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THE EFFECTS OF AN EXPERIMENTER ON THE RESPONSE TO INEQUITY IN
CAPUCHIN MONKEYS (*CEBUS APELLA*)

by

SARA A. PRICE

Under the Direction of Sarah F. Brosnan

ABSTRACT

Extensive evidence compiled over the past decade demonstrates that many species of animals respond negatively to inequity across several different contexts. One context that remains unexplored is whether inequity responses are influenced by the experimenter. Experimenter effects remain an enduring concern within animal research. I investigated whether the presence of the experimenter influences responses to inequity in a nonhuman primate species, the capuchin monkey (*Cebus apella*). In the presence or absence of an experimenter, monkeys worked in pairs to complete a computerized task, following which individuals received rewards that were either equal or unequal in comparison to the partner's rewards. Monkeys had difficulty learning the task, but after learning, rates of refusals were influenced by the individual reward received rather than the social comparison or the actions of the experimenter. I consider reasons for their frustration with the task and their subsequent lack of an inequity response in this context.

INDEX WORDS: Inequity, Experimenter, Experimenter effects, Capuchin monkeys, *Cebus apella*, Computerized task

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SARA A. PRICE

A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Arts

in the College of Arts and Sciences

Georgia State University

2014

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Sara Alexandra Price
2014

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CAPUCHIN MONKEYS (*CEBUS APELLA*)

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DEDICATION

I would like to thank my family and friends for all of their support. Special thanks to my parents (Lisa and Vince), siblings (Andrew and Adrienne), and Matt McBride.

Thank you to the monkeys that participated in this study – in memory of Drella.

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1 INTRODUCTION

Several species of animals respond negatively to inequity, and research continues to explore how this response is influenced by different external factors. The negative response to inequity occurs in several primate species (Brosnan, 2006; de Waal, 1996; Flack & de Waal, 2000), as well as non-primates (dogs: Horowitz, 2012; Range et al., 2009; Range et al., 2012; corvids: Wascher & Bugnyar, 2013). One common experimental testing procedure to study the inequity response involves having animals complete a task with a human experimenter in order to receive a food reward. Two participants, one acting as a subject and the other as a partner, sit adjacent to one another in front of the experimenter and alternate participation, allowing them to observe what tasks the other completes and what reward the other receives (c.f. Brosnan & de Waal, 2003). Generally, their responses when the partner received a better food reward are compared to their responses in a baseline condition in which both individuals received a lower-value food reward, and a negative response to inequity is inferred through the frequency of refusals to exchange or refusing to consume the food reward.

However, the effect of the experimenter on this phenomenon has yet to be determined. A major concern in psychology is how experiments are affected by the very artificiality of the procedures (Davis & Balfour, 1992; Rosenthal, 1963; Rosenthal & Halas, 1962). Do individuals respond as they perceive the experimenters desire? Are their behaviors influenced by the setup in ways that human experimenters may not recognize? These concerns warrant a proper evaluation of what effects experimenters may have on results, both related to the inequity response and beyond. Experimenter effects have not received much attention in animal research as compared to human research (Davis & Balfour, 1992), which is problematic since results rely on overt behavioral measurements rather than introspection. This may be even more important in

cognitive and behavioral research with captive animals, since researchers often are intimately involved in the testing procedures. Moreover, the majority of research that has been done on experimenter effects investigates individual animals' behavior outside of a social context (Kintz et al., 1965; McGuigan, 1963), but how might an experimenter affect social animals that must solve problems in social contexts? The current study focuses on the latter concern in the context of experimenter-induced inequity.

Anecdotal accounts suggest that the experimenter may play an influential role in the response to inequity. In his studies on contrast effects, Tinklepaugh described a response in which the macaque subjects sometimes “looked or even shrieked ‘accusingly’ (if so anthropomorphic a term may be used) at the experimenter or onlookers” (1928, p. 233) after the subjects discovered a preferred reward had been surreptitiously replaced with a less-preferred reward. Also, chimpanzees that are treated inequitably will scream or throw the tokens at human experimenters instead of the conspecific partner, although these responses are sufficiently uncommon that they have not yet been empirically explored. Since the response to inequity requires an individual to pay attention to the rewards that another individual receives as compared to one's own rewards, it is important to investigate what role the experimenter may have in this interaction, and what a response directed towards the human rather than conspecific might mean. Specifically, is the social comparison alone enough to elicit the inequity response, or might animals perceive the experimenter as causing the inequity? Therefore, in this study I explored the influence of an experimenter's presence on the responses to inequity in one species of nonhuman primate, the capuchin monkey (*Cebus apella*). This study implemented new methodology that enabled an experimenter to be present or absent in order to better determine whether the experimenter affected the type of response to inequity.

1.1 The Inequity Response

Studying the response to inequity can provide us with a better understanding of a related concept in humans, fairness. The concept of fairness is highly developed in humans and pervasive in many aspects of our culture. Fairness, defined as the distribution of costs and benefits from a joint activity, is complex, involving both receiving less (disadvantageous inequity) and receiving more (advantageous inequity) than another individual (Fehr & Schmidt, 1999; Hatfield et al., 1978). These concepts have been studied extensively in the field of behavioral economics and psychology, where it has been demonstrated that humans react negatively to receiving a different outcome than a social partner. Fairness in humans also incorporates inherent social norms and standards, and ties into complex emotions such as greed and envy (Fehr & Schmidt, 1999; Hatfield et al., 1978). Fairness is a complex, socially-based concept that is linked to morality (Frank, 1988), which implies an underlying motivation to maintain equity and maintain social norms. Although other species do not share the complete sense of fairness that humans often exhibit, they do show aspects of it, which can be studied empirically (Brosnan, in press). Additionally, even in humans, we cannot fully understand “fairness” without understanding its constituent parts. Typically this is done by exploring subjects’ responses to unequal outcomes, or inequity aversion.

Inequity aversion in humans may be influenced by many things, including an individual’s culture (Henrich et al., 2001), personality (Colquitt et al., 2006; Wiesenfeld et al., 2007), and the quality of the relationship between the individuals involved (Attridge & Berscheid, 1994; Clark & Grote, 2003); nonetheless, these responses are largely present across different societies and contexts (Haidt, 2012). Aside from behavioral consistency, there is also neurological evidence of consistent responses to inequity across humans. Unfair offers elicit activity in areas of the brain

associated with negative emotional affect and physical disgust (Sanfey et al., 2003). Considering this widespread consistency in multiple domains, inequity aversion may be considered a universal human cognition (Henrich et al., 2001). Thus, recent research has focused on examining why this behavior may have evolved – what the function is, why it is of importance, and what causes the variation we see among individuals and cultures.

A negative response to inequity occurs when an individual's expectations are violated based on a comparison of one's own efforts and rewards with the effort and rewards of a social partner. These responses to inequity come in different forms. In their typical social interactions, animals sometimes react in ways that indicate that they are not satisfied with their outcomes. For example, chimpanzees will often have temper tantrums when they do not receive what they want. Such tantrums might occur both with kin or non-kin, as for instance when offspring protest if their mother does not share (de Waal, 1996). These reactions are not limited to feeding situations. One male chimpanzee would display tantrums when he began losing female support in a struggle for dominance against another male; when females refused to extend support, or avoided him, he would throw himself on the ground and roll around screaming (de Waal, 2007).

Such behavior is not limited to primates. Canids have a set of social rules surrounding social play (i.e. what signals to display, how rough to play), and these rules are maintained as a group norm (Bekoff, 2001). Social play often involves action patterns used in other contexts, like predatory behavior, and therefore, it is crucial that canids display signals that demonstrate the desire to play before initiating these action patterns. Moreover, individuals that follow the social rules will self-handicap to reduce asymmetries in a play interaction; for example, an individual may not play as aggressively if the playmate is younger. Individuals that violate these rules or deceive playmates (such as displaying a play signal but acting inappropriately aggressive

towards the playmate) are not selected as play partners as often as those who do not violate these social rules. Ravens also follow a social norm in which an individual that possesses food can maintain possession in the presence of other individuals; those that violate this norm by attempting to steal food from the possessor will be attacked in an apparent instance of third party enforcement (Heinrich, 1999).

Of course such observations are intriguing, but do not provide the level of empirical support possible through controlled experiments. While we do not expect to see a full sense of fairness in other species, evidence is building that several species, including nonhuman primates, share at least some underlying behaviors related to fairness (Brosnan & de Waal, 2012). Specifically, we can test whether they monitor their own outcomes compared to those of a social partner, and whether they recognize and respond to discrepancies. Therefore, we can use nonhuman primates as a model system to study the precursor behaviors from which fairness may have evolved. We can study elements of fairness in other species, which may someday tell us the ways in which our own sense of fairness is and is not unique.

1.2 What Does Inequity Look Like in Other Species?

Studies on the inequity response in animals generally measure subjects' reactions to getting a different reward as compared to a partner, subsequent to both individuals completing the same work (Brosnan, 2006a). In the typical procedure, two subjects from the same social group, seated adjacent to one another, alternate performing a task (such as exchanging a token with a human experimenter) for a reward. The subject in question receives less than (disadvantageous inequity) or more than (advantageous inequity) the partner, and their response is compared to a control condition when both receive the same food reward. The subjects can easily observe the task that the other individual completes and the reward they both receive

during these interactions. Behavioral responses generally manifest as negative reactions such as refusing food rewards or refusing to continue participating in the task, and individuals may even toss the food reward at the experimenter.

One immediate finding is that the response is quite variable across contexts and individuals. In fact, responses amongst primates are not always consistent, even within the same species or within the same study (e.g., Brosnan et al., 2005; Brosnan et al., 2010b). This causes two problems; first, it is difficult to use a “check-box” approach to determine which species do and do not show the reaction. This is exacerbated by the fact that procedures and methodology vary among studies, and it is not always clear how to interpret two conflicting results. Second, this variability makes finding underlying causes and mechanisms more challenging, as they presumably interact with other features of the individual, the relationship, and the context.

Past studies on inequity have manipulated one (or more) of several factors to determine which features are more likely to lead to a negative reaction to inequity. These factors include the type of task (if any), the seating arrangement of subjects, and the distribution of rewards. One critical feature that has not yet been manipulated is the presence or identity of the experimenter. Given that the experimenter is the individual causing the inequity, this seems a critical next step.

1.2.1 Individual vs. Social Contrast

An important aspect in studying inequity is implementing the correct methodology to more clearly distinguish contrast effects from social comparison effects. Inequity differs from contrast effects by the referent of the comparison. Inequity is the comparison of an individual's own rewards to a partner's rewards (or social contrast; Brosnan, 2011), while contrast effects are the comparison of an individual's current rewards to a previously received reward or something in the environment (or individual contrast; Reynolds, 1961). Contrast effects were first studied in

macaques by Tinklepaugh (1928). Monkeys watched as the experimenter hid preferred food items under cups, which the monkeys could then access the next day. Sometimes, these preferred food items were surreptitiously replaced with non-preferred items (i.e., lettuce), and monkeys responded negatively when outcomes violated their expectations (i.e., receiving lettuce rather than the preferred food item). These contrast effects are widespread across different species (Range et al., 2012; Roma et al., 2006; Talbot et al., 2011; Wascher & Bugnyar, 2013). Contrast effects are essential to control for in order to determine whether “inequity” responses are actually social in nature, or whether the social partner is irrelevant. In other words, it is possible that in the response to ‘inequity,’ the individual is responding to the presence of a higher value reward, not to a social partner receiving that higher value reward.

To discriminate these possibilities, many researchers have included controls to differentiate between inequity responses and contrast effects. For instance, in one common control, subjects are shown one reward, then provided a different reward after completing a task; this entire procedure is done while seated next to a partner, who also is offered a different reward than they eventually receive (Brosnan et al., 2010b). In such tests, chimpanzees and capuchins do not react as strongly in the control (contrast) condition as they do in the inequity condition, where the partner received a better reward than the subject. This implies that nonhuman primates were indeed responding to the social contrast of the situation. On the other hand, squirrel monkeys show the opposite pattern, responding more strongly to individual than social contrast, although this is only the case in males; females respond to neither inequity nor contrast (Talbot et al., 2011). This difference between two very closely related primates (capuchin monkeys and squirrel monkeys are part of the same taxonomic Family) emphasizes the variability in this response across the Primates.

