

Clark's nutcrackers (*Nucifraga columbiana*) use gestures to identify the location of hidden food

Jan K. Tornick · Brett M. Gibson · David Kispert · Matthew Wilkinson

Received: 26 April 2010 / Revised: 16 August 2010 / Accepted: 19 August 2010
© Springer-Verlag 2010

Abstract Heterospecific cues, such as gaze direction and body position, may be an important source of information that an animal can use to infer the location of resources like food. The use of heterospecific cues has been largely investigated using primates, dogs, and other mammals; less is known about whether birds can also use heterospecific gestures. We tested six Clark's nutcrackers in a two-way object-choice task using touch, point, and gaze cues to investigate whether these birds can use human gestures to find food. Most of the birds were able to use a touch gesture during the first trial of testing and were able to learn to use point and gaze (eyes and head alternation) cues after a limited number of trials. This study is the first to test a non-social corvid on the object-choice task. The performance of non-social nutcrackers is similar to that of more social and related corvids, suggesting that species with different evolutionary histories can utilize gestural information.

Keywords Heterospecific communication · Gaze · Gestures · Social cognition · Object-choice · Pointing

Introduction

People rely upon facial cues and gestures during communication, as these cues convey information about our intentions and internal states to others (e.g. Emery 2000). Over the past decade, there has been much interest in examining what non-human animals may comprehend about the information conveyed in human facial

expressions and gestures (see Miklósi and Soproni 2006; Zuberbühler 2008; Emery and Clayton 2009 for reviews). Studies that have investigated what animals know about a social cue like human gaze, for example, provide an interesting example. On the one hand, animals may respond reflexively to a social cue like gaze. European starlings (*Sturnus vulgaris*) are sensitive to the presence and the direction of eye gaze (only eye orientation) during foraging (Carter et al. 2008), but this likely reflects the use of a simple and reflexive eye-detector mechanism (Emery 2000; see also Hampton 1994). Other work has found that animals will follow gaze (eye gaze alone or both head and eyes oriented) to a location (see Miklósi and Soproni 2006; Emery and Clayton 2009 for reviews), or even visually co-orient with the eye gaze of a human experimenter behind barriers (Tomasello et al. 1999; Bugnyar et al. 2004; Brauer et al. 2005). Indeed, eye gaze may inform observers about the internal states of others, perhaps diagnostic of a theory of mind (e.g. Premack 1988). One assumes that a person who sees an event occurring has knowledge of that event, while an observer who does not see the event has no knowledge of it. In a well-known study, Povinelli and Eddy (1996) allowed chimpanzees (*Pan troglodytes*) to beg from one of two human observers; one of the observers could see food, while the other had his vision blocked in some way. If the chimps were aware that the observer seeing the food had knowledge about the presence or absence of food, then the chimp should beg for food from that observer. However, the chimps generally did not discriminate between the two observers better than would be expected by chance.

One test that researchers have used to examine whether non-human animals can utilize human gestures is the two-way object-choice task (e.g. Anderson et al. 1995, 1996; Itakura and Anderson 1996). In the cooperative

J. K. Tornick (✉) · B. M. Gibson · D. Kispert · M. Wilkinson
Department of Psychology, University of New Hampshire,
10 Library Way, Durham, NH 03824, USA
e-mail: j.tornick@unh.edu

version of this task, an experimenter baits one of two opaque containers out of the view of the animal (e.g. behind a screen). The animal is then presented with the two containers, and the experimenter provides a cue indicating which of the two containers is baited (e.g. touching: Itakura and Anderson 1996; Itakura and Tanaka 1998; Nieworth et al. 2002; Miklósi et al. 2003; Byrnit 2004; Kaminski et al. 2005; Hauser et al. 2007; Schloegl et al. 2008a; Virányi et al. 2008, pointing: Call and Tomasello 1994; Itakura and Anderson 1996; Call et al. 1998; Itakura and Tanaka 1998; Peignot and Anderson 1999; Nieworth et al. 2002; Soproni et al. 2002; Miklósi et al. 2003; Byrnit 2004; Kaminski et al. 2005; Hauser et al. 2007; Schloegl et al. 2008a; Virányi et al. 2008; von Bayern and Emery 2009; Smith and Litchfield 2010, gazing, e.g., eyes only: Call et al. 1998; Itakura and Tanaka 1998; Peignot and Anderson 1999; Miklósi et al. 2003; Byrnit 2004; Virányi et al. 2008; von Bayern and Emery 2009; Smith and Litchfield 2010; or eyes and head: Itakura and Anderson 1996; Itakura and Tanaka 1998; Call et al. 1998; Peignot and Anderson 1999; Nieworth et al. 2002; Miklósi et al. 2003; Byrnit 2004; Kaminski et al. 2005; Hauser et al. 2007; Virányi et al. 2008; von Bayern and Emery 2009). The animal is then allowed to make a choice. Thus, the task is cooperative as the experimenter is providing a cue that can potentially be used to locate food.

The results of studies using the cooperative version of the two-way object-choice task with non-human primates have been surprisingly varied (see Emery and Clayton 2009 for a recent review). For instance, both chimpanzees (Itakura and Tanaka 1998; Wood et al. 2007) and gorillas (*Gorilla gorilla*; Peignot and Anderson 1999) are able to use point and touch cues to accurately locate food, though other studies have indicated that apes do not appear to understand the use of these cues (Povinelli et al. 1997; Tomasello et al. 1997). Non-human primates also have difficulty utilizing distal head and eye-gaze cues. Anderson et al. (1995, 1996) found that capuchin monkeys (*Cebus capucinus*) and rhesus macaques (*Macaca mulatta*) were not successful at using the direction of the experimenter's gaze to consistently find food. Similar results have also been reported for gorillas (Peignot and Anderson 1999). Chimpanzees have been shown to co-orient their gaze with both humans and other chimps (Povinelli and Eddy 1996; Tomasello et al. 1999; Hare et al. 2000), but in most studies were unable to use human gazing to find food in object-choice tasks (Povinelli et al. 1997; Call et al. 1998; Hare et al. 2000; Barth et al. 2005).

