

Clark's nutcrackers' (*Nucifraga columbiana*) ability to discriminate knowledge states of  
human experimenters during an object-choice task

by

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### Abstract

The present thesis examined whether the corvid, Clark's nutcracker, is able to discriminate knowledge states between human experimenters based upon gestural cues using an object-choice task. To do so, the knowledge state of two experimenters was manipulated – one experimenter was informed, and the other uninformed, as to the location of a hidden food reward. To find the reward, the birds had to use the gesture of the informed experimenter and refrain from using the unreliable gesture of the uninformed experimenter. The nutcrackers responded to the gesture of the informed experimenter at above chance levels when simultaneously presented with the uninformed experimenter's gesture. When the uninformed experimenter's gesture was presented alone, the birds continued to follow the gesture. These results suggest the birds learned the gesture was meaningful, perhaps by associative learning, yet when this mechanism was not reliable the nutcrackers based their choices on the knowledge states of the experimenters.

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## **Chapter 1: General Introduction**

When Premack and Woodruff (1978) originally coined the term Theory of Mind – the ability to impute the mental states of other individuals – their research focused on examining whether chimpanzees could understand the knowledge, intentions, and beliefs of others. Premack and Woodruff’s original Theory of Mind term, however, was not meant to be applied in a species-specific context. They were not concerned with whether chimpanzees possessed “human” minds so much as identifying what content chimpanzees used for inferring the minds of others. Indeed, their early work with the chimpanzee, Sarah, revealed the possibility that these animals have an elaborate Theory of Mind, albeit not necessarily the same Theory of Mind utilized by humans. For example, Premack and Woodruff presented Sara with a video of either a “kind” or “unkind” trainer attempting to solve various problems. After watching the video, Sarah was shown photographs of potential solutions to the problem. She consistently chose the correct solution to the problems, but only after watching the video with the “kind” trainer. Conversely, when the “unkind” trainer was portrayed, Sarah chose the incorrect or unfavorable solutions. This pattern of responding seemed to suggest that Sarah was ascribing different motivations or intentions to the human trainers and these altered whether she empathized (a form of perspective-taking) with that particular person.

Premack and Woodruff’s work was followed by other seemingly affirmative findings from observational data from naturalistic settings suggesting primates had a Theory of Mind (de Wall, 1986; Goodall, 1986; Cheney & Seyfarth, 1990; Whiten & Byrne, 1988). However, these studies often relied on anecdotal evidence and lacked the

control provided by laboratory studies (Premack, 1988), leading some to argue that no meaningful progress had been made in determining whether primates had a Theory of Mind (Heyes, 1998). Povinelli and Eddy (1996) developed a battery of laboratory tests to examine whether chimpanzees understood the relationship between ‘seeing’ and attending. In this work, chimpanzees witnessed a human experimenter with varying attentional states (e.g. facing forward or backward, blindfold placed over eyes or mouth, bucket placed on head) and the chimpanzees were required to beg to the person that could ‘see’ them and, therefore, would be able to provide a food reward. The chimpanzees did not preferentially beg to the experimenter that had visual access to the subject. This methodology was hailed as the most sound approach, with the most potential to differentiate between mentalist and behaviorist interpretations of the data (Heyes, 1998) and led some to speculate that only humans are capable of having a Theory of Mind (Penn & Povinelli, 2007; Saxe, 2006).

The work by Povinelli’s group (e.g. Penn & Povinelli, 2007) represented an important progression in the field – promoting experiments that require the animal to rely on mental states rather than simply attending to behavior to solve the task. Generally, laboratory-based experiments revealed that primates had little or no understanding of the mental states of other individuals; however, some argued that these null results were not evidence that primates were incapable of mental attribution, but rather that the paradigms employed were incapable of revealing such an ability because they lacked ecological relevance (e.g. begging, the use of blindfolds or buckets, Tomasello, Call & Hare, 2003a). Indeed, when primates were tested in competitive, rather than cooperative contexts, primates showed evidence for perspective-taking (chimpanzees: Hare, Call,

Agnetta & Tomasello 2000; Hare, Call, Tomasello, 2001) and sensitivity to attentional states (rhesus monkeys: Flombaum & Santos, 2005). These experiments prompted Tomasello and Call (1997) to revise their theory that chimpanzees did not possess a Theory of Mind, instead suggesting that chimpanzees understand some psychological states (e.g. competitive psychological states, Call, 2001), but not necessarily all the mental states that humans understand (e.g. cooperative psychological states, Tomasello, 1999).

Contemporary research has returned to Premack's (1988) approach to the study of Theory of Mind – subdividing Theory of Mind into components. Premack (1988) argued that Theory of Mind was comprised of various distinct cognitive skills and thus, subdivided Theory of Mind into three categories: perceptual (visual and attentional states), motivational (intentions), and informational (knowledge states and beliefs). Under the early definition of Theory of Mind, different species might possess some mental attributes of one or more categories while lacking others. Thus, according to Premack, a species did not necessarily have to possess the mental abilities within all categories to be considered to have a Theory of Mind. However, some researchers modified the required abilities, arguing that these categories must occur in combination or reworked the components to make them more stringent in order for a species to be considered to have Theory of Mind (e.g. understanding false-beliefs, rather than simply beliefs, required for Theory of Mind: Bennett, 1978; Dennett, 1978; Harman, 1978). The continuous modification of the definition of Theory of Mind resulted in the term coming to represent the mental capabilities of humans. At times, the debate has centered around the issue of whether or not animals possess a human Theory of Mind (see exchanges by



Povinelli & Vonk, 2003, 2004 and Tomasello, Call & Hare, 2003a,b). This debate, however, is inherently flawed in that no nonhuman species is capable of holding a human Theory of Mind, as it is just that, human. Whatever combination of inferences a species makes would represent its *own* Theory of Mind, uniquely adapted to promote the fitness of individuals within that species. Simply because a species possesses different theories about the minds of others rather than our own (for a discussion of potential differences see Tomasello, Call & Hare, 2003b, pg. 156) does not equate to not possessing any theories at all. Instead, it is likely that different species have certain components of Theory of Mind, or differently developed versions of the components that humans possess (Povinelli & Eddy, 1996). These alternative theories about the minds of others would then potentially represent the evolutionary building blocks for the Theory of Mind that humans know (e.g. Byrne, 1996).

The term Theory of Mind, increasingly connoting specific human mental processes, has since been replaced by many researchers by the less controversy-laden term, complex cognition (introduced by Emery & Clayton, 2004a) – which itself is comprised of four cognitive tools (causal reasoning, imagination, flexibility, and prospection) and Theory of Mind can be considered just one aspect of complex cognition (Emery, 2006). This shift in terminology, and more importantly in theoretical approach, changed the overarching question for researchers studying comparative cognition from “do non-human animals possess a human ToM?” to the more apt “what do non-human animals know about the minds of others?” and presumably how has that knowledge been advantageous to the individuals within a species given their specific ecology. It is under this general framework that the present thesis work was conducted.

