2010

Audience Effects in Cognitive Task Performance in Capuchin Monkeys (Cebus apella)

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Recommended Citation

Coyne, Sean Patrick, "Audience Effects in Cognitive Task Performance in Capuchin Monkeys (Cebus apella)" (2010). *Honors Theses*. 5.
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Audience Effects in Cognitive Task Performance in Capuchin Monkeys (*Cebus apella*)

by

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A Proposal Submitted to the Honors Council

For Honors in Animal Behavior

April 27, 2010

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Acknowledgements

This thesis was a long and sometimes difficult project and I would not have been able to succeed in my endeavors if not the generous help of many people. I would to thank the animal caretaking staff at Bucknell University, particularly Gretchen Long and Mary Gavitt, for their assistance in the care and management of the animals. Additionally, I would like to thank Casey Krause and Allison Fox for their assistance in collecting the data. Erica Dunayer has helped me with data collection, planning, writing, idea formation, and a variety of other things without which I would never have been able to complete my thesis. I would also like to thank Katie Bachmann who started with me in my research interests and has inspired me to achieve everything to the best of my ability. Finally, I would like to thank Dr. Judge, my advisor, for being patient with me and always giving me the advice and critique I need.

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Abstract

Primates as a taxonomic Order have the largest brains corrected for body size in the animal kingdom. These large brains have allowed primates to evolve the capacity to demonstrate advanced cognitive processes across a wide array of abilities. Nonhuman primates are particularly adept at social learning, defined as the modification of behavior by observing the actions of others. Additionally, primates often exploit resources differently depending on their social context. In this study, capuchin monkeys (*Cebus apella*) were tested on a cognitive task in three social contexts to determine if social context influenced their performance on the task. The three social contexts included: alone, having a dominant individual in an adjacent compartment, and having a subordinate individual in the adjacent compartment. The benefits to this design were that the social context was the only variable influencing performance, whereas in previous studies investigating audience effects other animals could physically and directly influence a subject's performance in an open testing situation. Based on past studies, I predicted that the presence of a dominant individual would reduce cognitive task performance compared to the other conditions. The cognitive test used was a match-to-sample discrimination task in which animals matched combinations of eight geometric shapes. Animals were trained on this task in an isolated context until they reached a baseline level of proficiency and were then tested in the three social contexts in a random order multiple times. Two subjects (Mt and Dv) have successfully completed trials under all conditions. Results indicated that there were no significant difference in task performance across the three conditions (Dv χ^2 (1) = 0.42, p=0.58; Mt χ^2 (1) = 0.02,

p=0.88). In all conditions, subjects performed significantly above chance (i.e., 39/60 trials determined by a binomial distribution). Results are contrary to previous studies that report low status monkeys “play dumb” when testing in a mixed social context, possibly because other studies did not account for aggressive interference by dominants while testing. Results of this study suggest that the mere presence of a dominant individual does not necessarily affect performance on a cognitive task, but rather the imminence of physical aggression is the most important factor influencing testing in a social context.

Introduction

Nonhuman primates demonstrate advanced cognitive processes across a wide array of abilities including the ability to use tools (e.g., Phillips 1998; Sugiyama 1994), to order quantities (e.g., Judge, Evans, & Vyas 2005), and even to learn human-like languages such as the symbolic word system used by bonobos, *Pan panisicus* (Savage-Rumbaugh, McDonald, Sevcik, Hopkins, & Rubert 1986). Some theories suggest that primates have developed their advanced cognitive abilities due to their sociality (Dunbar 1992; Byrne & Corp 2004). Primates, as a taxonomic Order, have the largest relative brain and neocortex size corrected for body size (Dunbar 1995). Further, there is a strong positive correlation between brain and neocortex size and group size, implying that more social animals evolved the capacity for higher intelligence (see Perez-Barberia, Shultz, & Dunbar 2007 for a review). One theory that attempts to explain why social complexity and brain size are positively correlated is the “Machiavellian Intelligence Theory” (Byrne & Whiten 1988). The Machiavellian Intelligence Theory proposes that since most primates live in unpredictable environments with patchy, highly contested resources, an “evolutionary arms-race” is established between group members. In this “arms-race,” individuals “win” by deceiving conspecifics so that they acquire a desired resource, such as mates or food. Additionally, individuals who are able to deceive social partners without the “loser” being made aware of their loss would be highly selected for since this deception can occur with minimal damage to group cohesion (Byrne & Whiten 1997).

However, this theory posits that primates evolved larger brains with increasing group size to deal with the complexities of having to outsmart more group members in larger groups.

The interpretation that brain evolution is driven by the constant motivation for greater strategies and counterstrategies to deceive conspecifics has also received criticism (e.g., Seyfarth & Cheyney 2002) because it usually assumes a level of consciousness that is higher than the capacity of most primates demonstrate. Another explanation for the relationship between social complexity and brain size is the Social Brain Hypothesis (Dunbar 2009), which suggests that primates are constantly participating in a "biological market," with, "animals as traders engaged in a mutually beneficial exchange of commodities," such as when baboons (*Papio hamadryas ursinus*) or chimpanzees (*Pan troglodytes*) groom for access to other valued commodities (Barrett, Henzi, & Dunbar 2003). This hypothesis posits that, since primates in larger groups have more possible "traders" to interact with, these animals have evolved larger brains to monitor a larger and more complex market with changing traders and variable commodity values. Thus, the gregarious tendency of primates is driving evolutionary selection for larger, more intelligent brains.

Social Interaction and Social Knowledge

Originally, primate social systems were thought to have evolved due to benefits derived from group living, such as collective predator defense, enhanced predator detection, foraging efficiency and shared defense from other species and conspecific groups of valuable resources such as food, territory, and mates (Strier 2007). Tomasello and Call (1997) discuss the complexities of primate "social fields" within such groups, and argue that a social field is similar to the spatial fields in which all animals live and interact. Social fields require the presence of four components: individuals specifically recognize other individuals in their group, individuals understand and can predict (to some extent) behavior of other individuals, animals form direct relationships with group members by remembering past experiences with those individuals, and individuals recognize and remember interactions that other individuals have had with each other.

There is extensive evidence for individual recognition. For example, tufted capuchins (*Cebus apella*) are able to recognize facial pictures of group mates (Pokorny & de Waal 2009). Squirrel monkeys (*Saimiri sciureus macrodon*) are able to recognize individual calls of group mates and respond differentially to playback calls of group mates compared to playback calls of neighboring groups or strangers (Biben & Symmes 1991). Studies have also demonstrated the ability of primates to predict the behavior of other individuals in their group. For example, in the 1970s, Menzel conducted work with a group of captive chimpanzees in which experimenters would hide food in an outdoor compound while the animals were locked inside. However, one individual was allowed to watch the hiding process. Eventually the chimps learned to identify the “watcher” and predict where the food was located by his movements (Menzel 1979). Further, there are many studies that have demonstrated individual recognition leading to direct relationship formation. The majority of this evidence has come from studies of kin selection where a crucial factor is the ability to recognize and interact selectively with relatives. For example, Charpentier, Peignot, Hossaert-McKey, and Wickings, (2007) have demonstrated that mandrills (*Mandrillus sphinx*) selectively affiliate with maternal and paternal half-siblings significantly more often than non-relatives. Finally, there is extensive evidence that primates are able to discriminate relationships between two others. For example, during “redirected aggression” an individual who is the victim in an aggressive encounter may retaliate against their aggressor’s kin or associates (e.g., pigtail macaques, *Macaca neminstrina*, Judge 1982; vervet monkeys, *Cercopithecus aethiops* Cheyney & Seyfarth 1989) indicating that primates not only recognize the individuals involved in a conflict, but know the relationships these combatants share with others. Further, Judge (1991) found that pigtail macaques engage in triadic reconciliation, in which the kin of victims in a fight will reconcile with their kin’s aggressor, suggesting that these animals are both recognizing third party relations and predicting others’ behavior based on their actions. Finally, Bachmann (2009) has demonstrated that captive hamadryas baboons (*Papio hamadryas hamadryas*) who witness a fight decrease behavioral indicators stress when they witness reconciliation between former combatants, where reconciliation is defined as the friendly post-conflict reunion between former opponents that functions as conflict resolution (de Waal & van Roosmalen 1979). The results indicated that primates are able to track rapid changes in the relationships between two other individuals, since the baboons quickly altered their behavior as the relationship between two combatants changed.