There is some evidence indicating that social organization has a role in the utilization of heterospecific cues during object-choice tasks. In a series of experiments, Flombaum and Santos (2005) presented a grape between a rhesus monkey and two human competitors to create a

competitive version of an object-choice task (see also Hare 2001). One of the competitors was able to see the grape, while the other was not able to do so. The authors reasoned that the monkeys would be able to utilize gaze cues in paradigms that are more comparable to the competitive social foraging environment in which such cue usage evolved. The results revealed that the monkeys were more likely to utilize gaze cues and take food from the competitor who was not able to see the grape than the competitor who could see the food. In addition, many domesticated animals also excel in utilizing social cues during object-choice tasks. In a well-cited study, Hare et al. (2002) examined the ability of seven adult domestic dogs (*Canis familiaris*) and seven adult wolves (*Canis lupus*) to use gaze + point + tap, gaze + point, or point cues to locate food during the cooperative version of the object-choice task mentioned above. Notably, each of the dogs performed above chance during one or more of these cue conditions, whereas none of the wolves were able to do so. Subsequent experiments revealed that the effects were not due to experience with the human owners, as litter-reared dog pups were just as competent as human-reared dog pups in utilizing gaze and point cues. Interestingly, in a recent study (Smith and Litchfield 2010), dingoes (*Canis dingo*) were able to use all cues except gaze (eyes only), gaze and point, and pointing from an incorrect location. Thus, dingoes, which have a history of domestication but have been wild for several thousand years, perform better than wolves, but not as well as dogs. In another study (Proops and McComb 2010), horses (*Equus caballus*) were able to discriminate between attentive and inattentive experimenters and were sensitive to human attentional cues, including gaze. This suggests that domestication may play a role in the ability to read human-given gestures; however, more work is needed to confirm this hypothesis.

Although the ability to utilize human-generated social cues has been studied extensively in primates and other mammals, less is known about whether birds can utilize and comprehend these cues. Giret et al. (2009) examined the use of human gestures in three African gray parrots (*Psittacus erithacus*) using the two-way object-choice task described above. During several pointing conditions, an experimenter extended their finger to one of two boxes while looking ahead until the bird made a choice. The parrots were able to use proximal pointing (experimenter's hand and arm extended ~10 cm from correct box), but not more distal or transitory point cues. The parrots were unable to utilize the gaze of an experimenter (eyes and head oriented toward the correct box until a choice was made) that was ~100 cm away from the box. Schloegl et al. (2008a) reported that young ravens (*Corvus corax*) preferentially paid attention to one of two objects that a human touched. These same ravens were not able to utilize proximal point (experimenter

pointed ~20 cm away from object for 5 s with arm while looking straight ahead) or gaze cues (experimenter bent forward and turned his eyes toward one of the objects) in the same way (however, see also Schloegl et al. 2008b). von Bayern and Emery (2009) examined the ability of another corvid, the jackdaw (*Corvus monedula*) to use point and gaze cues during both a competitive choice task (see Flombaum and Santos 2005 above), as well as a cooperative two-way object-choice task. The jackdaws took longer to take the food during the competitive task when the experimenter was directing their eyes toward the food than when their gazing was directed away. During the cooperative object-choice task, the experimenter pointed across their body ~25 cm away from the correct container, alternated their gaze between the bird and the correct container, oriented their eyes only toward the correct container, or oriented their head and eyes toward the correct container. Notably, the jackdaws were able to successfully utilize cross-body pointing and gaze alternation, but not the static gaze or head and gaze cues. Finally, Jaime et al. (2009) recently found that young bobwhite quail (*Colinus virginianus*) will respond to the gaze (eyes and head) directed toward one of two approach areas.

In the current study, we examined the ability of the Clark's nutcracker (*Nucifraga columbiana*) to use human-generated cues (touch, point, and gaze consisting of eyes and head alternation) to locate food during a two-way object-choice task. The Clark's nutcracker is a seed-caching corvid inhabiting mountainous regions of western North America. Each season, nutcrackers cache between 22,000 and 33,000 pine seeds that they relocate using spatial memory (for reviews, see Balda and Kamil 1988; Gibson and Kamil 2009). Although much is known about the nutcracker's spatial abilities (e.g., Gibson and Wilks 2008; LaDage et al. 2009; Kelly 2010), we know far less about their other cognitive abilities. Additionally, the nutcracker is closely related to other corvids like the raven and the jackdaw (Ericson et al. 2005), which have been recently examined for their ability to use point and gaze cues provided by a human experimenter. The social organization of these corvids is different, however (see Clayton and Emery 2007 for a review). Ravens live in groups early during their life and may join groups of juveniles after becoming independent. Jackdaws, the most social of the three, live in large colonial groups through adulthood even after pair-bonding has occurred, and are cooperative breeders. The nutcracker, however, is relatively solitary in its social organization compared with other corvids like ravens and jackdaws. They form breeding pairs and jointly defend a territory; at other times, they can be found in small family groups of two to four individuals (Mewaldt 1956). Nutcrackers may show a different pattern of performance than related birds that are more social given comparable tasks

since, as noted previously, social organization may influence the use or comprehension of such cues (e.g. Giret et al. 2009). As Miklósi and Soproni (2006) have recently suggested, a comparative analysis of the use of gestures is critical to understanding the factors responsible for the ability to use such cues.