Woodruff and Premack (1979) pioneered the methodological approach used in this thesis – that of the object-choice task. In this study, chimpanzees were presented with two opaque containers, one of which contained a hidden food reward. To select a container, the chimpanzees had to indicate to the trainer which container they believed to hold the reward. The trainer present was either cooperative (gave the reward to the chimpanzee once it was found) or a competitive trainer (kept the reward and ate it himself). Two of the four chimpanzees learned to indicate the correct container to the cooperative trainer and the incorrect container to the competitive trainer suggesting these subjects might have appreciated the intentions of the trainer present. Although this early work could not differentiate this mentalist interpretation from the possibility that the chimpanzees simply learned the reward contingencies through associative learning (Tomasello & Call, 1994), it introduced a promising new methodology to studying the minds of animals.

Since Woodruff and Premack's (1979) seminal work, many species have been tested in object-choice tasks as a means for studying a variety of issues in comparative cognition (e.g. inhibition: Amici, Aureli & Call, 2008; exclusion: Schloegl, 2011; gesture use: Miklosi & Soproni, 2006; social cognition: Emery & Clayton, 2009). Traditionally, most of the research examining intelligence in animals (including studies utilizing the object-choice paradigm) has focused on primates due to their shared ancestry with humans (Emery, 2006; Rogers & Kaplan, 2004) – the notion being that genetic relatedness would result in the most closely related minds in terms of organization and function. However, recent evidence has shown that other species outperform primates in object-choice tasks, particularly domestic dogs (Brauer, Kaminski, Riedel, Call &

Tomasello, 2006; Dorey, Udell & Wynne, 2009; Hare & Tomasello, 2005) and dolphins (Pack & Herman, 2006); thus, non-primate brains may be better suited in some respects for solving certain complex social cognition problems. For example, domestic dogs generally perform very well in object-choice tasks that require the animal to use the communicative gestures of a human experimenter (Udell, Dorey & Wynne, 2010), a success attributed to their evolution being shaped by domestication with humans (Hare, Brown, Williamson & Tomasello, 2002; Hare & Tomasello, 2005). Similarly, the impressive performance of dolphins during object-choice tasks has been argued to be a result of selection pressure for joint attention, presumably a result of dolphins extracting information from the echolocation calls of conspecifics (Pack & Herman, 2006). Thus, evidence indicates specific ecological factors throughout a species' evolution seem to promote the ability to understand mental states and, in the case of dogs and dolphins, shaped sensitivity to the cooperative mental states needed to succeed in most object-choice tasks.

Recently, some species of birds have been tested with object-choice tasks. If the assumption that a primate brain, or a mammalian brain for that matter, is not needed to solve complex social problems, then studying the brain and behavior of birds may be particularly revealing of the neuroanatomy and ecological pressures that are important for the development of complex social cognition abilities. The avian neural architecture is quite different from that of mammals, although, functionally the brains are very similar (Güntürkün, 2005; Jarvis & Consortium, 2005). Thus, despite 250 million years of separate evolution between birds and humans (Evans, 2000), birds may solve problems and reason in much the same way as mammals. Indeed, corvids, the group of birds with

the largest forebrains (Emery & Clayton, 2004b), thought to be the result of an array of ecological factors that promote intelligence (Lefebvre & Sol, 2008), show a variety of behaviors that suggest they have an impressive understanding of the minds of others, in many cases, rivaling that of primates (Emery & Clayton, 2004a). Thus, the deeply rooted assumption that primates are the animals most likely to possess complex social cognition abilities (or those resembling human abilities) is called into question. Casting aside these traditional assumptions, this thesis aims to examine Clark's nutcrackers' ability to utilize gestural information and to make inferences based on their perception of the mental states of human experimenters. The findings will then be discussed in the broader comparative context of past performance of corvids and primates tested with the object-choice task.

**Chapter 2: Clark's nutcrackers' (*Nucifraga columbiana*) ability to discriminate knowledge states of human experimenters during an object-choice task**

Research suggests that corvids may share many cognitive abilities with primates making these birds intriguing research subjects for the study of complex social cognition (Emery & Clayton, 2004). By comparing distantly related species it is possible to identify some of the common ecological factors that have driven the convergent evolution of social cognition skills in corvids and primates. As evidence for their complex social cognition abilities, primates have been reported to take into account various aspects of an observer to predict behavior, including: the observer's attentional state (Flombaum & Santos, 2005), dominance status (Hare, Call, Agnetta & Tomasello, 2000; Hare, Call & Tomasello, 2001), or knowledge state (Kaminski, Call & Tomasello, 2008). Likewise, corvids have been reported to use social cognition to alter their behavior as a function of whether another individual is present. Corvids have been shown to change the way they cache and retrieve food depending on whether or not they have been observed, both in the wild (Bugnyar & Kotrschal, 2002; Heinrich, 1999; Heinrich & Pepper, 1998; James & Verbeek, 1983) and in the laboratory (Bugnyar, 2010; Bugnyar & Heinrich, 2005; Bugnyar & Heinrich, 2006; Emery, Dally & Clayton, 2004). When another individual is present, corvids will tend to cache in areas where an observer would have reduced visual access to information regarding cache location, such as behind obstructions (Bugnyar & Kotrschal, 2002) or in shaded areas (Dally, Emery & Clayton, 2004). They have also been shown to preferentially cache when an observer is distracted or inattentive (Heinrich & Pepper, 1998), as well as take into account an observer's dominance status (Bugnyar & Heinrich, 2006; Paz-y-mino, Bond, Kamil & Balda, 2004). Ravens for instance, are more

likely to steal cached food if the caching bird is subordinate but not if it is dominant (Bugnyar & Heinrich, 2006). Additionally, if witnessed making a cache, corvids have been shown to re-cache their food when the observing bird has left the area (scrub jays: Emery, Dally & Clayton, 2004) and retrieve cached food preferentially when a competitor is knowledgeable of a cache's location (ravens: Bugnyar, 2010; Bugnyar & Heinrich, 2005; Clark's nutcrackers: Clary & Kelly, 2011; scrub jays: Dally, Emery & Clayton, 2006). These findings suggest that many corvids are sensitive to what other individuals see and know (much like some primates) and also recognize that other individuals may have intentions to steal their caches.

To date, research into the complex social cognition abilities of corvids has primarily focused on the domain of food caching. Whether such behavior seen in the context of food caching is truly indicative of sensitivity to knowledge states (i.e. having a mental representation of what information another individual possesses: Bugnyar, 2010; O'Neill, 1996) as opposed to simpler associative mechanisms, and whether this ability is flexible, such that it may be applied to non-ecologically relevant situations outside of the food-caching domain, is uncertain. Therefore, establishing that corvids are indeed capable of complex social cognition, by challenging them in contexts that do not facilitate the use of instinctual behaviors, is necessary before attempting to isolate the ecological similarities underlying the convergent evolution of corvid and primate cognition.