Social Learning

Clearly, there is extensive evidence for the four components of the primate “social field” (Tomasello and Call 1997). However, the existence of a primate social field does not confer an adaptive advantage unless primates can exploit the field to their advantage.

Social learning is one means that primates exploit this social field. Fragaszy and Visalberghi (2004) define social learning as the modification of behavior through experience, whereby an animal gains information about stimulus-response contingencies by observing the actions of others. One of the earliest documented cases of social learning was seen in the Japanese macaques (*Macaca fuscata*) at Koshima, Japan (Kawai 1965). The researchers provided the monkeys with sweet potatoes on the beach on a regular basis. Initially, an 18-month old was the first and only troop member to wash her potato pieces free of sand in the nearby ocean, but within three months her mother and two playmates also began to wash their potatoes. Within two years almost half the troop engaged in the behavior. These observations generated interest in social learning and the possibility of cultural transmission.

Since the early Koshima studies, several types of social learning have been documented and in a variety of primate species. For example, Tarnaud and Yamagiwa (2008) found in Japanese macaques that infants preferentially watch older group members to learn what foods are best to eat and how to process them. Specifically, infants were preferentially watching their mothers and sub-adult females, as opposed to juveniles or adult males, and these mothers and sub-adult females were foraging significantly on fruits, leaves, and invertebrates. The highest time of intensive observation by the infants was during the weaning period when mothers were limiting suckling time and infants were forced to explore the environment for new food items. Further, Humle, Snowdon, and Matsuzawa (2009) demonstrated that wild chimpanzee mothers preferentially use tools to fish for ants at certain time periods and locations that maximize infant learning. The chimpanzee mothers engaged in low-risk foraging on trails rather than high-risk foraging at ant-nests to reduce the possibility of swarming. The timing and location allowed infants to have a longer observation and practice period. Further, they demonstrated that the longer the mother spent showing the infant ant-dipping behavior, the more the offspring spent later engaging in the behavior itself.

Many studies investigating social learning demonstrate that specific relationships between two individuals, particularly mother-offspring and kin, influence infant learning. However, cultural transmission of another species' behavior has also been documented. In a study by de Waal and Johanowicz (1993), the authors investigated whether the reconciliation behavior of one species could be influenced by members of a different species. De Waal and Johanowicz (1993) studied a group of rhesus macaques (*Macaca mulatta*) co-housed with stumptail macaques (*Macaca arctoides*). In general, rhesus macaques are a highly aggressive species with a low reconciliation rate and low social tolerance, while stumptail macaques are a highly social tolerant species, reconciling frequently following aggression. The authors demonstrated that the rhesus macaques learned social tolerance and reconciled with each other three times more often than control individuals not housed with stumptail macaques. They concluded that cultural transmission of the stumptail macaque tendency to reconcile more and show a higher social tolerance had been passed on to the rhesus macaques. Additionally, Whiten, Horner, and de Waal (2005) demonstrated that a particular solution to a tool use apparatus with two different solutions was transmitted through two chimpanzee groups by cultural transmission. In this study, the authors designed a tool use task that could be solved by one of two methods. They then trained one high ranking female from each of two separate groups to be a “model,” but both models learned different ways of solving the task. Then the rest of the group watched the model perform the task and was given the task to perform themselves. Members of both groups significantly adopted their models’ method (i.e., performed their models method statistically more often than the alternative method). Interestingly, the authors noted that some individuals independently discovered the alternative method, but continued to reliably perform their group’s method, which the authors interpreted to be “cultural conformity.”

Tomasello and Call (1997) point out that during social learning primates do not usually imitate a response or teach another individual about a stimulus response contingency. Often, when individuals learn from others, stimulus or local enhancement draws other group members to use the same stimuli, but not necessarily to emulate the exact behavior with full understanding. For example, Call and Tomasello (1994) taught orangutans (*Pongo pygmaeus*) to use a rake to obtain out of reach food but the rake could be used in two different ways, one of which was more appropriate depending on the experimental context. These orangutans were then used as models for their group mates to watch. While many of the group members attempted to use the rake they saw the models using, no subject was reliably able to emulate the correct method in the correct experimental condition. So, while imitative social learning was thought to be a widespread phenomenon, there was also evidence that less complex cognitive processes such as *stimulus enhancement* (attraction to a certain stimulus) or *local enhancement* (attraction to a certain location to perform a behavior) were occurring. However, for the purposes of this study, what is most relevant is that individuals alter their behavior after observing other group members altering or exploiting the environment to advantageous ends.

Coordinated Behavior

Another way that primates adjust their behavior to others is to coordinate behavior in order to meet a goal that would be much more difficult, if not impossible, if performed in a solitary context. One of the most common occurrences of coordinated behavior is seen in the formation of coalitions and alliances. De Waal and Harcourt (1992) define ethological coalitions and alliances as, “a joining of forces of several parties in order to gain an advantage over another party.” The general idea is that individuals are cooperating in order to gain a competitive advantage in a direct competition against others (de Waal & Harcourt 1992). There is extensive evidence of coalitions and alliances forming among all four ape species, virtually all cercopithecine primates, (Tomasello & Call 1997), and even some New World species (e.g., tufted capuchins Ferreira, Izar, & Lee 2006). Coalitions and alliances can form for a variety of reasons, and can vary greatly in their duration. Indeed, many primates have developed stereotyped behaviors that are directed at group members in order to solicit their help in agonistic situations (see Walters & Seyfarth 1987 for a review). For example, Silk, Alberts, and Altmann (2004) report that female savannah baboons (*Papio hamadryas cynocephalus*) provide coalitionary support to solicitations in approximately 5% of aggressive interactions, with kin members and higher ranking females solicited most often. Kin members are motivated to provide support in aggressive encounters because of kin selection, while high ranking females are motivated to provide support because they risk losing benefits of a gregarious lifestyle if the lower ranking females leave the group. This pattern of coalition formation can be seen in nearly every cercopithecine as well as the great apes (de Waal & Harcourt 1982).

Another form of coordinated behavior seen in the wild is hunting behavior in chimpanzees. Boesch (2002) reports on the variation and type of hunting seen in different chimpanzee groups in the Tai National Forest, Côte d'Ivoire. In his observations, Boesch reports that various chimpanzee groups have developed coordinated hunting parties in which members assume different roles such as ambusher, chaser, blocker, and driver. The hunts usually require the specificity of all these roles, as well as anticipation of prey movements. Only males participate in hunting parties, beginning at age 10, but do not develop sophisticated skills until after approximately 20 years of practice (i.e., age 30). The amount of meat shared is proportional to the effort and role invested in the hunt. The Tai hunts are successful approximately half of the time and are more complex than hunts reported in other chimpanzee populations. For example, the hunts observed in the Gombe forest rarely have the specified roles seen in the Tai hunting parties and usually just involve a group ambushing a prey item (see Boesch 2002 for a review). Regardless of job specificity and coordination, groups are more likely to cooperatively hunt only if it increases the chances of a successful prey capture (Boesch 1994).