1.2.2 Task

The type of task (or the absence thereof) has a major influence on how subjects respond to inequity. Nonhuman primates are more likely to respond to unequal rewards when effort in the form of a task is required than they are to receiving rewards for “free” (i.e., not having to complete a task to receive the rewards), in which case no response to inequity has ever been documented (Brosnan & de Waal, 2003; Brosnan et al., 2010b; Brosnan et al., 2011a; Freeman et al., 2013; Neiworth et al., 2009; Talbot et al., 2011; van Wolkenten et al., 2007). There are several possible explanations for this. First, studies testing the negative response to inequity involve captive animals, who regularly receive food provisioned by human caretakers. Food is often distributed unequally, either because some animals need more or because dominants are more likely to receive food. The latter may be because they are more likely to come up and accept food from an experimenter or because they actively block subordinates from receiving food. As a result, some individuals are accustomed to getting more (or less) food than others and so may learn that there is no point in protesting food being handed out for “free.”

Additionally, the presence of a task may cue the subject to a context in which sensitivity to inequity is important. That is, if a purpose of inequity aversion is to help individuals recognize and avoid those situations in which a partner is receiving a greater benefit for a joint interaction (e.g., cooperation, see Section 1.4, below), then inequity aversion is more important in contexts in which there has been joint interaction than those in which there has not. This may cause individuals to respond differently when they work for the rewards than in those “gift reward” situations in which no task is present (Bräuer et al., 2006; Dindo & de Waal, 2007; Roma et al., 2006).

Therefore, one critical element of designing any study of inequity, including the current one, is including a task. Although the majority of studies have relied on an exchange paradigm, recent evidence indicates that individuals respond similarly to different types of tasks (e.g., a targeting task versus an exchange task; Freeman et al., 2013). Incorporating a task was a challenge in this study, which was designed to test the role of the experimenter in subjects' responses, because it required conditions in which no experimenter was present. Exchanges and other typically-employed tasks are impossible in the absence of an experimenter; therefore, I developed a computerized task that allowed me to maintain a task even in the absence of the experimenter (see Section 2.3, below).

1.2.3 Subjects' Relative Position and Control of Reward Distribution

Small differences in experimental protocols, such as how the subjects are seated with respect to one another, may make big differences in responding to inequity. Takimoto et al. (2010) found behavioral differences in capuchins based on visual contact, which suggests that any sense of separation, either visually or physically, affects behavior. Additionally, orientation may play a role. There is great variability in responses in chimpanzees and, while multiple factors vary, one feature that may be important is relative position; individuals responded to inequity when seated next to one another in a shared enclosure (Brosnan et al., 2005; 2010b) but not when seated across from one another in separate enclosures (Bräuer et al., 2006; 2009). In humans, the orientation of the subjects has also proven important (Sommer, 1965; 1967). Humans prefer to sit opposite one another in competitive tasks, apparently due to a strong interest in eye contact in a competitive situation, but prefer to sit adjacent to each other in cooperative ones. Unfortunately subjects' relative positioning is something that is often beyond

the control of researchers, particularly with large species such as the great apes (and positioning may not always affect behavior; e.g., Silk et al., 2005).

Aside from physical orientation, the degree of contact between subjects may play a role. A vital part of the inequity paradigm is that individuals expend effort on a task and receive the rewards that are intended for them. Consequently, if the subject that is designated as the disadvantaged individual ends up stealing the better rewards from their partner (common behavior from dominant individuals), we will not be able to measure an appropriate response to inequity. To control this, subjects are often separated from one another (e.g., by a mesh partition), which reduces stealing without requiring the intervention of the experimenter (which may also lead to experimenter influences on subjects' behavior; see Chapter 2). However, this separation may also inhibit reactions to unequal outcomes, due to decreased proximity between the animals (Talbot et al., in prep). This creates a problem for studies like the current one, without an experimenter. Given that capuchins do respond in some situations with a barrier (Brosnan et al., 2010b; Brosnan & de Waal, 2003; van Wolkenten et al., 2007), I chose to include a barrier in order to maintain the reward division in the experimenter absent condition.

1.3 Experimenter Effects

A consequence of working with animals in a laboratory setting is that over repeated interactions, humans and animals form relationships that can affect both the humans' and animals' behavior. Human experimenters may form different behavioral expectations for certain animal subjects, which may lead to cuing. Moreover, animals can discriminate among humans, causing them to act differently in the presence of certain individuals based on factors such as familiarity and the nature of interactions (Davis, 2002), which can ultimately affect cognitive performance and motivation in tasks (Cibulski et al., 2014). For example, some animals may be

more neophobic to unfamiliar individuals (Russel, 1973). Research is lacking on experimenter effects on the response to inequity, although it is an important issue to study for both practical and theoretical reasons. Below I discuss several of these issues in more detail.

1.3.1 Unintentional Cuing and Reinforcement

A big concern in animal research is that, despite implementing controls to encourage natural behavior, humans will emit unintentional cues, influencing the animals to act in a certain way to get a desired result. The effects of experimenter characteristics on animal behavior were first investigated by Carl Stumpf and Oskar Pfungst in 1904 in the famous case of Clever Hans, the horse that could ostensibly count. It was determined that unconscious cuing and reinforcement from the horse's trainer were driving this behavior (Pfungst & Stumpf, 1907). The "Clever Hans effect," in which an animal responds in the way in which the experimenter seemingly wants the animal to respond, remains an important factor to control for in experimental studies.

Since that time, researchers have found that experimenters may influence every step of the experimental process, from implementing the independent variables and handling subjects to measuring and reporting data (Kintz et al., 1965). A problematic phenomenon occurs when an experimenter receives feedback from an experiment through observing a behavior or partial result, creating a bias in the experimenter regarding predictions about general principles and expectancies for future responses (Rosenthal & Fode, 1963). Although this process is not well understood, it is possible that the experimental feedback might change the mood of the experimenter if data contradict the hypothesis or it might exaggerate an interpretation if the data do support a prediction. Either way, these types of biases run the risk of contaminating subsequent results and interpretations.

One study found that experimenters' expectancies of what they will observe in subjects can influence data obtained; experimenters were provided instructions involving what frequencies of contractions and head turns to expect in planaria undergoing classical conditioning, and although subjects' responses were not affected, the experimenters reported the frequencies that they expected to see (Cordaro & Ison, 1963). In another study looking at rats' performances in a simple T maze, subjects were randomly assigned to one of two groups of experimenters. One group was instructed that their subjects were "maze-bright" (bred for brightness) and the other experimenter group was instructed that their subjects were "maze-dull". Despite random subject assignment and arbitrary labels given to the two groups, the supposed "maze-bright" rats performed significantly better than the "maze-dull" rats (Rosenthal & Fode, 1963). It is possible that the experimenters' expectancies based on the instructions they received may have influenced their attitudes, which may have caused differences in signals transmitted through tactual and sensory modalities or differences in handling the animal subjects. A recent study specifically assessed how observer expectancies influence subjective scoring of behavior. Veterinary students applied different scoring methods in which they were shown duplicated video recordings of the same animals, an original version and a slightly modified version of the same clip. When scoring the clips, the students were provided either false or correct information about the conditions in which the animals had been filmed. In all trials, there was evidence that expectation bias formed from the contextual information provided influenced how the students scored the identical behaviors they observed (Tuytens et al., 2014).

Indeed, the way humans handle animal subjects may also cause behavioral differences. In a study on the effects of alcohol on learning the avoidance response in rats, the alcohol itself did not produce any differences in results. However, differences were observed based on the

team of experimenters employed to handle the animal subjects (Harris et al., 1964). Even the experimenter's personality and experience level can influence responses. McGuigan (1960) compared experimenters' traits scores on personality tests with behavioral scores of human subjects and found high correlations; for example, subjects performed more poorly with more neurotic experimenters. In another study, naïve and experienced experimenters each trained a group of rabbits on a conditioned shock-avoidance response and recorded acquisition speeds. The rabbits of the experienced experimenters reached criterion faster, and when a naïve experimenter was provided another group to train, there was a significant practice effect (Brogden, 1962).

These effects are all based on rather large experimenter influences, but nonhuman primates may be sensitive even to the eye movements of the experimenter (Povinelli & Eddy, 1996), which means that experimenters must work very hard to avoid unintentional cuing. In some cases, experimenters have worn sunglasses or baseball caps to avoid cuing by eye gaze (Call, 2001; de Blois et al., 1998; Pepperberg et al., 1997), but eye gaze is not the only type of unintentional cuing. Even subtle body movements may provide cues that can alter animals' performances. This concern is not limited to primates; Johnson (1913) showed that allegedly successful auditory discrimination made by dogs were actually the result of a reliance on subtle cues provided by the experimenter, such as respiration, posture, and the tensing and relaxing of muscles. The dogs were no longer able to discriminate when experimenters who were interacting with the animals or collecting data were blind to the conditions and desired results.

Not surprisingly, given how good animals are at discerning unintentional cues, they may also evaluate interactions between experimenters and learn the reputation of an experimenter based on these interactions. Indeed, several species of primates seem to be aware of others'

intents and can distinguish between the intentional and accidental acts of an experimenter (Call et al. 2004; Phillips et al. 2009; Wood et al. 2007). In these studies, typically framed as whether or not animals can learn reputations, individuals either interact with two experimenters, one of whom gives rewards (i.e., the generous experimenter) and one of whom does not (i.e., the selfish one), or watch another individual interact with them. When given a choice between experimenters, chimpanzees prefer to interact with the generous one whether they have personal experience with them (Subiaul et al., 2008) or have just watched another chimpanzee interact with them (Russell et al., 2008). Dogs show the same preference (Kundey et al., 2011; Marshall-Pescini et al., 2011). It may be that the apes' and dogs' ability to learn reputation are based on an understanding of the experimenter's intent, either due to advanced cognition or specific selection to pay attention to human cues, as with dogs (Hare & Tomasello, 2005).

On the other hand, capuchin monkeys, who are also highly cooperative and respond to inequity, do not discriminate between experimenters who "cheat" by failing to give offered rewards and those who do not (Brosnan & de Waal, 2009; see also Sheskin et al., 2013). However, capuchins do clearly discriminate experimenters and pay attention to their behavior; monkeys look longer at humans who imitate them, and they also spend more time in proximity and choose to interact more frequently with these imitators (Paukner et al., 2009). Capuchins also can point to communicate to a cooperative human (Mitchell & Anderson, 1997). Therefore, if capuchins do take into consideration past experiences with a human, we might expect that capuchins would respond differently to inequity based on the relationship with a specific human experimenter.

Like any experimental paradigm, the inequity response may be influenced by experimenters in the ways discussed above. One concern is that all of the previous task-based

experiments have required interaction with an experimenter, who distributes rewards to the correct individuals. This ultimately means that the experimenter must know the condition ahead of time, so as to provide the correct individual with their respective reward. With this knowledge, it is possible that the experimenter might be unintentionally cuing the subjects to respond in a certain way that would fit the predictions for that condition. For example, unintentional cuing via body language or watching the animal perform a task could affect motivation levels or performance on the task. Moreover, the experimenter's cuing might unexpectedly promote a negative reaction (or the animals may refuse to work due to experimenter influences rather than noticing and responding to the actual inequity).

In the recent exchange-based studies, there have been safeguards built in to avoid potential cuing. Experimenters will give subjects a consistent (and typically considerable) amount of time to respond without the experimenter feeling pressured to get the animal's attention, and individuals who are blind to conditions (e.g., not the experimenter collecting the data) can code for behavioral reactions. While these procedures ensure that the experimenter and the blind coder reliably agree on the response, it does not necessarily prevent the experimenter from cuing in the first place. For the current study, the main focus was to avoid any experimenter cuing by removing the interaction with the experimenter and most critically, by providing a control to see how the monkeys responded in the complete absence of an experimenter. To remove experimenter interaction, I implemented a computerized task instead of an exchange-based paradigm, and rewards were provided via an automatic dispenser. Also, because the experimenter was not directly interacting with the subjects and the reward distribution was automatic, cuing was less of a concern when the experimenter was present, too, even though the experimenter was not blind to the condition.