Object-choice tasks provide one promising means for exploring whether the abilities shown by corvids are in fact a representation of complex social cognition. In a common variant of this task – the two-way object-choice task – the animal is required to infer the underlying knowledge state of a human experimenter through the use of a human

experimenter's gestural cue to locate a food reward hidden under two or more opaque containers (e.g. primates: Byrnie, 2004; Call & Tomasello, 1994; Itakura & Anderson, 1996; Itakura & Tanaka, 1998; Nieworth, Burman, Basile & Lickteig, 2002; Peignot & Anderson, 1999; canids: Soproni, Miklósi, Topál & Csányi, 2002; Virányi, et al., 2008; cetaceans: Pack & Herman, 2004; Tschudin, Call, Dunbar, Harris & van der Elst, 2001). Studies examining whether corvids can use human gestures during this task have shown mixed results. Schloegl, Kotrschal and Bugnyar (2008a) presented ravens (*Corvus corax*) with an array of five containers and a human experimenter pointed to one container, which had been previously baited, with his ipsilateral arm. The birds did not choose this container more often when the experimenter pointed to it than if no cue was given. Conversely, von Bayern and Emery (2009) showed that jackdaws (*Corvus monedula*) were able to use a pointing cue during a similar task. However, in this study the experimenter extended his arm across his body (i.e., the contralateral arm) to indicate which of two containers was baited. It is not known whether this seemingly subtle gestural difference may account for the disparate findings of these two studies, or if that difference is attributable to species differences between ravens and jackdaws. When non-avian species have been tested with both an ipsilateral and contralateral gesture, the results indicate similar comprehension with either gestural form (dogs: Soproni, et al., 2002; dolphins: Pack & Herman, 2004; Herman, et al., 1999; seals: Shapiro, Janik & Slater, 2003). If non-avian species are any indication, then the difference between ravens and jackdaws likely represents a species difference in the ability to extract information from human gestures rather than a methodologically driven difference.

Tornick, Gibson, Kispert and Wilkinson (2011) reported that Clark's nutcrackers

(*Nucifraga columbiana*) were proficient at using a variety of gestural cues, when presented independently, to find a food reward hidden in one of two containers. The nutcrackers were able to use a touch gesture (a baited cup was touched using the ipsilateral arm and picked up by the experimenter) and a pointing gesture (the experimenter's ipsilateral arm and finger were directed to a baited cup) to locate the food reward at above chance levels early in testing. With additional training, the nutcrackers were also able to use eye gaze as a cue (the experimenter's eyes and head were alternated between the bird and the baited cup).

In addition to being able to examine gesture use, the two-way object-choice paradigm has the potential to elucidate whether animals can discriminate between experimenters with different knowledge states. Capitalizing on the apparent ability of Clark's nutcrackers to readily use human gestural cues (Tornick, et al., 2011), the current study examined whether Clark's nutcrackers are able to use the knowledge states of human experimenters during a two-way object-choice task. The experiment was conducted in two phases. During Phase 1 of this experiment, nutcrackers were tasked with locating a hidden food reward by using a combined look-point-touch gesture (from here on referred to simply as "gesture") from a familiar or novel human experimenter; this ability was a necessary prerequisite for Phase 2.

During Phase 2 of this experiment, the same nutcrackers were required to discriminate between an informed and uninformed human experimenter, and use only the gesture cues from the informed experimenter to locate a hidden food reward. The results from this modified two-way object-choice task can be used to examine whether nutcrackers are able to use the knowledge states of other individuals and whether the



cognitive abilities of nutcrackers can be used in non-ecologically relevant situations.

Thus, if nutcrackers' previously reported social cognition abilities (Clary & Kelly, 2011) are flexible and indicative of complex cognition, then they should show evidence of discrimination between the two human experimenters with differing knowledge of the hidden food reward's location, despite being tested in a non-ecologically relevant task.

### **Chapter 3: Methods**

#### **Subjects**

Ten (5 male and 5 female) wild-caught, sexually mature Clark's nutcrackers (*Nucifraga columbiana*) were used in the experiment. Birds had been in captivity for 8-16 years and were housed in individual cages (73 cm high x 48 cm wide x 48 cm deep) throughout the experiment. The birds were provided with a diet consisting of turkey starter, parrot pellets, sunflower seeds, pine seeds, mealworms, oyster shells, and a vitamin supplement. Each individual was food restricted to 85% of its *ad lib* weight for the duration of the experiment. All birds had previous experience with spatial and functional lateralization tasks. The colony room maintained a 12:12 light-dark cycle with light onset at 0700 and a temperature of 21°C. All housing and experimental conditions were approved by the local animal care committee and met the guidelines of the Canadian Council on Animal Care.

## Apparatus

Birds were tested in an experimental cage (66 cm high x 48 cm wide x 48 cm deep) surrounded by white curtains to create a uniform environment (200 cm long x 175 cm wide). The experimental cage allowed the birds to make choices through two openings at the front of the cage (see Figure 1). Birds could insert their heads through one opening at a time to obtain a food reward from a container situated on a tray (51 cm long x 23 cm wide) outside the cage. Two laterally positioned containers (8.5 cm diameter) were placed in this tray. A swivel lid was attached to each of the containers such that the contents could be occluded. To control for odor cues, each container had a layer of pine seeds along the bottom. The rest of the volume was filled with grit so that a single pine seed could be placed on the surface of the grit, in view of the test subject, when the container's swivel lid was open. The tray was attached to a pulley system operated by an experimenter located outside of the testing room. This system allowed the experimenter to pull the tray away from the cage once the subject had made a choice. Each trial was viewed and recorded using a Sony Mini DV digital videocassette recorder attached to an EverFocus 1/3" color digital camera mounted on the ceiling above the test cage.

## Procedures

**Habituation.** Prior to the experiment, the birds were given one container, filled with grit and a food reward, in their home cages so that they could explore the container and learn how to remove the lid to obtain the pine seeds inside. Once birds were readily approaching and reliably opening the containers in their home cage, the birds were

individually placed in the experimental cage and allowed to select freely from the containers which were placed flush against the two openings of the experimental cage with the swivel lids opened. On the following four days the swivel lids were closed and the birds were allowed to explore the containers and open the lids to retrieve a hidden pine seed from each container. Once birds were consistently opening the containers in less than 30 seconds they began participating in the experiment.

### **Phase 1**

**Training.** Training procedures for Experiment 1 were similar to those used by Tornick, et al. (2011). During training, birds received one daily session consisting of eight trials. During half of the trials the gesture was performed by an experimenter familiar to the birds (herein referred to as the “familiar experimenter”), whereas during the other half of the trials the gesture was performed by an experimenter unfamiliar to the birds (herein referred to as the “novel experimenter”). The trials were counterbalanced and pseudo-randomized so as not to have the same experimenter gesturing during more than two consecutive trials. During training, an experimenter entered the enclosure and stood at a central location behind the tray. The experimenter then placed an opaque barrier against the front of the bird’s cage so that the bird could not see the experimenter who proceeded to bait one of the two containers. During half of the trials, the pine seed was placed in the left container and during the other half of trials, in the right container. The baited side was counterbalanced across trials and pseudo-randomized so that the seed was never baited in the same container for more than two consecutive trials.