Methods

Subjects and housing

Six adult nutcrackers were trapped in western North America and housed at the University of New Hampshire. The birds were of unknown sex and age. They were kept in individual cages (48 × 48 × 72 cm) in an environmentally controlled room (10 h light/14 h dark cycle). Birds were maintained at 90% of their free-feeding weight, by regulating their intake of turkey starter, pigeon pellets, striped sunflower seeds, and mealworms following experimental sessions. They had previously been used in tests of spatial orientation and navigation (Gibson and Kamil 2001, 2005; Gibson and Wilks 2008), but were naïve to the current task. The birds had unlimited access to grit and water for the duration of the experiment.

Apparatus

The nutcrackers were trained and tested in a white melamine experimental chamber measuring 45 × 45 × 60 cm. A perch was centered 5 cm above the floor of the chamber. The front of the chamber was constructed of clear Plexiglas® and had two choice holes near the base each measuring 5 cm in diameter. Two identical cylindrical and opaque PVC food cups with opaque pivoting lids could be positioned in front of the choice holes. A bird in the chamber could insert its head through the hole and remove the lid from a cup positioned outside of the chamber. The food cups were situated on a sliding tray that could be moved towards or away from the two holes in the front wall of the chamber by the experimenter. The use of the tray ensured that the cups were always positioned in the same location in front of the choice holes.

Familiarization and training

The birds were first trained to open the food cups with their beaks in their home cages. Next, the birds were acclimated to the experimental apparatus by placing pine nuts in open food cups outside of the choice holes. The experiment began once the birds were readily opening cups in their home cages and regularly obtaining food in the experimental apparatus.

During each trial of training, a bird was placed in the apparatus, and the experimenter sat on a stool while facing the transparent front wall of the apparatus (experimenter's head was ~ 60 cm from the cups). The experimenter then presented a single pine nut to the bird for 3 s or until the bird appeared to have seen the food. Next, the experimenter raised a barrier that prevented the bird from seeing the experimenter bait one of two food cups. The lids on both cups were then closed, and the cups were placed onto the sliding tray. The barrier was removed and the cups were positioned in front of the choice holes of the chamber but just beyond the reach of the bird. Using the ipsilateral hand, the cup to the left of the experimenter (to the right of the bird) was first opened for 3 s and then closed, and then the right cup was opened for 3 s and then closed, so that the bird had seen the contents of both cups. Next, the tray holding the cups was positioned near the front wall of the apparatus, an opaque curtain between the bird and the experimenter was closed (to reduce unintentional cuing by the experimenter). The bird was then allowed to make a single choice. An overhead camera was used to view the bird's behavior. White noise was projected into the room through an overhead speaker.

If a correct choice was made, the bird was allowed to eat the food before the experimenter opened the curtain and prepared the next trial. If the bird made an incorrect choice, the tray was slid back from the apparatus, and the house light was extinguished for 10 s. The position of the baited cup was randomized between the left and right positions, with no more than two trials on the same side consecutively. Also, the cups were pseudo-randomized between the two locations to ensure that the birds could not use any unforeseen differences in the two food cups as a cue to find the food. Birds were given one session per day, consisting of eight training trials. If a bird did not make a choice within 30 s, the trial was repeated. The criterion required to begin testing was a minimum of seven out of eight correct

choices for five consecutive days; training lasted an average of 12.33 days (SEM = 2.23).

Testing

Each bird was given one session per day, consisting of seven trials of training and one test trial. The test was administered between the third and sixth trials of the session (randomly determined). The procedures for testing were comparable to those described for training above except where noted below. The birds encountered four different types of test conditions (Fig. 1) (1) *Touch*: The experimenter picked up the baited cup with the ipsilateral hand and held it for 5 s while keeping her head and eyes directed straight ahead; the cup was then returned to the same position in the sliding tray. (2) *Point*: The experimenter pointed 5–6 cm away with the extended index finger of the hand ipsilateral to the baited cup for 5 s with head and eyes directed ahead. (3) *Gaze*: The gaze of the experimenter alternated between the location of the food cup and the eyes of the bird (both the experimenter's head and eyes moved) for 5 s, with ~ 3 alternations. (4) *Control/No cue*: Birds were not shown the contents of either cup following the baiting and no systematic gestures were made; the experimenter's head and eyes were directed straight ahead for 5 s. The birds were motivated to obtain food and attended at a high level to the experimenter during the experimental sessions. If the bird did not appear to be attending to the presented cue (very rarely occurred), the experimenter continued to present the cue until attention appeared to have been captured by the cue.

The order of presentation of the test conditions was randomized across days, with the exception that the same condition could not be repeated for more than two consecutive days. During testing, if a bird made a correct choice, it received the food; if it made an incorrect choice, it did not receive food and the next trial ensued. Each bird

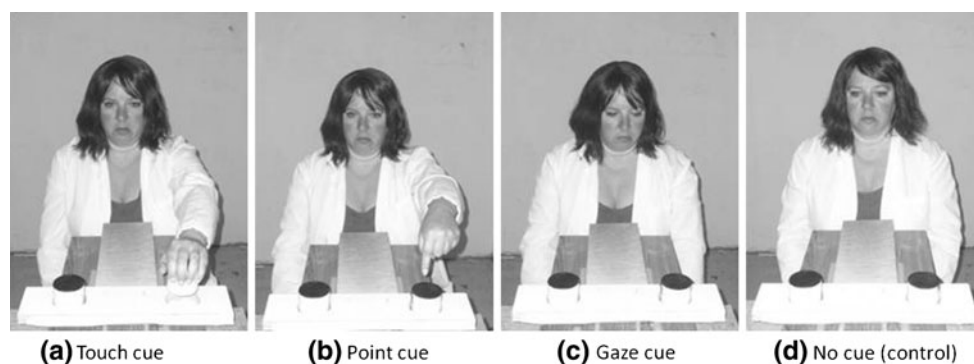


Fig. 1 Photographs of the test conditions. The four cues were **a** Touch: the experimenter picked up the baited cup while keeping her head and eyes directed straight ahead; **b** Point: the experimenter pointed with the extended index finger with head and eyes directed