1.3.2 Relationship with the Experimenter

While we have strong evidence that animals are sensitive to cues given by experimenters within a study, one feature that has been poorly explored is how the relationship between the experimenter outside of the experimental context influences the subjects' behavior in studies of behavior and cognition. This is potentially important for tests in which experimenters create inequity. In humans, responses to inequity differ depending on the relationship between the individuals involved (Clark & Grote, 2003), and this may be the case in other species as well. Although no study has directly addressed inequity, we do know that animals are sensitive to these relationships. One study suggests that the length of time working with an animal may influence their behavior in cognitive tasks. Corvids are sensitive to familiarity of an experimenter, participating more often and showing better performance in an exchange task with an experimenter with whom they have a more long-term relationship as compared to an unfamiliar experimenter (Cibulski et al., 2014); however, the possibility of experimenter effects cannot be ignored. Additionally, features of the experimenter may influence behavior prior to interaction. Female dogs readily approach unfamiliar humans of either sex, but male dogs tend to avoid unfamiliar male humans (Lore & Eisenberg, 1986).

Another consequence in captivity is that for some individuals, the interaction with the experimenter may be more rewarding than the reward itself, which means that the responses of the animal are not based on the reward distribution that the experimenters provide. This may be especially likely in domesticated animals or animals that interact intensively with humans, in which social interaction with the experimenter may have a higher value than the actual food reward since these animals are so accustomed to human attention and affection. In addition, because captive and domesticated animals are trained to obey human commands, animals could

be completing the task just to please the experimenter, without paying attention to the partner's efforts and reward outcomes. Therefore, the opportunity to interact with a human may overshadow any negative response or distract the animal from paying attention to a partner's efforts and reward outcomes. Additionally, the reaction to inequity may consequently be directed more towards the experimenter.

In a recent inequity study, dogs responded to an unequal distribution of rewards when tested with a conspecific, but they did not indicate sensitivity to quality of food or effort expended (Range et al., 2009), whereas nonhuman primates have shown this sensitivity (Massen et al., 2011; van Wolkenten et al., 2007). It has been postulated that the dogs reacted more to the commands of experimenters rather than responding to the quality and effort inequity conditions (Horowitz, 2012; Range et al., 2009; 2012). Therefore, it is plausible that nonhuman primates in captivity that are used to interacting with humans and obeying human commands may be prone to a similar phenomenon. Thus, another of the goals of this study was to begin to explore the degree to which the animals' relationship with the experimenter influenced their responses.

1.4 Inequity and Cooperation

It has been hypothesized that a sense of fairness evolved with cooperation. Humans with a sense of fairness are proposed to be more likely to succeed in cooperative interactions (Fehr & Schmidt, 1999), due to their greater ability to recognize and thus avoid cooperative interactions or partners which are not in their best interests, such as freeloaders who will exploit a shared effort without splitting the outcome. Many social nonhuman primate species (and those in other taxa) also cooperate both in the wild and in laboratory experiments, and thus this link between cooperation and inequity may exist in species besides humans (see Price & Brosnan, 2012, for an

overview). Indeed, the current study focuses on capuchin monkeys, who cooperate both in the wild (Rose, 1997) and in the laboratory (de Waal & Berger, 2000).

Capuchin monkeys can monitor their own contributions to a cooperative activity and the resulting outcomes, as well as a partner's (Brosnan, 2011), and consequently, can recognize whether they are being exploited and determine whether to continue contributing (Hatfield et al., 1978). Therefore, a negative response to inequity may be a signal to a partner that they are not being fair. However, the question remains as to where the negative response is being directed – towards the conspecific, or towards another source, such as the experimenter? Specifically, when the monkeys complete a task with the experimenter, do they view the experimenter as the cooperative partner, or do they view the experimenter as a mediator for a cooperative task involving subject and partner? It presumably makes a difference in responses depending on whether monkeys perceive themselves as cooperating with the experimenter or a conspecific.

Determining whether the negative response to inequity is directed towards the experimenter or the conspecific can also tell us about how individuals perceive this interaction. If an individual responds differently when an experimenter is present than when an experimenter is absent, this indicates that they see the experimenter as the cause of the inequity, which may indirectly imply that the individual has some understanding of human's intentions. Humans respond less strongly to distributions determined by a computer than by other humans (Blount, 1995), and cooperation with a human partner rather than a computer is associated with more brain activity for striatal mechanisms related to reward (Rilling et al., 2002), demonstrating that humans are sensitive to intentionality. Some nonhuman primates have demonstrated the ability to understand the intentional actions of others (Call et al., 2004), so while we cannot assume similar

underlying neural mechanisms, such similarity in outcomes would provide some evidence that they may understand aspects of intent.

On the other hand, if subjects do not respond differently to the presence or absence of the experimenter, then the results imply that the subjects are focused on the outcome of the interaction, not the underlying causes (i.e., not the experimenter). This has several implications. First, it implies that they are more outcome-focused than intent-focused, although the fact that they respond more strongly to a partner getting an outcome than to the mere presence of a higher-value outcome means that this is still a social response. We also cannot disentangle that they are sensitive to intent, but are more focused on conspecifics than humans. It is interesting to note that there may be less cause for concern over experimenter effects if subjects are insensitive to the presence of the experimenter, not because the experimenter is not a cause of bias, but because the subjects are not paying as much attention to the experimenter.

1.5 Purpose

In the current study, I used a novel methodology to assess whether the presence or absence of the experimenter affects the types of responses to inequity in one species of nonhuman primate (the capuchin monkey, *Cebus apella*). The primary goal of this study was to compare the responses to inequity when an experimenter was absent from the room versus when an experimenter was present and was “providing rewards.” There was an identical procedure for both conditions, so the only variable that changed was whether the experimenter was physically present, touching the reward dispensers. These results would determine whether the monkeys were responding to the experimenter’s presence or the conspecific’s outcomes. If the monkeys respond to inequity when an experimenter is present, but not when the experimenter is absent, this would imply that the monkeys are responding to the experimenter’s actions, rather than the

reward distribution. From this we could infer that the subjects are sensitive to the intent of the individual that creates the inequity. If the subjects respond the same regardless of whether the experimenter is present, this would imply that the monkeys are responding to the distribution, not the actions that led to that distribution. From this we could infer that the subjects are not as sensitive to intent or cause as they are to outcome. I do not expect the monkeys to respond to inequity when the experimenter is absent, but to do so when the experimenter is present, due to earlier results showing inequity when the experimenter was present (all previous studies have involved a present experimenter). However, if the subjects respond more strongly in the absence of an experimenter, this might imply a mediating effect of the experimenter on their willingness to respond negatively to inequity.

In order to do this, I developed a new methodology that allowed for both a task and a means of distribution of the food rewards to the appropriate monkey without human mediation. I created a joint-computer task that required the monkeys to expend effort to earn rewards, which were distributed by an automatic dispenser. Monkeys were separated from one another, which ensured that each monkey received its intended reward.

2 GENERAL METHODS

2.1 Subjects and Housing

Data were collected on 11 capuchin monkeys (*Cebus apella*) housed at Georgia State University's Language Research Center (LRC) in Atlanta, Georgia. Capuchins came from two social groups housed at the LRC; Group 1 consisted of 2 adult males, 2 adult females, and 2 juvenile females, and Group 2 consisted of 3 adult males, 2 adult females, and 1 juvenile male. All subjects were housed in social groups at the LRC and had indoor/outdoor access and

extensive environmental enrichment (climbing structures, barrels, swings, and other toys). All subjects had *ad libitum* access to water and were fed their usual diet consisting of primate chow, fruits and vegetables throughout the study. At no time were the subjects food or water deprived. No subject was tested twice in the same day.

All subjects were tested in pairs. These pairs were to remain the same throughout the study, although individuals that did not consistently complete the task were removed from these pairings and some individuals were re-paired (see Appendix A). All subjects participated voluntarily, coming when called to the testing cages in their indoor living areas for the experiment. Separating subjects out from their social group in this way limited distractions during the experiment. Animals were initially chosen to participate in the study if they reliably separated and had a potential partner that they tolerated from within their social group that also reliably separated.

2.2 Computer Task

The computer task was a CHASE task, in which individuals used a joystick to move a cursor on the computer screen so as to make contact with each of two moving green circles on the screen. The form of the task involved a white background with red cursors and green circles as targets. At the beginning of a trial, both circles appeared on the screen. The circles moved randomly and independently deflected off the borders of the playing area. Each circle disappeared when contacted with the cursor, and when both circles had been contacted, the individual received his/her reward.

Because this was a joint task, individuals shared a split screen (a black line split the screen in half) and each individual had a view of his/her own and the partner's cursor movements. Individuals alternated taking turns; when it was one player's turn, both circles

appeared on the playing individual's side of the screen while the non-playing individual's side of the screen went blank (with no cursor). Once the playing individual completed the trial and received the corresponding rewards, a new trial began for the partner while the other side of the screen in turn went blank. The ITI (inter-trial interval) and the presence of a partner's cursor varied depending on the version of the program (see Section 3.5.1 and Table 1). Within an individual's turn, any continuous 30 seconds without deflecting the joystick was defined as a "refusal." A refusal resulted in the individual losing his/her chance to play that trial, and play reverted back to the partner.

Table 1. Summary of modifications made across studies.

| Study | ITI | Components on Screen | |
|-------------|------------|---------------------------|-----------------------------|
| | | Playing Individual | Non-playing Individual |
| Studies 1-4 | 10 seconds | Moveable cursor + targets | Blank screen |
| Study 5 | 5 seconds | Moveable cursor + targets | Moveable cursor, no targets |

All subjects completed the same version of the CHASE task (involving touching two moving targets with the cursor, as described above). Once an individual touched both targets, an automatic dispenser released one of two reward types, either a low value reward (LVR - 1 reward) or a high value reward (HVR - 4 rewards). Each session involved 60 alternating trials for each individual (i.e., 120 trials total). All sessions were run to completion. Thus, individuals' statistics referred to the number of trials completed or refused out of 60 trials per session. Not all pairs of monkeys completed the same number of sessions within each study (see Appendix A), however final statistics are based on each pair's full set of 8 completed sessions. Although computer tasks have not been used specifically to look at the response to inequity alone, all of the capuchin subjects had prior experience using the described CHASE task (e.g., Beran &

Evans, 2009; Evans et al., 2008) and were used to paying attention to differential rewards through tasks that examined economic decision-making (e.g., Brosnan et al., 2011b).

2.3 Setup

Each pair consisted of a subject and partner. Each individual in a pair was tested in both roles. In order to ensure that rewards would be distributed to the intended individual, all subjects were separated from their partners by a clear barrier (see Section 1.2.3). This procedure with the barrier is consistent with previous joint-computer studies (Brosnan et al., 2011b). One concern, as noted above, is that subjects' responses to inequity may be influenced by proximity to the partner, thus the barrier may inhibit reactions. However, use of the barrier was necessary to appropriately distribute rewards, and there is evidence that capuchins will still respond to inequity when physically separated (Brosnan et al., 2010a; Brosnan & de Waal, 2003; Fletcher, 2008; Takimoto et al., 2010; van Wolkenten et al., 2007).

Capuchin monkeys were tested in a testing box (24 in. tall, 56 in. long, 27.5 in. wide) attached to the home enclosures. The testing box had a pair of clear panels separating the animals from the computer apparatus, allowing the monkeys clear visual access to both their and their partner's side of the computer screen, with metal mesh surrounding the sides of the panel (Figure 1). A clear barrier was also used to separate the two monkeys into separate testing areas (each 28 in. long and 27.5 in. wide), but allowed them to see each other, each other's work, and each other's rewards. Only one animal pair was tested at a time.