After baiting one of the containers from behind the barrier, the experimenter closed both of the containers, removed the barrier, and proceeded to show the bird the contents of each container, one at a time. To do so, the experimenter opened the lid of one of the containers for three seconds (or until the bird directed its gaze at the open container), closed the lid, and then proceeded to do the same for the other container. The location (left or right) of the container that was opened first was counterbalanced across trials. After this presentation the experimenter pushed the tray flush against the cage. The experimenter immediately left the experimental room to allow the bird to make a choice in private. Birds were allowed to make a single choice. If the bird chose the rewarded container it was allowed to obtain the seed before the tray was pulled away. If the bird chose the unrewarded container, a 10 second blackout ensued (experimental room lights extinguished) and the tray was pulled away from the cage. After the bird's choice, a 30 second inter-trial interval was instituted. Once a bird was reliably making a choice within 30 seconds or less, and made accurate choices during seven of the eight trials for five consecutive days, the bird was presented with the testing sessions.

**Testing.** Testing was conducted over two blocks (ten test days per block), with one session per day consisting of eight trials: six training trials and two test trials. The procedures for the six training trials were exactly as described above. The two test trials occurred randomly between trials two through seven (trials one and eight were always training trials), but were never presented consecutively. One test trial was conducted by the familiar experimenter, and the other test trial was conducted by the novel experimenter. For each test trial, the experimenter baited one container as during training. However, once the barrier was removed the experimenter gestured to the baited

container, which now had the swivel lid closed, by looking (orienting his head and eyes towards the container), pointing (extending his ipsilateral arm towards container), and touching (making contact with container using his finger tip). This gesture was held for three seconds or until the bird attended to the gesture by tilting its head in each direction allowing the bird to view the situation with each eye. If the bird correctly chose the rewarded container, defined as removing the swivel lid, it was allowed to retrieve the seed. However, if it chose the unrewarded container the tray was pulled away. Unlike the training trials, blackout periods were not presented for incorrect choices during testing to reduce the potential for associative learning.

## **Phase 2**

During Phase 2 the birds were challenged to use the knowledge states of two experimenters simultaneously in order to find the reward. To accomplish this, we needed to ensure that the birds were able to reliably use the gesture; therefore, during Phase 2, all of the birds from Phase 1 were now explicitly trained to use the gesture. A new person was used as the novel experimenter during Phase 2.

**Training.** Birds were trained in three stages. During stage one, the training procedures were the same as those of testing during Phase 1 with the exception that once the barrier was removed the experimenter baited one of the containers in full view of the bird. The experimenter then gestured to the open and baited container for three seconds before the bird was allowed to make a choice.

Stage two was identical to stage one with the exception that after the container was baited the experimenter closed both containers before gesturing to the baited container.

During stage three the visual barrier was erected and from behind this barrier the experimenter repositioned the containers so that they were vertically aligned on the tray (at this point neither of the container's were baited; see Figure 2). This alignment prevented the birds from being able to use the experimenter's arm position during the baiting process as a reliable cue for the position of the baited container (see below). Once the containers were aligned, the barrier was removed and the experimenter positioned a cardboard stand (28.5 cm x 45 cm) in front of the tray. This stand allowed the experimenter to bait one of the two containers without the bird seeing which of the containers was baited. After the container was baited, the experimenter moved both containers back to their lateral positions, removed the cardboard stand, and proceeded to gesture to the baited container (the location of the baited container now unknown to the bird). The tray was placed flush against the cage and the experimenter left the room permitting the bird to make a choice in private. The bird was allowed to retrieve the seed after making a correct choice whereas an incorrect choice was followed by a 10 second blackout period.

**Testing.** Testing was conducted over two blocks (eight test days per block), with one session per day consisting of eight trials: six training trials and two test trials. The procedures for the six training trials were exactly as described above. The two test trials occurred randomly between trials two through seven (trials one and eight were always baseline trials), but were never presented consecutively. There were two testing conditions: the *Uninformed Gesture Condition* and the *Gesture Conflict Condition*. One test trial of each condition was administered during a daily session. Testing involved two knowledge states; the Informed Experimenter, who was responsible for baiting the

container and therefore was informed as to the location of the reward, and the Uninformed Experimenter, who was not involved in the baiting processes and therefore uninformed of the location of the reward. The familiar and the novel experimenter played both the roles of Informed Experimenter and Uninformed Experimenter equally often.

During the *Uninformed Gesture Condition*, the Informed Experimenter presented the trial as in stage three, except after removing the cardboard stand the Informed Experimenter left the experimental room and was replaced by the Uninformed Experimenter; thus this condition only involved one knowledge state (uninformed). The Uninformed Experimenter gestured to a predetermined container; during half of the trials this container was the rewarded one and during half of the trials it was the unrewarded one. The gesture was held for three seconds after which the tray was pushed flush against the cage, the experimenter left the room allowing the bird to make a choice in private. During this condition, if the bird was able to use the knowledge state of the Uninformed Experimenter it should determine that the gesture was not informative as to the location of the reward. This condition allowed us to examine whether the birds would use the gesture information even when it was uninformative, in which case the birds should follow the gesture of the Uninformed Experimenter, or whether the birds would refrain from using the uninformative gesture and either choose randomly between the two containers or adopt a side preference.

During the *Gesture Conflict Condition*, the Informed Experimenter prepared the trial as in stage three, except once the cardboard stand was removed the Uninformed Experimenter also entered the enclosure. Both experimenters proceeded to gesture

(simultaneously) to a predetermined container. Specifically, the Informed Experimenter gestured to the rewarded container whereas the Uninformed Experimenter gestured to the unrewarded container. The gestures were held for three seconds, after which the tray was pushed flush against the cage and both experimenters left the room, allowing the bird to make a choice in private. In order to choose correctly, the bird had to use some aspect of the experimenters' knowledge states. For instance, the bird could use the knowledge state of the Informed Experimenter to choose the rewarded container or use the knowledge state of the Uninformed Experimenter to avoid choosing the unrewarded container – or a combination of both strategies.

For both test conditions, if a bird chose the rewarded container it was allowed to recover the seed prior to the tray being pulled away, whereas if the unrewarded container was chosen the tray was pulled away (but no blackout period was administered) and a 30 second inter-trial interval ensued.

### **Statistical Analysis**

For all analyses alpha was set at 0.05. Choice accuracy was analyzed using repeated measures ANOVAs with Experimenter and Testing Blocks as variables. One-sample t-tests were used to compare the choice accuracy against chance (50% accuracy).



## Chapter 4: Results

### Phase 1

Eight birds progressed to testing after an average of 27 training days. Two birds failed to reach training criterion after 60 days and did not progress to testing during Phase 1.