ahead; **c** Gaze (eyes and head alternation): the eyes and head of the experimenter alternated between the location of the food cup and the eyes of the bird; and **d** Control/No cue: no gestures were made. Each bird was given only one test trial per day

encountered an initial block (Block 1) that included 64 trials of testing (16 tests for each of the four test conditions). If performance during testing for a given bird did not reach significance for the touch, point, or gaze conditions, one or two additional blocks of testing were administered with that gesture. While other studies have examined performance over a relatively short interval, we were also interested in examining whether birds that initially failed to use the cue would show an ability to do so after repeated testing. An additional block of control tests were also run concurrently as described above. For instance, if a bird continued testing with gaze cues for a second block (but not the touch or point cues), it would also encounter the control condition. We administered two tests, rather than one, during each daily session for birds that encountered testing during Blocks 2 and 3. Finally, four of the birds (Susan, Fitz, Starr, and Betsy) encountered initial testing (one block) with the gaze and point conditions during the summer of 2008. Eight months later, these birds encountered all four test conditions. The other two birds (Sony and Puck) began testing in the spring of 2009 with the four test conditions.

Analysis

The performance of the birds was analyzed individually across blocks. The number of correct choices for the touch, point, gaze, and control conditions was compared to chance performance (8 of 16) for each block using binomial tests. Family-wise type I error rate was controlled using a step-down Holm-Bonferroni procedure (Holm 1979; Ludbrook 1998). Adjusted alphas (α_{obt}) are reported. All tests were two-tailed.

Results

Five of the six nutcrackers (Susan, Fitz, Starr, Sony, and Puck) were able to use the touch cue to locate hidden food significantly better than would be expected by chance (Fig. 2, first row). In the first block of 16 trials, Susan selected the cup that had been touched during 15 of 16 trials (93.75%, $\alpha_{\text{obt}} = 0.013$, $P < 0.001^*$), Sony on 14 of 16 trials (87.5%, $\alpha_{\text{obt}} = 0.013$, $P = 0.002^*$), Puck on 14 of 16 trials (87.5%, $\alpha_{\text{obt}} = 0.013$, $P = 0.002^*$), Fitz on 13 out

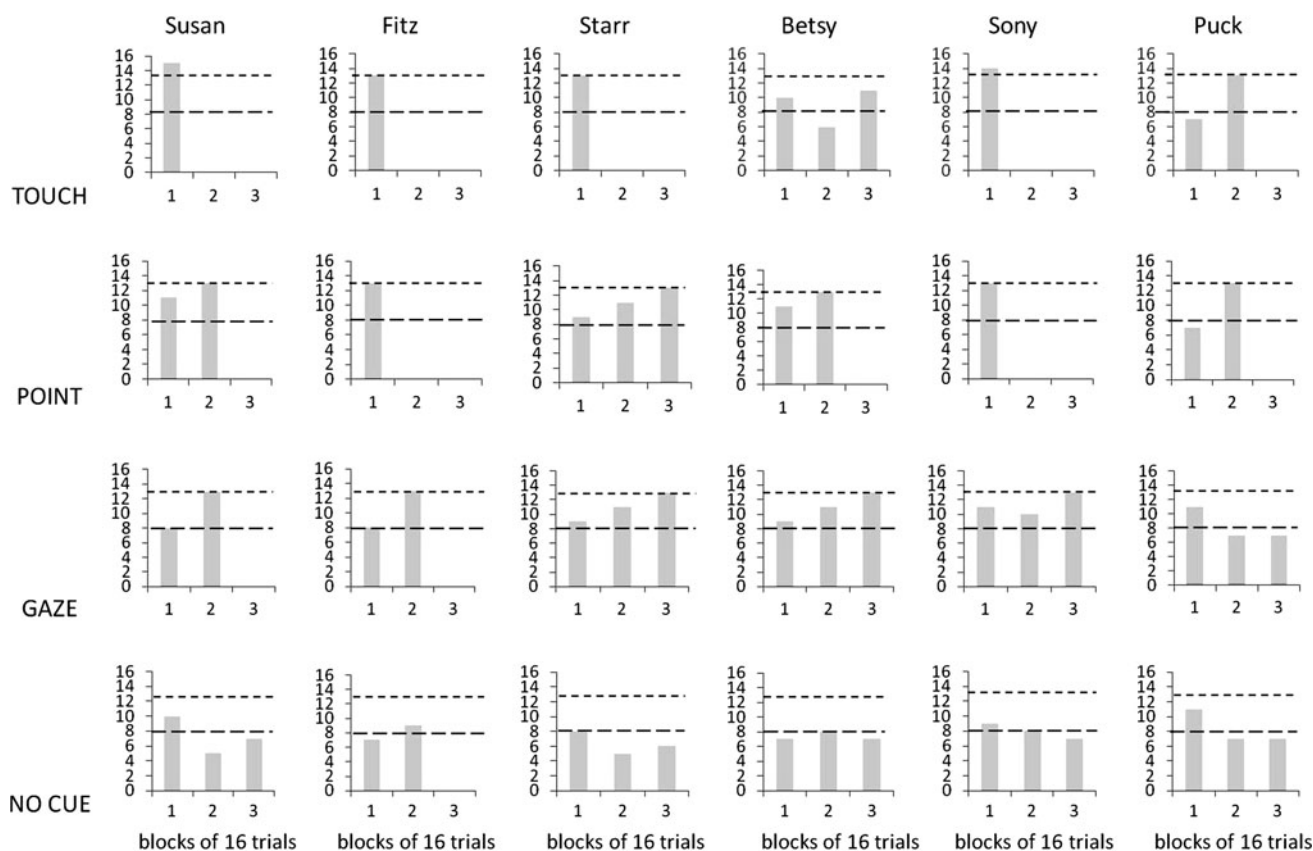


Fig. 2 The number of correct responses (out of 16) made by individual birds during the touch, point, gaze, and control (no cue) conditions across blocks of testing. Data for each condition are presented in rows, and data for individual birds are presented in