There is evidence for naturally occurring coordinated behavior in other Old World primates and apes, and even in prosimians such as the coordinated group movements of sifakas, *Propithecus verreauxi* (Trillmich, Fichtel, & Kappeler 2004). Much laboratory evidence indicates that many primates are able to cooperate on a task, although the degrees to which they understand the role of other individuals in the task is quite variable. For example, Chalmeau, Lardeux, Brandibas, and Gallo (1997) report that two orangutans were able to perform a coordinated task without being trained to work together. The task required that two levers be pulled simultaneously in order to obtain food, but the levers were too far apart to for one individual to pull both. The orangutans demonstrated an untrained understanding of the requirements of this task and the authors concluded that they were similar to chimpanzees in their ability to engage in coordinated behavior without explicit training, such as the behaviors chimpanzees display while hunting. Coordination has also been seen in a variety of monkey species. Mason and Hollis (1962) trained rhesus macaques to operate a mechanism that pulled food rewards towards both individuals in the pair. The task had four levers each connected to a pair of food trays, only one of which contained food. The food dishes were visually occluded so that only one individual in the pair could see the food and only the other individual in the pair could operate the pulley to bring the food rewards to the pair. Therefore, the “seer” had to inform the “puller” as to the location of the food. The macaques were able to learn this task, but unable to reverse roles without further training. A similar result occurred in a study with tufted capuchin monkeys (Chalmeau, Visalberghi, & Gallo 1997). The task was similar to the lever task for the orangutans described above. However, the capuchins required training in order to coordinate their behavior and did not seem to understand the role of the other individual in the task. Therefore, these and other studies lead to the conclusion that monkeys are able to coordinate their behavior, but do not fully understand cooperative problem solving. Regardless of the level of understanding, the primates are adjusting their behavior in the presence of other individuals.

Deception

Another area of primate behavior that involves a context specific alteration of behavior toward another is seen in the phenomenon of deception. There are a myriad of anecdotes providing evidence that primates are able to deceive conspecifics. For example, de Waal (1998) reports observing a low ranking male chimpanzee hiding his erection from higher ranking males while soliciting a female. Also, Van Elsacker, Meuleman, and Savini (2001) describe an incident in which an adult male bonobo hid preferred food items in an indoor enclosure. He would not start to eat these highly prized items until after the other adult male started eating in the presence of the higher ranking females. These higher ranking females would pester the male who was eating in their presence and often took his food. The authors concluded that hiding the valued items and waiting until the females were distracted was evidence of tactical deception.

There are also many reports of deceptive behavior in monkeys, particularly in capuchin monkeys (see Fujita, Kuroshima, & Masuda 2002). For example, Wheeler (2009) reports that wild tufted capuchins use alarm calls in a deceptive manner, which he referred to as the “monkeys crying wolf.” Alarm calls exist in many primate species and are specific vocalizations that alert conspecifics to the presence of predators. Alarm calls can result in a variety of anti-predator behaviors such as freezing or moving to out-of-sight locations (Zuberbuhler, Noe, & Seyfarth 1997; Zuberbuhler 2002). However, false alarm calls can be valuable if they succeed in distracting dominant individuals from foraging. The author predicted that if calls were used in this manner, the subordinate monkeys would give false alarm calls more often than dominant monkeys because they have more limited access to food. Wheeler (2009) observed that calls did succeed in distracting dominant individuals, they were given significantly more when food was most highly contested in areas of high animal density, and that the false alarm callers were in a spatial position where the call facilitated usurpation of the available resources. Wheeler concluded that subordinate individuals selectively altered their alarm calling behavior depending on the specific social context to maximize resource consumption.

Amici, Call, and Aureli (2009) tested three species of monkeys to determine the amount of deception the species exhibited, if any, and under what conditions. The authors presented spider monkeys (*Ateles geoffroyi*), tufted capuchins, and long-tailed macaques (*Macaca fascicularis*) with two tasks. In each task, subordinate individuals were trained to perform the task while dominant individuals were not. The first task involved an opaque box that had a reward hidden inside. The second task involved a clear box which allowed the reward to be seen by both individuals, but only the subordinate individual was informed on how to open the box. The results showed that the subordinates of all three species often waited to open the box until dominant individuals were further away or not looking, indicating that they were able to withhold information from dominant individuals.

In all of the deceptive situations described above, a distinct and purposeful change in behavior occurred due to the presence of other individuals, particularly dominant individuals. Subordinates changed their behavior in specific contexts in a predictable manner both experimentally (e.g., Amici, Call, & Aureli 2009), and under naturalistic conditions (e.g., Wheeler 2009; de Waal 1998).

Audience Effects

Although it is fairly well established that primates change their behavior in a context specific manner, the systematic study of "audience effects" is a relatively new line of research that did not emerge until the late 1990s. Some research comes from the detrimental effects of high visitor density on zoo animals. For example, Wells (2005) reports that in a group of zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*) the animals exhibit significantly more behavioral indicators of stress, including conspecific aggression, abnormal behavior (such as repetitive teeth clenching, body rocking, or spinning), and autogrooming, during periods of high visitor density. Hosey (2000) reports similar results in a review of a variety of New World monkey, Old World monkey, and ape behavior in zoos. In contrast, during periods of low visitor density the animals exhibited significantly more normative behaviors indicative of relaxation.

Two studies that systematically studied how audience composition affected vocalizations were done by Pollick, Gouzoules, and de Waal (2005) on capuchins and Slocombe and Zuberbuhler (2007) on chimpanzees. In the capuchin study, the authors investigated how food calling varied during different social contexts. The authors predicted that capuchins would adjust their food vocalizations based on both the amount of food and the composition of their audience. The test involved 12 adult females under two food conditions (small amount and large amount) and five total audience conditions (higher ranking female, higher ranking male, lower ranking female, lower ranking male, whole group, and solitary). The results indicated that subjects called more for large amounts of food than for small amounts, and that high ranking subjects called significantly less often than middle or low ranking individuals. Further, there were significantly more calls made in the presence of the whole group than for any other context, which may be more reflective of kin presence than group size. In the chimpanzee study, the authors investigated the acoustic properties of recruitment screams in wild chimpanzees, in which animals attempt to recruit aid during agonistic encounters. The authors found that victims of aggression would exaggerate their recruitment screams to make them seem as if they were receiving more severe aggression than what they are actually experiencing if there was a group member present whose rank either matched or surpassed the aggressor. These two studies demonstrate evidence of naturally occurring and laboratory produced audience effects on primate behavior.

Perhaps one of the most interesting studies of audience effects was reported by Drea and Wallen (1999). In this study, the authors wanted to test whether an individual's audience affected its performance on a cognitive task. A group of rhesus macaques was divided into two subgroups based on rank and trained to separate into the high ranking and low ranking groups for testing. They were then trained on a simple discrimination task involving two sets of colored foraging boxes, in which one color (blue) contained a food reward of peanuts and the other color (red) contained similarly sized rocks. Initially all animals were trained in a common testing arena, and during this time only the dominant animals seemed to successfully learn the discrimination task as they spent significantly more time than subordinates foraging at the baited blue boxes. The next two phases of the study involved testing animals in their subgroups split by rank. First the animals were tested on the same task but using a new color scheme (baited yellow and non-baited green). In the split condition, in which dominants only tested with other dominants and subordinates only tested with other subordinates, both groups demonstrated superior ability on the task by selectively foraging only at the correct yellow boxes. The next phase involved split testing again, but this time using the original color scheme (red and blue), which the subordinate individuals initially seemed unable to perform accurately. However, while split, both groups demonstrated the ability to correctly perform the task. The final stage of the experiment involved recombining the groups and testing them using the yellow and green color scheme, on which both groups performed accurately while in the split conditions. When both groups tested together, only the dominant animals demonstrated the ability to select the correct boxes, and the subordinates no longer performed correctly. The authors concluded that the low status monkeys were purposefully “playing dumb” on the combined group task since they had already demonstrated the ability to perform the task in the split group condition.

