Physical and Social Cognition in the White-handed Gibbon (*Hylobates lar*)

**DISSERTATION**

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

By

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Abstract

While the cognitive capacities of primates have been studied for nearly a century, it is only relatively recently that scientists have begun to systematically compare the cognition of non-human primates with one another, humans, and other animals. These comparisons have been used to formulate hypotheses on the nature of cognitive change that may have led to human cognition. Knowledge about which species share cognitive characteristics can be used to understand why these characteristics exist and how they are used within their natural environments. Chimpanzees have long been the model subject, as they are the closest living relatives to humans and exhibit many complex behaviors in their natural environments and in captivity; among monkeys, capuchins have been most studied for similar reasons. It has become increasingly difficult to understand the full picture of non-human primate cognition, however, based on a limited number of species. With this in mind, it is useful to test a range of primates to pinpoint cognitive similarities and differences among groups. Gibbons are an important subject in this regard, as their cognition has received very little study, yet they occupy a unique phylogenetic position as lesser apes, which diverged from a common human ancestor between the time of Old World monkeys and great apes.

In the present research, a range of physical and social cognitive tests were used to gain a better understanding of gibbon cognition. In the domain of physical cognition, gibbons were tested in the areas of quantity and causality. Results on numerosity
comprehension indicate that gibbons’ discriminability threshold likely falls between that of chimpanzees and rhesus macaques, although further study is needed to confirm this. In the causality experiments, gibbons were successful in using changes in an object’s shape to locate hidden food (Experiment 2B). They were less successful in Experiment 2C, however, especially with variations on the basic support problem and they also had difficulty utilizing noise to locate hidden food in Experiment 2A.

In the second set of experiments, gibbons were tested in the domain of social cognition, specifically in the areas of communication and theory of mind. They were much less successful in this group of studies. The gibbons were not able to utilize the communicative cues of the experimenter to locate a hidden reward whether they were provided in a basic informative context (Experiment 3A) or a more intentional one (Experiment 4B). While they were able to indicate the location of a reward to a naïve experimenter in Experiment 3B, they failed to attend to the attentional state of the experimenter in Experiment 3C. In addition, in Experiment 4A they were able to follow combined head and eye gaze, yet failed to follow eyes alone or follow head/eye gaze behind a barrier.

Based on these results, gibbon cognition seems to have important differences from that of great apes and more generally resembles that of monkeys. Implications of this research and areas for future study are discussed.
Dedication

Dedicated to my loving and supportive husband, John, and our ray of sunshine, Caden;
and, of course, the amazing group of gibbons who made this research possible.
Acknowledgments

First, I would like to thank my advisor, Dr. Sally Boysen. Sally encouraged me to continue on with primate research despite numerous set-backs along the way and modeled perseverance and determination. This work also would not have been possible without the support and guidance of my other committee members, Vladimir Sloutsky and Dawn Kitchen. Vladimir and Dawn provided important comments on my research and encouraged me to ask new questions along the way. In addition, all of my committee members remained flexible and helpful as we struggled to coordinate dates and schedules for meetings.

I would also like to extend my heartfelt gratitude and thanks to Pam and Don White, owners and founders of the American Primate Educational Sanctuary where I was able to conduct my research with the gibbons. Pam and Don were always available to help in whatever way they could and often took time from their busy days to assist me with the logistics of testing the gibbons. In addition, they were always happy to lend an ear to discuss my musings on gibbon cognition and offer their fresh perspectives.

I am grateful for the help of undergraduate research assistant, Katie Wilson, who coded all of the gibbon data. She jumped in quickly and was instrumental in establishing reliability in all of the tasks.
I would never have made it through graduate school without the support of my husband, John. He constantly provided reassurance and the encouragement I needed to achieve my goals. He was always there to discuss the latest primate news and even provided his assistance to edit papers along the way. He has also been there to share the trials and tribulations of parenthood with me, and helped me carve out extra time to work on my research.

Lastly, I would like to thank my son Caden for reminding to enjoy the little things in life. He has helped me to gain a new perspective on child development and cognition, which has shaped my scientific interests. Through watching him grow, I am continually amazed at the wonder of human cognition and development.
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Fields of Study

Major Field: Psychology

Areas of Emphasis: Comparative Cognition; Developmental Psychology
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Chapter 1: Introduction

Despite the wealth of new information about primate cognition that has been gained in recent years, much about the evolution of primate cognition remains unknown. While many similarities and differences between humans, other great apes, and monkeys have surfaced, it is still not clear whether certain cognitive capacities vary in accord with phylogenetic relationships or if similar capacities have surfaced through convergent evolution. The former would predict that species more closely related to humans would share more human-like cognitive skills that were derived from a common ancestor (Maestripieri & Roney, 2006; Suddendorf & Whiten, 2001), while the latter proposal would allow for relatively unrelated species to show similar cognitive capacities and skills due to similar environmental factors, such as diet (Parker & Gibson, 1977). One group that is in a unique phylogenetic position to help with these problems is the gibbon, although there has been little scientific study of gibbons’ cognitive capacities thus far (e.g. Cunningham, Anderson, & Mootnick, 2006). Since gibbons are taxonomically apes, they fall intermediately between Old World monkeys and great apes, sharing a common ancestor with the great apes. Comparatively investigating the cognitive capacities of the gibbon will allow for a more complete picture of the cognitive relationship among non-human primates.

The specific aims of the present set of studies are to gain an understanding of the physical and social cognitive capacity of the white-handed gibbon (Hylobates lar) and
how these cognitive capacities compare to those of other primates. The tasks presented focus on areas that are ecologically valid to all primates. Physical cognition will be examined in terms of the subjects’ understanding of numerosity and causality, both of which would be helpful in keeping track of food resources and predators and exploiting the environment most efficiently. Social cognition will be examined in terms of the ability to use and understand social communicative cues and precursors to theory of mind, which would allow individuals to exploit knowledge of conspecifics to gain access to food rewards, avoid predators, and form alliances.

Throughout the next introductory sections I will 1) provide a brief review on the literature concerning the theories of cognitive evolution, 2) discuss the history of the field of primate comparative cognition and why I studied the areas of physical and social cognition, 3) review what is currently known about gibbon cognition, and 4) provide a detailed overview of the experiments conducted to test the cognitive capacity of white-handed gibbons (*Hylobates lar*).

1.1 The Nature of Cognitive Evolution

The day-to-day lives of humans look much different than that of their great ape cousins. Clearly, a variety of differences abound. However, it is not immediately clear if these observable differences are a result of large scale, generalized intelligence differences that provide humans with advanced capabilities in many different areas or if the differences are a result of more subtle changes that have occurred in particular domains, such as physical or social cognition. Although an increase in brain size throughout the primate lineage has been well-documented (Matsuzawa, 2007), there is
still much debate surrounding why and how these changes occurred (Healy & Rowe, 2007; Shettleworth, 2010). Several hypotheses have been proposed to explain the evolution of cognition in primates (Dunbar, 2010; Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; Parker & Gibson, 1977). I will review the following hypotheses concerning the evolution of cognition: a) general intelligence, b) ecological intelligence, and c) social intelligence.

An important area receiving renewed attention is whether primate cognition is more of a domain-general or domain-specific ability (Deaner, van Schaik, & Johnson, 2006; Reader & Laland, 2002). As one might expect, the general intelligence hypothesis advocates for a domain-general view of intelligence. Proponents of the general intelligence hypothesis often cite energetic limitations, such as body size and longevity, or structural constraints as the selection pressures behind the changes in primate brains (Barrickman, Bastian, Isler, & van Schaik, 2008; Dunbar, 2010). In this view, more advanced cognition overall is achieved through more efficient brain functions, such as learning, memory, planning, etc. (Deaner, et al., 2006, Herrmann, et al., 2007). The technical intelligence hypothesis advocates that enhanced domain-general cognition in great apes is the result of “technical” problems, such as foraging, extended home range, arboreal locomotion, and nest building, which resulted from their large body size (Russon, 2004). Recent meta-analyses of studies with non-human primates conducted by Deaner and colleagues (2006) and Reader and Laland (2002) lend support to the technical intelligence hypothesis, as well as other general intelligence views. Deaner and colleagues (2006) examined the cognitive abilities of 24 primate genera and found
significant differences in overall performance between groups. Most notably, great apes were more successful than the other groups across all paradigms tested, including detour problems, object permanence, tool use, discrimination learning, and delayed response, among others. This analysis, however, did not use data from social research paradigms, which are an important area of cognitive study, as the lives of primates involve so many social factors (Parker & McKinney, 1999; Tomasello & Call, 1997).

Consistent with the general intelligence view, another plausible scenario driving the evolution of large brains and complex cognition in primates involves their responses to environmental challenges. Ecological intelligence hypotheses focus on environmental factors such as the switch to a frugivorous diet, expanded home range size, the use of extractive foraging, and other forms of innovative tool use (Dunbar, 2010, Parker & Gibson, 1977; Reader & Laland, 2002). These hypotheses view survival, and hence selection, in terms of securing food resources under more and more challenging conditions. Specifically, the extractive foraging hypothesis has been proposed to explain tool use behavior observed in capuchin monkeys, lion-tailed macaques, baboons, and great apes as a convergent response to the same environmental challenge of embedded fruit (Parker & Gibson, 1977; Parker & McKinney, 1999). Additional support for ecological hypotheses comes from the large-scale analysis of published reports of executive brain size, social learning, tool use, and innovation (Reader & Laland, 2002). Reader and Laland (2002) found a strong correlation between brain size and rates of innovation, tool use, and social learning. They concluded that their findings were most consistent with ecological hypotheses, as the social behaviors cited were frequently used
in the context of foraging. Specifically, in the vein of Jolly (1966), Reader and Laland (2002) proposed that:

Individuals capable of inventing new solutions to ecological challenges, or exploiting the discoveries and inventions of others, may have had a selective advantage over less able conspecifics, which generated selection for those brain regions that facilitate complex technical and social behavior (p. 4440).

They went on to hypothesize that nonsocial and social behaviors may be based on the same processes that evolved together, providing support for domain-general hypotheses of intelligence (Reader & Laland, 2002).

Social intelligence hypotheses focus on how primates meet survival challenges socially and maximize survival through their intense social connections with others (Dunbar, 2003; Dunbar, 2010). Byrne and Whiten (1988) coined the term “Machiavellian Intelligence” for the range of complex, and often manipulative, social behaviors exhibited by monkeys and apes, which then sparked extensive interest in the social lives and corresponding cognition of primates. Indeed, many social factors have been correlated with brain size. For example, Byrne & Corp (2004) found that the frequency of tactical deceptions observed in the field was correlated with neocortex size in primates. This data supports the view that social challenges served as a major factor influencing the expansion of the neocortex in primates. In addition, Reader and Laland (2002) found that there was a relationship between the number of instances of innovation/social transmission and brain size. Other social factors correlated with neocortex volume in primates include grooming clique size, frequency of social play,
social group size, and the extent of social skills used in male mating (Dunbar, 2003). While not denying that simple environmental selection pressures (namely frugivory) may have been involved, Dunbar (2003, 2010) proposed that intensely bonded social groups and social skills were likely the most important selection pressures for the evolution of large brains. Dunbar (2003) hypothesized that predation risk necessitated an increase in group size, which then selected for an increase in brain size, as larger brains were necessary to deal with more bonded and complex social relationships.

The cultural intelligence hypothesis is a recent extension of social intelligence hypotheses and posits that culture selects for intelligence (Herrmann, et al., 2007; Whiten & van Schaik, 2007). Herrmann and colleagues (2007) contend that specific forms of social intelligence would be most important to sustain culture and these are the areas that separate humans from other great apes and allow for human’s unique and extensive cultural systems of living with one another and transmitting knowledge. Herrmann and colleagues (2007) tested human children, chimpanzees, and orangutans, on a number of physical and cognitive skills. They hypothesized that there would be no significant differences between the performance of human children (~2.5 years) and other great ape species in the domain of physical cognition. However, they anticipated significant differences between the human children and non-human primates in the field of social cognition. Indeed, Herrmann and colleagues (2007) found that human children generally performed similarly to the other apes (chimpanzees and orangutans) in the domain of physical cognition (measured through knowledge of space, quantities, and causality), while the children out-performed the other apes in the domain of social cognition.
Based on their results, Herrmann and colleagues (2007) concluded that humans differed specifically from great apes in the area of social cognition. These findings are problematic for the general intelligence hypothesis, as supporters of this view would have predicted equivalent differences in both cognitive domains.

The back and forth debate on cognitive evolution has left some researchers overwhelmed and frustrated (Healy & Rowe, 2007). Healy and Rowe (2007), among others, urge the consideration of multiple selection pressures on brain evolution (Seyfarth & Cheney, 2002). To begin to untangle the complex relationship of brain size, social factors, life history, and diet, among other variables, carefully planned experiments with a wide-range of genera and in a number of cognitive domains are vital.

1.2 Experimental Testing of Cognition in Primates

The cognitive abilities of primates have been studied for nearly a century, with the pioneers of this research area, such as Kohler and Yerkes, asking experimental questions that are still investigated today (Tomasello & Call, 1997). In studying comparative cognition, researchers have historically relied on a developmental framework to guide their research designs and protocols (Parker & McKinney, 1999; Tomasello & Call, 1997). Upon reviewing the field of primate cognition up to 1997, Tomasello and Call (1997) divided the research areas into “physical” and “social” cognition to reflect the major domains of knowledge often compared across monkeys, apes, and human children. Each of these domains has several sub-domains; commonly, physical cognition includes studies of space, categorization, causality, and number, while social cognition includes
areas such as communication, comprehension, self-awareness, imitation, and theory of mind (Herrmann, et al., 2007; Parker & McKinney, 1999; Tomasello & Call, 1997).

Based on their meta-analysis of primate cognition in 1997, Tomasello and Call concluded that there were no overarching differences between non-human apes and monkeys in terms of their physical cognition (based on the relevant literature in the areas of spatial knowledge, causality, categorization, and quantities). They further asserted that while there may be species differences or differences in the speed and flexibility of learning, these differences are not synonymous with overall differences in “intelligence” between apes and monkeys (Tomasello and Call, 1997).

Although they conceded that there were more differences between the groups in the areas of social cognition, they posited that these did not translate into a qualitative difference between the social cognitive representations and perceptions of monkeys and apes. Rather they claimed that these differences were more likely a by-product of a tendency to focus on chimpanzees (often with enculturated backgrounds) as representative of the great apes and one or two species of monkeys, such as capuchins, as representative of all monkeys. With these ideas in mind, Tomasello and Call (1997) proposed that non-human primate cognition should be viewed more in terms of degrees of separation rather than looking for large scale differences between the divisions of monkeys and apes. In line with other reports at the same time, they also proposed that non-human primates, in general, had distinctively different social cognitive capacities than humans. They posited that while chimpanzees, in particular, seemed to understand
much about the behavior of others, they showed no understanding of any psychological states (Povinelli & Eddy, 1996; Tomasello & Call, 1997).