columns. Note that some birds encountered more than one block (16 trials) of testing with each cue (see text). The coarse dashed line indicates chance performance, and the fine dashed line indicates the above chance threshold for significance

of 16 of trials (81.25%, $\alpha_{\text{obt}} = 0.014$, $P = 0.009^*$), and Starr during 13 of 16 trials (81.25%, $\alpha_{\text{obt}} = 0.014$, $P = 0.009^*$). Betsy chose the cup that had been touched on 10 of 16 trials during the first block (62.5%, $\alpha_{\text{obt}} = 0.017$, $P = 0.122$); on 6 out of 16 during the second block (37.5%, $\alpha_{\text{obt}} = 0.05$, $P = 0.122$); and on 11 out of 16 trials (68.75%) during the third block ($\alpha_{\text{obt}} = 0.025$, $P = 0.067$). Five of the nutcrackers made a number of their correct responses early during the first block of testing. Susan used the touch cue correctly during the first 15 trials, and Fitz made nine correct choices initially. Starr and Puck correctly used the touch cue on the first five consecutive trials, and Sony did so in the first four.

All six nutcrackers were also able to use the point cue to locate hidden food significantly better than would be expected by chance, though following different durations of testing (Fig. 2, second row). Two birds were able to accurately use pointing during the first block. Sony made a correct choice on 13 out of 16 trials (81.25%, $\alpha_{\text{obt}} = 0.017$, $P = 0.009^*$), and Fitz did so on 13 out of 16 trials (81.25%, $\alpha_{\text{obt}} = 0.014$, $P = 0.009^*$). Three other birds were able to utilize pointing following two blocks of testing. Susan made a correct choice on 11 out of 16 trials during the first block (68.75%, $\alpha_{\text{obt}} = 0.017$, $P = 0.067$) and on 13 of 16 trials (81.25%) during the second block ($\alpha_{\text{obt}} = 0.02$, $P = 0.009^*$). Betsy used the point cue on 11 out of 16 trials during the first block (68.75%, $\alpha_{\text{obt}} = 0.013$, $P = 0.067$); and on 13 out of 16 trials (81.25%) during the second block ($\alpha_{\text{obt}} = 0.014$, $P = 0.009^*$). Puck made a correct choice on 7 of 16 trials (43.75%) during the first block ($\alpha_{\text{obt}} = 0.05$, $P = 0.175$); and on 13 out of 16 trials (81.25%) during the second block ($\alpha_{\text{obt}} = 0.017$, $P = 0.009^*$). Finally, Starr used the point cue on 9 out of 16 trials (56.25%) during the first block ($\alpha_{\text{obt}} = 0.02$, $P = 0.175$); on 11 out of 16 trials during the second block (68.75%, $\alpha_{\text{obt}} = 0.02$, $P = 0.067$); and on 13 out of 16 trials (81.25%) during the third block ($\alpha_{\text{obt}} = 0.02$, $P = 0.009^*$). The time-course of correct responses during the first block of testing was quite different than that reported for the touch condition. Only one of the nutcrackers (Sony) displayed a strong early pattern of correct choices using pointing (seven tests in a row).

Five of the six nutcrackers were able to use the gaze cue (Fig. 2, third row) to locate hidden food significantly better than would be expected by chance; though, like with the point cue, following different intervals of testing. Three birds were able to use the direction of gazing by the second block of testing. Betsy selected the cup that was indicated by gazing on 9 of 16 trials (56.25%) during the first block ($\alpha_{\text{obt}} = 0.033$, $P = 0.175$), and on 13 of 16 trials (81.25%) during the second block ($\alpha_{\text{obt}} = 0.014$, $P = 0.009^*$). Fitz made a correct choice on 8 out of 16 trials during the first block (50%, $\alpha_{\text{obt}} = 0.025$, $P = 0.196$), and on 13 of 16

trials (81.25%) during the second block ($\alpha_{\text{obt}} = 0.025$, $P = 0.009^*$). Susan made a correct choice on 6 of 16 trials (37.5%) during the first block ($\alpha_{\text{obt}} = 0.033$, $P = 0.122$), and on 13 of 16 trials during the second block (81.25%, $\alpha_{\text{obt}} = 0.02$, $P = 0.009^*$). Two additional birds were also able to use the direction of gaze during third block of testing. Sony used the gazing cue on 11 of 16 trials (68.75%) during the first block ($\alpha_{\text{obt}} = 0.025$, $P = 0.067$); 10 of 16 trials (62.5%) during the second block ($\alpha_{\text{obt}} = 0.033$, $P = 0.122$), and on 13 of 16 trials during final block (81.25%, $\alpha_{\text{obt}} = 0.025$, $P = 0.009^*$). Starr used the direction of gaze on 9 of 16 trials (56.25%) during the first block ($\alpha_{\text{obt}} = 0.02$, $P = 0.175$), 11 of 16 trials (68.75%) during the second block ($\alpha_{\text{obt}} = 0.02$, $P = 0.067$), and on 13 of 16 trials during the last block (81.25%, $\alpha_{\text{obt}} = 0.02$, $P = 0.009^*$). One bird failed to use gazing cues entirely. Puck made 11 of 16 correct choices (68.75%) during the first block ($\alpha_{\text{obt}} = 0.017$, $P = 0.067$); 7 of 16 correct choices (43.75%) during the second block ($\alpha_{\text{obt}} = 0.05$, $P = 0.175$); and 7 of 16 correct choices during the third block (43.75%, $\alpha_{\text{obt}} = 0.033$, $P = 0.175$). None of the birds showed a systematic pattern of correct choices early during the first block of testing.