A possible alternative explanation for Drea and Wallen’s (1999) results is that the dominant individuals were simply physically preventing subordinate individuals from accessing the baited boxes. Although the authors did not witness any heavy aggression, there was significantly more threatening of individuals near the testing zone. Further, although they report that dominant and subordinate subgroups received the same amount of threats, they did not report the pattern of threats. Within each subgroup, there were three matrilines related through maternal kinship: a dominant, a mid-ranking, and a lower ranking matriline. Therefore, the relative rank of the different matrilines changed depending on the testing condition. For example, the third ranking matriline in the dominant subgroup was dominant to approximately half the group under the combined conditions, but when testing in the split group condition, they ranked the lowest. During the split testing condition, the highest ranking matriline in each subgroup gathered the most peanuts, but because the directionality of aggression was not reported, it is unclear if, or to what degree, the top matrilines threatened conspecifics during the various testing conditions. The authors proposed that because monkeys were able to anticipate behavioral consequences, the subordinate individuals were purposefully inhibiting their behavior in order to avoid being punished for countermanding the dominance hierarchy (Drea and Wallen 1999). However, it is still difficult to determine if the presence of dominant individuals caused subordinate individuals to "play dumb" because they were threatened away in the testing area, because they learned a simple stimulus-response contingency in which obtaining food in the presence of more dominant individuals resulted in physical aggression, or because the subordinates were purposefully withholding correct responses to avoid possible retribution.

Proposed Research

The goal of this study was to investigate the extent to which the mere presence of an audience affects the ability of tufted capuchins to perform a cognitive discrimination task. A touch-screen computer was used to administer a shape-matching discrimination task under three social contexts: alone, with a subordinate audience, and with a dominant audience. Unlike the Drea and Wallen (1999) study, individuals could not physically interact during testing. The audience was only seen and heard nearby in an adjacent compartment. If individuals performed significantly lower with a dominant individual nearby and not the subordinate audience, that would seem to give support to Drea and Wallen's (1999) explanation that subordinate animals willingly inhibit successful behavior in order to avoid transgressing hierarchical rules. If individuals performed significantly worse in both social contexts, but not when alone, then the presence of any individual, regardless of its rank, might be acting as a distracting influence and lower performance. Finally, if there were no significant differences in performance across social contexts, then that would seem to indicate that the capuchins are not subject to audience or distraction effects while performing a cognitive task.

I predicted that the tufted capuchins in this study would act similarly to the rhesus macaques reported in the Drea and Wallen (1999). Dominance hierarchies in both species are similar in that they are linear and are determined by dyadic contests over food and space (Wheeler 2009; Drea & Wallen 1999). Dominant individuals by definition should have first access to preferred food items because of an elevated status over subordinate individuals (de Waal 1986); subordinate capuchins might suppress correct performance in order to avoid breaking hierarchical rules that might encourage future punishment from dominant individuals. On the other hand, capuchins are known to be a more socially tolerant species than rhesus macaques and this might influence audience effects(capuchins de Waal 1997; rhesus macaques Cooper & Bernstein 2008). For example, de Waal (1997) demonstrated that capuchins regularly share food with both kin and non-kin group mates, while Maestripieri (2007) states that rhesus macaques do not share food under any circumstance. Therefore, unlike the rhesus macaques of Drea and Wallen's (1999) study, capuchins may not withhold behavior in the presence of dominant individuals.

Methods

Subjects and Housing

Subjects were two adult male tufted capuchin monkeys housed in a colony of fourteen animals at Bucknell University's Animal Behavior Laboratory. The group was established from six animals acquired in 2000 and all individuals were born in captivity. Both animals had previous experience using touch screen computers to perform discrimination tasks. They were used as subjects because they were the only two to reach a training criterion. A training criterion was required because an animal needed to demonstrate some level of proficiency on the discrimination task before it could be tested for performance changes in the presence of different audiences. Although the goal was to test more subjects, the alpha male Monet (Mt) and the subordinate adult male DaVinci (Dv) were the only two to reach the criterion.

The group's enclosure was constructed of plastic paneling and stainless steel welded-wire caging with linoleum floors covered with cedar chips. Compartments were furnished with perches, swings, and climbing structures to promote species-typical movement (Judge, Evans, and Vyas 2005). Subjects were fed twice per day, once in the morning with standard monkey biscuits, fruit, and vegetables and once in the afternoon with canned primate diet, bread, peanuts, raisins, and a "snack," such as popcorn or pretzels after the completion of testing. Water was available *ad libitum*.

The entire enclosure consisted of 3 rooms with 15 interconnecting compartments (Figure 1). Chambers were connected to each other by mesh-wire doors that could be manually operated from outside the caging to separate specific chambers. Where chambers were interconnected by overhead tunnels, they could be blocked off by portable metal panels. When not testing or serving as an audience, animals were moved to a room of the enclosure (“Room A” Figure 1) where they were completely visually occluded from the room where animals were tested (“Room C” Figure 1). Subjects and audience members were trained to move into two compartments in Room C (labeled *1 and *2 in Figure 1) for testing. Testing and audience chambers 1 and 2 measured 1.0 x 2.3 x 2.4m and 1.65 x 2.3 x 2.4m respectively.