The views proposed by Tomasello and Call (1997) have been the subject of much speculation, debate, and research over the last decade. With a dearth of new research in primate cognition, it has become increasingly clear that great ape cognition is, in many ways different, and possibly more complex, than that seen in other primate species (Kaminski, Call, & Tomasello, 2008; Tomasello, Call, & Hare, 2003). New testing paradigms in the area of social cognition in particular seems to indicate that, unlike Tomasello and Call’s original ideas (1997), great apes may indeed possess the capacity to understand some psychological states in others (Tomasello, et al., 2003). Work in the domain of theory of mind has been especially helpful in causing a revision of thinking about the social cognitive skills of non-human primates, indicating that at least chimpanzees may understand something about the knowledge states of humans and conspecifics (Kaminski, et al., 2008; Tomasello, et al., 2003).

Great apes are not alone in their recent success in more complex cognitive paradigms, as a number of other positive results have been found with a variety of non-primate species (Emery & Clayton, 2004; Hare, Brown, Williamson, & Tomasello, 2002; Shettleworth, 2010). Many species of birds have excelled in tool property and tool use paradigms originally tested with non-human primates, as well as tests in their comprehension of social behaviors (Emery & Clayton, 2004; Weir & Kacelnik, 2006). In addition, domestic dogs and young puppies have been found to reliably follow human eye gaze and respond successfully to human communicative cues. Dogs, compared to
wolves, seem to have a predisposition to focus on human eyes and other communicative signals, perhaps indicating a role for domestication in selecting for qualities useful in human social cognition (Hare, et al., 2002). The co-occurrence of such behaviors in distantly related species such as great apes and birds or dogs indicates that interpretations of any success must be viewed in terms of that species’ unique evolutionary and ecological niche. Such comparative research highlights the idea that similar behaviors can arise in distantly related species to solve various ecological problems, which provides support for theories of convergent evolution.

Despite the amount of recent research and unique insights, the extent of similarities or differences between the cognition of humans and other great apes, and if likewise similarities or differences can be seen among great apes, lesser apes, and monkeys, is still unclear. Important questions that remain include: Is physical cognition indeed essentially equivalent across the primate order, specifically between monkeys, apes, and humans, as predicted by the cultural intelligence hypothesis (Herrmann, et al., 2007)? Further, are the differences in social cognition between humans and other great apes reflected in other evolutionary relationships, such as that between monkeys and non-human apes?

1.3 Gibbon (Hylobatidae) Background

1.3.1 General

Gibbons (Family: Hylobatidae) are part of the superfamily Hominoidea, along with orangutans, gorillas, bonobos, chimpanzees, and humans (Rowe, 1996). Based on molecular estimates, it is believed that gibbons were the first group to split from the
common ape ancestor, between 25-12 million years ago (Goldman, Giri, & O’Brien, 1987; Hasegawa, Kishino, & Yano, 1985; Sibley & Ahlquist, 1987). There are several superficial differences that distinguish gibbons from the great apes. For example, quite different from the great apes, gibbons do not build nests and instead sleep in tree branches on their sitting pads. In addition, gibbons primarily travel via brachiation, which is often described as a “pendulum” swing (Bartlett, 2007). In terms of life history, the gestation length, brain size, and life span of gibbons are all intermediate between Old World monkeys and great apes (Matsuzawa, 2007; Parker & McKinney, 1999).

Gibbons are a primarily arboreal group found throughout Asia, with the majority of their diet consisting of fruit that is found high in the canopy. They live in small, pair-bonded groups (average size: 4-6), and travel regular routes in search of ripe fruit. Gibbons are considered to be a moderately social taxonomic group and are known for regular vocal displays and songs. These songs seem to serve a territorial function and also help to reinforce the bond between pair mates (Bartlett, 2007).

1.3.2 Cognition

While there has been a collection of work investigating the vocalizations and songs produced by gibbons (Geissmann, 2002), there have been relatively few studies to systematically investigate the cognitive processes of any gibbon species. The few experimental studies including more than one gibbon subject are dispersed in a number of different areas of cognition, including object permanence, tool use, mirror recognition, and social communication (Cunningham, et al., 2006; Fedor, Skollar, Szerencsy, & Ujhelyi, 2008; Hyatt, 1998; Liebal, Pika, & Tomasello, 2004).
In terms of physical cognition, gibbons have recently participated in tests of object permanence and tool use with mixed results. Fedor and colleagues (2008) tested several gibbon species with object permanence tasks, including single visible displacement, single invisible displacement, and double invisible displacements. They found great individual variation within the group and concluded that only one of their subjects (out of 10 tested) was able to spontaneously solve the single visible displacement trials. Cunningham and colleagues (2006) found more favorable results in their tests of object manipulation in hoolock gibbons. Specifically, they found that all subjects (n = 4) were able to use a rake-like object to pull food within their reach during their first trial. In more difficult trap-tube trials, however, only half of the subjects were significantly above chance across all trial blocks.

Similar to research in physical cognition, very little is known about the social cognition of gibbons. Two recent mirror recognition tests with a total of 27 gibbons (including the genera *Hylobates*, *Symphalangus*, and *Nomascus*) showed no indication of visual self-recognition, as none of the subjects used the mirror to investigate an experimental mark on their head (Hyatt, 1998; Suddendorf & Collier-Baker, 2009). This evidence for a lack of self-recognition in gibbons is in contrast to the performance of chimpanzees, orangutans, and gorillas. At least some subjects from each of great ape species tested (note: bonobos have not yet been formally tested using the mark procedure) were able to pass the mark test in a paradigm similar to that tested with gibbons (Parker, 1994; Posada & Colell, 2007; Swartz, Sarauw, & Evans, 1999).
In the area of communication, Liebal and colleagues (2004) observed the social behaviors of 14 siamangs (*Symphalangus syndactylus*) and concluded that gibbons may have a more extensive knowledge of social communication than once believed. The behaviors of the gibbons resembled monkeys in terms of their lack of manual or object-related gestures and their tendency to use primarily tactile gestures. However, the flexibility the gibbons exhibited in when and how to use their gestures was more characteristic of the social behavior observed in chimpanzees (Liebal, et al., 2004).

The sporadic and largely inconclusive data from cognitive research studies with gibbons is problematic considering the gibbon’s unique evolutionary position. Their performance on cognitive tasks could help further define relative cognitive similarities and differences between monkeys, lesser apes, and great apes. In the next section I will present an overview of the experiments conducted with gibbons in the areas of physical and social cognition.

### 1.4 Overview of Experiments

Four groups of experiments were utilized to test the physical and social cognition of white-handed gibbons. A total of nine subjects participated in the experiments, including five males and four females. However, despite that fact each subject was given the opportunity to participate in every experiment, some animals would not engage in certain testing paradigms and, thus, the number of subjects varied slightly depending on the experiment. Each experiment was designed to be comparable to studies with a variety of other species, such as chimpanzees, orangutans, rhesus monkeys, and capuchins. Several of the basic paradigms are similar to selected tasks in the Primate
Cognition Test Battery (PCTB) compiled by Herrmann and colleagues (2007). The PCTB was not be tested identically with gibbons, however, as some of the measures have been conducted with other populations of gibbons (e.g. object permanence) and other measures from the PCTB have been altered to better assess potential confounds and necessary controls absent in the original design (Experiments 1, 3A, 4A). Specifically, the experiments were chosen to represent a variety of physical and social tasks with ecological relevance for primate species and also to allow more straightforward comparisons between gibbons and other primate species. That fact that many of these tasks have been tested with other non-human primates will be especially helpful in making comparisons between gibbons, great apes, Old Work monkeys, and New World monkeys. The performance of gibbons will provide new insight into the cognitive abilities of lesser apes and the relationship of relative successes and failures of different species will be helpful in understanding more about the nature of cognition in primates. Chapters 2 and 3 will examine physical cognition (see Table 1 for experiment summaries), while Chapters 4 and 5 will measure social cognition (see Table 2 for experiment summaries). Each experiment will utilize a relative small number of experimental test trials to assess spontaneous knowledge in gibbons and avoid excessive learning effects.
<table>
<thead>
<tr>
<th>Quantity</th>
<th>Experiment</th>
<th>Number of Trials (per subject)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1: Numerosity Discrimination</td>
<td>84 (4 trials for each numerosity pair)</td>
</tr>
<tr>
<td>Causality</td>
<td>2A: Noise</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>a. full</td>
<td>a. 3</td>
</tr>
<tr>
<td></td>
<td>b. empty</td>
<td>b. 3</td>
</tr>
<tr>
<td></td>
<td>c. conditioning control</td>
<td>c. 3</td>
</tr>
<tr>
<td></td>
<td>2B: Shape</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>a. board</td>
<td>a. 3</td>
</tr>
<tr>
<td></td>
<td>b. cloth</td>
<td>b. 3</td>
</tr>
<tr>
<td></td>
<td>2C: Tool Properties</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>a. cloth side (support 1)</td>
<td>a. 3</td>
</tr>
<tr>
<td></td>
<td>b. cloth bridge (support 2)</td>
<td>b. 3</td>
</tr>
<tr>
<td></td>
<td>c. ripped cloth (connectedness 1)</td>
<td>c. 3</td>
</tr>
<tr>
<td></td>
<td>d. broken string (connectedness 2)</td>
<td>d. 3</td>
</tr>
<tr>
<td></td>
<td>e. tray circle (connectedness 3)</td>
<td>e. 3</td>
</tr>
</tbody>
</table>

Table 1 Physical cognition experiments
### Table 2 Social cognition experiments

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Number of trials (per subject)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Communication</strong></td>
<td></td>
</tr>
<tr>
<td>3A: Comprehension</td>
<td>15</td>
</tr>
<tr>
<td>a. look</td>
<td>a. 3</td>
</tr>
<tr>
<td>b. point</td>
<td>b. 3</td>
</tr>
<tr>
<td>c. marker</td>
<td>c. 3</td>
</tr>
<tr>
<td>d. goal-switch</td>
<td>d. 3</td>
</tr>
<tr>
<td>e. location control</td>
<td>e. 3</td>
</tr>
<tr>
<td>3B: Pointing Cups</td>
<td>4</td>
</tr>
<tr>
<td>3C: Attentional State</td>
<td>4</td>
</tr>
<tr>
<td>a. away</td>
<td>a. 1</td>
</tr>
<tr>
<td>b. towards</td>
<td>b. 1</td>
</tr>
<tr>
<td>c. away: body-facing</td>
<td>c. 1</td>
</tr>
<tr>
<td>d. towards: body-away</td>
<td>d. 1</td>
</tr>
<tr>
<td><strong>Theory of Mind</strong></td>
<td></td>
</tr>
<tr>
<td>4A: Gaze Following</td>
<td>18</td>
</tr>
<tr>
<td>a. head &amp; eyes</td>
<td>a. 3</td>
</tr>
<tr>
<td>b. back</td>
<td>b. 3</td>
</tr>
<tr>
<td>c. eyes</td>
<td>c. 3</td>
</tr>
<tr>
<td>d. head/eye control</td>
<td>d. 3</td>
</tr>
<tr>
<td>e. barrier</td>
<td>e. 3</td>
</tr>
<tr>
<td>f. barrier control</td>
<td>f. 3</td>
</tr>
<tr>
<td>4B: Intentions</td>
<td>6</td>
</tr>
<tr>
<td>a. trying</td>
<td>a. 3</td>
</tr>
<tr>
<td>b. reaching</td>
<td>b. 3</td>
</tr>
</tbody>
</table>

1.4.1 Physical Cognition

Experiment 1 investigates the ability of gibbons to discriminate the larger of two numerosities and compares their performance on a range of test ratios. From the data generated, the plateau of numerosity discrimination abilities for this group of gibbons will be discussed, and notably compared to monkeys, great apes, and humans that have been tested in similar paradigms (Barth, Kanwisher, & Spelke, 2003; Beran, 2007; Cantlon & Brannon, 2006; Hanus & Call, 2007; Hauser, Tsao, Garcia, & Spelke, 2003; Lipton & Spelke, 2003; Stevens, Wood, & Hauser, 2007; Tomonaga, 2008).
Experiments 2A and 2B examine gibbons’ knowledge of causality through their use of auditory and visual information to locate hidden food. During Experiment 2A, the gibbons were given a choice between two closed, opaque containers. In one condition (“full”), the experimenter shook the baited container and simply held the unbaited container for the same length of time. In the other condition (“empty”), the experimenter shook the unbaited container and held the baited container for the same length of time. During Experiment 2B, a food reward was placed under one of two identical stimuli choices (either cloth or cardboard), altering the shape of the baited choice. The gibbons were then able to choose between the two stimuli. Experiment 2C analyzes gibbons’ knowledge of tool properties. The basic on/off cloth support problem (condition “cloth side”), along with several other means-end tool tasks were presented to the gibbons. These three causality experiments are discussed in terms of the gibbons’ ability to understand unseen causal forces and make inferences. Comparisons with other non-human primates previously tested in these paradigms are discussed (Call, 2004; Call, 2007; Hauser, Kralik, & Botto-Mahan, 1999; Herrmann, et al., 2007; Yocom & Boysen, in press). Causality is a very interesting area comparatively, as great apes have often been more successful than monkeys when presented with novel problems in these areas.

1.4.2 Social Cognition

Non-human primate social cognition remains a rather divided arena filled with much debate about the extent of the abilities of non-human primates compared to one another and to humans (Povinelli, 2000; Tomasello & Call, 1997; Tomasello, Call, & Hare, 2003). To contribute additional data to this area, Experiments 3 and 4 were
designed to measure areas that are very important in navigating the social world of primates.

The first in this series, Experiment 3, examines the gibbons’ abilities to both understand human communicative signals and produce their own communicative signals to obtain to food reward. Social communication (both production and comprehension) allows primates to disperse information about food sources and predators quickly and efficiently (Dunbar, 2003). Specifically, Experiment 3A tests the ability of gibbons to utilize human communication signals, such as pointing, gaze behavior, and replica markers to locate a reward hidden under one of two opaque cups. Experiment 3B requires gibbons to produce communicative signals to direct a naïve human experimenter toward a baited container. In addition, Experiment 3C investigates whether gibbons take the attentional state of an experimenter into account when begging or trying to obtain food. Comparisons are made with past studies of monkeys and great apes in these paradigms (Anderson, Montant, & Schmitt, 1996; Hattori, Kuroshima, & Fujita, 2010; Herrmann, et al., 2007; Itakura, Agnetta, Hare, & Tomasello, 1999; Leavens & Hopkins, 1998).