Finally, the number of correct choices during the control (no cue) condition fluctuated near chance during each block of testing (Fig. 2, fourth row). Binomial tests confirmed this observation and indicated that none of the six nutcrackers chose the baited cup significantly above chance during the control condition during any block of testing (all $P_s > \alpha_{\text{obt}}$).

Discussion

Five of the six nutcrackers were able to use information about which cup the experimenter touched, to locate food at levels that were significantly above chance. Notably, performance was high for many birds during the initial trials of the first block of testing. The fact that nutcrackers use a touch cue to locate an object is consistent with the findings from Schloegl et al. (2008a) showing that young ravens, a closely related but relatively more social corvid (see “Introduction”) preferentially inspected toys that were touched by a human experimenter. These findings are also consistent with the work showing that a number of mammalian species also use a touch cue to locate food. Captive gorillas (Peignot and Anderson 1999), cotton-top tamarins (*Saguinus oedipus*), rhesus monkeys, and chimpanzees (Wood et al. 2007), goats (*Capra hircus*; Kaminski et al. 2005), and dogs and some captive wolves (Hare and Tomasello 1999; Virányi et al. 2008) have all been reported to use touching as a cue during a cooperative food choice task.

Two of the six nutcrackers were able to use pointing (~ 10 cm from the cup and held for 5 s) as a cue during the first block of testing; the other four birds were able to acquire the use of the point cue after 32 additional point condition trials. Nutcrackers' performance appears to be comparable to that of most of the other birds thus far examined. One African gray parrot was able to initially use a proximal (~ 10 cm) pointing cue, and two others learned to do so after additional experience (Giret et al. 2009). The parrots were not able to use pointing cues if the cues were more transitory or more distal to the target, however. The jackdaw, a social corvid closely related to the nutcracker, has also been shown to use cross-distal pointing (25 cm from container and held until a choice was made) to find a target during a cooperative two-way object-choice task (von Bayern and Emery 2009). Four out of the nine jackdaws were able to use point cues to locate food within 24 trials. While the ability of jackdaws and nutcrackers to utilize pointing cues would appear to be comparable, such conclusions must be tentative, as the point cues provided to the jackdaws were more subtle than those given to the nutcrackers. Notably, the other corvid thus far examined, the raven, failed to use pointing cues to explore one of several toys (Schloegl et al. 2008a) even after 20 such trials. In that study, the pointing cue was farther away (approximately 20 cm) than in the current study but held for approximately the same duration.

None of the nutcrackers successfully used the direction of gaze during the first block of testing, but three birds did so after 32 trials and another two after 48 trials. In other work, ravens were not capable of detecting hidden food solely by relying on a human's eye gaze (held for 5 s) or the direction or body orientation of a conspecific (Schloegl et al. 2008a); though, ravens have been reported to follow the direction of gaze around and behind barriers (Bugnyar et al. 2004). Jackdaws, when choice data were collapsed across birds, were reported to utilize gazing when the experimenter alternated the direction of eye gaze between the correct location, but not when eye gaze was fixed at the correct location (until the bird made a choice). The analysis of the individual data (supplemental data) indicated that none of the nine jackdaws were capable of using gaze alternation after 24 trials at a level that was above chance, however. African gray parrots generally appear unable to use direction of eye gaze (held until bird made a choice), though one subject learned to do so after extensive training (Giret et al. 2009). The nutcrackers' ability to use gaze would appear comparable to that of the jackdaw, which successfully used gaze alternation to locate a goal. However, the cues provided to the nutcrackers may have been more salient than those provided to these other species, since both the head and eye orientation alternated between the goal and the bird for 5 s, whereas in these other studies

the gaze was fixed (parrot, jackdaw, and raven) or only the eyes alternated (jackdaw).

The results of the current study reveal that there is substantial overlap in the use of touch, point, and gaze cues used by nutcrackers and more social corvids like ravens and jackdaws. As noted above, comparisons across the studies using the object-choice task with birds have utilized somewhat different information, or held the cue for different durations. Such differences can make it difficult to draw strong conclusions about social organization and the ability to utilize social cues. To make stronger conclusions, it will be important to compare birds that are closely related but diverge in social organization, and to use the same task and cues.

Although the current work indicates that nutcrackers are capable of using all three gestures examined here, the mechanism(s) underlying the use of these cues is unclear. One strong possibility is that the nutcrackers acquired the ability to use all three cues via a combination of associative learning and local stimulus enhancement. Nutcrackers may have acquired the ability to use both touch and point cues very early during testing in a single trial. One-trial learning might account for the strong early performance of the birds with the touch and point cues in this study (Sokolov 1963; MacDonald 1994; Menzel 1999; Pravosudov and Clayton 2001; Schwartz et al. 2002). Additionally, because we monitored performance across multiple blocks of testing, we could follow gradual improvements in the use of the gestural information that would also be consistent with a more typical pattern of learning. Indeed, this type of pattern would appear to well characterize the ability of the nutcrackers to utilize the gaze cue in the current study, as most nutcrackers appeared to use the cue after two or more blocks of testing.

The nutcrackers' use of the three cues might also be explained by the theory of local enhancement. Schloegl et al. (2008a) suggested that the stronger response to a pointing cue may simply arise because there is a smaller distance between the fingertip and the cup than the face and the cup in the gazing condition. This line of reasoning could explain why the nutcrackers' performance was better in the touch condition than the point condition, and better in the point condition than the gaze condition. Local enhancement has also been suggested as the mechanism underlying similar behavior in ravens (Fritz and Kotrschal 1999), goats (Kaminski et al. 2005), wolves (Miklósi et al. 1998, 2003), and horses (McKinley and Shambrook 2000).