A repeated measures ANOVA examining choice accuracy with Experimenter (Familiar and Novel) and Testing Blocks (1 and 2) did not show a main effect of Experimenter (Familiar:  $M = 0.5688$ ,  $SE = 0.024$  and Novel:  $M = 0.6063$ ,  $SE = 0.046$ ;  $F_{(1, 7)} = 1.615$ ,  $p = 0.244$ ), showing that the birds' accuracy was similar regardless of which experimenter was performing the gesture. The birds' accuracy was also similar across Testing Blocks (Block 1:  $M = 0.5688$ ,  $SE = 0.048$  and Block 2:  $M = 0.6063$ ,  $SE = 0.033$ ;  $F_{(1, 7)} = 0.612$ ,  $p = 0.460$ ). Although choice accuracy was low, a one-sample t-test showed that the birds were choosing the correct container significantly more than expected by chance, supporting that the birds had learned to use the gesture ( $M = 0.5875$ ,  $SE = 0.034$ ;  $t_{(7)} = 2.593$ ,  $p = 0.036$ ).

### Phase 2

Four birds met the training criterion after an average of 43.5 days of stage three training, and therefore progressed to testing. The remaining six birds did not meet the training criterion after 85 training days, and did not progress to testing.

**Uninformed Gesture Condition.** A repeated measures ANOVA examining choice accuracy with Experimenter (Familiar and Novel) and Testing Blocks (1 and 2) did not

show a main effect of Experimenter (Familiar:  $M = 0.8438$ ,  $SE = 0.060$  and Novel:  $M = 0.8438$ ,  $SE = 0.031$ ;  $F_{(1, 3)} = 0.000$ ,  $p = 1.000$ ) showing that the birds' accuracy was similar regardless of which experimenter was performing as the Uninformed Experimenter. The birds' accuracy was also not significantly different across Testing Blocks (Block 1:  $M = 0.7813$ ,  $SE = 0.060$  and Block 2:  $M = 0.9063$ ,  $SE = 0.031$ ;  $F_{(1, 3)} = 6.000$ ,  $p = 0.092$ ).

The nutcrackers followed the Uninformed Experimenter's gesture at above chance levels ( $M = 0.8438$ ,  $SE = 0.040$ ,  $t_{(3)} = 8.521$ ,  $p = 0.003$ ). The bird's choice accuracy during the *Uninformed Gesture Condition* was not significantly different from baseline trials (test trials:  $M = 0.8438$ ,  $SE = 0.040$ ; baseline trials:  $M = 0.9317$ ,  $SE = 0.013$ ,  $t_{(3)} = -1.822$ ,  $p = 0.166$ ). Individually, three of four birds used the gesture at above chance levels (Sid: 13/16 trials, 0.8125, binomial:  $p = 0.021$ ; George: 14/16 trials, 0.8750, binomial:  $p = 0.004$ ; Tanthalas: 15/16 trials, 0.9375, binomial:  $p = 0.001$ ) and one bird missed significance by one response (Tasha: 12/16 trials, 0.7500, binomial:  $p = 0.077$  – see Figure 3). Thus, birds continued to rely on the experimenter's gesture to guide their choices despite the gesture not providing reliable information as to the goal's location.

**Gesture Conflict Condition.** A repeated measures ANOVA examining choice accuracy with Experimenter (Familiar and Novel) and Testing Blocks (1 and 2) did not show a significant main effect of Experimenter (Familiar:  $M = 0.5312$ ,  $SE = 0.079$  and Novel:  $M = 0.6250$ ,  $SE = 0.089$ ;  $F_{(1, 3)} = 0.325$ ,  $p = 0.608$ ) showing that the birds' accuracy was not significantly different depending on which experimenter was performing as the Informed Experimenter. The birds' accuracy was also similar across

Testing Blocks (Block 1:  $M = 0.6250$ ,  $SE = 0.094$  and Block 2:  $M = 0.5313$ ,  $SE = 0.074$ ;  $F_{(1, 3)} = 0.325$ ,  $p = 0.608$ ).

Overall, the nutcrackers chose the Informed Experimenter's gesture significantly more often than would be predicted by chance ( $M = 0.5781$ ,  $SE = 0.016$ ,  $t_{(3)} = 5.000$ ,  $p = 0.015$ ) and this choice accuracy was not significantly different across Testing Blocks (Block 1:  $M = 0.6563$ ,  $SE = 0.060$ ; Block 2:  $M = 0.5000$ ,  $SE = 0.090$ ;  $t_{(3)} = 1.058$ ,  $p = 0.368$ ). Individually, however, none of the nutcrackers chose the Informed Experimenter's gesture significantly greater than chance (Sid, Tanthalas, and Tasha: 9/16 trials, 0.5625, binomial:  $p = 0.804$ , and George: 10/16 trials, 0.6250, binomial:  $p = 0.454$  – see Figure 4). Choice accuracy remained very high on baseline trials ( $M = 0.9317$ ,  $SE = 0.013$ ;  $t_{(3)} = 32.974$ ,  $p < 0.001$ ).

## Chapter 5: Discussion

Learning to reliably use the gestures from two experimenters was clearly a difficult task for the nutcrackers as only four of the ten birds were able to acquire the training criterion during Phase 2. The birds showed that they could use the gesture at above chance levels from Phase 1, but many of the birds could not improve this accuracy in order to achieve the accuracy criterion needed for Phase 2 testing. The birds that did proceed to testing tended to use the gestural information from the Uninformed Experimenter during the *Uninformed Gesture Condition*, suggesting when birds did learn to use the gesture, the use of this gesture was robust and persisted even when it did not provide reliable information as to the reward's location. This may suggest that the birds were not sensitive to the knowledge state of the Uninformed Experimenter and relied

upon the Informed Experimenter to guide choices during training. However, when the gestures from the two experimenters provided conflicting information as to the location of the rewarded container, overall the birds chose the knowledgeable experimenter more often than would be expected by chance, showing that they may have been able to distinguish between the two experimenters to use the knowledge state of the Informed Experimenter. This performance suggests that nutcrackers base their decisions on whether an individual possesses rather than lacks information. These results are the first to show that nutcrackers may use knowledge states from human experimenters to guide choice behavior in a non-ecologically relevant task, an ability previously shown only by primates (Povinelli, Nelson & Boysen, 1990).

Overall, the nutcrackers chose the gesture of the Informed Experimenter despite a number of components of the task that could be considered non-ecologically relevant. The experiment required the birds to use the gestures and knowledge states of a distantly-related species. Considering the different forms that the gestures of primates and birds take (e.g. beak pointing versus limb pointing – see Kaplan, 2011 for avian gestures), the nutcrackers may have had difficulty recognizing that a referential gesture was being presented. Using knowledge states, however, may be a skill more easily applied across primates and corvids, as the circumstances leading to knowledge acquisition are likely similar (e.g. visual access to events leads to informed knowledge states; corvids: Bugnyar, 2010; primates: Hare, et al., 2001). The nutcrackers may have been able to use the experimenter's knowledge state, but were not proficient in using the gesture because the birds could not easily extract the information conveyed due to the divergent forms of avian and human (primate) gestures. This distinction would explain the difficulty the

birds experienced during training with a human gesture, and the evidence that they preferred the information provided by the Informed Experimenter once the gesture was learned. Combining these different task components likely would have increased the difficulty of the task – an idea proposed by Call and Tomasello (1999), who suggested the object-choice task is difficult because “the subject is asked to master both the logistics of the task and to display an understanding of other minds at the same time” (p. 382).