It is still not clear, however, what components of common human communication skills, if any, can be utilized by other primates. For instance, beyond basic communication skills, are non-human primates able to read and reason about goal-directed human behaviors? In this vein, a hallmark of social cognition, which is often thought of as a unique human skill, is theory of mind (Kaminski, et al., 2008). Since non-human primate experiments designed to test theory of mind through false beliefs have
been unsuccessful (Kaminski, et al., 2008; Tomasello & Call, 1997), I instead tested some of the complex social components that are likely precursors to theory of mind.

The last set of experiments measure the presence of two components associated with theory of mind, gaze and intentionality (Tomasello, et al., 2003). Experiment 4A investigates whether gibbons spontaneously follow the gaze of a human experimenter, including around a barrier. Lastly, Experiment 4B examines whether gibbons can use the intentional movements (i.e. “trying”, “reaching”) of a human experimenter to select a baited container of food. The results are compared with similar studies of capuchins, spider monkeys, rhesus monkeys, and great apes (Amici, Aureli, Visalberghi, & Call, 2009; Emery, Lorincz, Perrett, Oram, & Baker, 1997; Vick & Anderson, 2000).

Together, this compilation of nine experiments will help provide insight concerning the capabilities and limitations of gibbon cognition in these particular areas of physical and social cognition, while allowing for comparisons with other non-human primate species.
Chapter 2: Numerosity

Recently, it has been proposed that all animals may share an ancient system for detecting and comparing numerosities, or a “number sense” (Brannon, 2005; Dehaene, Dehaene-Lambert, & Cohen, 1998; Hauser, et al., 2003; Nieder & Miller, 2003). Extensive research on non-human animals’ understanding of numerosity indicates that a variety of animals, ranging from salamanders to chimpanzees, can indeed compare two sets of items (Boysen & Berntson, 1995; Brannon & Terrace, 1998; Emmerton, Lohmann, & Niemann, 1997, Hanus & Call, 2007; McComb, Packer, & Pusey, 1994; Smith, Piel, & Candland, 2003; Uller, Jaeger, Guidry, & Martin, 2003). This skill has been documented in naturalistic settings (Kitchen, 2004; McComb, et al., 1994; Wilson, Hauser, & Wrangham, 2001), as well as in captive studies (Beran, 2001; Brannon & Terrace, 1998; Hanus & Call, 2007). While most studies have examined how animals judge small numerosities, more recently it has been shown that discrimination abilities in non-human primates remain accurate even for larger numerosities of up to 30 items (Cantlon & Brannon, 2006). Further, even when studies disentangled other continuous variables that would normally change in accordance with the number of items presented (e.g. rate of presentation, surface area, brightness, etc.), both rhesus macaques and tamarins maintained the same level of accuracy in their performance (Beran, 2007; Cantlon & Brannon, 2006; Hauser, et al., 2003).
Human infants have also been tested in numerosity discriminations. By 6-months of age, infants are able to judge the larger of two sets (Xu & Spelke, 2000; Xu, Spelke, & Goddard, 2005). Similar to the control measures used in animal studies, recent work by Cordes and Brannon (2009) indicates that infants do not represent number as a last resort strategy, but can successfully discriminate sets based on numerical cues even when other continuous cues, such as contour length and area, are available. The infants numerical discriminations held for small sets (2 vs. 3), large sets (8 vs. 16), and comparisons between small and large sets (2 vs. 8) (Cordes & Brannon, 2009).

A closer look at the performance of both non-human animals and human children indicates that both groups exhibit size and distance effects in their responses (Brannon, 2005; Starkey & Cooper, 1980; Xu & Spelke, 2000), just as human adults do (Barth, et al., 2003). For example, in rhesus monkeys, numerosity judgments on a computerized match-to-sample task are more error prone as the numerical distance between two items decreases (i.e., 5:6 would produce more errors than 5:9), illustrating the distance effect. In addition, while distance remains constant, they also tend to make more errors as the size of the numerosities increases (i.e. 14:19 would produce more errors than 5:10), illustrating the size effect (Nieder & Miller, 2003). The size effect indicates that differences among small numerosities are easier to discriminate than similar differences among large numerosities. While differing theories have been proposed to account for the size and distance effects (Brannon, Wusthoff, Gallistel, & Gibbon, 2001; Dehaene, 2001), recent neurophysiologic work indicates that animals possess a logarithmically scaled representation of number (Nieder & Miller, 2003). According to the logarithmic
hypothesis, small numbers are more easily discriminated since they have less cognitive
“overlap,” while larger numbers are compressed and thus will have more cognitive
overlap, making them more difficult to discriminate (Dehaene, 1997). Behavioral studies
reinforce these findings of a logarithmically scaled number representation for pigeons
(Roberts, 2005), rhesus macaques (Nieder & Miller, 2003) and human children (Siegler
& Opfer, 2003).

Some have posited there may be an “upper limit” to the numerosity of stimuli that
can be differentiated without a verbal numerical system (Hauser, et al., 2003). However,
in their work with rhesus macaques, Nieder & Miller (2003) found that the ratio between
two sets, as opposed to their absolute numerical value, controlled their level of
discrimination. The difficulty of discriminations became more complex, and errors more
common, as the ratio between items decreased (“ratio” being calculated as the numeric
value obtained from dividing the larger numeral in a set by the smaller) (Nieder & Miller,
2003). This study, in accord with other numerosity tasks with non-human primates,
indicates there is not a set upper limit on the number of items that can be discriminated,
but instead representations become more approximate (e.g. less accurate) for larger
numbers (Beran, 2007; Nieder & Miller, 2003).

It is possible that while all species may share a nonverbal “number sense,”
different species may each have a different threshold discriminability ratio for number. If
this is the case, there may be slight changes in discriminability in accordance with
phylogenetic changes among groups. For example, humans may have the lowest, or most
fine-tuned, discriminability threshold ratio, followed by other apes, and then monkeys.
Indeed, human adults have very fine-tuned discrimination abilities, with an average discriminability threshold of approximately 1.15-1.2 (Barth, et al., 2003; Pica, Lemer, Izard, & Dehaene, 2004; Van Oeffelen & Vos, 1982). Human infants show a slightly worse discriminability ratio threshold between 1.5 and 2.0 at 6-months old, although it does improve quickly with age to between 1.25 and 1.5 at 9-months old (Lipton & Spelke, 2003). The chimpanzees, bonobos, orangutans, and gorillas tested by Hanus and Call (2007) were able to discriminate ratios up to the level of 1.11 (e.g. 9:10), yet they were not tested at any more difficult ratios. In a more extensive test of numerosity discrimination by Tomonaga (2008), the discriminability threshold ratio of chimpanzees, averaged over two subjects, was 1.2, which placed them in the same range as the adult humans tested (Barth, et al., 2003; Pica, Lemer, Izard, & Dehaene, 2004; Van Oeffelen & Vos, 1982). Based on several studies utilizing various numerosities, rhesus monkeys have a discriminability threshold ratio in the range of 1.4-1.5 (Beran, 2007; Cantlon & Brannon, 2006; Nieder & Miller, 2003). Only slightly worse than rhesus monkeys, tamarin and marmoset monkeys both have a threshold ratio of approximately 1.5, as they were able to successfully select the greater quantity of discrimination ratios 2:3 or higher, but not 4:5, which has a smaller ratio between the two numerosities (Hauser, et al., 2003, Stevens, et al., 2007).

Due to their phylogenetic position between monkeys and great apes, it is possible that gibbons’ discriminability ratio would fall between that of great apes and rhesus. Alternatively, specific ecological pressures, such as availability of food, may have
contributed to lower or higher discriminability ratios for gibbons than would be predicted by phylogeny.

2.1 Experiment 1: Numerosity Discrimination

To investigate these possibilities, the discrimination abilities of gibbons were tested on a range of numerosity ratios. Three numerosity pairs for each ratio of interest were tested, with ratios ranging from 2.5 (e.g. 2:5, a two and a half-fold difference in numerosity) to 1.2 (e.g. 5:6, a 1.2-fold difference in numerosity). I predicted that gibbons would have a discriminability ratio between that of rhesus monkeys (1.4-1.5) and apes (1.1-1.2). Further, I predicted that the ratio variable would have a large influence on performance, as other investigators have found that this variable significantly affects the performance of great apes and monkey species (Beran, 2007; Hanus & Call, 2007; Hauser, et al., 2003; Neider & Miller, 2003; Tomonaga, 2009).

Method

Subjects

Six white-handed gibbons (*Hylobates lar*), including three males and three females, participated in Experiment 1. Since not all subjects participated in all experiments, Table 3 shows each subject’s experimental participation, along with age, sex, and rearing history.
The gibbons were housed at the American Primate Educational Sanctuary (A.P.E.S.) in series of inter-connected indoor/outdoor enclosures, with ample environmental enrichment. They were tested in their outdoor enclosures and were able to freely move around and could discontinue participation at any time by simply leaving the testing area. The gibbons were fed their normal diet of fruits, vegetables, and chow twice a day, along with water ad libitum. Food deprivation was not used at any time during any of the experiments. None of the gibbons housed at A.P.E.S. have ever been part of any previous cognitive or behavioral studies.

**Design and Procedure**

Two small bowls, positioned behind an occluder, were baited with different numbers of grape halves. The bowls were then placed on the tray, always from left to right, approximately 10 inches from one another. The subjects were permitted to observe the dishes for approximately three seconds, following which the tray was pushed forward,
allowing the subjects to reach through the mesh of their enclosure and choose between the two dishes. When the subject moved one of the bowls or food rewards, the other bowl was then removed while the subject retrieved the contents of the selected dish.

After the subject emptied the selected dish, the platform was retracted and a new trial was initiated.

Each subject received four trials of each of the 21 number pairs, for a total of 84 trials per subject (see Table 4 for list of numerosity pairs). The numerosity pairings were presented randomly, with the side of the larger numerosity counterbalanced, such that no more than two trials with the larger numerosities on the same side of the tray were presented in consecutive order. For each subject, a session consisted of 10 or fewer trials based on the subject’s willingness to participate and level of attentiveness.

<table>
<thead>
<tr>
<th>Discriminability Ratios (B/A)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.5</td>
</tr>
<tr>
<td>2:5</td>
</tr>
<tr>
<td>4:10</td>
</tr>
</tbody>
</table>

Table 4 Numerosity sets presented to each subject

All trials were coded by the experimenter during testing. A choice was considered correct if the subject selected the dish with the larger numerosity. In addition, the trials were video-recorded and 40% of the trials were coded offline by a second, naïve coder in order to calculate inter-rater reliability. Agreement between the experimenter and coding assistant was very high (Cohen’s K = 0.98).
It is important to note that surface area and numerical value were confounded in this experiment. Previous studies with non-human primates have found that both factors contribute to discriminatory food choices and suggest that similar processes may underlie both discriminations (Beran, Evans, & Harris, 2008; Boysen & Berntson, 1995; Stevens, et al., 2007). With this in mind, to more closely resemble a natural foraging decision, food and surface area were allowed to co-vary.

Results & Discussion

To analyze the group’s performance, the number of correct choices for each numerosity set and larger ratio group were compared with chance (assuming a 50% probability of selecting either numerosity) using two-tailed binomials (p level = 0.05). Table 5 indicates the gibbons’ performance at each numerosity set and ratio group.
<table>
<thead>
<tr>
<th>Ratio</th>
<th>Numerosity Set</th>
<th>Percent Correct</th>
<th>Ratio Correct</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.5</td>
<td>2:5</td>
<td>70.83</td>
<td>70.83*</td>
</tr>
<tr>
<td></td>
<td>4:10</td>
<td>79.17*</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6:15</td>
<td>62.5</td>
<td></td>
</tr>
<tr>
<td>2.0</td>
<td>1:2</td>
<td>66.67</td>
<td>56.94</td>
</tr>
<tr>
<td></td>
<td>2:4</td>
<td>66.67</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3:6</td>
<td>37.50</td>
<td></td>
</tr>
<tr>
<td>1.67</td>
<td>3:5</td>
<td>58.33</td>
<td>68.12*</td>
</tr>
<tr>
<td></td>
<td>6:10</td>
<td>68.18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9:15</td>
<td>78.26*</td>
<td></td>
</tr>
<tr>
<td>1.5</td>
<td>2:3</td>
<td>62.50</td>
<td>67.61*</td>
</tr>
<tr>
<td></td>
<td>4:6</td>
<td>82.61</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6:9</td>
<td>58.30</td>
<td></td>
</tr>
<tr>
<td>1.33</td>
<td>3:4</td>
<td>78.26*</td>
<td>62.86*</td>
</tr>
<tr>
<td></td>
<td>6:8</td>
<td>43.48</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9:12</td>
<td>66.67</td>
<td></td>
</tr>
<tr>
<td>1.25</td>
<td>4:5</td>
<td>58.33</td>
<td>57.14</td>
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<tr>
<td></td>
<td>8:10</td>
<td>56.52</td>
<td></td>
</tr>
<tr>
<td></td>
<td>12:15</td>
<td>56.52</td>
<td></td>
</tr>
<tr>
<td>1.2</td>
<td>5:6</td>
<td>50.00</td>
<td>59.72</td>
</tr>
<tr>
<td></td>
<td>10:12</td>
<td>58.33</td>
<td></td>
</tr>
<tr>
<td></td>
<td>15:18</td>
<td>70.83</td>
<td></td>
</tr>
</tbody>
</table>

Table 5 Percent correct for each numerosity set and ratio (* indicates $p < 0.05$)

While the gibbons were generally most successful with the larger ratios (e.g. 2.5), there was one noteworthy exception. The gibbons’ performance in the 3:6 numerosity was especially low considering the small numbers involved and large two-fold ratio difference between them. Without the 3:6 numerosity set in the data, the 2.0 ratio group would have 66.67% correct, which is significantly above chance ($p < 0.05$, two-tailed
binomial). Yet, because it is unclear why the group performed so poorly for this set, performance on the 3:6 set was initially left in the data analysis.

To understand which factors were most influential in subjects’ responses, a step-wise multiple regression analysis was conducted. The dependent variable was the percentage of correct responses for each numerosity pair and the independent variables were ratio, absolute difference in number between the sets, and total quantity. The model was not significantly affected by any of the independent variables (p > 0.05) and the largest amount of variance explained by a model ($R^2 = 0.004$) included all three independent variables.