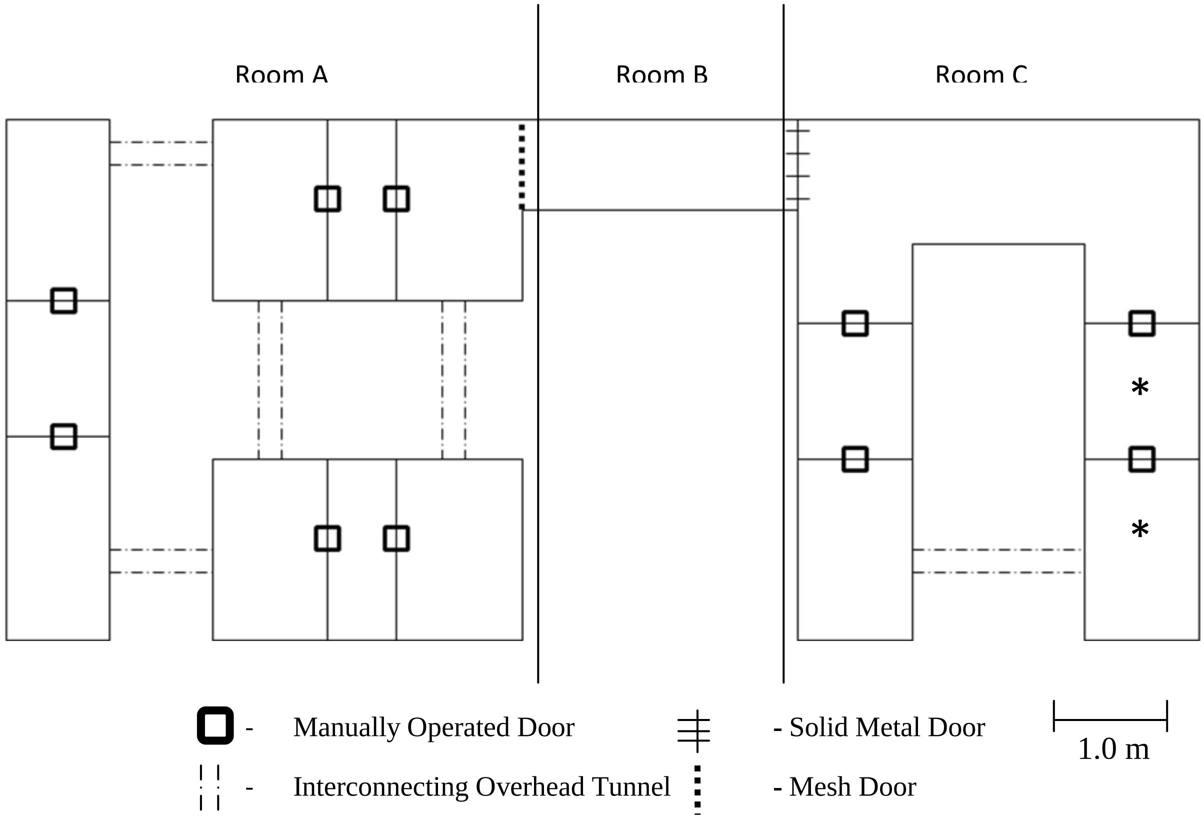


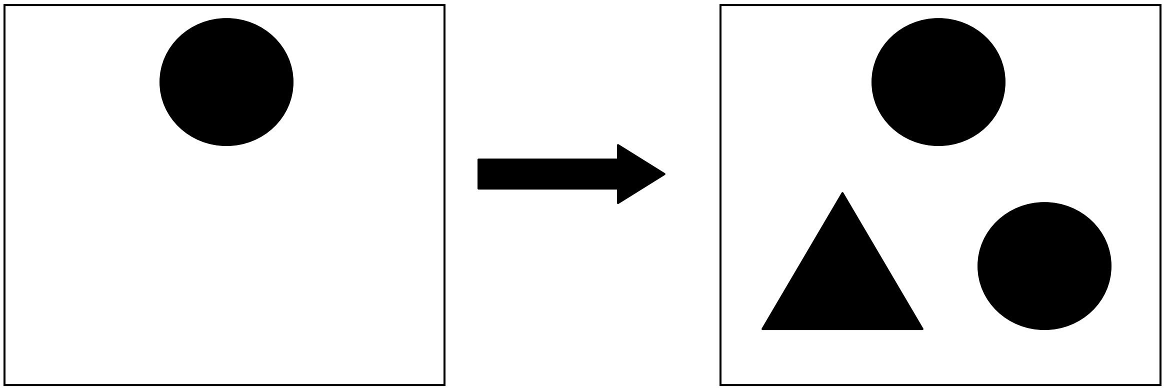
Figure 1. Diagram of the entire enclosure indicating two testing and audience chambers marked with an asterisks

Discrimination Task and Apparatus

The discrimination task was presented on a 15” Elo Touch Systems Model ET1525C-40WE-3 touch screen computer run on a Power Macintosh G3, both of which were placed on a rolling cart (Figure 2). The apparatus was rolled up to the caging where a testing perch was 25cm from the screen, a comfortable distance for the subjects to reach. The PsyScope 1.2.5 software package (Cohen, Mac-Whinney, Flatt, & Provost, 1993) was used to present a simultaneous match-to-sample (MTS) task of all possible paired combinations of eight geometric shapes (e.g., circle, triangle).

Figure 2. The testing apparatus. The touch screen faces the subject while the operating computer faces the experimenter.

The task required that the animals first touch a sample stimulus. When touched, the sample stimulus would make a "boing" sound indicating that it had been activated and two choice stimuli would appear beneath the sample stimulus (Figure 3). If the subject then touched the matching stimulus, a "beep" sound would occur and a green box would surround the correct choice indicating that it had been selected. The subject would then be given a preferred food reward by the experimenter and the next trial would begin after a 2 second intertrial interval (ITI). If the subject made the incorrect choice, no reward was provided and the screen would go black for a 3 second time out before the next trial would begin. A test session included 60 trials on the MTS task. The sample stimulus, pairs of choice stimuli, and side of correct stimuli were all randomized by the software package. Testing was grouped in blocks, in which a block consisted of a testing session in each of the three social contexts (alone, dominant audience, and subordinate audience). Both subjects completed a minimum of three blocks. The audience for one subject on any given day was independent of the other because each subject had a separate randomized order of audience context. In order to ensure animals were aware of the task requirements, baseline training occurred prior to data collection. An animal was considered to know how to perform the task if it performed above chance (39/60 trials determined by a binomial distribution) for two consecutive sessions. These initial scores were used as a "baseline" score for later comparisons.



a.

b.

Figure 3. The match-to-sample task in which subjects touched the top sample (a) which made two choices appear (b). Subjects were then required to touch the matching choice to receive a reward.

Testing Procedures

Testing occurred in the afternoon five days a week. Each animal would only test in one audience condition per day. Initially, all animals were moved out of the testing room into a room behind a visually occluding door (Room A Figure 1). Subjects and their audience member were then moved back into the testing room (Room C Figure 1) by opening and closing interconnecting doors. Animals were rewarded with a grape for moving into the proper chambers. The order of testing for the two subjects was somewhat random in the sense that whichever subject or audience member separated first also dictated the first one tested. For both subjects, the “subordinate” audience was one of the two lowest ranking females (Natalie or Delicious). For Dv, Mt served as the “dominant” audience; the alpha female (Sally) served as Mt’s “dominant” audience.

To begin testing, the test animal would be separated into their preferred testing chamber (DaVinci tested in room *1 while Monet preferred to test in room *2; see Figure 1) while the audience member was moved to the adjacent compartment, where it could be both seen and heard through the interconnecting wire cage doorway. While the animals could physically touch each other through the door, physical contact was limited as they could only fit a hand through, and could in no way physically prevent the other animal from performing the MTS task. When both animals had consumed their grape reward for moving into the chamber, the testing apparatus would be rolled up to the caging and testing would commence.

Since the presence of another animal might influence the subjects’ willingness to test, latency was recorded from the time the apparatus was presented until the time the subject pressed the sample stimulus. Latencies between trials were also recorded to evaluate willingness to test. Both latency measures were used to score when an animal was refusing to test. An animal's test session was terminated if it would not touch the touch screen for five consecutive minutes.

To minimize effects of the investigator presence on the animal's performance, only one experimenter would administer rewards at the cage while all others stood or sat off to the far side of the room and silently record latency information. Additionally, the investigator operating the testing apparatus was unable to see the choices on the subjects' computer screen, so could not give any cues as to the correct choice. Reward distribution was based on hearing the auditory cue given by the computer for a correct choice. Once the test concluded, the animal was given a grape reward for completing the testing session and returned to the rest of the group. If an animal refused to test he was returned to the group with no grape reward.

Data Analysis

Correct and incorrect MTS choices and refusals to test were recorded for each session and grouped by social context. To test for differences across social conditions, a 3x2 χ^2 contingency table analysis was conducted with social context as one variable and trial outcomes (correct versus incorrect) as the second variable. To determine if scores differed across the entire testing period, a 2x2 χ^2 contingency table analysis was conducted with condition (baseline versus testing) as one variable and trial outcomes (correct versus incorrect) as the second variable. It was important to measure this variable in order to determine if variations in task performance were due to audience effects and not a general decline in performance over time. The last two “alone” social context scores were used as a comparison to the last two baselines scores obtained prior to testing. All tests were conducted with α set at $p < .05$.

Results

Training

Although attempts were made to train seven subjects to perform the MTS task, only two subjects, DaVinci and Monet, were able to reach the performance criterion required to participate. Their performance on the MTS task was correct above chance level (39/60 trials) for two consecutive testing sessions as determined by a binomial distribution. For both criterion sessions, Dv scored 57/60, while Mt scored 44/60 and 49/60. All other animals failed to reach criterion after 5 months of training, and were not used as subjects.

Testing

Neither subject differed significantly in their MTS scores over the duration of the study when baseline scores were compared to the last two “alone” scores (Dv χ^2 (1, n = 120) = .42, p = .58; Mt χ^2 (1, n = 120) = .02, p = .88; Figure 4).