Additionally, object-choice tasks have been argued to be a cooperative task (Hare, 2001), which may be less ecologically relevant and consequently less intuitive for a relatively non-social species like the Clark’s nutcracker. Clary and Kelly (2011) made a similar argument when describing how the cache protection strategies of nutcrackers compare to those of more social corvid species. After experiencing cache theft nutcrackers were found to decrease the number of caches made over time, the opposite pattern of the more social Western scrub-jay (Emery, et al., 2004), which increased caching behavior after experiencing pilferage. Thus, the authors suggested that nutcrackers may view caching interactions as competitive, whereas social species may view them as cooperative. If less social species view social interactions as competitive, this may explain why the majority of the nutcrackers had difficulty consistently following the experimenter’s gesture during the current study. This could explain the above chance, yet low accuracy performance of the nutcrackers in Phase 1 and the inability of many birds to achieve maximum accuracy in Phase 2.

In terms of the nutcrackers’ ability to use gestures, the results seem to be at odds with those recently reported by Tornick, et al. (2011). The nutcrackers in this previous study learned to use gestural cues to locate a food reward quickly and effectively,

whereas the majority of the birds in the current study were unable to learn to use the human-based gesture despite being explicitly trained to follow the gesture through additional training trials and the implementation of correction procedures after incorrect choices.

Several procedural differences were introduced in the current study (e.g. combined gesture, multiple experimenters) in order to examine knowledge state discrimination compared to the methods employed by Tornick et al. (2011), which may account for some of the differences in gesture learning. The results of the current study do not support the likelihood that the nutcrackers were learning to use the gesture cue through local enhancement strategies (Tornick, et al., 2011; Schloegl, et al., 2008a). Tornick, et al. suggested that this simpler strategy may have accounted for subjects' superior performance with pointing and touch cues over eye gaze because these cues reduce the distance between the cue and the goal location. However, in the current study, both the point and touch cue of the gesture were presented together and offered no distance between the cue and the container, yet the nutcrackers struggled to learn to follow the gesture. Thus, even though we increased the physical contact with the rewarded container, arguably increasing local enhancement, the nutcrackers were not able to use this local information to improve choice behavior.

The results agree with other studies showing that static eye gaze (at least in the context of the object-choice task), is particularly difficult for corvids to use (ravens: Schloegl, et al., 2008a; rooks: Schmidt, Scheid, Kotrschal, Bugnyar & Schloegl, 2011; jackdaws: von Bayern & Emery, 2009) and that alternating eye gaze may be more salient for some species (jackdaws: von Bayern & Emery, 2009; nutcrackers: Tornick, et al.,

2011). Ravens have also succeeded in using human eye gaze if the experimenter is able to ‘see’ the hidden food (Schloegl, Kotrschal & Bugnyar, 2008b) or if asked to track human gaze behind visual barriers (Bugnyar, Stowe & Heinrich, 2004), even though alternating gaze cues were not used in these procedures. Thus, it may be that object-choice tasks require animals to use information in a way that differs from how cues are used in more ecologically relevant problems.

Specifically because the object-choice task is difficult, and non-ecologically relevant for corvids (perhaps especially so for less social species), the evidence that corvids can succeed in these tasks is particularly revealing as to the extent of their cognitive capabilities. The results presented here, suggesting that Clark’s nutcrackers may be capable of discriminating the knowledge states of humans, highlight the flexibility and complexity underlying nutcracker cognition. If the nutcrackers are capable of making judgments about the mental states of others in this purposefully difficult context, then it is certainly conceivable that these birds are using these abilities regularly and more proficiently in natural situations (e.g. during caching interactions). This study also indicates that nutcrackers may share with primates the ability to determine the knowledge states of others individuals, a skill thought to underlie complex social cognition – further suggesting that the similarities in behavior and cognition between corvids and primates represents evidence for convergent evolution.

## **Chapter 6: Future Directions**

The study presented in this thesis is the first to examine a species of corvid using the object-choice task with the explicit purpose of explicating what these birds know

about the mental states of others. The results are intriguing; yet alone they cannot provide a strong argument for the definitive ability of corvids to discriminate knowledge states. The strength of this study was the performance of the nutcrackers despite the difficult nature of the task; the nutcrackers clearly had difficulty understanding the communicative nature of the gesture. Therefore, future endeavors should work towards creating tasks that reduce the ambiguity introduced by the human gesture, either by modifying how the gesture is trained and presented, or by eliminating it altogether.

The presented study has potential for identifying which aspects of the experimenter-animal interaction are complicating the object-choice task by comparing the current methodology with that of the Tornick, et al. (2011) study. Both the nutcrackers used here and in Tornick, et al. come from the same population of birds, caught at the same time, and brought into the same original laboratory, so regional differences or experimental history are unlikely to be the cause of the divergent results found in terms of nutcracker gesture use. Rather, these differences suggest that the subtle procedural differences between these two studies affected how the birds understood the gesture being presented. In the presented study, there were four major departures from the methodology of Tornick, et al.:

- Tornick et al. (2011) tested the nutcrackers with each gesture independently whereas during Phase 1 of the current study the three cues were combined with the purpose of creating a “super stimulus” gesture that would be more salient to the birds and enhance learning. This clearly was not the case – the combined stimulus did not enhance learning and instead the combination of the cues may have been distracting for the birds.



- The nutcrackers in the current study had to learn the same gesture but from two different experimenters; this was not so with the Tornick et al. (2011) study which used a single experimenter to train (and test) each gesture. The experimental question posed in Phase 2, whether nutcrackers could discriminate the knowledge states of human experimenters, required the birds to be trained with two experimenters. Thus, during Phase 1, although the birds did not show a difference in choice accuracy when the gesture was presented by either the familiar or novel experimenter, requiring the birds to use the gesture from two experimenters, rather than one, may have made the task more difficult.
- During Phase 1 training and in Tornick et al. (2011), one container at a time was opened for the birds to view the contents. During the current study, the order of container presentation was counterbalanced, whereas in Tornick et al. the left container was always opened first. The birds in Tornick et al. may have capitalized on this predictability and developed a strategy around this procedure – possibly directing the bird’s attention in a more step-wise fashion through the procedures.
- Finally, during Phase 1 testing and throughout Phase 2, unlike in Tornick, et al. (2011), the gaze cue was not alternated between the bird and the container; instead the gaze, along with head orientation, was directed at the container of interest for the duration of the gesture. This procedure was used in anticipation of the *Gesture Conflict Condition* so as not to bias the birds to choose the experimenter that last moved their gaze. Given that Tornick, et al. found that nutcrackers were least proficient in using eye gaze to locate a hidden reward it is unlikely that this

modification would have disrupted the birds' performance to the degree that was observed.