While none of the variables tested had a large effect on the performance of the gibbons, it is possible that more experience with the numerosity choices would have yielded different results. Many studies with non-human primates have utilized a training procedure in which the subjects are rewarded for selecting the larger of two numerosities over hundreds or even thousands of trials and then presented with novel numerosity choices during testing (Beran, 2007; Cantlon & Brannon, 2006; Stevens, et al., 2007; Tomonaga, 2008). Since the gibbons in the present study were not food deprived in any way, a training procedure which focused them on the numerosity variable may have helped them attend to it more readily during testing. Indeed, Cantlon & Brannon (2007) found that numerosity was more a salient cue for rhesus monkeys that had received prior training to attend to this cue.

Spontaneously, the gibbons may have been biased by the amount of food present, which may have occasionally been in conflict with the numerosity (i.e., in a 2:3 set, two
grape halves may have been slightly larger than three grape halves, or the two group may have had the largest food piece overall). Studies with chimpanzees, tamarins, and marmosets indicated that they primarily based their choices on the amount of food present rather than the number of food items when the two variables conflicted (Beran, et al., 2008; Stevens, et al., 2007). Further, Beran and colleagues (2008) found that chimpanzees often selected a choice with the largest individual food item, even when the choice had the smaller total amount of food. Based on these results, it is possible that such unintentional factors in the present study could have affected the gibbons’ judgments; although given the incrementally small potential differences in the sizes of the grapes used, this seems unlikely to have caused a large effect.

Further analyses of the data set revealed no significant differences among the ratio groups for the percent correct (p > 0.05, Kruskal-Wallis), yet there was a trend for the gibbons to perform worse as the ratios decreased (see Table 5). As mentioned, the numerosity set 3:6 was an outlier within the 2.0 ratio group, as the gibbons only chose the larger numerosity on 37.50% of the trials for this set. While it is not clear why the gibbons performed so poorly on this particular set, it was most likely due to some combination of low levels of attention and lack of motivation.

Without the outlier set 3:6 in the data, a pattern emerged in which the gibbons’ performance was significant (p < 0.05, two-tailed binomials) from the largest ratio group, 2.5, until the two smallest ratio groups 1.25 (p = 0.282, two-tailed binomial) and 1.2 (p = 0.125, two-tailed binomial). No clear pattern was evident, however, among the three numerosity sets within each ratio group, as sometimes those numerosity sets with larger
numerical differences (i.e., 6:15, difference = 9, 62.5% correct) had a lower success rate than those with a smaller numerical difference (i.e., 4:10, difference = 6, 79.17% correct) (see Table 5). It, therefore, seems likely that the gibbons’ discriminability threshold would fall into the range of 1.33-1.25, which would place them directly between chimpanzees and rhesus macaques (Beran, 2007; Cantlon & Brannon, 2006; Hanus & Call, 2007; Nieder & Miller, 2003; Tomonaga, 2008). However, before any definitive conclusions can be reached, steps should be taken to 1) investigate why gibbons’ correct performance was relatively low across all the categories, and 2) further test the 3:6 numerosity pair to better understand why gibbons had particular difficulty with this set.
Chapter 3: Causality

Causality has long been a primary area of interest for studies of cognitive development (Leslie, 1982, 1984; Piaget, 1971). This area has been studied in infants to better understand the dynamics of inferential causality. Although precursors to adult causal reasoning have been found in infants, the precise mechanism or mechanisms behind such inferences remains debated (Cohen & Amsel, 1998; Leslie, 1982; Leslie & Keeble, 1987). Comparative studies using non-human primate have recently been helpful in exploring the possible evolutionary emergence of causal reasoning and similarities between species. Several methodological approaches using a range of primate species have been used to investigate the domain of causality. The most widely used methods and results from these experiments will be briefly reviewed, with emphasis on non-human primate studies.

The first of the paradigms, also used widely in infant research, is the looking time task (Baillargeon, Needham, & DeVos, 1992; Leslie, 1982; Schlesinger & Langer, 1999). This task analyzes the amount of time that subjects spend looking at novel scenarios, when compared to a familiarization or habituation period. The basic approach relies upon the investigation of complex phenomena without imposing significant task demands for either human infants or non-human animals which do not have the linguistic, or perhaps motor, competency to respond to more complex methodologies. Infants have been tested with this approach using direct launching sequences (Cohen & Amsel, 1998;
Leslie, 1984), hand/object pick-up sequences (Leslie, 1982), and object retrieval (through pulling) sequences (Schlesinger & Langer, 1999; Sommerville & Woodward, 2005). Throughout the looking time studies, if infants looked longer at a non-causal or impossible event following a familiarization period with the causal or possible event, the longer looking times were interpreted as reflecting a violation of the infant’s casual expectations. With this in mind, it was assumed that the infants with longer looking times were exhibiting an understanding and therefore, knowledge of, causality (e.g., Leslie, 1982, 1984). Based on such manipulations, some investigators have posited that infants have an innate understanding of causality that is evident by 27 weeks of age (Leslie & Keeble, 1987), while others contend that causal reasoning develops more slowly over the first year of life (Cohen & Amsel, 1998; Cohen, Rundell, Spellman, & Cashon, 1999).

Recently, looking time measures have been used to assess non-human primate knowledge of causal relations and the results have supported similar responses in great apes as those shown by human infants (e.g. Cacchione & Krist, 2004; O’Connell & Dunbar, 2005). Cacchione and Krist (2004) analyzed differences in chimpanzee looking times between possible and impossible support scenes, using a banana fully supported by a table compared with a banana touching only the edge of a table, yet appearing to remain supported. They concluded that chimpanzees have an understanding of support in terms of the amount of contact that is necessary for one object to support another, though their understanding of object orientation may be slightly different from that of humans (Cacchione & Krist, 2004). Similarly, in a modification of Leslie’s (1982) hand/object
pick-up sequences, O’Connell & Dunbar (2005) found that chimpanzees looked longer at non-causal events, such as a banana “following” a hand off the screen, when such instances followed causal sequences, such as a hand picking up a banana and moving off the screen. The authors explained their results as a violation of the chimpanzees’ sense of causality. The interpretation of looking time methods, however, remains highly controversial, even with human infants (Aslin, 2000; Cashon & Cohen, 2000), so currently it is difficult to fully assess the understanding of causality by non-human primates based on these studies alone.

Another method that has been widely used to study causality in non-human primates involves the use of object manipulation tasks. The most common form of such tasks are tool use studies in which an object must be used, and sometimes manipulated or altered, in order to retrieve another object, often a desired food, that is out of reach. Visalberghi and Limongelli (1994) used a creative “trap-tube” design in which a stick could be used to push a reward out of the middle of a clear tube. The trap tube had a hole in the center of the tube and a small clear trap attached. Success on the task required the subjects to attend to which side of the tube they inserted the tool. In order to avoid losing the reward, the monkey had to note the specific location of the candy, relative to the trap, and insert the tool such that it would push the candy away from the trap and out the other end of the tube. This invariably meant that the monkey had to push the candy away from themselves, which was counterintuitive for accessing the reward. The three capuchins tested had very limited success in this task, with the only successful monkey using a trial-and-error strategy that eventually resulted in the determination of a perceptual rule that
lead to more optimal performance (Visalberghi & Limongelli, 1994). When chimpanzees were tested on the same task, two of the five subjects demonstrated the ability to solve the task without using the associative strategy shown by capuchins (Limongelli, Boysen, & Visalberghi, 1995). Recently, Cunningham and colleagues (2006) found that hoolock gibbons also were successful on a variation of the trap-tube task, although these authors could not definitively conclude that the gibbons were using a causal strategy and not an associative one to solve the problem. What remains unclear is if the capacity to understand the causal relationships inherent during tool use tasks is present in all non-human primates, since a number of captive species show expertise with tool tasks under captive conditions, yet show no similar propensity to use tools in the wild (e.g. gibbons: Cunningham, et al., 2006).

Another common method for studying causality in non-human primates uses a forced-choice task involving a selection between two (or more) different tools, containers, or objects. These tasks can be fairly straightforward, such as pulling a length of cloth with a reward placed directly on it, rather than a length of cloth with the food reward placed next to it (Hauser, et al., 1999). Tamarins and capuchins can learn to be successful on such tasks after many trials, and are able to then generalize their understanding of the task to variations of some other perceptual features of the problem, such as changes in cloth color and shape (Hauser, et al., 1999; Yocom & Boysen, in press). In these instances, however, the monkeys do not demonstrate spontaneous, or immediate, causal knowledge about the relationship between the cloth and the food. A recent replication using chimpanzee subjects revealed greater initial success in the task.
Yocom and Boysen (in prep) found that chimpanzees could spontaneously solve the basic “On/Off” support problem, including complex variations during which examples of full support were contrasted with imminent contact or perceptual containment (although see Povinelli, Reaux, Theall, & Giambrone, 2000 for different results and interpretation of chimpanzees’ knowledge of support).

Other studies have used the object-choice method to investigate the ability of primates to make causal inferences in the auditory and visual domains (Braeuer, Kaminski, Riedel, Call, & Tomasello, 2006; Call, 2004; Call, 2007; Paukner, Huntsberry, & Suomi, 2009; Sabbatini & Visalberghi, 2008). Both Call (2004) and Braeuer et al. (2006) found that great apes were able to infer which of two containers contained a food reward based on the noise produced when the baited container was shaken, and, in a separate experiment, when no noise was produced when an empty container was shaken. In contrast, capuchins monkeys were unable to spontaneously determine which container was baited based upon auditory signals, yet showed success after hands-on experience with the same containers (Paukner, et al., 2009; Sabbatini & Visalberghi, 2008). In the visual domain relative to shape, all four species of great apes were able to infer which of two boards had a food reward underneath, based on the way the presence of the reward altered the orientation of the board versus another board that was lying flat (Braeuer, et al., 2006; Call, 2007). To date, only the great apes have been tested in the shape causality paradigm.

While some animals have demonstrated more initial skill in some causality experiments than others, the evidence for causal reasoning in each of these paradigms
remains highly debated (see Tomasello & Call, 1997; Penn & Povinelli, 2007; Shettleworth, 2010). Under scrutiny is the determination of which species, in addition to humans, can demonstrate an understanding of causal relationships and if this understanding develops through experience or is obvious upon an animal’s initial encounter with a new problem (Bania, Harris, Kinsley, & Boysen, 2009; Herrmann, Wobber, & Call, 2008; Povinelli, 2000; Sabbatini & Visalberghi, 2008; Tomasello & Call, 1997).

The methods and procedures used to examine causality are also important. As with infants, it is possible that increased looking times to non-causal events shown by non-human primates may reflect their reaction to simply viewing a perceptual oddity, or an over-interpretation of data by experimenters, rather than an understanding of causality. Consequently, these questions remain as part of a contentious debate (Cacchione & Krist, 2004; Cashon & Cohen, 2000; Haith, 1998). Furthermore, tool use tasks may require a degree of physical dexterity and manipulation that is unavailable to all primate species, even though the underlying cognitive capacities may be present (Mulcahy & Call, 2006). With these limitations in mind, in the present set of studies, object choice tasks were chosen to examine the performance of gibbons for comparison with the performance of other non-human primate species. Specifically, the tasks were used to analyze gibbons’ inferential reasoning about sound (Experiment 2A), shape (Experiment 2B), and tool properties (Experiment 2C), in order to obtain a food reward.
3.1 Experiment 2A: Noise

Experiment 2A examined gibbons’ knowledge of the causal properties associated with auditory signals. Although gibbons do make use of elaborate vocalizations, there have not been any reports of the vocalizations coinciding with food (i.e., alerting others of a food source, etc.) (see Bartlett, 2007). Taking into consideration this issue and the cognitive inferences involved in the experimental paradigm, I hypothesized that gibbons would have difficulty using auditory signals to locate a food reward.

Method

Subjects

Six white-handed gibbons (Hylobates lar), including two males and four females, participated in Experiment 2A (see Table 3).

Procedure

While an occluder blocked two opaque cups, the experimenter hid several peanuts and two grapes in one of the cups and placed removable lids on both containers. Next, the occluder was moved and the experimenter manipulated the cups in one of the following ways:

a. full – the baited cup was shaken three times (so the food inside rattled) and then the empty cup was lifted and held for the same length of time (approximately three seconds) without shaking it.

b. empty – the empty cup was shaken three times, producing no noise, and the baited cup was lifted and held for the same amount of time (approximately three seconds) without shaking it, therefore producing no noise.
Following each of the manipulations above, the platform was pushed forward, allowing the subjects to choose between the two cups.

Each subject participated in one session per day, with a session including six or less trials. Position of the correct choice was pseudo-randomized such that the correct cup was not presented on the same side of the tray for more than two trials in a row. Each subject participated in three trials for each condition, with the full condition always preceding the empty condition.

Subjects were free to discontinue participation at anytime by simply leaving the testing area. Each subject’s choice was coded during testing. The trials were also video-recorded and 70% were coded offline by a naïve assistant to establish inter-rater reliability. Inter-rater reliability was very high (Cohen’s K = 0.96).

Results and Discussion

The group’s performance was not significantly different from chance for either of the two conditions (61% correct for both conditions, empty: p > 0.05, two-tailed binomial), indicating that the gibbons were not successful in using an auditory cue to infer the location of a hidden food reward. In addition, there were no differences in the number of correct choices between the full and empty conditions (p > 0.05, Mann-Whitney U).

Although the gibbons did not perform successfully with the two conditions, it is possible that they could not spontaneously solve the problems due to a lack of relevant experience with tasks that combined food and auditory variables. Consequently, a
follow-up experimental condition was designed to examine the role of experience on gibbons’ performance in this paradigm.

c. **conditioning control**

A noise conditioning procedure was introduced to determine if the gibbons could solve the auditory detection problem after explicit pairings of the noise/food combination for the subjects. The same gibbons that participated in the previous full and empty conditions were each presented with three noise conditioning trials, followed by repeating the three trials from the original full condition.

Similar to the previous conditions, while an occluder blocked two opaque cups, the experimenter hid several peanuts and two grapes in one of the cups and placed removable lids on both. When the occluder was removed, the experimenter shook the baited cup three times, removed the lid, dumped the food onto the tray and pushed the tray toward the subject. After three such conditioning trials were completed, the full condition was repeated in the same manner as the original test.

All choices were coded during the test session. All trials were video-recorded and 50% were coded offline by a naïve assistant to establish inter-rater reliability. Agreement between the experimenter and coding assistant was excellent (Cohen’s $K = 1.0$).

**Overall Results and Discussion**

The group did not perform significantly different from chance in the conditioning control condition (67% correct, $p > 0.05$, two-tailed binomial). The group’s performance in the full conditions before and after conditioning was also compared using a Mann-Whitney U test to see if there was a significant difference in the number of correct
choices between the two conditions. No significant difference was found (p > 0.05, Mann-Whitney U), indicating the performance of the gibbons had not improved due to the training procedure.