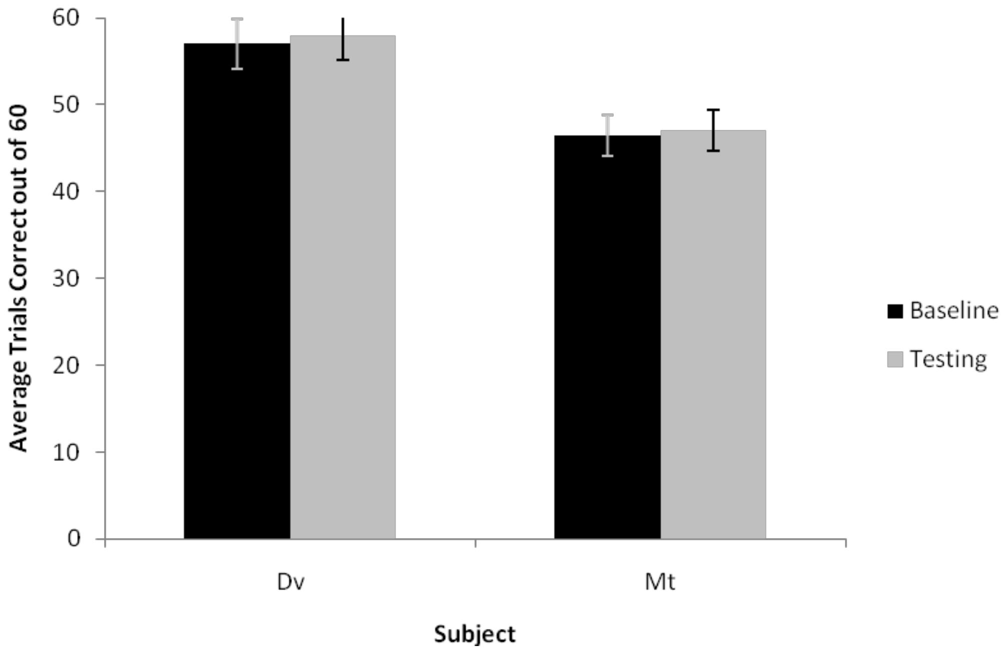


Figure 4. Comparison of performances between baseline and the end of the testing period. Error bars represent +/- one standard error.

Both subjects performed significantly above change across all audience conditions (Figure 5). A Chi-squared analysis on each subject revealed no significant relationship between the number of trials correct and the social context of testing (Dv χ^2 (2, n = 540) = .324, p = .851; Mt χ^2 (2, n = 180) = 1.713, p = .425). The animals' performance did not change across any social context.

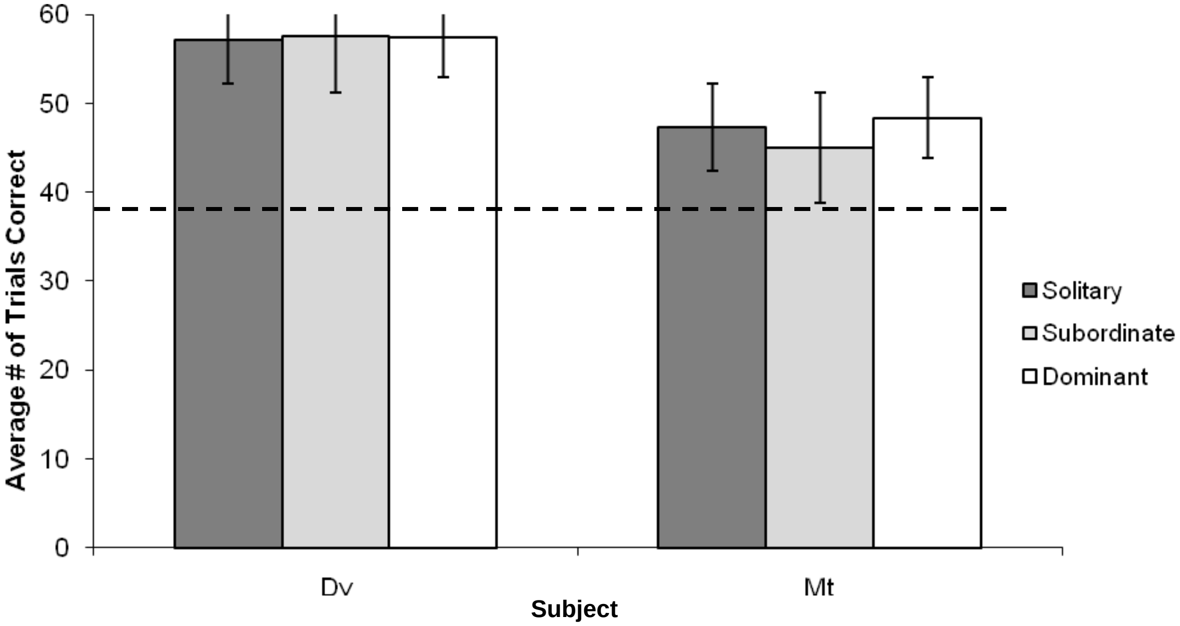


Figure 5. Subjects' average scores across 60 trials in the different audience conditions. The dashed line indicates above chance performance. Error bars represent +/- one standard error.

Refusals to test were rare and only occurred on approximately 7% of possible testingsessions (N=3/41). Further, there is no discernable pattern suggesting that certain audience conditions caused subjects to refuse (Figure 6). Mt refused once in the "dominant" audience condition whereas Dv refused twice, once in the dominant condition and once in the control condition. Latency to begin testing revealed no trend because, except for the rare cases when a subject refused to test in which the latency was the maximum five minutes (300 sec), subjects always began testing as soon as the apparatus was pushed up to the caging.

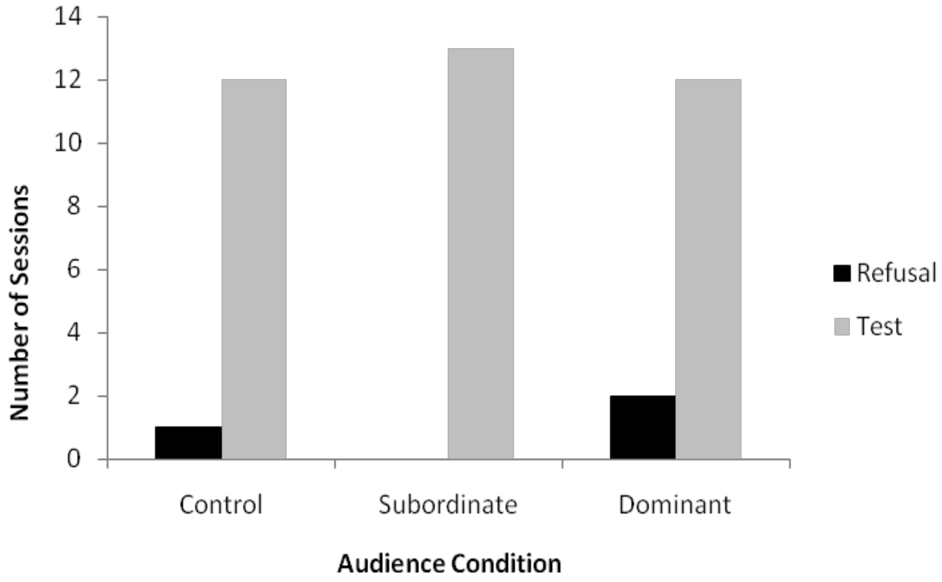


Figure 6. Occurrences of refusals in the different social contexts combined across both subjects.

Discussion

Results of this study indicated that capuchin monkeys were not subject to an audience effect while performing a cognitive task. Regardless of the social condition under which they tested, the animals' MTS discrimination scores were near identical (Figure 5). These results contradict reports by Drea and Wallen (1999) that subordinate individuals purposefully suppress successful performance on a discrimination task in the presence of dominant individuals. Further, it seems that capuchins are also not subject to additional distractions while testing with other individuals present since performance in the alone condition was no different than either social condition.

Dominant individuals were unable to physically prevent subordinate individuals from either performing the task or receiving a reward. Additionally, subordinate individuals ignored any threats they received and continued to test as if they were alone. Unlike the animals in the Drea and Wallen (1999) study, threats in this study could not result in physical aggression, at least during testing. The lack of consequence for breaking hierarchy rules should then encourage subordinate individuals to test to the best of their ability in order to maximize the number of rewards received, especially if they were unable to monopolize preferred food items during times when no testing occurred. Although no dominant individuals engaged in physical aggression during testing, it is possible that animals may have waited until testing was over to punish the subordinate animals for receiving rewards in their presence, although this was not evaluated in the current study. If punishments were a *post hoc* event, then one would expect that the animals would initially perform successfully but decline over the course of the testing period as a result of repeated punishments after successful performances. This scenario is unlikely as the animals' MTS performance did not change over time (Figure 4).