Additionally, experimenter-animal communication in this task could be enhanced by considering the natural communicative system of the species being studied. For birds, the work of Kaplan (2011) documenting how magpies gesture to conspecifics holds particular promise for this issue. The identification of the specific features that corvids attend to in natural gestural exchanges could guide how the gestures of future object-choice experiments are presented to the bird. For instance, given the descriptions provided by Kaplan that magpies 'point' by aligning their body both in the horizontal and vertical dimensions toward a predator, corvids may preferentially attend to the body orientation of the communicating individual – a gestural component neglected in the current literature. Instead of directing the head or eyes to the rewarded container, if the experimenter simply aligned his body towards the correct container, then the birds may find this communication more meaningful and intuitive.

Considering that birds routinely turn their head side to side to view dynamic situations with a lateral gaze (Moldonado, Maturana & Varela, 1988; Koboroff, Kaplan & Rogers, 2008), the birds may not realize that the head movement of the experimenter is of added importance and thus, do not extract information from this gesture. If birds use body alignment more so than eye or head orientation, it would make the current debate over static versus alternating gaze moot (see discussion). Small modifications to the procedures have been shown to alter the performance of animals in object-choice tasks (e.g. hiding food in tubes instead of bowls, Call, Hare & Tomasello, 1998), so

conceivably this small, yet perhaps not insignificant modification may improve the birds' performance.

Utilizing conspecifics rather than human experimenters would be another novel modification that could potentially facilitate the communication of experimental questions to the animal being studied. This idea has been utilized in one intriguing scenario to date (Kaminski, Call & Tomasello, 2008). The use of conspecifics instead of human experimenters inevitably sacrifices some experimental control; however, the use of recorded images of natural animal gestures may ameliorate this concern. If, for instance, a recording is shown of birds "pointing", thereby taking advantage of communication originating from a conspecific to indicate the reward container, the ambiguity that using a human experimenter inevitably introduces would be eliminated entirely. Application of this concept may be particularly difficult for birds, however, considering video screens are designed for the trichromatic visual system of humans and not the tetrachromatic visual system of birds. However, video screens that exceed the 90 Hz time resolution of the avian visual system (Bischoff, 1988; Powell, 1967) have been shown to effectively mimic a real moving image (Galoch & Bischoff, 2006; Ikebuchi & Okanoya, 1999). Additionally, although these images lack ultraviolet information, video recordings still elicited courtship behaviors (Adret 1997, Shimizu 1998, Ikebuchi & Okanoya 1999) suggesting that the video recording technique may be valid for mimicking a conspecific for the purposes of future object-choice tasks.

If such modifications are implemented, the animals may show improved performance, allowing more complex concepts to be tested and with more confidence that the results will provide meaningful insight into whether the animal is or is not

inferring mental states as opposed to simply struggling to cope with task demands. As previously mentioned (see General Introduction), some researchers have argued that understanding false-beliefs would be convincing evidence for a Theory of Mind. Previous attempts to examine whether primates understand false-beliefs have been hampered by the difficulty with the object-choice tasks devised (Call & Tomasello, 1999). Thus, null results can either be interpreted as a failure to understand the false-belief or a failure to understand all of the sequential components of the task. If, however, the confusion introduced by the human experimenters can be minimized or eliminated altogether, then the results of such experiments could hold more interpretative value.

Clearly, the method employed in object-choice tasks has an important (and poorly understood) impact on the animal's ability to understand the question being asked. Yet, if the task can be fitted to the species under investigation, the paradigm has great potential for revealing what animals know about the minds of others, and what aspects of complex social cognition are unique to humans, or other species for that matter.

This thesis has shown that Clark's nutcrackers may have the potential to ascribe different knowledge states to experimenters. Unlike, many studies plagued by the confound that the animal is simply basing its decisions on the behavior of others, this experiment requires the birds to rely on the knowledge states of the experimenters to find the goal at better than chance levels. During the *Gesture Conflict Condition* both experimenters gesture simultaneously, thus the gestures can't be differentiated other than by each experimenter's underlying knowledge state; hence the bird must base its decision on mental states rather than behavior. Furthermore, the results of the *Uninformed Gesture Condition* show that associative processes and cognition-based decisions may

work in parallel, and that the mere presence of associative learning does not preclude further complex cognition from occurring. Only by accounting for the associative learning and behavior reading hypotheses proffered (Penn & Povinelli, 2007; Heyes, 1998) can meaningful conclusions be made about the abilities of animals to attribute mental states to others. The presented thesis addresses these concerns. The task was difficult, yet there was evidence of knowledge state discrimination nonetheless – a revealing addition to the literature on what the corvid mind is capable.

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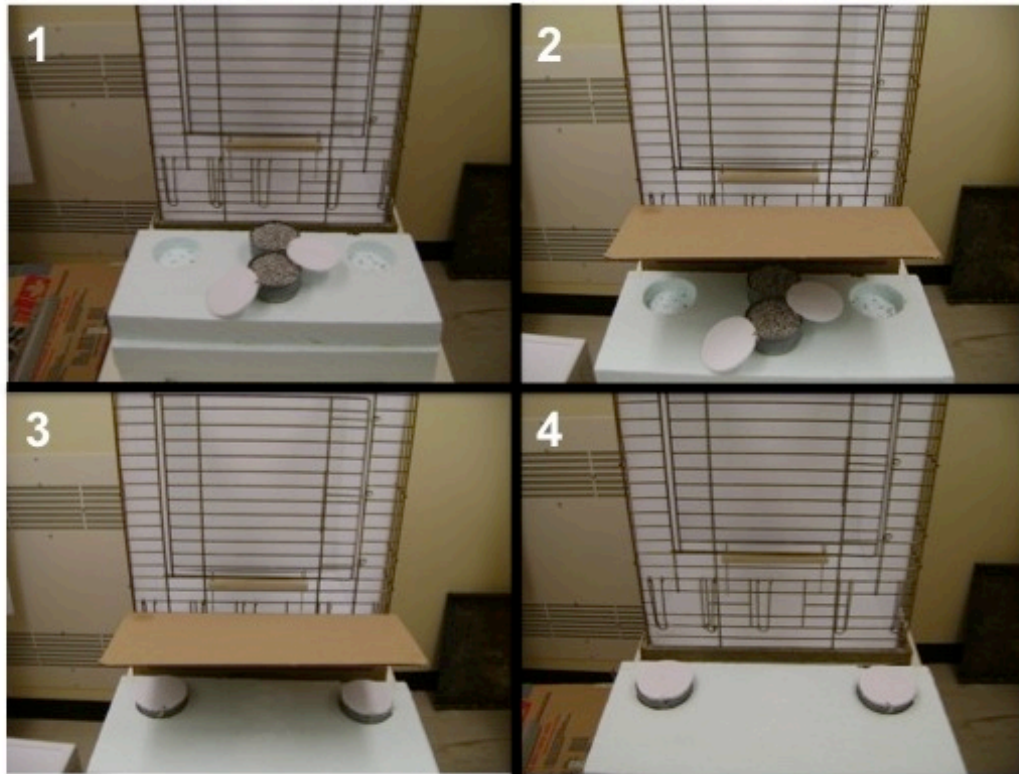
Figure 1: Photo of Experimental Cage and Tray



*Figure 1.* The front of the experimental cage. Two openings were located on either side of the cage to allow the bird access to either of the containers positioned laterally on the tray outside the cage.