The gibbons’ overall performance is in contrast to chimpanzees, bonobos, orangutans, and gorillas that were able to successfully solve both the full and empty conditions in a similar study (Call, 2004). Beyond the great apes performance as a group, the individual analyses of Call (2004) revealed that 33% (9 out of 27) of individual great apes were significantly above chance in the full condition and 33% (3 out of 9) were above chance individually in the empty condition. Capuchin monkeys tested in the same paradigm were able to solve both conditions only after a period of experiential learning, in which they were provided both full and empty containers that they could freely manipulate for a total of 30 minutes (Sabbatini & Visalberghi, 2008). Following the experiential learning, the number of successful subjects in the full condition increased from one to three (out of eight total). Four of the capuchins with the best performance in the full condition were tested in the empty condition and two out of four were able to successfully solve the problem (Sabbatini & Visalberghi, 2008). In a different study that did not utilize any sort of familiarization or training, capuchins were not successful in using auditory information to locate hidden food (Paukner, et al., 2009). These results indicate that following training, capuchins’ performance, including the more difficult inference by exclusion in the empty condition, is similar to great apes. Spontaneously, however, great apes have been more successful in noise causality paradigms than capuchins.

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Individual analyses of each gibbon’s performance failed to show any drastic differences from the group analyses. One gibbon (Trevor) did have a 100% success rate for both the full and empty conditions (prior to conditioning), indicating that it is possible that the species may have the capability to make auditory inferences. While the training seemed to provide little benefit in helping the gibbons solve the full condition, more training trials or a different kind of training, such as that used with the capuchins tested by Sabbatini & Visalberghi (2008), may have been more useful. Specifically, physical manipulation of the stimuli may have been more beneficial than observation in highlighting the important auditory component of the task.

3.2 Experiment 2B: Shape

Visual shape/form is a very important factor in locating ripe fruit in the wild. Indeed, the visual cortex in the brains of primates has expanded during brain evolution (Dunbar, 2010). With that in mind, I hypothesized that gibbons, who feed primarily on fruit and leaves, would be successful in using the subtle visual cue of altered shape to locate a hidden reward.

Method

Subjects

Seven white-handed gibbons (*Hylobates lar*), including three males and four females, participated in Experiment 2B (see Table 3).

Design & Procedure

With an occluder blocking the subject’s view, the experimenter hid a food reward under one of two identical pieces of hard cardboard or flimsy cloth. The occluder was
then removed, the platform pushed forward, and the subject allowed to select one of the two objects.

*a. cardboard* – a banana slice was hidden under one of the two rigid cardboard pieces. The correct choice was visually apparent since one of the cardboard pieces was placed over the food and, therefore, inclined, while the other piece remained flat on the platform.

*b. cloth* - a grape piece was hidden under one of the two flimsy cloth pieces. The correct choice was visually apparent since one of the cloth pieces was placed over the food and, therefore, showed a raised bump, while the other remained flat on the platform.

Each subject participated in one session per day, with a session including six or less trials. The order of the correct choice was pseudo-randomized in that the correct choice was not presented on the same side of the tray for more than two trials in a row. Each subject received three trials for each condition, with the cardboard condition always preceding the cloth condition. Subjects were free to discontinue participation at anytime by simply leaving the testing area.

The experimenter coded all side choices during testing. The trials were also video-recorded and 75% were coded offline by a naïve assistant to establish inter-rater reliability. Agreement between the experimenter and coding assistant was 100% (Cohen’s $K = 1.0$).

**Results & Discussion**

The group’s performance, collapsed over both conditions, was significantly above chance ($p = 0.001$, two-tailed binomial test). A separate analysis of each condition
revealed that the group’s performance in the cardboard condition was significantly above chance \( (p = 0.027, \text{ two-tailed binomial}) \), while their performance in the cloth condition was not significantly different than chance \( (p = 0.189, \text{ two-tailed binomial}) \). Performance in the cloth condition, however, was heavily weighted by one of the subjects, Yoda, who did not choose the correct cloth on any of his trials and in fact, seemed to noticeably avoid the correct cloth with a raised bump indicative of the food reward. Since Yoda was an extreme outlier (see Figure 1), the data was re-analyzed without Yoda’s data for both conditions.

![Figure 1](image-url)  

Figure 1 Range of average number correct per subject (* indicates \( p < 0.05 \)). Dashed line indicates chance.
Upon re-analysis, the group’s performance remained significant overall and during the cardboard condition \((p < 0.05, \text{two-tailed binomials})\), and was now also significantly above chance for the cloth condition \((p = 0.031, \text{two-tailed binomial})\). Further, the group’s performance was now identical between the two conditions \((78\% \text{ correct for each condition})\) indicating there was no significant difference in performance between the cardboard and cloth conditions.

The gibbons were able to use the visual change in shape of both cardboard (incline) and cloth (bump) to correctly choose the stimuli that covered the food reward. This is very similar to the performance seen in chimpanzees, bonobos, orangutans, and gorillas, who were also able to successfully solve a condition with a food reward hidden under a board using a small number of test trials \((\text{Brauer, et al., } 2006; \text{Call, } 2007; \text{Herrmann, et al., } 2007)\). No other species can be compared, as others have not yet been tested in this paradigm.

This task has ecological relevance for gibbons as they primarily feed on ripe fruits, high up in the forest canopy. The ability to quickly visually discern the location of ripe fruit \((\text{e.g. behind a branch, under leaves, etc.})\) would be very beneficial for them on a day-to-day basis. While experience in the wild would likely enhance and refine this skill, gibbons in the current study have had very limited opportunities to previously use this type of causal information as their food is not generally hidden or covered in any way. In addition, six out of the seven gibbons tested in this experiment chose the correct piece of cardboard to uncover on their first trial, possibly indicating that they were able to immediately understand the problem. The ability to understand the visual interplay of
physical properties may, therefore, be a primitive part of folk physics that does not require specific training or experiences to develop.

3.3 Experiment 2C: Tool Properties

While Experiment 2C falls under the umbrella of causality, the basic support paradigm is often viewed as straightforward means-end discrimination. Several monkey species are able to solve many variations of this paradigm, yet this only occurs after extensive training (Hauser, et al., 1999; Spaulding & Hauser, 2005; Yocom & Boysen, in press). Recent evidence with great apes, however, indicates that they may be more skilled than monkeys in making such discriminations with no prior training (Cunningham, et al., 2006; Furlong, Boose, & Boysen, 2008; Herrmann, et al., 2008; Povinelli, et al., 2000; Yocom & Boysen, in prep). With this in mind, I hypothesized that with no prior experience, gibbons would have limited success. I predicted that they would be successful in the basic On/Off paradigm (cloth side condition), yet would have difficulty utilizing their knowledge to solve other variations of the problem.

Method

Subjects

Eight white-handed gibbons (Hylobates lar), including five males and three females, participated in Experiment 2C (see Table 3).

Design & Procedure

Behind an occluder, the experimenter placed two different tools and two equally sized food rewards on the platform, out of the subject’s reach. One tool was considered “functional”, which the subjects could use to access the reward, while the other tool was
non-functional. After giving the subject approximately five seconds to examine the tool choices, the platform was pushed forward so that the subject could choose one of the tools and attempt to retrieve the reward. Each subject participated in the following tool property conditions:

\textit{a. cloth side} (support 1) – the two tools were identical pieces of cloth; a reward was placed on one piece of cloth and next to the other piece of cloth. Only the cloth that supported the reward was effective in retrieving the food.

\textit{b. cloth bridge} (support 2) – the two tools were identical pieces of cloth and each cloth had a Plexiglas bridge over the end farther away from the subject. The first reward was placed directly on one piece of cloth, underneath the bridge; the second reward was placed on the Plexiglas bridge that was above the other cloth tool. Only the cloth that supported the reward was effective in retrieving the food.

\textit{c. cloth ripped} (connectedness 1) – the two tools were pieces of cloth: one was a continuous length of cloth, while the other was two separate pieces of cloth, positioned with a visible space between them. In the latter tool, the two pieces, when combined, had identical dimensions to the intact cloth. The rewards were placed on the end of the intact cloth farthest from the subject; for the two-cloth tool, the reward was placed on the smaller piece of cloth farthest from the subject (which could not be reached by the subject). Only the intact cloth was useful to obtain the reward.

\textit{d. broken string} (connectedness 2) – the two tools were pieces of wool string: one tool was an intact length of string with a food reward tied at the far end, the other tool included two pieces of string with a visible space between them and a food reward tied to
the far end of the string piece that was inaccessible to the subject. Only the intact string was useful to obtain the reward.

*e. tray circle* (connectedness 3) – the tools were two cardboard trays. One tray had a circle cut out of the middle and a banana slice placed in the cut-out circle; the other tray had a U-shape cut out and a banana slice placed in the cut-out U. Both trays had a string attached, so that a subject could pull the tray toward himself. However, when the trays were moved, only the tray with the cut-out circle was useful in obtaining the reward.

Each subject participated in one session per day, with a session including nine or less trials. The order of the correct choice was pseudo-randomized in that the correct choice was not presented on the same side of the tray for more than two trials in a row. Each subject received three trials for each condition. Subjects were free to discontinue participation at anytime by simply leaving the testing area.

The experimenter coded all choices during testing. The trials were also video-recorded and 50% of the trials were coded offline by a naïve assistant to establish inter-rater reliability. Agreement on the side chosen was very high (Cohen’s K = 0.96).

Results & Discussion

Binomial tests were used to compare the gibbons’ performance in each condition with chance, which was a 50% probability of selecting either cloth. A Bonferroni correction was used to set the p-values at $\alpha = 0.05/5 = 0.01$ for the binomial tests. The gibbons performed best in the cloth side condition (75% correct, $p = 0.023$, two-tailed binomial test), yet their performance was not significantly different than chance in any of
the conditions tested ($p > 0.01$, two-tailed binomial tests). A Kruskal-Wallis test was used to compare the number of correct choices in each of the five conditions and no significant differences were found ($p > 0.05$) (see Figure 2).

![Figure 2 Average number correct +/- SEM. Dashed line indicates chance.](image)

The cloth side condition, which the gibbons were able to most easily solve, was the most straightforward condition tested. The gibbons’ performance is especially notable, however, in that they were able to solve this condition at a high level of success with no prior training or experience. While several species of monkeys have been successful with similar test conditions in tool property experiments, their successes
involved extensive training with the basic on/off (e.g. cloth side) paradigm until a criterion level was reached, which was then followed by presentation of other conditions (Hauser, et al., 1999; Spinozzi & Poti, 1989; Yocom & Boysen, in press). A closer analysis of previous studies with similar conditions revealed that during their first session of the cloth side condition, the performance of tamarins (~50-75% correct range for those starting with the side condition, Hauser, et al., 1999) and capuchins (average ~64% correct, Yocom & Boysen, in press) was below gibbons’ initial level of success (average 75% correct). In contrast, a recent study aimed at measuring great ape comprehension of the functional properties of tools after limited experience found that chimpanzees, bonobos, orangutans, and gorillas all performed significantly above chance in conditions similar to the present cloth side, cloth bridge, cloth ripped, and broken string conditions after only six trials (Herrmann, et al., 2008). In a follow-up experiment, sanctuary chimpanzees and orangutans, who were completely naïve to the testing materials, performed significantly above chance in the same conditions after only three test trials (Herrmann, et al., 2008).

The gibbons’ limited overall success in the support problem indicates that they may have a more restricted spontaneous understanding of support than great apes. It is also possible that gibbons require more noticeable or blatant differences than great apes to solve the variations of this problem. This could be due to attention differences between the groups. Although most of the gibbons would sit for testing, getting them to focus on the stimuli was sometimes challenging. Alternatively, gibbons may require more experience to solve the conditions, as opposed to great apes. Since their
performance was near significance level in the side condition, it seems likely that if gibbons were provided with the extensive training in the side condition seen in studies with monkeys they would have had been more successful in the other conditions as well.

Overall, the pattern of results seen with the gibbons does not directly mirror that of monkeys or great apes previously tested. Instead, gibbons seem to fit into a niche intermediate between monkeys and great apes in which they have a high level of spontaneous success with the basic support problem, but cannot extend this performance to more challenging conditions.

3.4 General Discussion

Over all the causality experiments, the gibbons performed best in Experiments 2B and 2C, indicating that they were able to use visual information to obtain a reward more easily than auditory information. While they were not successful in all conditions tested, the number of successful choices is more impressive since it resulted from spontaneous performance with unfamiliar tasks and materials. Compared to other species, gibbons performed worse (Experiments 2A & 2C) or equivalent (Experiment 2B) to great apes, and equivalently (Experiment 2A) or better (Experiment 2C) than monkeys tested in similar studies.
Chapter 4: Communication

Notably, social communication serves as a rather important skill for both human and non-human primates in their natural environments. In terms of non-verbal communication, humans can express themselves through gestures, body and head orientation, and eye gaze, among others. Studies of these communicative abilities in young children and infants have revealed that by 12-months of age infants can follow gaze referentially (Meltzoff & Brooks, 2007; Senju, Csibra, & Johnson, 2008) and use pointing as a signal of object-directed action (Woodward & Guajardo, 2002).

The ability of non-human primates to understand social communicative signals, such as gaze and pointing, has been tested in object-choice tasks. While there have been several variations, the basic set-up entails a human (although sometimes tested with a conspecific) providing the subject with a choice of two or more opaque containers, one of which hides a food reward. The experimenter then indicates the location of the reward by approaching, pointing, gazing, or otherwise marking the correct container in some way (Itakura, et al., 1999; Tomasello, Call, & Gluckman, 1997). The results of these studies have been mixed, possibly as a result of methodological differences in the studies or variations in rearing histories of the subjects (Call & Tomasello, 1994; Hare & Tomasello, 2004; Tomasello, et al., 1998). The emerging picture, however, seems to indicate phylogenetic differences that roughly reflect the natural developmental sequence at which great apes, specifically chimpanzees, are able to comprehend these behaviors.
In a longitudinal study, Okamoto-Barth and colleagues (2008) found that infant chimpanzees showed a progression of understanding human communicative skills in the following order: tap, touch, whole-hand point, close-point, distant-point, close-head/eye gaze, distant-head/eye gaze. Indeed, capuchins and rhesus macaques can be trained to use pointing to find a hidden reward, but not gaze (Anderson, et al., 1996; Anderson, Sallaberry, & Barbier, 1995). Likewise, local enhancement through tapping on and pointing to the baited container are the most beneficial cues for adult gorillas and chimpanzees, while their success has been more sporadic with cues involving only eye gaze (Call, Agnetta, & Tomasello, 2000; Itakura, et al., 1999; Peignot & Anderson, 1999).