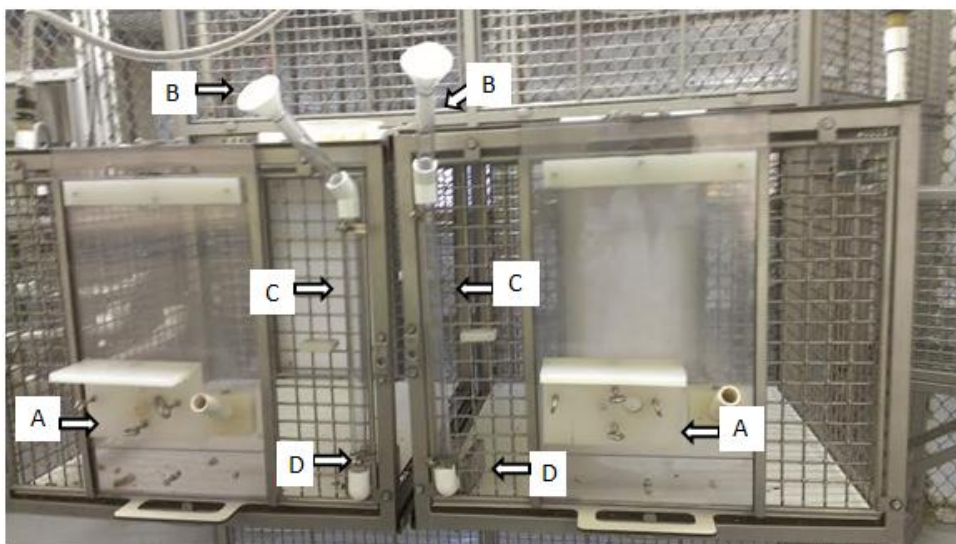


Figure 1. Diagram of the joint testing box (front view). Joystick controllers are inserted into the mounts (A). Reward pellets fall into the funnels (B) and travel through clear plastic tubing (C) into reward cups (D).

The computer rested on a moveable cart. A large screen was placed at the monkey's eye-level to allow the animals to sit in front of the caging in their respective areas and watch a split-screen (Figure 2). Joysticks were connected to the computer on either side of the cart, and were inserted into mounts built into the clear front panels, allowing the animals to control a cursor with the joystick. Two automatic reward dispensers were attached to the cart on both sides and fruit-flavored pellets sat at the top of each reservoir. Each reward was released one-by-one from a reward dispenser and rolled down clear tubing into one of two clear PVC pipes that were attached to the metal mesh and positioned centrally between subject and partner, landing into an individual's respective reward cup that was attached to the inside of the testing box (Figures 1 and 2). The reward delivery and reward cups were visible to both individuals through the clear barrier or mesh separation.



Figure 2. Diagram of the joint testing box (side view). Reward pellets sit in the reservoir (A) and are released by an automatic dispenser (B). Monkeys have a split-screen view on the computer screen (C) and control a cursor by moving a joystick on the controller (D) to touch moving targets.

It was vital that the monkeys could see each other's rewards as clearly as possible. If they did not know what their partner got, they would not realize that the outcomes were inequitable. In previous inequity studies with the token exchange task, the experimenter would hold up each individual's reward so that both monkeys could see it before handing it over to the intended individual. However, because this new methodology required automatic reward distribution, the clear tubing and reward cups situated on either side of the barrier helped ensure the best chance for both monkeys to see each other's pellets being distributed automatically. Additional visual and auditory cues were also used to make this reward delivery as noticeable as possible to both individuals. As each reward was released from the dispenser, the rewarded player's side of the

screen flashed. In addition, a tone played once for each reward earned. This tone was the same for both individuals.

The procedure for reward distribution was the same for experimenter present and experimenter absent conditions. In conditions in which there was a human experimenter, the experimenter stood behind the screen. The experimenter touched the playing monkey's corresponding dispenser, as if she were controlling the release of the pellet into the dispenser. The experimenter knew ahead of time which reward each individual would be receiving based on the type of equity condition (Table 2), but she fixed her gaze at a spot on the caging during testing; thus, she could not see the screen and the reward distribution was automatic, which limited inadvertent cuing (see Section 1.3.1).

Table 2. Summary of the different test types and conditions.

| Experimenter condition | Test type | Equity condition | Number of Rewards | |
|--------------------------------|---------------------|--------------------------|-------------------|---------|
| | | | Subject | Partner |
| Experimenter present or absent | Low equity control | Low equity | 1 | 1 |
| | High equity control | High equity | 4 | 4 |
| | Inequity | Disadvantageous inequity | 1 | 4 |
| | | Advantageous inequity | 4 | 1 |

Prior to the beginning of testing, the monkeys were acclimated to the joint-computer testing box setup. Whereas the capuchins previously have participated in joint-computerized testing in smaller individual testing boxes (Brosnan et al., 2011b), as well as joint manual tasks in the larger testing box, they had never participated in a joint-computer task in the larger testing box. For the acclimation period, the setup was the same as described above, except that the computer screen was not turned on and joystick controllers were not attached for the monkeys to

manipulate (therefore, no task was required). Each monkey pair was given a total of two 10-minute sessions, on separate days, in which the experimenter manually provided them pellets by pushing the release button on the automatic dispenser. The monkeys received two pellets every 30 seconds (40 pellets in total). This also functioned to train the monkeys to associate the experimenter with the release of rewards (although in the actual testing sessions, it would be automatic). All sessions were videotaped with two Canon cameras, one pointing toward each side of the testing box to capture both players' behaviors and proximity to the joystick. The reaction time (time it took to first touch the joystick from the start of the trial) and completion time (time it took to touch both targets) were also recorded.

2.4 Conditions

To determine whether the monkeys responded to inequity, responses in control tests were contrasted with responses in inequity tests (Table 2). There were four equity-type conditions: low equity (LE), in which both players received 1 reward (1 reward for subject, 1 reward for partner), high equity (HE), in which both players received 4 rewards (4 rewards for subject, 4 rewards for partner), disadvantageous inequity (DI), in which the subject received less than the partner (1 reward for subject, 4 rewards for partner), and advantageous inequity (AI), in which the subject received more than the partner (4 rewards for subject, 1 reward for partner). These four conditions were randomized across sessions, and individuals were tested in both subject and partner roles. In addition, there were two experimenter conditions: experimenter present and experimenter absent. Thus, each pair of monkeys completed 8 sessions: 2 low equity, 2 high equity, and 4 inequity (two when the subject was disadvantaged and two when the subject was advantaged). Half of these sessions were experimenter present and the other half were experimenter absent.

3 STUDIES 1-5, METHODS AND RESULTS

3.1 Study 1

3.1.1 *Study 1 Methods*

I initially tested five pairs of monkeys (see Appendix A, Study 1) that had reliably worked together on previous joint-computer tasks (Price et al., in prep). The computer task, setup, and conditions were as described above.

3.1.2 *Study 1 Results*

Unexpectedly, 4 of 10 monkeys (affecting 3 of the 5 pairs) failed to participate in the study, completing 0 trials within one or two sessions, and thus never received a reward. Analysis of the video tapes revealed that these monkeys did not even approach the joystick, indicating that this failure was not an inability to do the task *per se*, but an unwillingness to participate (see Appendix A). The remaining 6 monkeys actively participated (Appendix A). Because the 4 monkeys that failed to participate represented a large proportion of the subjects and in order to prevent experience effects, I decided to terminate the study as soon as the problem emerged, which was after 5 of 6 pairs had completed two sessions.

3.1.3 *Study 1 Discussion*

This study was aborted as soon as it became apparent that there might be a problem with the task or setup. After 2 sessions, only two of the monkeys completed, on average, more than half of the trials in the session. To remain blind to results, I did not look at the number of refusals after each session was completed, but upon noticing a pattern of inactivity among several monkeys, I examined the data. The low patterns of responses could not be explained by the type of condition (i.e., low response rates were not limited to low equity conditions or to those individuals that were disadvantaged). These monkeys had all previously participated in joint-

computerized tasks with a shared screen and separate joysticks and pellet dispensers, as in the current study; however, as the apparatus was modified (in order to maximize the degree to which they could see their partner's rewards) there was the possibility that their refusals were due to unfamiliarity with the novel apparatus. To investigate this, I tested all of the pairs on a familiar joint-computerized task that they had recently completed (the Chicken Game; Price et al., in prep). If subjects' performance on the Chicken Game with the new apparatus differed from the previous study with the original apparatus, then this difference was likely caused by the apparatus. On the other hand, if their performance was the same, then the refusal to participate was due to some element of the current task.

3.2 Study 2

3.2.1 Study 2 Methods

For this stage, I tested the same five monkey pairs (Appendix A) on a joint economic decision-making game called the Chicken Game (Price et al., in prep), using the same setup in the joint testing box as in Study 1. The Chicken Game required the monkeys to make joint decisions that would affect both of the monkeys' payoff outcomes. Pairs shared a split-screen view and could see their partner's decision. At the beginning of each trial, two different icons representing two separate strategies appeared on both players' sides of the screen. Each individual had to move his or her cursor to touch one of the two icons, and each player's selection stayed up on the screen until the monkeys received their payoff outcomes. Depending on each individual's selection, subject and partner received different payoff outcomes (ranging from 0 to 4 pellets). All pairs had participated in this computerized game for the past year, but they had never played in the joint testing box.

In each of the previous Chicken Game sessions, all pairs had routinely completed 200 trials (the maximum number of trials offered) within two hours, so for the current study, pairs were given two hours to complete as many trials as they could within each session. To meet criterion, pairs had to complete two full sessions of 200 trials in this time on two separate days. If pairs completed over 100 trials by the end of the session, I gave them another attempt the following day; however, if pairs failed to reach 100 trials for two sessions in a row, testing was terminated. Pairs that passed criterion were re-tested on the inequity task following the procedure described in Study 1.

3.2.2 Study 2 Results

Three of five pairs passed criterion (Appendix A, Study 2). Of these pairs, two of the six monkeys (affecting two of the three pairs) subsequently did not participate in the inequity task, completing 0 trials across all sessions (Appendix A) until testing was aborted after 2 or 3 sessions.

3.2.3 Study 2 Discussion

The results suggest that the difficulties were caused by both the apparatus and the task. Considering the first of these, two pairs were dropped from this study when they failed to reach criterion on the Chicken Game, with which they had previous experience. This suggests that their failure to work was due to the novel testing apparatus. Whereas each pair was provided with two 10-minute acclimation sessions receiving free rewards (see Section 2.3), no task was provided during acclimation. This was done in part to make sure the monkeys focused on the new type of reward distribution (receiving rewards automatically in the joint testing box rather than being handed rewards), but meant that the apparatus was still largely novel. I also wanted to ensure that

the monkeys paid attention to the novel type of pellet delivery, which involved the pellets traveling through the clear tubing and landing in the reward cups.

Of the six monkeys who passed the task criterion, two individuals subsequently failed to participate in the inequity test (Appendix A), suggesting that some aspect of the inequity task was aversive. For the next study, I re-paired the monkeys to determine whether the difficulties on the inequity task would persist across new pairs. Individuals were dropped from those pairs in which either player did not pass the Chicken Game criterion or did not participate in the inequity task following passing criterion. Three new pairs were created (two pairs using monkeys that had both been previously tested in Studies 1 and 2, and one pair using a previously tested monkey in Studies 1 and 2 and one that had never been tested).

3.3 Study 3

3.3.1 Study 3 Methods

I paired only monkeys that performed trials in the previous experiment and re-tested them following the procedures described in Study 1 (Appendix A). I continued to test one pair that had consistently met the criteria in the two previous studies. To determine whether the performance problems were persisting across the new pairs, each pair was provided 4 sessions. Each individual had to reach a criterion of an average of 20 completed trials over 4 sessions in order to continue testing.

3.3.2 Study 3 Results

Six of eight individuals passed criterion for the four sessions (Appendix A, Study 3). One failed to do so after 4 sessions, but her partner met criterion. For another pair, testing was terminated early after two sessions. In this pair, one individual was likely to pass criterion but her partner completed only 3 trials within two sessions. Upon inspection, this was not due to

rewards; this individual completed only one trial when advantaged and two trials when disadvantaged. Moreover, video footage confirmed that he only touched the joystick once in one session and twice in the other session. Therefore, testing was terminated as soon as this motivational problem emerged to prevent possible experience effects in both monkeys in the pair. As a comparison, the subject with the second lowest average had completed 13 trials and 7 trials respectively in her first two sessions. Because this subject completed at least some trials in each session, she was not dropped even though she ultimately did not pass criterion after four sessions. The two pairs for which both monkeys passed criterion completed all 8 sessions.