Most of the nutcrackers were able to utilize the touch cues early during testing which is comparable to the performance of ravens, a species closely related to the nutcracker. The ability of the nutcrackers to use point and gaze cues did not appear until after 16 or more trials of testing for most birds. Related, more social corvids showed comparable performance to the nutcrackers regarding the use of

pointing and gazing cues. As indicated previously, social factors may play a role during two-object tasks; domesticated dogs, for instance, utilize gestural information at a higher level than related wolves. In part, this may reflect the fact that dogs have been bred to better attend to communicative information. Likewise, the corvids that have been examined thus far using object-choice tasks (jackdaws, ravens) are more social than nutcrackers (see “Introduction”) and have been enculturated at an early age. These factors may have been expected to provide jackdaws and ravens with an advantage in using touch, point, and gaze information to locate a hidden goal, compared to the wild trapped and less social nutcrackers used in the current study. In contrast, nutcrackers performed comparably to the other birds. It may be the case that the cues used in these studies are acquired via basic associative mechanisms that all three of the corvids discussed would appear to already employ to learn about cues in an environment. Other uncontrolled and methodological factors (e.g., differences in the nature of the cues, conditions) across these studies may have accounted for similarities in the pattern of performance between nutcrackers and more social corvids, however. Future work with naïve social and non-social corvids given comparable tasks will be important. In addition, we anticipate that future work will be needed to determine which mechanisms (learning, logical comprehension) are responsible for the ability of birds (and other non-human animals) to utilize gestural information.

Acknowledgments We thank Robert Drugan and William Stine for their advice and support; Kasandra Babineau for testing and animal care; and Erika Wells for photography. The experiment complies with the US laws concerning animal care, and was reviewed and approved by the University of New Hampshire (UNH) Institutional Animal Care and Use Committee (IACUC). The authors declare that they have no conflict of interest.

References

- Anderson JR, Sallaberry P, Barbier H (1995) Use of experimenter-given cues during object-choice tasks by capuchin monkeys. *Anim Behav* 49:201–208
- Anderson JR, Montant M, Schmitt D (1996) Rhesus monkeys fail to use gaze direction as an experimenter-given cue in an object-choice task. *Behav Process* 37:47–55
- Balda RP, Kamil AC (1988) The spatial memory of Clark’s nutcrackers (*Nucifraga columbiana*) in an analogue of the radial arm maze. *Anim Learn Behav* 16:116–122
- Barth J, Reaux JE, Povinelli DJ (2005) Chimpanzees’ (*Pan troglodytes*) use of gaze cues in object-choice tasks: Different methods yield different results. *Anim Cogn* 8:84–92
- Brauer J, Call J, Tomasello M (2005) All great ape species follow gaze to distant locations and around barriers. *J Comp Psychol* 119:145–154
- Bugnyar T, Stöwe M, Bernd H (2004) Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proc Biol Sci* 271:1331–1336
- Byrmit JT (2004) Nonenculturated orangutans (*Pongo Pygmaeus*) use of experimenter-given manual and facial cues in an object-choice task. *J Comp Psychol* 118:309–315
- Call J, Tomasello M (1994) Production and comprehension of referential pointing by orangutans (*Pongo pygmaeus*). *J Comp Psychol* 108:307–317
- Call J, Hare B, Tomasello M (1998) Chimpanzee gaze following in an object-choice task. *Anim Cogn* 1:89–99
- Carter J, Lyons NJ, Cole HL, Goldsmith AR (2008) Subtle cues of predation risk: starlings respond to a predator’s direction of eye gaze. *Proc R Soc Lond B Biol Sci* 275:1709–1715
- Clayton NS, Emery NJ (2007) The social life of corvids. *Curr Biol* 17:R652–R656
- Emery NJ (2000) The eyes have it: the neuroethology, function, and evolution of social gaze. *Neurosci Biobehav Rev* 2000:581–604
- Emery NJ, Clayton NS (2009) Comparative social cognition. *Annu Rev Psychol* 60:87–113
- Ericson GP, Jansen A, Johansson US, Ekman J (2005) Inter-generic relationships of the crows, jays, magpies and allied groups (Aves: *Corvidae*) based on nucleotide sequence data. *J Avian Biol* 36:222–234
- Flombaum JL, Santos LR (2005) Rhesus monkeys attribute perceptions to others. *Curr Biol* 15:447–452
- Fritz J, Kotschal K (1999) Social learning in common ravens, *Corvus corax*. *Anim Behav* 57:785–793
- Gibson BM, Kamil AC (2001) Search for a hidden goal by Clark’s nutcrackers (*Nucifraga columbiana*) is more accurate inside than outside a landmark array. *Anim Learn Behav* 29:234–249
- Gibson BM, Kamil AC (2005) The fine-grained spatial abilities of three seed-caching corvids. *Learn Behav* 33:59–66
- Gibson BM, Kamil AC (2009) The synthetic approach to the study of spatial memory: have we properly addressed Tinbergen’s “four questions?”. *Behav Process* 80:278–287
- Gibson BM, Wilks T (2008) The use of self-motion cues and landmarks by Clark’s nutcrackers (*Nucifraga columbiana*) during a small-scale search task. *Anim Behav* 76(4):1305–1317
- Giret N, Miklósi Á, Kreutzer M, Bovet D (2009) Use of experimenter-given cues by African gray parrots (*Psittacus erithacus*). *Anim Cogn* 12:1–10
- Hampton RR (1994) Sensitivity to information specifying the line of gaze of humans in sparrows (*Passer domesticus*). *Behav* 130:41–51
- Hare B (2001) Can competitive paradigms increase the validity of experiments on primate social cognition? *Anim Cogn* 4:269–280
- Hare B, Tomasello M (1999) Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *J Comp Psychol* 113:1731–1777
- Hare B, Call J, Agnetta B, Tomasello M (2000) Chimpanzees know what conspecifics do and do not see. *Anim Behav* 59:771–785
- Hare B, Brown M, Williamson C, Tomasello M (2002) The domestication of social cognition in dogs. *Science* 298:1634–1636
- Hauser M, Glynn D, Wood J (2007) Rhesus monkeys correctly read the goal-relevant gestures of a human agent. *Proc R Acad B* 274:1913–1918
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scand J Statist* 6:65–70
- Itakura S, Anderson JR (1996) Learning to use experimenter-given cues during an object-choice task by a capuchin monkey. *Curr Psychol Cogn* 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*). *J Comp Psychol* 112:119–126
- Jaime M, Lopez JP, Lickliter R (2009) Bobwhite quail (*Colinus virginianus*) hatchlings track the direction of human gaze. *Anim Cogn* 12:559–565