For non-verbal social communication to be most effective, one must take into account whether or not the recipient of your gestures is paying attention, or is aware of your presence. When trying to gain the attention of an experimenter to receive a hidden reward, chimpanzees will move until they are visually facing the experimenter before beginning any visual food begging gestures (Liebal, Pika, Call, & Tomasello, 2004). In addition, chimpanzees are able to take into account an experimenter’s body and head orientation and will only visually gesture toward an experimenter for food when they are being watched (Hostetter, Cantero, & Hopkins, 2001; Kaminski, Call, & Tomasello, 2004), particularly if the experimenter’s eyes are visible (Bulloch, Boysen, & Furlong, 2008). Further, chimpanzees will produce spontaneous communicative gestures in situations that do not involve food rewards (Russell, et al., 2005).
What is not clear, however, is if these intentional communicative behaviors are a relatively recent development among ape species in the primate lineage. If this is indeed the case, we should expect the lesser apes to be less skilled than chimpanzees and humans, but perhaps more skilled than monkey species. A study of spontaneous social behavior among siamangs, indicates that they do seem to fall at an intermediate level between the complex, flexible gestures used by chimpanzees and the primarily tactile gestures of monkeys (Liebal, et al., 2004). Specifically, the siamangs did not produce the manual and object-based gestures commonly seen in chimpanzees and instead seemed to favor the use of tactile over visual gestures (Liebal, et al., 2004; Tomasello, et al., 1997). The siamangs did, however, produce a majority of their visual gestures and facial expressions when the recipient of their behaviors was visually attentive (Liebal, et al., 2004). Pileated gibbons studied in a visual co-orientation study with static photographic images also seemed to respond based on the attentional state of the experimenter or conspecific’s photograph (Horton & Caldwell, 2006).

To understand if gibbons can utilize human social communication skills, they were tested using the basic object-choice task with pointing, head and eye gaze, and replica markers of food as the communicative cues. In order to judge their ability to follow a goal object, they participated in trials in which the distinct goals were switched after the subjects’ witnessed the experimenter hiding the food reward under one of the objects. To assess the ability of gibbons to produce social communicative skills, another experiment measured their spontaneous production of gestures toward a naïve experimenter after witnessing a reward being hidden in a location out of the subject’s
reach. In addition, a final experiment assessed whether or not they were able to take the attentional state of a naïve experimenter into account when producing communicative gestures toward hidden food. The performance of the gibbons was compared to that of great apes and monkeys who were tested in similar paradigms.

4.1 Experiment 3A: Comprehension

Experiment 3A examined the ability of gibbons to understand commonly used human communicative signals. It also tested whether gibbons can track goals, as human infants do, or instead, only keep track of spatial/environmental information (Woodward, 1998). Due to the difficulties of great apes in similar experiments, I hypothesized that gibbons would have limited success with any of the communicative signals, with the least success in the gaze condition. Further, I predicted that gibbons would have difficulty tracking the goal of the experimenter.

Method

Subjects

Seven white-handed gibbons (*Hylobates lar*), including three males and four females, participated in Experiment 3A (see Table 3).

Design and Procedure

Behind an occluder, the experimenter baited one of two opaque plastic cups on a movable platform and gave one of the following social cues.

*a. look* – the experimenter alternated her gaze between the subject and baited cup three times while calling the subject’s name. The experimenter continued to look at the
baited cup, pushed the platform forward, and kept her gaze focused on the baited cup
until the subject made a choice.

b. point – the experimenter pointed towards the baited cup with the index finger
of her contra-lateral hand. At the beginning of the point, the experimenter also alternated
her gaze between the subject and baited cup three times while calling the subject’s name.
The experimenter continued to look at the baited cup, pushed the platform forward, and
kept her gaze focused on the baited cup and her finger pointed in the same direction until
the subject made a choice.

c. marker – the experimenter placed a photo of the food reward (grapes) on top of
the baited cup. Before placing the marker, the experimenter alternated her gaze between
the photo and the subject three times, while calling the subject’s name.

d. goal-switch -- the experimenter baited one of two distinctly colored (white and
black) opaque cups in full view of the subject. Following the baiting, an occluder was
raised and the experimenter switched the position of the two cups. Next, the occluder
was removed and the tray was pushed toward the subject, so that the subject could choose
one of the cups (with no cuing). The experimenter focused on the handle of the tray
behind the two cups as the subject made a choice.

e. location control -- this condition was used as follow-up control for the goal-
switch condition above. The experimenter baited one of two distinctly colored (white
and black) opaque cups, by lifting the cup and placing food directly underneath of it, in
full view of the subject. Directly following the baiting, the tray was pushed toward the
subject, so that the subject could choose one of the cups. The experimenter focused on the handle of the tray behind the two cups as the subject made a choice.

Each subject participated in one session per day, with a session including six or less trials. The order of the correct choice was pseudo-randomized in that the correct choice was not presented on the same side of the tray for more than two trials in a row. Each subject received three trials for each condition. Subjects were free to discontinue participation at anytime by simply leaving the testing area.

The experimenter coded all choices during testing. The trials were also video-recorded and 70% were coded offline by a naïve assistant to establish inter-rater reliability. Agreement between the experimenter and coding assistant was excellent (Cohen’s K = 1.0).

Results & Discussion

The results of Experiment 3A are present in Figure 3. The gibbons’ performance was significantly above chance only in the location control condition (p = 0.007, two-tailed binomial; p > 0.05, two-tailed binomials for all other conditions). In addition, there was a significant difference in the number of correct choices between the location control condition and the goal-switch condition (p = 0.026, Mann-Whitney U). There were no significant differences in the number of correct choices between any of the other conditions (p > 0.05, Kruskal-Wallis).
These results indicate that the gibbons were able to solve the location control condition from witnessing the hiding of the food reward, yet they were not able to use any of the communicative information from the experimenter, such as pointing, looking, a picture of the food reward, or the color/appearance of the cup concealing the reward to solve the problem. Likewise, other non-human primate species have also had difficulty using human communicative cues to find hidden food. In a similar object choice task, cotton-top tamarins were not able to use pointing, tapping, looking, or glancing to find the baited container at a level significantly greater than chance (Neiworth, Burman,
Basile, & Lickteig, 2002). Similarly, both rhesus and capuchin monkeys fail to use gaze as a cue in an object choice paradigm; while they have had more success with pointing as a cue, their success was measured over hundreds of trials, allowing the possibility of learning during the test trials (Anderson, et al., 1996; Anderson, et al., 1995). Great apes have experienced only slightly more success than monkeys in these paradigms. They have continually failed to use pointing alone as a communicative cue and require an iconic cue (i.e. a photograph) with a very close spatial relation to the baited object to solve the problem (Herrmann, Melis & Tomasello, 2006; Tomasello, et al., 1997). In the present experiment, aside from performance in the location control condition, the gibbons’ performance in marker condition was the most successful (71% correct), yet not significantly different from chance (p = 0.08, two-tailed binomial). Other studies with chimpanzees have revealed that they continually fail to use the gaze of a human or conspecific to locate a hidden reward, however they are more successful when gaze (or another cue) is combined with a vocalization or when the experimenter (or conspecific) simply approaches the baited container (Call, et al., 2000; Itakura, et al., 1999).

It is possible that gibbons’ inability to use the communicative cues is due to a lack of experience with cooperative communication activities. Chimpanzees, for example, have been more successful in competitive rather than cooperative tests utilizing communicative cues (Hare & Tomasello, 2004). Hare and Tomasello (2004) found that chimpanzees were able to use the cue of an outstretched arm and hand to find food when it was provided by an experimenter or conspecific who was competing with them for the food (e.g. experimenter reaching for same reward that was beyond his reach), yet not
when an experimenter was cooperating with them through the same body gestures toward a food reward that was within the experimenter’s reach (e.g. outstretched arm and hand in a pointing gesture). Chimpanzees and rhesus macaques have also been successful in other competitive paradigms, leading researchers to conclude that at least some species, perhaps those with a despotic social structure, understand social communication best under more ecologically valid, competitive conditions (Hare, Call, & Tomasello, 2001; Rosati, Santos, & Hare, 2010). Since gibbons have a unique social structure and typically live in pair-bonded groups, it is not clear whether they would perform better under competitive conditions, as seen in chimpanzees and rhesus.

Based on the results of this experiment, it seems most likely that gibbons are not able to understand this set of communicative, or goal-directed, human social cues or track an occluded food reward. It remains possible that gibbons could understand other types of communicative cues, such as approaching and visually inspecting the correct container (e.g., Itakura, et al., 1999), which may be more similar to social cues used in the wild. Further, gibbons may have more success with cues provided by conspecifics, although studies comparing the results from human experimenters and conspecifics have not revealed a clear consensus on whether this is an influential factor on performance (Hare & Tomasello, 2004; Horton & Caldwell, 2006; Itakura, et al., 1999; Neiworth, et al., 2002). Instead, the relationship of the subject with the experimenter (familiarity and interactions) or conspecific (dominant versus subordinate) may have more of an effect on success (Call, et al., 2000; Horton & Caldwell, 2006; Shepherd & Platt, 2010).
4.2 Experiment 3B: Pointing Cups

Experiment 3B required the gibbons to convey to a naïve experimenter the location of a hidden reward. While chimpanzees produce a number of communicative/begging gestures in many different situations, the extent of gibbon communicative abilities is not known (Hostetter, et al., 2001; Russell, et al., 2005). Liebal and colleagues (2004) found that one species of lesser apes, siamangs (*Symphalangus syndactylus*), do not rely on the same communicative repertoire as chimpanzees, yet they do express numerous social behaviors in captivity, including tactile, facial, and visual gestures, and seem to be able to take a conspecific’s attentional state into account when gesturing. Horton and Caldwell (2006) also found evidence that pileated gibbons (*Hylobates pileatus*) could use a photograph of a human or conspecific to judge attentional state and alter their behavior to co-orient with the photographed face. With that in mind, I predicted that gibbons would have moderate success in communicating the location of the baited cup to the experimenter.

Method

Subjects

Six white-handed gibbons (*Hylobates lar*), including four males and two females, participated in Experiment 3B (see Table 3).

Design & Procedure

One opaque cup was placed on each of two separate platforms. A human caretaker hid a banana slice under one of the cups in full view of the subject and then left the testing area. A naïve experimenter centered the ape by crouching equidistant between
the platforms and calling the subject’s attention. Then, the experimenter waited until the subject approached or indicated one of the cups (maximum time: one minute). When a cup was indicated by gazing or pointing, the experimenter lifted the indicated cup and, if correct, provided the reward to the subject. If the cup was not indicated at the end of one minute, or if the incorrect cup was chosen, the reward was shown to the subject and then all stimuli were removed from the testing area.

Each subject participated in one session per day, with a session including four or less trials. The side of the baited cup was pseudo-randomized in that the correct choice was not presented on the same side for more than two trials in a row. Subjects were free to discontinue participation at anytime by simply leaving the testing area.

The experimenter coded all choices during testing. The trials were also all video-recorded and coded offline by a naïve assistant to establish inter-rater reliability. Agreement between the experimenter and coding assistant on the frequency of gaze and pointing behaviors was high (Cohen’s K = 0.75).

**Behavioral Coding**

For each trial, the subjects’ responses were scored as correct, incorrect, or no response. If a subject indicated the correct cup to the experimenter through any form of head/eye gaze or pointing gestures, the corresponding trial was recorded as correct (note: pointing was defined as an outstretched arm, hand, or fingers). If a subject indicated the incorrect (unbaited) cup to the experimenter, the trial was scored as incorrect, while if a subject failed to indicate either cup to the experimenter during a trial, that trial was
counted as a no response. The experimenter also recorded any other unique gestures, no matter which cup they were directed toward.

Results & Discussion

The gibbons indicated a cup (either correct or incorrect) to the experimenter on 83% of all trials through either gaze or pointing behaviors. Out of these trials, the group selected the correct cup 80% of the time, which was significantly greater than chance ($p = 0.012$, two-tailed binomial). The gibbons used gaze and pointing behaviors equally to indicate their choice and, thus, there was no significant difference between utilization of the two behaviors ($p = 1.0$, Mann-Whitney U). No other gestures or behaviors were used by the gibbons during testing.

These results indicate that the gibbons were able to use baiting information to direct a naïve experimenter toward a food reward. This is consistent with research from chimpanzees which indicates that they also rely heavily on pointing and gaze to convey the location of food to a naïve experimenter (Leavens & Hopkins, 1998). Compared to gibbons, however, chimpanzees utilize more of a variety of referential gestures, including gaze alterations, vocalizations, food begging, whole-hand point, index-finger point, and a combination of these and other unique gestures (Leavens & Hopkins, 1998). In contrast, monkeys do not exhibit the same flexibility with gestures as apes (Call & Tomasello, 2007).

4.3 Experiment 3C: Attentional State

Experiment 3C required gibbons to take the attentional state of the experimenter into account when requesting food that was visually unavailable to the experimenter.
Similarities and differences to Experiment 3B, made this an intriguing follow-up experiment. For instance, some aspects of this experiment are less complex than the previous experiment, such as the fact that the food was not hidden and remained visually available to the subject throughout testing. Yet this experiment adds on the complex requirement of awareness of the experimenter’s attentional state. In other words, the experimenter can only help if she is aware of the subject’s attempts to communicate. Based on positive results in this regard with siamangs (Liebal, et al., 2004) and gibbons successful communication in Experiment 3B, I hypothesized that the gibbons would be successful in differentiating between the varying attentional states of the experimenter.

Method

Subjects

Five white-handed gibbons (Hylobates lar), including three males and two females, participated in Experiment 3C (see Table 3).

Design & Procedure

A caretaker hid a grape out of the subject’s reach on either the left or right side of the testing area in full view of the subject and then left the testing area. A naïve experimenter then entered the testing area and stood on the side opposite of the reward in each of four different attentional states.

a. away – the experimenter oriented her whole body away from the reward (e.g. with her back toward the reward). The subject then had to approach the side/front of the experimenter in order to be visible. If the subject approached in this way within 30 seconds, the experimenter turned around and waited for the subject to direct her attention
toward the reward. If the subject approached the reward location and indicated it to the experimenter within another 30 seconds, the experimenter gave the reward to the subject.

b. towards - the experimenter faced toward the reward. If the subject approached the reward location and indicated it to the experimenter within 30 seconds, the experimenter gave the reward to the subject.

c. away: body-facing – this manipulation is identical to “away”, except the experimenter’s body faced toward the reward and her face was oriented in the opposite direction.

d. towards: body-away – this manipulation is identical to “towards”, except the experimenter’s body faced away from the reward and her face was oriented in the direction of the reward.

For all the attentional states, if the subject never approached the reward or overtly indicated the location to the experimenter in the allotted time, the reward was removed and the next trial was initiated.