For the two pairs for which both monkeys passed criterion, behavior in the subsequent eight testing sessions did not differ across equity conditions in any of the dependent measures, whether the experimenter was present (refusals: $X^2(3)=.600$, $p=.896$; average reaction time: $X^2(3)=1.8$, $p=.615$; average completion time: $X^2(3)=1.5$, $p=.682$) or absent (refusals: $X^2(3)=2.1$, $p=.552$; average reaction time: $X^2(3)=3.9$, $p=.272$; average completion time: $X^2(3)=4.5$, $p=.212$). The monkeys also did not respond differently to any condition in the experimenter present versus absent conditions for refusals (LE: $z=-.730$, $p=.465$; HE: $z=-.730$, $p=.465$; DI: $z=-1.095$, $p=.273$; AI: $z=-1.461$, $p=.144$), average reaction time (LE: $z=-1.095$, $p=.273$; HE: $z=-1.461$, $p=.144$; DI: $z=-1.095$, $p=.273$; AI: $z=-1.826$, $p=.068$), and average completion time (LE: $z=-1.095$, $p=.273$; HE: $z=-1.461$, $p=.144$; DI: $z=-1.095$, $p=.273$; AI: $z=-.365$, $p=.715$). An overview of results can be found in Figures 3 and 4.

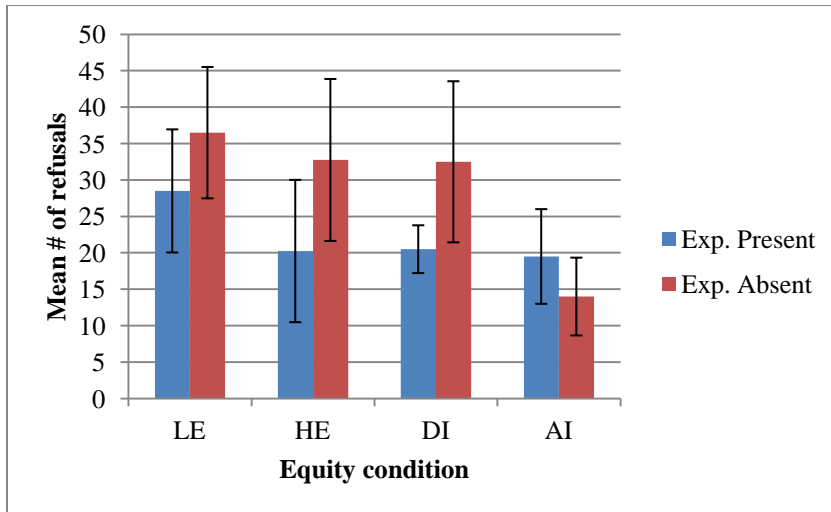


Figure 3. Overview of mean refusals out of 60 trials across the 8 conditions in Study 3 (n=4). Equity conditions are LE (low equity), HE (high equity), DI (disadvantageous inequity), and AI (advantageous inequity).

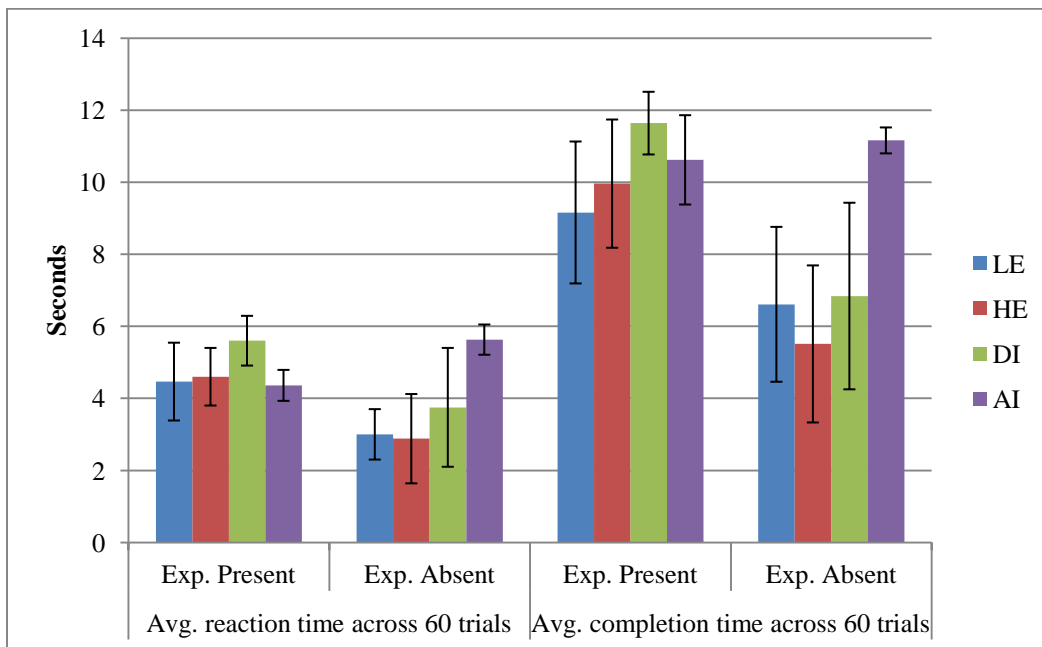


Figure 4. Overview of average reaction time and average completion time across 60 trials in the 8 conditions in Study 3 (n=4). Equity conditions are LE (low equity), HE (high equity), DI (disadvantageous inequity), and AI (advantageous inequity).

3.3.3 Study 3 Discussion

Two pairs passed criterion and completed all 8 sessions of the inequity task. It is possible that the problems experienced in Studies 1 and 2 were due to individual motivation issues, because the individuals that were re-paired continued to work well in their new pairs. However, individuals within the other two pairs showed low response rates, despite having worked well in their previous pair.

The four monkeys that completed the study did not respond differently across equity conditions or experimenter conditions. It is possible that the sample size ($n=4$) was too small to find any effects, or it may also be that the task and setup prevented these monkeys from noticing or responding to differential reward outcomes. Therefore, to clarify this issue, I decided to make modifications in order to help the two remaining pairs who did not meet criterion and therefore to increase the sample size. Prior to each inequity task, I tested the monkeys on the Chicken Game for 10 minutes to rule out the possibility that a failure to participate was due to a lack of motivation. If monkeys worked on the Chicken Game but then failed to participate in the inequity task immediately following, it would indicate that their disinterest in participating was due to the task, not the apparatus or a generalized lack of interest. However, if the monkeys failed to complete the Chicken Game, this would mean that the lack of interest extended beyond the inequity task and was a more general lack of motivation to work that day, and consequently, I did not test them on the inequity task.

3.4 Study 4

3.4.1 Study 4 Methods

The two pairs that did not pass criterion in Study 3 were tested on the Chicken Game, following the setup in Study 2. Individuals were provided the chance to complete as many trials

as they could within 10 minutes to receive rewards. On average, individuals typically completed a minimum of 60 trials within 60 minutes; therefore, the criterion was set so that if each individual completed at least 10 trials in the 10 minutes, they were immediately tested on the inequity task, starting with conditions that they had yet to experience.

3.4.2 Study 4 Results

One pair passed Chicken Game criterion, but immediately following, one subject in the pair completed a low number of trials on the inequity task (5; see Appendix A, Study 4) and only touched the joystick 6 times. Upon further inspection, this session was an advantageous inequity condition in which this particular individual was receiving the better reward; therefore, it was clear that this was not due to frustration due to inequity or receiving a low value reward in comparison with the possible payoffs of four pellets in the Chicken Game (the highest reward possibility was four pellets in both the Chicken Game and inequity task). The other pair failed to pass criterion. Because this test requires both individuals' input to receive rewards, either one or both individuals did not participate long enough to reach the 10 trials (Appendix A).

3.4.3 Study 4 Discussion

Again, the results from this study indicated problems with both the apparatus and the inequity task. One pair failed to pass the Chicken Game criterion; because this game requires both individuals to make a selection before receiving rewards, the failure to complete the task may have been influenced by a single monkey or both monkeys not participating. This indicated either a dislike of the new apparatus or a more generalized lack of motivation to work. The other pair passed the Chicken Game criterion but on the subsequent inequity task one individual failed to participate despite receiving the better rewards. Unlike the other pair that refused to work on either task, this individual's pattern of behavior indicates that he was willing to participate on a

familiar task but lost motivation to work when the task was switched to the inequity task immediately following. Based on the collective results from Studies 1-4, I modified some parameters of the task to help the remaining monkeys better understand it (Table 1). It is possible that some monkeys found the ITI to be too long, which might have caused them not to view the task as a joint task for which they should carefully pay attention to their partner's outcomes. Monkeys might have also been confused because the non-playing individual did not have a cursor on his side of the screen. Therefore, the non-playing individual moved his joystick, and when the cursor movements did not correlate with his joystick movements, he consequently might have lost interest or become frustrated. These two factors combined might have caused monkeys not to realize that the task was a joint task in which the players alternated turns, which may have been a motivating factor for the lack of participation.

3.5 Study 5

3.5.1 Study 5 Methods

I modified the inequity task parameters (Table 1) by shortening the ITI to keep the monkeys' attention and adding a functioning cursor on the non-playing individual's side of the screen so that the individual might be more aware of their cursor movements versus their partner's cursor movements. The two pairs were tested following the setup in Study 1.

3.5.2 Study 5 Results

Both pairs completed all eight sessions (Appendix A, Study 5). When the experimenter was present, their behavior differed across equity conditions in refusals ($X^2(3)=8.333, p=.040$) but not average reaction time ($X^2(3)=.900, p=.825$) or average completion time ($X^2(3)=.900, p=.825$). Post-hoc analysis with Wilcoxon signed-rank tests was conducted with a Bonferroni correction applied, resulting in a significance level set at $p < .0083$. With this correction, there

were no significant differences between any of the equity conditions. When the experimenter was absent, the monkeys' behavior did not differ across equity conditions (refusals: $X^2(3)=3.9$, $p=.272$; average reaction time: $X^2(3)=6.30$, $p=.098$; average completion time: $X^2(3)=1.5$, $p=.682$). They also did not respond differently to any condition in the experimenter present versus absent conditions for refusals (LE: $z= .000$, $p=1$; HE: $z= -1.069$, $p=.285$; DI: $z= -.272$, $p=.785$; AI: $z= -1.826$, $p=.068$), average reaction time (LE: $z= -.730$, $p=.465$; HE: $z= -.730$, $p=.465$; DI: $z= -1.461$, $p=.144$; AI: $z= .000$, $p=1$), and average completion time (LE: $z= -.730$, $p=.465$; HE: $z= -.730$, $p=.465$; DI: $z= -1.095$, $p=.273$; AI: $z= -.730$, $p=.465$). An overview of results can be found in Figures 5 and 6.

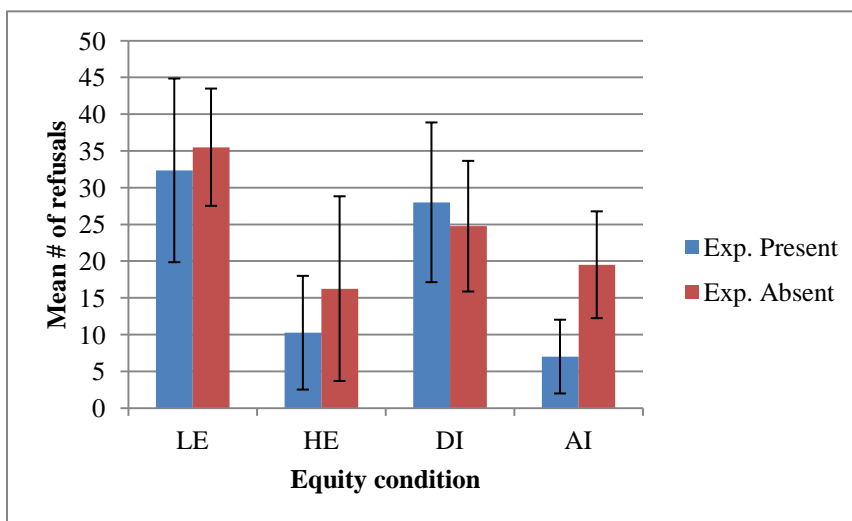


Figure 5. Overview of mean refusals out of 60 trials across the 8 conditions in Study 5 (n=4). Equity conditions are LE (low equity), HE (high equity), DI (disadvantageous inequity), and AI (advantageous inequity).