Another explanation for the differences in audience effect in this study versus the Drea and Wallen (1999) study may be attributed to possible differences in social tolerance between capuchins and rhesus macaques. For example, de Waal (1997) demonstrated that because of high social tolerance and affiliative tendency, tufted capuchins willingly allow other individuals to take food in their presence. In particular, male capuchins share food more willingly and are less discriminatory in what they expect in return from social partners. In comparison, Schaub (1996) demonstrated that long-tailed macaques (*Macaca fascicularis*) have a tendency to engage in "spiteful" behavior, in that they specifically do not to share food items with non-relatives. Rhesus macaques are similar to long-tailed macaques in displaying low social tolerance. Further, Maestripieri (2007) reports, with a high degree of certainty, that rhesus macaques never share food under any circumstances. Further, there are possible social structure differences in punishment between macaques and capuchins. For example, there is evidence that macaques engage in kin-oriented revenge systems (Aureli, Cozzolino, Cordischi, and Schucchi 1992), whereas no such system has been seen in capuchins. It is very likely that the dominant individuals in Drea and Wallen's (1999) study refused to allow subordinate individuals to attempt to perform the discrimination task. Similarly, subordinate individuals in that same study may have been unwilling to try and succeed on the task knowing that they were very likely to be punished for attempting to perform or succeeding at the task because of the low social tolerance by their more dominant group mates. In contrast, capuchins may not have evolved the cognitive capacity to anticipate such retribution if their society lacks the "revenge systems" seen in macaques.

Despite the small amount of subjects, results indicate that capuchins were not subject to the same audience effects suggested by Drea and Wallen (1999) in rhesus macaques. Clearly, the presence of conspecifics had no noticeable effect on these two specific animals' performances. Results, however, may have been unique to these particular animals and the audiences chosen. Different subjects with different combination of audiences may have shown an effect. Regardless, the results ultimately imply that the most important factor in an audience effect is the imminence of physical harm, and not the mere presence of others. The ability to physically harm subordinate individuals is the critical methodological difference between this study and the one conducted by Drea and Wallen (1999). The authors interpreted their results as rhesus macaques consciously aware of hierarchical rules and knowingly playing dumb to appease the dominant individuals in the hierarchy. I suggest that the rhesus macaques were “playing dumb” because they learned a simple stimulus-response contingency, in which peanut retrieval in the presence of dominant individuals resulted in physical harm.

Capuchins regularly engage in all aspects of the “social field” described by Tomasello and Call (1997). They recognize conspecifics, predict the behavior of others, form long-term relationships with group mates, and recognize the relationships between others. Their engagement in the social field allows capuchins to make decisions regarding how to act around other members of their group based on both the direct relationship they have with group mates, as well as their ability to anticipate the behavior of others based on past experience. Because physical interaction was limited methodologically in this study, the capuchins had no motivation to engage in either self-denying or deceptive behavior in which they hid their knowledge of correct task performance from dominant individuals. Similar to capuchins in Wheeler’s (2009) study, where subordinate individuals used context specific false alarm calls to usurp food resources, capuchins in this study were maximizing available resources by performing correctly a majority of the time on the cognitive task. However, in Wheeler’s study capuchins had to withhold behavior until the social context enabled them to be successful. In this study, subjects were rewarded most during this time of physical separation of the group because they could receive food rewards without any competition, and should therefore have always performed the task to the best of their ability in order to ensure the most rewards possible. Indeed, all animals in the group have observed conspecifics that have been separated for husbandry purposes. They may have learned, via social learning, that separation from the group facilitates uncontested food resources.

Although capuchins in this study did not exhibit evidence of audience effects, there is evidence that they have the cognitive capacity to engage in such interactions. For example, Brosnan and de Waal (2003) conducted a study on inequity aversion in capuchins. Their study investigated origins for motivation to cooperate, and utilized a bartering task in which the monkeys exchanged tokens for food items with human experimenters. In some trials, individuals would exchange tokens for the same food reward, while in others one would exchange tokens for more preferred rewards (grapes) while the other individual traded for a less preferred food reward (cucumbers). In conditions where the rewards were not equal, the monkeys were significantly more likely to delay the exchange or refuse to exchange at all. Results indicated that capuchins are aware of what other individuals consumed, how they received those rewards, and made conscious decisions on participation based on comparing their own situation with others. The results reported by Brosnan and de Waal (2003) are relevant to the study here because they indicate that the capuchins in this study most likely had the cognitive capacity to assess the audience contexts while testing and made decisions based on their observations.

Just as I suggested that the rhesus macaques of Drea and Wallen’s (1999) study merely acted in response to a learned stimulus-response contingency, the capuchins in the present study most likely did not make complex decisions weighing the pros and cons of testing correctly in varying social contexts. Rather, individuals most likely learned that when separated from the rest of the group, regardless of who is watching, they were able to receive whatever rewards were offered free of any negative consequences. Even though capuchins possess the ability to withhold their knowledge from others, or “play dumb” as Drea and Wallen suggest, the design of this study motivated subjects to exploit the available resources while they were free from harassment of their group mates and separate from the “social field” in general. Different experimental designs may have produced a variety results depending on the degree to which animals had to directly or physically compete over the preferred rewards. Therefore, we should be careful of interpreting poor cognitive performance in any primate, including humans, as the willingness to appease more dominant individuals, but rather that these subordinate individuals feel threatened into poorer performance.

Bibliography

Amici, F., Call, J., & Aureli, F. (2009). Variation in withholding of information in three monkey species. *Proceedings of the Royal Society: Biological Sciences*, *276*, 3311-3318.

Aureli, F., Cozzolino, R., Cordischi, C., & Scucchi, S. (1992). Kin-oriented redirection among Japanese macaques – An expression of a revenge system. *Animal Behaviour*, *44*, 283-291.

Bachmann, K.A. (2009). The influence of reconciliation on the quadratic post-conflict interactions of Hamadryas baboons (*Papio hamadrays hamadryas*). Masters Honors Thesis, Bucknell University

Barret, L., Henzi, P., & Dunbar, R. (2003). Primate cogncition: from 'what now?' to 'what if?'. *Trends in Cognitive Sciences*, *7,* 494-497.

Biben, M. & Symmes, D. (1991). Playback studies of affiliative vocalizing in captive squirrel monkeys: Familiarity as a cue to response. *Behaviour*, *117,* 1-19.

Boesch, C. (1994). Cooperative hunting in wild chimpanzees. *Animal Behaviour*, *48,* 653-667.

Boesch, C. (2002). Cooperative hunting roles among Tai chimpanzees. *Human Nature,* *13*, 27-46.

Brosnan, S.F., & de Waal, F.B.M. (2003). Monkeys reject unequal pay. *Nature*, *425*, 297-299.

Byrne, R.W. & Corp, N. (2004). Neocortex size predicts deception rates in primates. *Proceedings of the Royal Society of London: Biological Sciences, 271*, 1693-1699

Byrne, R.W. & Whiten, A. (1988). *Machiavellian intelligence. Social expertise and the evolution of intellect in monekys, apes, and humans*. New York: Oxford University Press.

Call, J. & Tomasello, M. (1994). The social learning of tool use by orangutans (*Pongo pygmaeus*). *Human Evolution, 9*, 297-313.

Chalmeau, R., Visalberghi, E., & Gallo, A. (1997). Capuchin monkeys, *Cebus apella*, fail to understand a cooperative task. *Animal Behaviour, 54*, 1215-1225.

Chalmeau, R., Lardeux, K., Brandibas, P., & Gallo, A. (1996). Cooperative problem solving by orangutans (*Pongo pygmaeus*). *International Journal of Primatology, 18*, 23-31.

Charpentier, M.J.E., Peignot, P., Hossaert-McKey, M., & Wickings, E.J. (2007). Kin discrimination in juvenile mandrills, *Mandrillus sphinx*. *Animal Behaviour, 73*, 37-45.