Each subject participated in one session per day, with a session including four or less trials. The side of the reward was pseudo-randomized in that the correct choice was not presented on the same side for more than two trials in a row. Subjects were free to discontinue participation at anytime by simply leaving the testing area.

All experimental trials were coded live by the experimenter and videotaped for review by a naïve assistant to establish inter-rater reliability. Agreement ratings on the occurrence of gesture and gaze behaviors was high (Cohen’s K = 0.80).
Behavioral Coding

Each experimental trial was coded as correct or incorrect. If a subject indicated the reward to the experimenter, then the experimenter gave the reward to the subject and that trial was counted as correct. If the subject did not indicate the reward to the experimenter in the allotted time that trial was counted as incorrect. In addition, the frequencies of the following “directed” behaviors were scored for each trial: gesturing/pointing (arm or hand out-stretched) and gaze (eyes/head toward experimenter).

Results & Discussion

Gibbons were only able to successfully direct the experimenter’s attention to the reward on one trial (Deana; condition: towards: body-away). Gestures of any kind were only recorded in small percentage of the total trials (45%) and were evenly distributed across the experimental conditions (p = 0.302, Kruskal-Wallis,). With this in mind, the gibbons were not affected by the differing postures and attentional states of the experimenter.

These results are in contrast to the gibbons’ behavior in Experiment 3B, in which they used both gaze and reaching behaviors to successfully indicate the baited cup to the experimenter. Several factors may have contributed to the gibbons’ poor performance in this experiment. First, in this study the experimenter remained standing and never faced directly toward the gibbon (as opposed to the experimenter’s body orientation in Experiment 3B). It is possible that the gibbons could have viewed all of the trials as “inattentive” and, therefore, did not produce any referential behaviors. Alternatively, the gibbons may not have been able to handle the two-step procedure of gaining the
experimenters’ attention and then requesting the food. Hattori et al. (2010) found that capuchin monkeys were able to show an understanding of human attentional states only when food was being held by an experimenter, and not in a separate condition in which the food was on a table next to the experimenter. They proposed that requesting situations in which food is separate from a human experimenter are too difficult and confusing for primate subjects and do not accurately measure their ability to judge attentional states.

In a study with great apes, Kaminski and colleagues (2004) found that chimpanzees, bonobos, and orangutans were sensitive to both an experimenter’s body orientation and face orientation when requesting food from a table in front of an experimenter, but not to an experimenter’s eye gaze (eyes open versus closed). Further, the chimpanzees studied by Hostetter et al. (2001) used a differing combination of vocalizations and gestures, depending on whether an experimenter holding a food reward was facing toward them or away from them. The chimpanzees were more likely to vocalize when the experimenter was faced away from them and more likely to use visual gestures when the experimenter faced toward them (Hostetter, et al., 2001). In another requesting paradigm, without the use of food rewards, chimpanzees used referential gestures, dependent on the experimenter’s attentional state (e.g. towards the subject versus away from the subject) to request a tool from the experimenter (Russell, et al., 2005).

Thus, although gibbons may possess some knowledge of the attentional states of others, at least at the lowest level of “engaged” in Experiment 3B (in which they
gestured) versus possibly “inattentive” in Experiment 3C (provided no gestures), they are clearly not as skilled as the great apes, most notably chimpanzees, who were tested in the attentional state paradigms discussed above. As gibbons are largely arboreal and often have limited visual contact with their relatively small social group, it would likely be inefficient for them to use primarily visual gestures to communicate with one another (e.g., Liebal, et al., 2004). In fact, during social observations, Liebal and colleagues (2004) found that siamangs used tactile gestures (e.g. gentle touch, nudge, pull, slap) most frequently followed by facial expressions and actions, while visual gestures were used the least.

4.4 General Discussion

In Experiment 3A the gibbons were not able to use any of the experimenter’s social cues to locate the hidden food and could not track the food when the location of the goal container was moved. They were able to successfully remember the location of the food in control trials, however, indicating that they did understand that they could locate the hidden food under one of the cups. The gibbons were more successful in Experiment 3B, as they were able to indicate the food location to a naïve experimenter in the majority of trials. However, they were not able to demonstrate this knowledge when the experimental paradigm was changed slightly in Experiment 3C. In Experiment 3C the gibbons did not indicate the food to the experimenter in any condition and showed no differences in their behavior between the various attentional conditions.

Overall, these experiments show that while gibbons do not demonstrate evidence of understanding the referential nature of human social cues, they are able to produce
interpretable communicative cues toward a human experimenter. Their overt communication appears to be limited, however, likely based on an experimenter’s body orientation or other social/methodological factors. Compared to the great apes tested in similar paradigms, gibbons seem to have more limited forms of communication. Their ability to interpret and express communicative cues seems to be more similar to monkeys species tested in similar areas. The unique ecology and social structure of gibbons likely contributed to their performance during this set of communication tasks.
Chapter 5: Theory of Mind

The term of “theory of mind” actually encompasses a number of unique social-cognitive skills, such as understanding goal-directed behavior, intentions, perceptions, knowledge, and beliefs of others. For human infants, these skills seem to develop quickly during the first year, with children showing skill in discerning goals (Gergely, Nadasdy, Csibra, & Biro, 1995), intentions (Schwier, van Maanen, Carpenter, & Tomasello, 2006), and knowledge of others (Moll & Tomasello, 2007; Onishi & Baillargeon, 2005) by their first birthday. It is not until around 4 years of age, however, that children are able to understand, what seems to be the most complex aspect of theory of mind, false-beliefs (for meta-analysis see Wellman, Cross, & Watson, 2001). While there is still no evidence that any non-human primates can pass a non-verbal false belief task, experimental evidence now indicates that at least some species of non-human primates are aware of many of the same psychological states as two year-old human children (Call & Tomasello, 1999; Kaminski, et al., 2008; Tomasello, et al., 2003).

Eye gaze has been extensively studied in infants and non-human primates as a developmental precursor to understanding the intentions of others (Brooks & Meltzoff, 2002; Johnson, Slaughter, & Carey, 1998; Moll & Tomasello, 2004; Rosati & Hare, 2009). The results from human infants indicate that they are able to follow an experimenter’s eye gaze to a location behind a barrier at 12 months of age (Moll & Tomasello, 2004). Despite the limited success of chimpanzees and orangutans in using
gaze as a cue to locate hidden objects (Call, et al., 2000; Call, Hare, & Tomasello, 1998; Itakura, et al., 1999), all species of great apes can follow the gaze of an experimenter and will even alter their orientation in order to take the visual perspective of an experimenter (Braeuer, Call, & Tomasello, 2005; Rosati, et al., 2010). Similarly, while monkeys cannot spontaneously locate food in an object choice task using only the gaze cue, macaques, mangabeys, baboons, capuchins, tamarins, marmosets, and lemurs have been shown to follow gaze, at least in some conditions (Rosati & Hare, 2009). In addition, capuchins and spider monkeys show some evidence for perspective taking, as they will alter their body position to follow an experimenter’s gaze around a barrier (Amici, et al., 2009). In contrast to great apes, however, neither spider monkeys nor capuchins have exhibited any “looking back” behaviors, indicating that a high level or perspective taking explanation may be premature (Amici, et al., 2009; Brauer, et al., 2005). Further, capuchins, tamarins, and lemurs respond to overt changes in face/head/body orientation, but not to changes in the direction of the eyes only (Neiworth, et al., 2002; Shepherd & Platt, 2008; Vick & Anderson, 2000). These results seem to indicate that while gaze-following behaviors may be wide-spread across the Primate order, the underlying psychological mechanisms and the information that is gained from following the gaze of others may vary between species, and notably between great apes and monkeys (Rosati, et al., 2010).

Based on the rational imitation paradigm pioneered by Gergely and colleagues (2002), Wood, et al. (2007) tested the ability of New World monkeys (tamarins), Old World monkeys (rhesus macaques), and great apes (chimpanzees) to discern the goal-
directed, intentional action of a human. All three species were able to infer the
experimenter’s goal, and select the cued container, when an experimenter acted on it in
an intentional (hand grasp) or rational (elbow touch when hands full) manner.
Conversely, the animals picked between the two containers randomly, when the contact
was unintentional (hand flop) or not rational (elbow touch when hands empty) (Wood,
Glynn, Phillips, & Hauser, 2007). This seems to indicate that much like human infants,
several other species of primates can indeed use intentional and rational behavior to
identify goals (Wood, et al., 2007).

The exact nature of species differences among the use of eye gaze and
understanding of intentions remains elusive, perhaps due to a limited number of species
and paradigms that have been tested. It is possible that some aspects of theory of mind,
such as the understanding of intentions or eye gaze may be a common part of all primate
cognitive capacities and more complex aspects, such as knowledge of others beliefs, may
be uniquely human. Alternatively, there may be further divisions among primates,
perhaps such that Old World monkeys and apes share some social cognitive skills that
New World monkeys do not. In the following experiments, the ability of gibbons to
follow gaze (Experiment 4A) and understand intentions (Experiment 4B) were measured
and then compared to the performance of monkeys and great apes.

5.1 Experiment 4A: Gaze Following

Experiment 4A tested the gibbons’ ability to spontaneously follow the gaze
of a human experimenter. As evidence for gaze following is widespread across many
primate species (Amici, et al., 2009, Tomasello, et al., 1998), I hypothesized that gibbons
would follow the head/eye gaze of an experimenter. However, since the “high level”, or perspective taking, explanations for gaze following have been limited to great apes (Brauer, et al., 2005), I hypothesized that gibbons would have more difficulty using eyes alone and following gaze around a barrier.

Method

Subjects

Five white-handed gibbons (*Hylobates lar*), including one male and four females, participated in Experiment 4A (see Table 3).

Design and Procedure

The experimenter sat in front of the subject and provided a grape to center the subject’s attention. When the subject looked at the experimenter, a trial was initiated. Each of the subjects received the following three gaze manipulations on different days to minimize habituation.

a. head & eyes – the experimenter sat facing the subject, called the subject’s name, showed him a piece of food and then hid it in her hand in front of her body. The experimenter then looked up toward the sky with her head and eyes (which remained open) for 10 seconds.

b. back – the experimenter sat with her back towards the subject, called the subject’s name, showed him a piece of food, and then hid it in her hand next to her shoulder. The experimenter then looked up with her head and eyes (which remained open) for 10 seconds. During this time, the experimenter looked over her shoulder three
times to ensure that the subject was attentive. If the subject was not paying attention when the experimenter glanced the second time, the trial was repeated.

c. eyes - the experimenter sat facing the subject and called the subject’s name, showed him a piece of food and then hid it in her hand in front of her body. The experimenter then looked up with only her eyes (which remained open) for 10 seconds, while her face remained oriented toward the subject.

d. forward control (no look) – the experimenter sat facing the subject and called the subject’s name, showed him a piece of food and then hid it in her hand in front of her body. The experimenter then looked toward the subject’s chest keeping her head and eyes facing forward for 10 seconds.

Each subject participated in one condition per day, with a condition including three trials. Subjects were free to discontinue participation at anytime by simply leaving the testing area.

Behavioral Coding

The frequency of each subject’s “looking up” and “looking back” behaviors were scored. A subject’s response was coded as “looking up” if the subject moved his eyes and/or head up toward the sky in the direction of the experimenter’s gaze. In addition, a subject’s response was coded as “looking back” if the subject looked up, looked at the experimenter, and then looked up again consecutively within a five-second period. All trials were double coded off-line by the experimenter and a naïve assistant to establish inter-rater reliability. Agreement between the experimenter and naïve assistant on the number of looking behaviors was excellent (Cohen’s K = 0.80).
Results

Only one looking back behavior occurred (Abigale; condition: head & eyes) during the experiment. The total number of looking up behaviors varied among the four conditions (see Figure 4). The number of looking up behaviors was significantly different between the head/eyes and control conditions ($p = 0.031$, Mann-Whitney U), as well as between the head/eyes and eyes only conditions ($p = 0.025$, Mann-Whitney U). No other significant differences were found between any of the other conditions ($p > 0.05$). This indicates that gibbons were able to follow the gaze of a human conspecific when both head and eyes were used as a cue, but not when the back of the head or eyes were used alone.
In order to better understand the extent of gibbons’ gaze following abilities, four of the subjects that participated in the above gaze conditions were tested in the following barrier conditions.

*e. barrier gaze* – the experimenter sat facing the subject, with a wooden barrier (18 x 24 inches) placed directly beside her. The experiment called the subject’s name, showed him a piece of food and hid it in her hand in front of her body and then looked with her head and eyes behind the barrier for 10 seconds. In order for the subject to

Figure 4 Average frequency of looking up +/- SEM (* indicates p < 0.05). Dashed line indicates chance.
follow the experimenter’s eye gaze, he would need to move and reorient himself to a position in which he/she could see behind the barrier.

*f. barrier control* - the experimenter sat facing the subject, with the same wooden barrier as described above directly next to her. The experimenter then called the subject’s name, showed him a piece of food and hid it in her hand in front of her body. The experimenter looked toward the subject’s chest keeping her head and eyes facing forward for 10 seconds.

Each subject participated in both conditions, with a condition including three or less trials. Subjects were free to discontinue participation at anytime by simply leaving the testing area.

*Behavioral Coding*

The number of “looking over” and “directed movement” behaviors were measured for each subject. A subject’s response was coded as looking over if the subject moved his eyes or head up and over, as if peering behind the wooden barrier. In addition, a subject’s behavior was coded as directed movement if the subject moved into a position in which they could see behind the barrier, by either climbing up the fence or moving to the side of the barrier.

All trials were double coded off-line by the experimenter and a naïve assistant to establish inter-rater reliability. Agreement between the experimenter and coding assistant on the frequency of looking over and directed movements was high (Cohen’s K = 0.80).

*Results & Discussion*
The gibbons showed no response when the experimenter’s head and eye gaze was directed behind the wooden barrier. As a group, they did not reliably make any attempts to move and see what the experimenter was gazing toward or look in the same direction. Further, there were no differences in their behaviors between the barrier gaze and barrier control conditions (frequency of looking and directed movement in each condition were zero).

The gibbons’ performance in the barrier conditions combined with their initial performance in the first four conditions point to two important conclusions. First, it indicates that gibbons can follow the gaze direction of an experimenter if they are able to rely on combined head and eye movements, yet the performance falters when it is based on orientation of the back of the head or only the eyes. Further, it does not appear that gibbons have knowledge that an experimenter’s gaze is directed toward a goal, as they did not follow the experimenter’s gaze behind a wooden barrier that would have required them to move or change their orientation in some way.