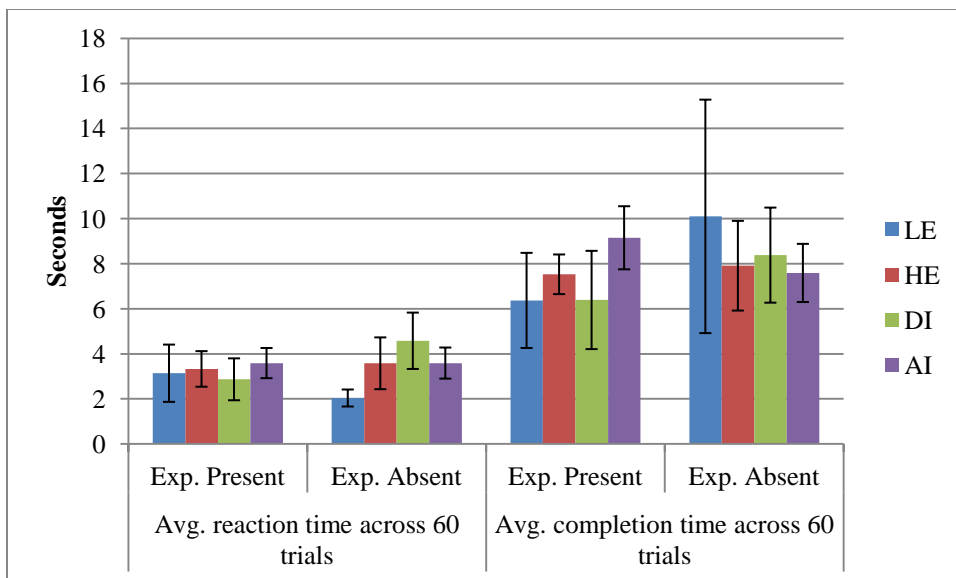


Figure 6. Overview of average reaction time and average completion time across 60 trials in the 8 conditions in Study 5 (n=4). Equity conditions are LE (low equity), HE (high equity), DI (disadvantageous inequity), and AI (advantageous inequity).

3.5.3 Study 5 Discussion

With the modifications, two additional pairs of monkeys completed all 8 sessions of the inequity task. Given that I found no statistically significant comparisons (except the overall Friedman's for Study 5, for which there were no significant comparisons following Bonferroni corrections), I combined the data from Study 3 and Study 5 to increase the sample size and re-ran the analyses.

3.6 Combined Data

3.6.1 Combined Data Results

I analyzed the combined data using factorial repeated-measures GLM. I conducted analyses across the full 60 trials for refusals, average reaction time, and average completion time (see Figures 7 and 8 for overview). For all results reported, the assumption of sphericity was met.

Experimenter presence or absence did not have a significant effect on any dependent variables (refusals: $X^2(1)=2.17, p=.14$; average reaction time: $X^2(1)=.74, p=.39$; average completion time: $X^2(1)=.65, p=.42$). The type of equity condition did have a significant effect on refusals ($X^2(3)=14.59, p=.002$) but not average reaction time ($X^2(3)=4.96, p=.17$) or average completion time ($X^2(3)=2.74, p=.43$). There were no interactions between experimenter and equity condition for any of the dependent variables (refusals: $X^2(3)=.43, p=.93$; average reaction time: $X^2(3)=3.22, p=.36$; average completion time: $X^2(3)=1.35, p=.72$). Planned contrasts revealed that subjects refused significantly more in the low equity condition compared to any other condition, $b = -3.33, t(42) = -2.63, p=.012$ (Table 4). After collapsing the data to compare performance as a function of absolute food amounts, subjects' refusals differed significantly depending on whether they received a single reward or four rewards, $z = -2.1, p=.036$.

I also examined whether refusal rates changed across time as the session progressed. Refusal rates significantly decreased across trials in the high equity condition ($r_s(960) = -.147, p<.001$) and low equity condition ($r_s(960) = -.149, p<.001$), but not the advantageous inequity condition ($r_s(960) = -.010, p=.751$) nor the disadvantageous inequity condition ($r_s(960) = -.052, p=.107$). Comparing the correlation coefficients from each condition confirmed the above findings. The correlation between refusal rates across the duration of the session in the high equity condition differed significantly from the correlations between refusal rates across the duration of the session in the disadvantageous inequity condition ($z = -2.1, p=.036$) and the advantageous inequity condition ($z = -3.02, p=.003$) but not the low equity condition ($z = 0.04, p=.968$). The correlation between refusal rates across the duration of the session in the low equity condition differed significantly from the correlation between refusal rates across the duration of the session in the disadvantageous inequity condition ($z = -2.15, p=.032$) and the

advantageous inequity condition ($z = -3.07, p = .002$). The correlations between refusal rates across the duration of the session in the advantageous inequity condition and the disadvantageous inequity condition did not differ significantly, $z = -0.92, p = .358$.

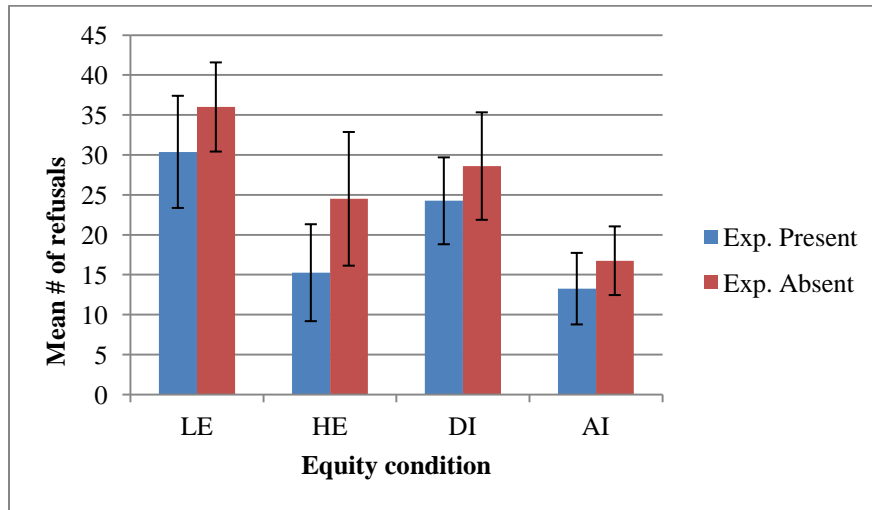


Figure 7. Overview of mean refusals out of 60 trials across the 8 conditions in Studies 3 and 5 (combined data, $n=8$). Equity conditions are LE (low equity), HE (high equity), DI (disadvantageous inequity), and AI (advantageous inequity).

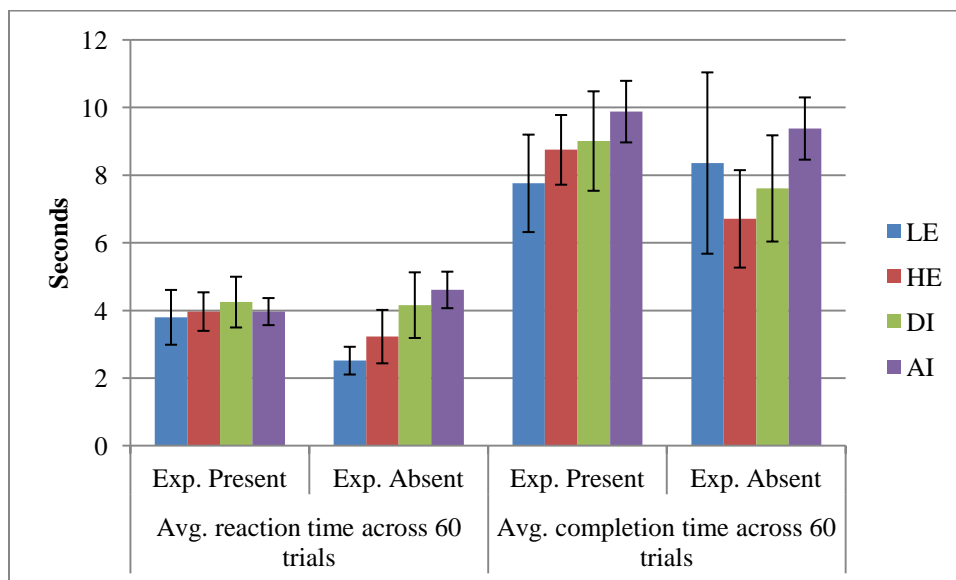


Figure 8. Overview of average reaction time and average completion time across 60 trials in the 8 conditions in Studies 3 and 5 (combined data, $n=8$). Equity conditions are LE (low equity), HE (high equity), DI (disadvantageous inequity), and AI (advantageous inequity).

Table 3. Results for analysis of contrasts for refusals. Equity conditions are LE (low equity), HE (high equity), DI (disadvantageous inequity), and AI (advantageous inequity). Refusals in the low equity condition differed significantly from any other condition, $b = -3.33$, $t(42) = -2.63$, $p = .012$.

| Contrast | b | SE_b | df | t | p |
|---------------------------------|-------|--------|----|-------|-------|
| Experimenter Present vs. Absent | -2.84 | 1.79 | 7 | -1.59 | 0.16 |
| LE vs. other conditions | -3.33 | 1.26 | 42 | -2.63 | 0.012 |
| DI vs. AI | 4.88 | 5.06 | 42 | 0.96 | 0.34 |
| DI vs. other conditions | -0.42 | 2.19 | 42 | -0.19 | 0.85 |

3.6.2 Combined Data Discussion

Overall, the pattern of results suggests that monkeys were sensitive to receiving a single reward, but were not sensitive to either their reward as compared to their partner's (i.e., equity versus inequity) or the presence of the experimenter. In the combined data, I found that the overall number of refusals differed significantly across equity conditions, and the monkeys refused the most when both individuals were receiving a low value reward. Moreover, although this was not statistically significant, monkeys also refused at high rates when disadvantaged as compared to a partner, which was the other condition in which they received a single reward, suggesting that the monkeys were sensitive to getting a single reward as opposed to the four rewards. Indeed, this was confirmed after analyzing performance as a function of food amounts, which revealed that the monkeys' refusals differed significantly depending on what amount of reward they received. Additionally, in no condition did the subjects' behavior change depending on whether the experimenter was present.

However, there was one finding that hints to the possibility that subjects were responding to the relative equity of the rewards. Although the overall number of refusals did not differ across conditions, the rate of refusal did. In the combined data, the subjects' rate of refusal did

not change in the two conditions that resulted in unequal outcomes, whether they were advantaged (AI) or disadvantaged (DI). On the other hand, they were less likely to refuse across the course of the session in the two conditions that resulted in equal outcomes, whether they received the preferred outcome (HE) or the less preferred one (LE), possibly indicating a social facilitation effect when their outcome matched their partner's. This finding is the one indication that the subjects noticed when their outcome differed from their partner's, regardless of whether they were relatively advantaged or disadvantaged. This result hints that this procedure might yield valuable insights with a larger sample size and an adapted procedure that takes in to account the changes that were in place in Study 5.