Cheney, D.L. & Seyfarth, R. M. (1989). Reconcilation and redirected aggression in vervet monkeys (*Cercopithecus aethiops*). *Behaviour, 110*, 258-275.

Cohen, J., MacWhinney, B., Flatt, M., & Provost, J. (1993). PsyScope: An interactive graphic system for designing and controlling experiments in the psychology laboratory using Macintosh computers. *Behavior Research Methods, Instruments, and Computers, 25,* 257–271.

Cooper, M.A., & Bernstein, I.B. (2008). Evaluating dominance styles in assamese and rhesus macaques. *International Journal of Primatology, 29*, 225-243.

de Waal, F.B.M. (1986). The integration of dominance and social bonding in primates. *The Quarterly Review of Biology, 61*, 459-479

de Waal, F.B.M. (1998). *Chimpanzee Politics Power and Sex among Apes*. New York: Johns Hopkins University Press.

de Waal, F.B.M., & Harcourt, A.H. (1992). Coalitions and alliances: a history of ethological research. In A.H. Harcourt and F.B.M. de Waal (Eds.), *Coalitions and Alliances in Humans and other Animals* (pp. 1-19). New York: Oxford University Press.

de Waal, F.B.M. & Johanowicz, D.L. (1993). Modification of reconciliation behavior through social experience: An experiment with two macaque species. *Child Development*, *64*, 897-908.

de Waal, F.B.M., & van Roosmalen, A. (1979). Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology, 5,* 55-66.

Drea, C.M. & Wallen, K. (1999). Low-status monkeys "play dumb" when learning in mixed social groups. *Proceedings of the National Academy of Science, 96*, 12965-12969.

Dunbar, R.I.M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution, 20*, 469-493.

Dunbar, R.I.M. (1995). Neocortex size and group size in primates: a test of the hypothesis. *Journal of Human Evolution*, *28,* 287-296.

Dunbar, R.I.M. (2009). The social brain hypothesis and its complications for social evolution. *Annals of Human Biology, 36,* 562-572.

Ferreira, R., Izar, P. & Lee, P.C. (2006). Exhange, affilitation, and protective interventions in semifree-ranging brown capuchin monkeys (*Cebus apella*). *American Journal of Primatology, 68*, 765-776.

Fragaszy, D. & Visalberghi, E. (2004). Socially biased learning in monkeys. *Learning & Behavior*, *32,* 24-35.

Fujita, K., Kuroshima, H., & Masuda, T. (2002). Do tufted capuchins (*Cebus apella*) spontaneously deceive opponents? A preliminary analysis of an experimental food-competition contest between monkeys. *Animal Cognition, 5,* 19-25.

Hosey, G.R. (2000). Zoo animals and their human audiences: What is the visitor effect? *Animal Welfare, 9*, 343-357.

Humle, T., Snowdown, C.T., and Matsuzawa, T. (2009). Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition*, *12,* S37-S48.

Judge, P.G. (1982). Redirection of aggression based on kinship in a captive group of pigtail macaques. *International Journal of Primatology, 3*, 301.

Judge, P.G. (1991). Dyadic and triadic reconciliation in pigtail macaques (*Macaca neminstrina*). *American Journal of Primatology, 23,* 225.

Judge, P.G., Evans, T.A., & Vyas, D.K. (2005). Ordinal representation of numeric quantities by brown capuchin monkeys (*Cebus apella*). *Journal of Experimental Psychology: Animal Behavior Processes, 31,* 79-94.

Kawai, M. (1965). Newly acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates, 6*, 1-30.

Maestripieri, D. (2007). *Macachiavellian Intellegence: How Rhesus Macaques and Humans Have Conquered the World*. Chicago: University of Chicago Press.

Mason, W.A. & Hollis, J.H. (1962). Communication between young rhesus monkeys. *Animal Behaviour, 10*, 211-221.

Menzel, E.J. Jr. (1979). Communication of objects-locations in a group of young chimpanzees. In D.A. Hamburg & E.R. McCown (Eds.), *The great apes* (pp. 259-371). Menlo Park, CA: Benjamin Cummings.

Perez-Barberia, F.J., Shultz, S., & Dunbar, R.I.M. (2007). Evidence for coevolution of sociality and relative brain size in three orders of mammals. *Evolution, 12*, 2811-2821.

Phillips, K.A. (1998). Tool use in wild capuchin monkeys (*Cebus albifrons trinitatis*). *American Journal of Primatology, 46*, 259-261.

Pokorny, J. & de Waal, F.B.M. (2009). Monkeys recognize the faces of group mates in photographs. *Proceedings of the National Academy of Sciences*, *106*, 21539–21543

Pollick, A. S., Gouzoules, H. & de Waal, F.B.M. (2005). Audience effects on food calls in captive brown capuchin monkeys, *Cebus appella*. *Animal Behaviour, 70*, 1273-1281.

Savage-Rumbaugh, S., McDonald, K., Sevcik, R.A., Hopkins, W.D., & Rubert, E. (1986). Spontaneous symbol acquisition and communicative use by pygmy chimpanzees (*Pan paniscus*). *Journal of Experimental Psychology: General, 115,* 211-235.

Seyfarth, R.M. & Cheyney, D.L. (2002). What are big brains for? *Proceedings of the National Academy of Sciences, 99*, 4141-4142.

Silberberg, A., Crescimbene, L., Addessi, E., Anderson, J.R., Visalberghi, E. (2009). Does inequity aversion depend on a frustration effect? A test with capuchin monkeys (*Cebus apella*). *Animal Cognition, 12*, 505-509.

Slocombe, K. E. & Zuberbuhler, K. (2007). Chimpanzees modify recruitment screams as a function of audience composition. *Proceedings of the National Academy of Science, 104*, 17228-17233.

Strier, K.B. (2007). *Primate Behavioral Ecology* (3rd ed.). Boston: Pearson Education, Inc.

Sugiyama, Y. (1994). Tool use by wild chimpanzees. *Nature*, *367*, 327.

Takimoto, A., Kuroshima, H. & Fujita, K. (2010). Capuchin monkeys (*Cebus apella*) are sensitive to others’ reward: an experimental analysis of food-choice for conspecifics. *Animal Cognition*, *13*, 249-261.

Tarnaud, L. & Yamagiwa, J. (2008). Age-dependent patterns of intensive observation on elders by free-ranging juvenile Japanese macaques (*Macaca fuscata yakui*) within foraging context on Yakushima. *American Journal of Primatology, 70*, 1103-1113.

Tomasello, M. & Call, J. (1997). *Primate Cognition*. New York: Oxford University Press.

Trillmich, J., Fichtel, C., & Kappeler, P.M. (2004). Coordination of group movements in wild Verreaux's sifakas (*Propithecus verreauxi*). *Behaviour*, *141*, 1103-1120.

Van Elsacker, L. Meuleman, B., & Savini, T. (2001). How a subordinate male bonobo leads dominant females up the garden path. *Folia Primatologica*, *72*, 33-36.

Walters, J.R., & Seyfarth, R.M. (1987). *Conflict and Cooperation*. In B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham, & T.T. Stuhsaker (Eds.), Primate Societies (pp. 306-317). Chicago: University of Chicago Press.

Wells, D.L. (2005). A note on the influence of vistors on the behaviour and welfare of zoo-housed gorillas. *Applied Animal Behaviour Science, 93*, 13-17.

Wheeler, B.C. (2009). Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society: Biological Sciences, 276*, 3013-3018

Whiten, A. (1997). *Machiavellian intelligence II: Extensions and evaluations*. Cambridge, U.K.: Cambridge University Press

Whiten, A., Horner, V., & de Waal, F.B.M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature, 437*, 737-740.

Zuberbuhler, K. (2002). A syntactic rule in forest monkey communication. *Animal Behaviour*, *63*, 292-299.

Zuberbuhler, K., Noe, R., & Seyfarth, R.M. (1997). Diana monkey long-distance calls: message for conspecifics and predators. *Animal Behaviour, 53*, 589-604.