The gibbons’ performance in the gaze following trials is similar to a number of other non-human primate species. For instance, macaques, capuchins, tamarins, and lemurs are able to follow combined head and eye cues, but not eyes alone (Emery, et al., 1997; Neiworth, et al., 2002; Shepherd & Platt, 2008; Vick & Anderson, 2000). The propensity of gibbons, as well as other non-human primates, to rely on cues other than eye gaze may have an ecological basis. The “gaze camouflage theory” posits that the dark colored sclera of all non-human primates, helps to disguise their eye gaze from other individuals, including conspecifics and predators (Kobayashi & Kohshima, 2001).
Kobayashi and Kohshima (2001) found that for the majority of non-human primates the
dark coloring of the sclera was similar to the coloring of their iris and/or face, making it
difficult to distinguish the iris position and/or eye outline in the face. Indeed, upon
reviewing the videotaped gaze following trials, it was often difficult to distinguish the eye
position of the gibbons, especially those with dark-colored faces (note: in this experiment
three subjects had light-colored faces and two had dark-colored faces). This is in contrast
to humans, the only primate species that have white sclera, which provides contrast to
easily distinguish the eye outline in the face and the iris position in the eye (Kobayashi &
Kohshima, 2001). Indeed, Tomasello and colleagues (2007) found that while human
infants preferred to follow the eye gaze cue, great apes, including chimpanzees, bonobos,
and gorillas, preferentially utilized the head cue, although they were still able to follow
some eye movements.

As for the psychological basis of their gaze-following, gibbons failure to attend to
the goal of an experimenter’s gaze or exhibit any looking back behaviors indicates that
they may not be able to use the gaze cue as flexibly as great apes (Braeuer, et al., 2005;
Tomasello, Hare, & Agnetta, 1999). Braeuer and colleagues (2005) found that great apes
will follow an experimenter’s gaze around barriers and even engage in looking back
behaviors when they cannot locate the target of an experimenter’s gaze. Gibbons
primarily arboreal lifestyle, dispersed in the forest canopy, may not necessitate using eye
gaze in the same way as great apes. Instead, gibbons gaze following may resemble the
behavioral tendencies of primates such as capuchins and marmosets, who do not seem to
appreciate what others can or cannot see (as opposed to chimpanzees tested in similar
studies) and instead base their behavior on the head or body movements of conspecifics (Burkhart & Heschel, 2007; Hare, Addessi, Call, Tomasello, & Visalberghi, 2003; Hare, Call, Agnetta, & Tomasello, 2000).

5.2 Experiment 4B: Intentions

Experiment 4B examined the gibbons' ability to utilize the intentional behavior of an experimenter to locate a hidden reward. Chimpanzees as well as capuchin monkeys have been successful in distinguishing between an experimenter’s unwilling and unable food sharing behaviors (Call, Hare, Carpenter, & Tomasello, 2004; Phillips, Barnes, Mahajan, Yamaguchi, & Santos, 2009). In addition, some non-human primates have been more successful using human social communicative cues when they are presented in an intentional manner, rather than a cooperative one. For instance, in an object choice task, orangutans and chimpanzees can distinguish between markers placed on top of a container in an intentional versus accidental manner (Call & Tomasello, 1998). Chimpanzees are also able to use the same type of hand/arm gesture when it is presented in a reaching or prohibitive manner (“Don’t touch that!), rather than a cooperative one (pointing) (Hare & Tomasello, 2004; Herrmann & Tomasello, 2006).

Since gibbons had difficulty in understanding the set of human social cues used in Experiment 3A, it is possible they may not have understood those actions as intentional forms of communication. In order to better understand gibbons’ comprehension of an experimenter’s overtly intentional behavior, gibbons were tested in an object-choice task in which the experimenter directed two types of intentional behaviors toward one of two opaque cups. I hypothesized that gibbons would choose the baited container in each of
these conditions at above chance levels, since the experimenter’s behaviors toward the baited cup were more obvious and directed (e.g. intentional) than in previous experiments.

Method

Subjects

Six white-handed gibbons (*Hylobates lar*), including three males and three females, participated in Experiment 4B (see Table 3).

Design & Procedure

Behind an occluder, the experimenter baited one of two opaque plastic cups on a movable platform, which was out of the subject’s reach. After removing the occluder, the experimenter provided one of the following social cues and then pushed the platform forward and allowed the subject to choose one of the cups.

a. trying – the experimenter tried unsuccessfully to twist off the lid of the baited cup while looking at the baited cup.

b. reaching – a mesh barrier blocked the experimenter’s access to the cups. The experimenter tried to reach toward the baited cup by fully extending the equilateral arm and gazing toward the correct cup, yet was unsuccessful in touching the cup due to the mesh barrier. The experimenter’s directed reach and gaze continued until the subject made a choice.

For each condition, the platform was pushed forward approximately three seconds after the experimental manipulation began.
Each subject participated in one session per day, with a session including six or less trials. The order of the baited choice was pseudo-randomized in that it will not be presented on the same side of the tray for more than two trials in a row. Each subject received three trials for each condition. Subjects were free to discontinue participation at any time by simply leaving the testing area.

All trials were coded online by the experimenter. They were also all videotaped and coded by a naïve assistant to establish inter-rater reliability. Inter-rater agreement was excellent (Cohen’s K = 1.0).

**Results & Discussion**

The group successfully chose the correct container in 61% of the trials for each condition, which was not significantly different from chance (p = 0.481 for trying and reaching conditions, two-tailed binomials). Further, there was no difference in the number of correct choices between the two conditions. This indicates that gibbons were not able to use intentional trying or reaching behaviors of a human experimenter to locate to hidden food. However, it remains possible that at least some subjects were able to understand the experimenter’s intentional behavior in the trying condition, as two subjects (Abigale and Stephanie) made no errors in the trying condition.

When compared to the pointing condition in Experiment 3A (52% correct), gibbons were only slightly more successful in the reaching condition (61% correct), which utilized the same basic gesture. This indicates that unlike chimpanzees, gibbons were not significantly more successful in the reaching condition that conveyed intentional behavior (p > 0.05, Mann-Whitney U).
While several species of non-human primates have shown some level of intention-reading abilities, success appears dependent on the nature of the task presented (i.e. cooperative versus competitive) and the format of testing (i.e. rational behavior paradigms, etc.) (Phillips, et al., 2009; Wood, et al., 2007; also see Rosati, et al., 2010 for review). It is possible that gibbons would perform more favorably with a competitive task design in which they had to compete with an experimenter or conspecific for food, instead of using an experimenter’s behavior in a cooperative way. In competitive selection tasks, the behavior of both chimpanzees and rhesus macaques indicate that they are aware of what others can see, and will modify their behavior to avoid being noticed by a competitor (Flombaum & Santos, 2005; Hare, et al., 2001). In addition, Kaminski et al. (2008) found evidence that chimpanzees are aware of what others know in a competitive paradigm with a conspecific. To fully understand the limitations of gibbons’ abilities to understand and use intentional behaviors of others and before any firm conclusions are made, it will be useful to test their abilities in a variety of contexts.

5.3 General Discussion

The results of Experiment 4A indicates that gibbons can only follow human gaze when the head and eyes are used together as a cue and that they do not seem to understand the referential quality of human’s looking behavior. This points to a low-level explanation for gibbon’s gaze following behavior, indicating that they may not be able to understand the goal of another’s gaze and their co-orienting may be more of an inflexible behavior. Similar claims have been made for several species of monkeys, while great apes do seem capable of more flexible and complex gaze following.
Experiment 4B showed that gibbons do not seem to understand intentional behaviors in the same way as several other species of non-human primates. Taken together, these experiments show that while gibbons do share some important social cognition skills with great apes, they appear to be more similar to monkeys in their social cognitive abilities. Although gibbons do not seem as advanced as the great ape species tested in these human-based precursors to theory of mind, more research is needed before any firm conclusions can be drawn.

The results of Experiments 4A and 4B do fit together, however, as understanding the referential nature of eye gaze and intention-reading may be linked. Gibbons’ failures in gaze following, as well as in understanding intentional behaviors, may be related to their specialized ecology and lifestyle. Their primarily arboreal lifestyle, with conspecifics spread out in the forest canopy, may not provide a need to link intentions or eye gaze with goals or actions. In addition, gibbons’ small, familiar social groups that do not exhibit an explicit dominance hierarchy may make complex social cognitive skills unnecessary.
Chapter 6: Conclusions

6.1 Summary of Results

Table 6 details the results of the nine experiments conducted on gibbon cognition. While it is not possible to directly compare the two areas, gibbons generally seemed to perform more successfully in the physical cognition studies compared to the social cognition experiments, over which they were largely unsuccessful. They also exhibited numerous differences from the performance of great apes in both the physical and social realm. Notably, great apes have excelled in several of the areas where the gibbons failed, such as Experiments 2A, 2C, 3C, 4A, and 4B. Overall, the performance of gibbons seems more consistent with monkeys, such as capuchins and macaques, who have been tested in similar studies.
<table>
<thead>
<tr>
<th>Experiment</th>
<th>Gibbon Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Physical 1: Numerosity</td>
<td>Successful with ratio groups 2.5, 2.0 (without 3:6 data), 1.67, 1.5, 1.33; Unsuccessful with ratio groups 1.25 and 1.2</td>
</tr>
<tr>
<td>2A: Noise</td>
<td>Failed to use noise as a cue</td>
</tr>
<tr>
<td>2B: Shape</td>
<td>Successful with both cardboard and cloth</td>
</tr>
<tr>
<td>2C: Tool Properties</td>
<td>Most successful in cloth side condition</td>
</tr>
<tr>
<td>Social 3A: Comprehension</td>
<td>Failed to utilize any communicative cues; successful with location control</td>
</tr>
<tr>
<td>3B: Pointing Cups</td>
<td>Successful in indicating the correct cup</td>
</tr>
<tr>
<td>3C: Attentional State</td>
<td>Failed to differentiate between attentional states</td>
</tr>
<tr>
<td>4A: Gaze Following</td>
<td>Follow head/eye gaze up, yet failed to follow back of head, eyes alone or gaze around a barrier</td>
</tr>
<tr>
<td>4B: Intentions</td>
<td>Failed to utilize trying and reaching behaviors</td>
</tr>
</tbody>
</table>

Table 6 List of gibbon performance in all experiments

6.2 Broader Implications

The combination of physical and social experiments conducted with gibbons marks an important contribution to understanding the origins of cognition in non-human primates. In each of the areas tested, the gibbons’ performance helps to clarify their understanding of the physical and social world. With this research, it is increasingly clear that gibbons do not fit neatly into any category. They do not seem to be quite as savvy as great apes in certain aspects of the physical cognition experiments (although some had similar results), nor as insightful as them at understanding human behaviors and intentions in the social cognition tasks. In contrast, the gibbons were able to solve some...
problems with much less experience than capuchins, and seem to have a more fine-tuned number discriminability threshold compared to monkey species.

Experiments 2A and 2B are helpful in evaluating competing intelligence hypotheses. The noise and shape experiments required inferential reasoning, which is often a complex process. Herrmann and colleagues (2007) found that, in addition to superior performance in social experiments, human children were moderately better than chimpanzees and orangutans in noise and shape causality experiments, leading them to speculate that instead of a specific socio-cultural advantage, humans may be distinct in “the ability to understand unobserved causal forces in general.” However, it is still possible that this ability may have first evolved in the social domain (Herrmann, et al., 2007; Tomasello & Call, 1997). Overall, gibbons were not as successful in the causality experiments as great apes or human children (Herrmann, et al., 2007). Further, gibbons performed successfully in the shape experiment, yet unsuccessfully in the noise experiment, indicating that they may understand causality differently in different sensory domains. This performance may have an ecological basis as well, as wild gibbons utilize visual features (e.g. food shape, color, etc) over auditory signals in their search for food (Bartlett, 2007), compared to chimpanzees who regularly exhibit referential food grunts for different types of food (Slocombe & Zuberbuhler, 2005).

The tool property conditions in Experiment 2C are especially interesting, as gibbons are morphologically restricted due to their hook-like hands that are specialized for brachiating (e.g. Cunningham, et al., 2006). It seems that although gibbons are not morphologically equipped to deal with challenging tool use, they may have the requisite
causal knowledge from a common ape ancestor to solve basic tool-use problems (Cunningham, et al., 2006). In this case, although gibbons do not have a need to exploit this trait in the wild, they can utilize it in captive situations. The gibbons’ performance in Experiment 2C is especially powerful, as they were tested on a limited amount of trials and had a high rate of spontaneous success in the cloth side condition.

The results of Experiments 4A and 4B help to tease apart the intricacies of theory of mind. Gibbons’ performance indicates that there may be a link between “high level” gaze following, which would include looking back behaviors and perspective taking, and understanding intentional behavior. Gibbons failed in both of these complex theory of mind components, suggesting that they may differ from great apes and humans in their ability to understand and reason about the thoughts of others (Herrmann, et al., 2007; Kaminski, et al., 2008).

6.3 Future Directions

While this compilation of experiments adds much to the field of comparative psychology, there remain many areas that require further study. An important factor to consider in future experiments is the role of experience or practice in gibbons’ performance. In particular, it would be helpful to re-test the causality paradigms of Experiments 2A, 2B, and 2C after providing different types and amounts of experience to subjects.

Specifically in social experiments, it would be interesting to compare performance in competitive and cooperative paradigms, as several species of non-human primates seem to perform better in competitive experimental situations, which may be
more intuitive for non-human primates (Hare & Tomasello, 2004; Rosati, et al., 2010). The performance of gibbons in this area could be particularly helpful, as their pair-bonded social structure superficially resembles that of humans and other researchers have cited social learning and cooperation as a point of divergence between humans and great apes (Herrmann, et al., 2007). Further, although several studies have found no effect of experimenter versus conspecific on performance, this would be another area that warrants investigation with this species, as occasionally non-human primates perform differently depending on their exact relationship with the other individual in the experimental testing situation (Rosati, et al., 2010; Shepherd & Platt, 2010). Additional tests in social areas previously studied with both monkeys and great apes, such as imitation, will prove beneficial in continuing to understand gibbon social cognition in both a species-specific and comparative manner.

6.4 Overall Conclusions

Together these cognitive experiments provide new and intriguing data on the nature and limitations of gibbon cognition. While gibbons did not perform in exactly the same way as either great apes or monkeys over the experiments, they were generally more similar to monkeys, notably in the realm of social cognition, although the reasons for these differences are not clear. Gibbons’ unique ecology and social structure must be kept in mind when evaluating different hypotheses of intelligence, as their cognition is likely affected by these factors.

The results from these studies can begin to fill a species void in comparative primate research that been cited continually for many years (e.g. Parker & McKinney,
1999; Tomasello & Call, 1997; Roasati, et al., 2010). While much work is still needed to understand gibbons’ folk physics, or naïve psychological reasoning about the world, and social expertise, these studies provide an important step in bridging the phylogenetic gap in studies on non-human primates.
References


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