- Kaminski J, Riedel J, Call J, Tomasello M (2005) Domestic goats (*Capra hircus*) follow gaze direction and use some social cues in an object choice task. *Anim Behav* 69:11–18
- Kelly DM (2010) Features enhance the encoding of geometry. *Anim Cogn* 13:453–462
- LaDage LD, Roth TC II, Fox AF, Pravosudov VV (2009) Flexible cue use in food-caching birds. *Anim Cogn* 12:419–426
- Ludbrook J (1998) Multiple comparison procedures updated. *Clin Exp Pharmacol Physiol* 25:1032–1037
- MacDonald SE (1994) Gorilla's (*Gorilla gorilla gorilla*) spatial memory in a foraging task. *J Comp Psych* 108:107–113
- McKinley J, Shambrook TD (2000) Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*). *Anim Cogn* 3:13–22
- Menzel CR (1999) Unprompted recall and reporting of hidden objects by a chimpanzee (*Pan troglodytes*) after extended delays. *J Comp Psych* 113:426–434
- Mewaldt JM (1956) Nesting behavior of the Clark's nutcracker. *Condor* 58:3–23
- Miklósi Á, Soproni K (2006) A comparative analysis of animals' understanding of the human pointing gesture. *Anim Cogn* 9:81–93
- Miklósi Á, Polgárdi R, Topál J, Csányi V (1998) Use of experimenter given cues in dogs. *Anim Cogn* 1:113–121
- Miklósi Á, Kubinyi E, Topál J, Gácsi M, Virányi Z, Csányi V (2003) A simple reason for a big difference: Wolves do not look back at humans but dogs do. *Curr Biol* 13:763–766
- Nieworth JJ, Burman MA, Basile BM, Lickteig MT (2002) Use of experimenter-given cues in visual co-orienting and in an object-choice task by a new world monkey species, cotton-top tamarins (*Saguinus oedipus*). *J Comp Psych* 116(1):1–3
- Peignot P, Anderson JR (1999) Use of experimenter given manual and facial cues by gorillas (*Gorilla gorilla*) in an object-choice task. *J Comp Psychol* 113:253–260
- Povinelli DJ, Eddy TJ (1996) Chimpanzees: joint visual attention. *Psychol Sci* 7:129–135
- Povinelli DJ, Reaux JE, Bierschwale DT, Allain AD, Simon BB (1997) Exploitation of pointing as a referential gesture in young children, but not adolescent chimpanzees. *Cogn Dev* 12:423–461
- Pravosudov VV, Clayton NS (2001) Effects of demanding foraging conditions on cache retrieval accuracy in food-caching mountain chickadees (*Poecile gambeli*). *Proc Biol Sci* 268:363–368
- Premack D (1988) “Does the chimpanzee have a theory of mind?” revisited. In: Byrne RW, Whiten A (eds) *Machiavellian Intelligence*. Oxford University Press, New York, pp 160–178
- Proops L, McComb K (2010) Attributing attention: the use of human-given cues by domestic horses (*Equus caballus*). *Anim Cogn* 13:197–205
- Schloegl C, Kotrschal K, Bugnyar T (2008a) Do common ravens (*Corvus corax*) rely on human or conspecific gaze cues to detect hidden food? *Anim Cogn* 11:231–241
- Schloegl C, Kotrschal K, Bugnyar T (2008b) Modifying the object-choice task: is the way you look important for ravens? *Behav Process* 77:61–65
- Schwartz BL, Colon MR, Sanchez IC, Rodriguez IA, Evans S (2002) Single-trial learning of “what” and “who” information in a gorilla (*Gorilla gorilla gorilla*): implications for episodic memory. *Anim Cogn* 5(2):85–90
- Smith BP, Litchfield CA (2010) Dingoes (*Canis dingo*) can use human social cues to locate hidden food. *Anim Cogn* 13:367–376
- Sokolov EN (1963) Higher nervous functions—orienting reflex. *Ann Rev Physiol* 25:545–562
- Soproni K, Miklósi Á, Topál J, Csányi V (2002) Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *J Comp Psychol* 116:27–34
- Tomasello M, Call J, Gluckman A (1997) Comprehension of novel communicative signs by apes and human children. *Child Dev* 68:1067–1080
- Tomasello M, Hare B, Agnetta B (1999) Chimpanzees, *Pan troglodytes*, follow gaze direction geometrically. *Anim Behav* 58:769–777
- Virányi Z, Gácsi M, Kubinyi E, Topál J, Belényi B, Ujfalussy D, Miklósi Á (2008) Comprehension of human pointing in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Anim Cogn* 11:373–387
- von Bayern AMP, Emery NJ (2009) Jackdaws respond to human attentional states and communicative cues in different contexts. *Curr Biol* 19:1–5
- Wood JN, Glynn DD, Phillips BC, Hauser MD (2007) The perception of rational, goal-directed action in nonhuman primates. *Science* 317:1402–1405
- Zuberbühler K (2008) Gaze following. *Curr Biol* 18:R453–R455