Figure 2: Sequence of Tray Formations during Stage 3 Training



*Figure 2.* Stage 3 training during Phase 2. Panel 1: both containers placed centrally on the tray outside the cage. Panel 2: a cardboard stand was introduced to occlude bird's view of containers. Panel 3: the containers were returned to the lateral positions. Panel 4: the cardboard stand was removed and the containers were placed in their final locations prior to making the gesture.

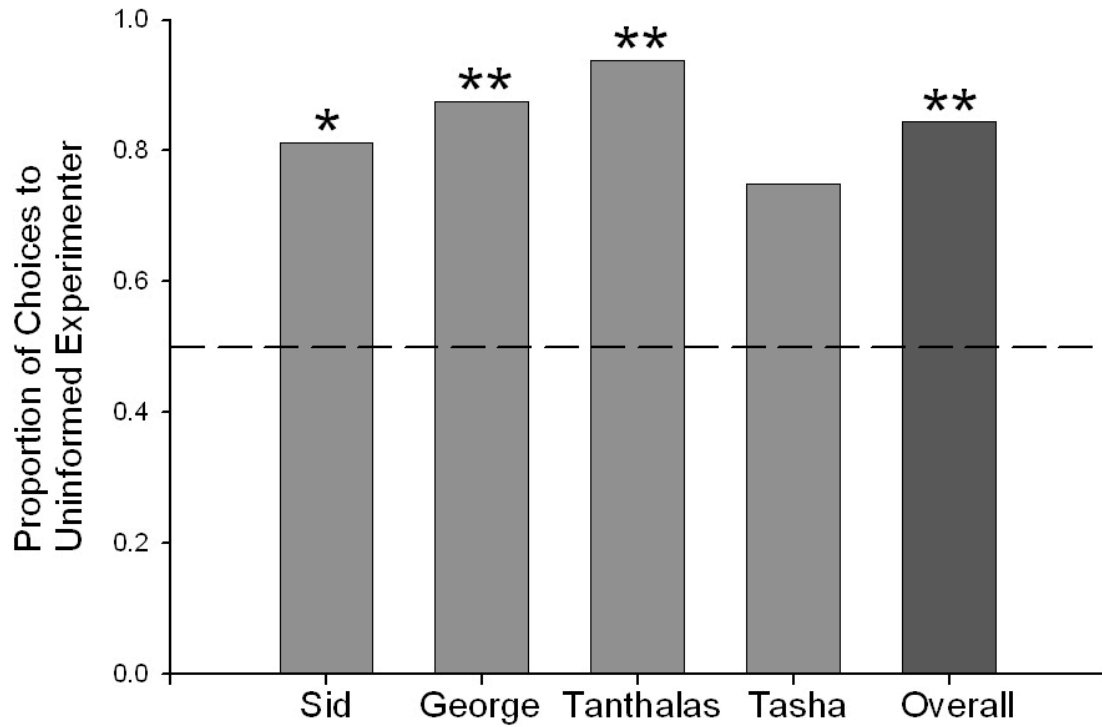
Figure 3: Choice Accuracy during *Uninformed Gesture Condition*

Figure 3. Comparison of each bird's choice accuracy and overall choice accuracy to chance responding during the *Uninformed Gesture Condition*. \* indicates significance at  $p < 0.05$ ; \*\* indicates significance at  $p < 0.01$ .

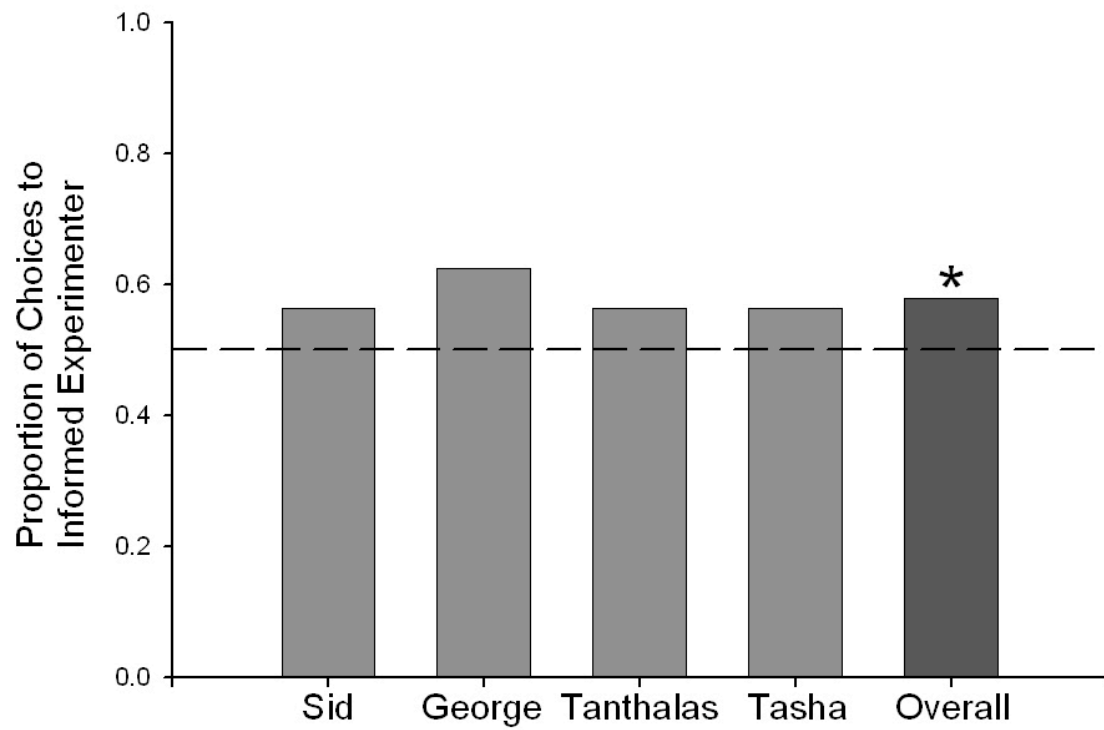
Figure 4: Choice Accuracy during *Gesture Conflict Condition*

Figure 4. Comparison of each bird's choice accuracy and overall choice accuracy to chance responding during the *Gesture Conflict Condition*. \* indicates significance at  $p < 0.05$ .