4 GENERAL DISCUSSION

My hypothesis that monkeys' responses would be influenced by the presence of the experimenter was not supported. Monkeys' behavior did not change in any condition depending on whether the experimenter was present or absent. However, it may still be surprising that the presence of the experimenter did not change their willingness to work and/or accept rewards (even if this was independent of the reward inequity, or lack thereof) for several reasons. First, it remains unclear what role the experimenter may play in a social interaction. On the one hand, the experimenter may provide additional cues that the context is a social one, causing the subjects to pay more attention. On the other hand, the experimenter may be distracting, as a recent study suggests; macaques performed significantly better on an object-choice task when the experimenter was hidden behind a curtain and only the arm of the experimenter was visible, suggesting that the presence of the experimenter distracted the monkeys away from the salient cues in the task (Schmitt et al., 2014). Second, whereas the procedures and apparatus were carefully constructed so as to remove interaction with the experimenter and prevent cuing, it is

challenging to eliminate all unintentional cuing. Whereas I tried to stay as consistent as possible in my movements as the experimenter and maintain my gaze straight ahead during testing, nonhuman primates are sensitive to eye movements (Povinelli & Eddy, 1996) and animals may be sensitive to subtle body movements (Johnson, 1913), such as respiration, posture, and the tensing and relaxing of muscles - processes that would be impossible for an experimenter to have full control over. Moreover, it is possible that the monkeys' unwillingness to work provided experimental feedback that negatively affected my mood, which conceivably could have further influenced unintentional cuing and changed monkeys' behavior (perhaps leading them to work less in the presence of the experimenter). Third, I have had years of experience with these monkeys and they are familiar with interacting with me, both in terms of experimental and husbandry-type interactions. Consequently, because capuchin monkeys can discriminate humans (Paukner et al., 2009), there was a risk that my past experience with these monkeys might influence their perception of me as the experimenter, and I thought they might be more willing to work in my presence because they are used to receiving rewards from me. So while on the one hand this is surprising, on the other hand it is good news that the experimenter's presence does not always influence behavior.

A second area of interest is why we did not see a strong response to inequity in this study, as has been found in some others (Brosnan et al., 2010b; Brosnan & de Waal, 2003; Fletcher, 2008; Takimoto et al., 2010; Takimoto & Fujita, 2011; Talbot et al., in prep; van Wolkenten et al., 2007; but see Fontenot et al., 2007; Silberberg et al., 2009; Talbot et al., in prep). In this study, the monkeys' responses seem to have been more strongly driven by their own immediate outcomes rather than how their outcomes compared to their partner's (as measured by their overall refusal rate). However, the correlations examining refusal rates across the duration of the

different sessions suggest that the monkeys were at least noticing inequity, even if they did not refuse more often overall in the inequity conditions. Refusal rates did not change over time in either disadvantageous or advantageous inequity conditions, but the monkeys refused less often across trials in the low equity and high equity conditions. This outcome is intriguing for several reasons. First, it was independent of the subject's actual outcome. This change was based on whether their outcome matched their partner's, not what they got. Second, it was equally strong whether they were more advantaged than a partner or less advantaged. This may indicate that what affected their behavior was the degree to which their outcome was the same as a partner's, possibly indicating that different foods are less preferred regardless of one's absolute or relative outcomes. Given evidence for both inequity (Brosnan et al., 2010b; Brosnan & de Waal, 2003; Fletcher, 2008; Takimoto et al., 2010; Takimoto & Fujita, 2011; Talbot et al., in prep; van Wolkenten et al., 2007) and prosocial behavior (Brosnan et al., 2010a; Lakshminarayanan & Santos, 2008) in capuchins in previous studies, this is a possibility that deserves further exploration.

A critical question is why the subjects did not respond to inequity in this task. First, there is an indication that they noticed it based on the change in refusal rates across sessions, which mirrors earlier findings with capuchins (Brosnan & de Waal, 2004). However, there were no changes in overall refusal rates as in other capuchin studies with different reward distributions. There are several possibilities for this. First, as discussed in Section 1.2.3, subjects' orientation and physical proximity may influence the animals' behavior. In fact, recent evidence from another study using a traditional token exchange procedure suggests that the same capuchin subjects did not respond to inequity when a barrier separated individuals, but they did respond in at least some circumstances once this barrier was removed (Talbot et al., in prep). Of course,

other studies have shown that capuchins do respond to inequity when separated by a barrier (Brosnan & de Waal, 2003; Brosnan et al., 2010b; van Wolkenten et al., 2007). Additionally, Talbot and colleagues found that these monkeys did not respond to differences in quantity of the same food, whether or not there was a barrier. However, monkeys do discriminate and respond to the difference between one and four pellets, as this same magnitude is used in the Chicken Game (Price et al., in prep). In the Chicken Game, these differences in rewards are associated with additional cues; each monkey in the pair chooses an icon that represents a strategy, and the resulting combination of chosen icons is displayed on the screen as the monkeys receive their corresponding rewards. Therefore, it is less likely that the magnitude of food rewards was problematic, but that the monkeys could not associate how their behavior resulted in a certain reward outcome.

One major challenge to this work was the subjects' disinterest in participating. This study provided evidence that the apparatus setup and the task both contributed to the problem. Regarding the former, in several cases, videotape analysis revealed that the monkeys were not even approaching the joystick, suggesting that it was not the task (which they never tried) that influenced their decision. In Study 2, some pairs failed criterion on a familiar task with which they had had previous success, again indicating that the novel testing apparatus was problematic. Despite receiving an acclimation period without a required task, subjects did not experience actually *using* the apparatus prior to testing. This was done to prevent any possible contrast effects, in which the monkeys would compare their testing experience to the acclimation period (which may have been problematic if their first exposure with the setup mimicked an equity session with an experimenter present). In retrospect, giving them prior exposure to the task with

the new apparatus would have been a beneficial prerequisite, and would have alerted me to the problems much earlier.

Moreover, the nature of the task may have influenced the low performance rates, although it is unclear which aspect was specifically problematic. There was an indication that the inequity task was problematic when, even after monkeys passed criterion for the Chicken Game, several subsequently failed to participate on the inequity task. One possibility is the alternation inherent in the task. The alternating inequity task was largely structured off a previous study, in which these same monkey subjects received extensive training to learn how to alternate taking turns on the CHASE task to reward their partner (Parrish et al., in prep). Although subjects in the previous study required significant training, they were able to learn it and as a result, I did not expect that these monkeys would have difficulty with another alternating task. The results in Study 5 point to two possible influences, the ITI and the presence of a second functional cursor for the non-playing monkey. Considering the first of these, monkeys certainly improved when the ITI was shortened from 10 seconds to 5 seconds in Study 5. However, in Parrish and colleagues' study, monkeys were ultimately able to wait as long as two minutes between turns. Whereas their study required significantly more scaffolding to reach these long ITIs, I still find it unlikely that the ITI alone influenced subjects' behavior so significantly.

The other difference was that in the testing phase of Parrish et al. (in prep), the non-playing individual's cursor was frozen in place, whereas in the current study (Studies 1-4), the non-playing individual's cursor was completely absent. Because the non-playing individual did not have a cursor on his/her side of the screen, s/he may have been confused about whether s/he was controlling the movement on the screen, and s/he may have become frustrated if these movements did not correlate with touching the joystick. Supporting this, adding a functional

cursor for the non-playing monkey was one of the changes linked to increased success in Study 5.

Whereas the issues with the ITI and the cursor cannot be disentangled, it is possible that in the current study, the alternating inequity task was not perceived as a joint task, in which both individuals should have paid attention to each other's performance and reward outcomes. It is also possible that the monkeys do not perceive the split screen in the way that I expected them to. Perhaps a more suitable task would be one that was more cooperative and required both players' inputs. For example, the monkeys could work on a single screen with different cursors and both individuals would be required to chase the same moving target to touch it. This might be more analogous to a task that requires both players to coordinate expended efforts to obtain rewards.

Another limitation to this study was finding the balance between staying blind to the results as the study progressed and monitoring possible procedural problems to potentially adapt the paradigm in the middle of the study. As discussed in the introduction, there is always a risk that an experimenter may form a bias based on how the study is progressing, causing expectancies for future behavior (Rosenthal & Fode, 1963). For example, if data support a hypothesis, it might cause the experimenter to exaggerate an interpretation. If data contradict the hypothesis, it might change the mood of the experimenter, who may emit unintentional cues or test additional subjects to increase power. For example, in the current study, I expected the monkeys to perceive the alternating task as a social one in which their partner mattered, however, without testing the monkeys in partner-absent conditions, it was impossible to know for sure. I also expected the monkeys to complete a certain number of trials for each session based on their efficiency on other computer tasks, therefore, I interpreted the low number of trials completed in sessions as problematic. On the other hand, it may be beneficial to track

performance on a novel task in order to determine whether subjects understand the contingencies of the task; this is especially important in animal research in which the subjects cannot ask questions for clarification or give feedback on what may have been confusing. Therefore, there needs to be a balance in the risk of experimenter bias and in the risk of poor performance on an unknown task.

One way to approach this problem is by creating objective criteria ahead of time in anticipation of problems, which requires tracking results to an extent but is established before testing has begun. However, this type of computerized inequity study with the joint testing box apparatus had never been attempted before, and so it was difficult to create criterion considering all of these new factors. In fact, based on results from Parrish et al. (in prep), it was expected that the monkeys were familiar and successful with the alternating CHASE task and were willing to wait for long periods in between receiving rewards, so it was surprising that the monkeys were not willing to work on this task. Also, because it was a computerized study, I assumed that the monkeys would complete a high number of trials because they easily complete 200 trials in other types of joint tasks (e.g. the Chicken Game).

Therefore, as the experimenter, I took the approach of staying as blind as possible to performance across the type of equity conditions and only examined the data once it became clear that several monkeys were not working. At this point, I did not want to give monkeys further negative experience if the apparatus or task was aversive or frustrating to several subjects. For this particular study, I believed it was beneficial to adapt the paradigm as problems persisted and it appeared likely early in the study that multiple subjects would not meet criterion. Often times, subjects were not even completing a single trial in order to determine what reward they were receiving, and as the comparison of rewards was the main requirement for inequity, it

was crucial to fix this problem as soon as possible. One of the problems with my approach was that different subjects received different numbers of sessions, so each subject had different experiences. This made it impossible to compare subjects' performance, meaning that even though I ultimately had four pairs complete the task, it is not clear how subjects may have been influenced differently by this different experience. In the future I would begin by testing all pairs on the same sub-selection of four conditions (in randomized order) and establish a criterion for average number of responses (as in Study 3); with this method, all pairs would receive the same experience with the number of sessions and types of conditions, and I could more properly assess differences among performances.

Of course the aforementioned problems with implementing the study make it difficult to extrapolate further; however, I note that the finding that the experimenter did not influence the subjects' behavior (irrespective of inequity condition) is not unprecedented. Previous research found that capuchins did not learn to prefer more reliable experimenters over those who cheated them (e.g., gave them less than anticipated; Brosnan & de Waal, 2009; Sheskin et al., 2013), so these studies combined with my current results suggest that capuchins are not particularly sensitive to either the experimenter's intent to cheat them (e.g., provide less than offered; Brosnan & de Waal, 2009; Sheskin et al., 2013) or to their intent to cause inequity (e.g., the current results). This may be different from chimpanzees, who do learn reputation (Russell et al., 2008; Subiaul et al., 2008) and therefore might be expected to respond differently based on the presence or absence of an experimenter.

Future research will be required to explore these questions further. Whereas there was tentative evidence that subjects in my study noticed inequity, suggesting the utility of a new study with a larger sample size, it is difficult to understand what our findings mean. Nonetheless,

experimenter effects remain an important area of research, especially when working with animals, and require further attention. Because it is virtually impossible to remove the experimenter from the experiment in all testing situations, researchers should have a better understanding of what role the experimenter plays overall in an attempt to control for these effects as much as possible. Moreover, the relationship between human experimenters and their animal subjects is fascinating in and of itself, and has important implications beyond research, such as how we can improve life in captivity for animal subjects.

REFERENCES

- Attridge, M., & Berscheid, E. (1994). Entitlement in romantic relationships in the United States: A social-exchange perspective. In M.J. Lerner & G. Mikula (Ed.), *Entitlement and the affectional bond: Justice in close relationships*, (pp. 117-148). New York: Plenum.
- Bekoff, M. (2001). Social play behaviour. Cooperation, fairness, trust, and the evolution of morality. *Journal of Consciousness Studies*, 8(2), 81-90.
- Beran, M. J., & Evans, T. A. (2009). Delay of gratification by chimpanzees (*Pan troglodytes*) in working and waiting situations. *Behavioural processes*, 80(2), 177-181.
- Blount, S. (1995). When social outcomes aren't fair: The effect of causal attributions on preferences. *Organizational behavior and human decision processes*, 63(2), 131-144.
- Bräuer, J., Call, J., & Tomasello, M. (2006). Are apes really inequity averse? *Proceedings of the Royal Society B: Biological Sciences*, 273(1605), 3123.
- Bräuer, J., Call, J., & Tomasello, M. (2009). Are apes inequity averse? New data on the token-exchange paradigm. *American Journal of Primatology*, 71(2), 175-181.
- Brogden, W. J. (1962). The experimenter as a factor in animal conditioning. *Psychological Reports*, 11, 239-242.
- Brosnan, S. F. (2006). Nonhuman species' reactions to inequity and their implications for fairness. *Social Justice Research*, 19(2), 153-185.
- Brosnan, S. F. (2011). A hypothesis of the co-evolution of cooperation and responses to inequity. *Frontiers in Neuroscience*, 5:43.
- Brosnan, S. F. (in press). Why an evolutionary perspective is critical to understanding moral behavior in humans. In M. Bergmann & P. Kain (Eds.), *Challenges to Moral and Religious Belief*. Oxford University Press.

- Brosnan, S. F., & de Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature*, 425(6955), 297-299.
- Brosnan, S. F. & de Waal, F. B. M. (2004). Reply to “Inequity aversion in capuchins” (Henrich and Wynne). *Nature*, 428, 140.
- Brosnan, S. F., & de Waal, F. B. M. (2009). *Cebus apella* tolerate intermittent unreliability in human experimenters. *International Journal of Primatology*, 30(5), 663-674.
- Brosnan, S. F., & de Waal, F. B. M. (2012). Conclusion to justice in animals. *Social Justice Research*, 25(3), 336-351.
- Brosnan, S. F., Flemming, T., Talbot, C. F., Mayo, L., & Stoinski, T. (2011a). Orangutans (*Pongo pygmaeus*) do not form expectations based on their partner's outcomes. *Folia Primatologica*, 82(1), 56-70.
- Brosnan, S. F., Houser, D., Leimgruber, K., Xiao, E., Chen, T., & de Waal, F. B. M. (2010a). Competing demands of prosociality and equity in monkeys. *Evolution and Human Behavior*, 31(4), 279-288.
- Brosnan, S. F., Schiff, H., & de Waal, F. B. M. (2005). Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 272(1560), 253-258.
- Brosnan, S. F., Talbot, C., Ahlgren, M., Lambeth, S. P., & Schapiro, S. J. (2010b). Mechanisms underlying responses to inequitable outcomes in chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 79(6), 1229-1237.
- Brosnan, S. F., Wilson, B., & Beran, M. J. (2011b). Old World monkeys are more similar to humans than New World monkeys when playing a coordination game. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1522-1530 .

- Call, J. (2001). Object permanence in orangutans (*Pongo pygmaeus*), chimpanzees (*Pan troglodytes*), and children (*Homo sapiens*). *Journal of Comparative Psychology*, *115*(2), 159-171.
- Call, J., Hare, B., Carpenter, M., & Tomasello, M. (2004). 'Unwilling' versus 'unable': chimpanzees' understanding of human intentional action. *Developmental Science*, *7*(4), 488-498.
- Cibulski, L., Wascher, C. A., Weiß, B. M., & Kotrschal, K. (2014). Familiarity with the experimenter influences the performance of Common ravens (*Corvus corax*) and Carrion crows (*Corvus corone corone*) in cognitive tasks. *Behavioural Processes*, *103*, 129-137.
- Clark, M. S., & Grote, N. K. (2003). Close relationships. In: *Handbook of Psychology: Personality and Social Psychology*. Vol. 5 (Ed. by T. Millon & M.J. Lerner), pp 447-461. New York: J. Wiley.
- Colquitt, J. A., Scott, B. A., Judge, T. A., & Shaw, J. C. (2006). Justice and personality: Using integrative theories to derive moderators of justice effects. *Organizational Behavior and Human Decision Processes*, *100*(1), 110-127.
- Cordaro, L., & Ison, J. R. (1963). Psychology of the scientist: Observer bias in classical conditioning of the planarian. *Psychological Reports*, *13*(3), 787-789.
- Davis, H. (2002). Prediction and preparation: Pavlovian implications of research animals discriminating among humans. *ILAR Journal*, *43*(1), 19-26.
- Davis, H. E., & Balfour, D. A. (1992). *The inevitable bond: Examining scientist–animal interactions*: Cambridge University Press.

- de Blois, S. T., Novak, M. A., & Bond, M. (1998). Object permanence in orangutans (*Pongo pygmaeus*) and squirrel monkeys (*Saimiri sciureus*). *Journal of Comparative Psychology*, *112*(2), 137-152.
- de Waal, F. B. M. (1996). *Good natured: The origins of right and wrong in humans and other animals*. Cambridge, Massachusetts: Harvard University Press.
- de Waal, F.B.M. (2007). *Chimpanzee politics: Power and sex among apes*. Baltimore, MD: The Johns Hopkins University Press.
- de Waal, F. B. M., & Berger, M. L. (2000). Payment for labour in monkeys. *Nature*, *404*(6778), 563.
- Dindo, M., & de Waal, F. B. M. (2007). Partner effects on food consumption in brown capuchin monkeys. *American Journal of Primatology*, *69*(4), 448-456.
- Evans, T. A., Beran, M. J., Chan, B., Klein, E. D., & Menzel, C. R. (2008). An efficient computerized testing method for the capuchin monkey (*Cebus apella*): Adaptation of the LRC-CTS to a socially housed nonhuman primate species. *Behavior research methods*, *40*(2), 590-596.
- Fehr, E., & Schmidt, K. M. (1999). A theory of fairness, competition, and cooperation. *The Quarterly Journal of Economics*, *114*(3), 817-868.
- Flack, J. C., & de Waal, F. B. M. (2000). Any animal whatever. Darwinian building blocks of morality in monkeys and apes. *Journal of Consciousness Studies*, *7*, *1*(2), 1-29.
- Fletcher, G. E. (2008). Attending to the outcome of others: disadvantageous inequity aversion in male capuchin monkeys (*Cebus apella*). *American Journal of Primatology*, *70*(9), 901-905.

- Fontenot, M., Watson, S., Roberts, K., & Miller, R. (2007). Effects of food preferences on token exchange and behavioural responses to inequality in tufted capuchin monkeys, *Cebus apella*. *Animal Behaviour*, 74(3), 487–496.
- Frank, R. H. (1988). *Passions within reason: The strategic role of the emotions*, New York: W.W. Norton & Company.
- Freeman, H. D., Sullivan, J., Hopper, L. M., Talbot, C. F., Holmes, A. N., Schultz-Darken, N., Williams, L.E. & Brosnan, S. F. (2013). Different responses to reward comparisons by three primate species. *PloS one*, 8(10), e76297.
- Haidt, J. (2012). *The righteous mind: Why good people are divided by politics and religion*. New York, NY: Penguin Books.
- Hare, B., & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, 9(9), 439-444.
- Harris, H., Piccolino, E., Roback, H., & Sommer, D. (1964). The effects of alcohol on counterconditioning of an avoidance response. *Quarterly journal of studies on alcohol*, 25, 490-497.
- Hatfield, E., Walster, G. W., & Berscheid, E. (1978). *Equity: Theory and research*: Boston: Allyn & Bacon.
- Heinrich, B. (1999). *Mind of the Raven*, New York: Cliff Street Books.
- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., & McElreath, R. (2001). In Search of Homo economicus: Behavioral experiments in 15 small-scale societies. *The American Economic Review*, 91(2), 73-78.
- Horowitz, A. (2012). Fair is fine, but more is better: Limits to inequity aversion in the domestic dog. *Social Justice Research*, 25(2), 195–212.

- Johnson, H. M. (1913). Audition and habit formation in the dog. *Behavior Monographs*, 2(8), 78.
- Kintz, B. L., Delprato, D. J., Mettee, D. R., Persons, C. E., Schappe, R. H. (1965). The experimenter effect. *Psychological Bulletin*, 63(4), 223-232.
- Kundey, S., De Los Reyes, A., Royer, E., Molina, S., Monnier, B., German, R., & Coshun, A. (2011). Reputation-like inference in domestic dogs (*Canis familiaris*). *Animal Cognition*, 14(2), 291-302.
- Lakshminarayanan, V. R., & Santos, L. R. (2008). Capuchin monkeys are sensitive to others' welfare. *Current Biology*, 18(21), R999-R1000.
- Lore, R. K., & Eisenberg, F. B. (1986). Avoidance reactions of domestic dogs to unfamiliar male and female humans in a kennel setting. *Applied Animal Behaviour Science*, 15, 261-6.
- Marshall-Pescini, S., Passalacqua, C., Ferrario, A., Valsecchi, P., & Prato-Previde, E. (2011). Social eavesdropping in the domestic dog. *Animal Behaviour*, 81(6), 1177-1183.
- Massen, J. J. M., van den Berg, L. M., Spruijt, B. M., & Sterck, E. H. M. (2011). Inequity aversion in relation to effort and relationship quality in long-tailed Macaques (*Macaca fascicularis*). *American Journal of Primatology*, 74(2), 145-156.
- McGuigan, F. J. (1960). Variation of whole-part methods of learning. *Journal of Educational Psychology*, 51, 213-216.
- McGuigan, F. J. (1963). The experimenter: A neglected stimulus object. *Psychological Bulletin*, 60(4), 421-428.
- Mitchell, R. W., & Anderson, J. R. (1997). Pointing, withholding information, and deception in capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 111(4), 351-361.

- Neiworth, J. J., Johnson, E. T., Whillock, K., Greenberg, J., & Brown, V. (2009). Is a sense of inequity an ancestral primate trait? Testing social inequity in cotton top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology*, *123*(1), 10-17.
- Parrish, A. E., Brosnan, S. F., & Beran, M. J. (in prep). I'll work for you and you work for me: Oh wait, you might not matter.
- Paukner, A., Suomi, S. J., Visalberghi, E., & Ferrari, P. F. (2009). Capuchin monkeys display affiliation toward humans who imitate them. *Science*, *325*(5942), 880-883.
- Pepperberg, I. M., Willner, M. R., & Gravitz, L. B. (1997). Development of Piagetian object permanence in grey parrot (*Psittacus erithacus*). *Journal of Comparative Psychology*, *111*(1), 63-75.
- Pfungst, O., & Stumpf, C. (1907). *Das Pferd des Herrn von Osten: der kluge Hans. Ein Beitrag zur experimentellen Tier-und Menschen-Psychologie*: Barth.
- Phillips, W., Barnes, J. L., Mahajan, N., Yamaguchi, M., & Santos, L. R. (2009). 'Unwilling' versus 'unable': capuchin monkeys' (*Cebus apella*) understanding of human intentional action. *Developmental Science*, *12*(6), 938-945.
- Povinelli, D. J., & Eddy, T. J. (1996). Chimpanzees: Joint visual attention. *Psychological Science*, *7*(3), 129-135.
- Price, S. A., & Brosnan, S. F. (2012). To Each According to his Need? Variability in the Responses to Inequity in Non-Human Primates. *Social Justice Research*, 1-30. doi: 10.1007/s11211-012-0153-z
- Price, S. A., Beran, M. J., Wilson, B. J., & Brosnan, S. F. (in prep). Responses to the Chicken Game.

- Range, F., Horn, L., Virányi, Z., & Huber, L. (2009). The absence of reward induces inequity aversion in dogs. *Proceedings of the National Academy of Sciences, 106*(1), 340-345.
- Range, F., Leitner, K., & Virányi, Z. (2012). The influence of the relationship and motivation on inequity aversion in dogs. *Social Justice Research, 1*-25.
- Reynolds, G. S. (1961). Behavioral contrast. *Journal of the Experimental Analysis of Behavior, 4*(1), 57-71.
- Rilling, J. K., Gutman, D. A., Zeh, T. R., Pagnoni, G., Berns, G. S., & Kilts, C. D. (2002). A neural basis for social cooperation. *Neuron, 35*(2), 395-405.
- Roma, P. G., Silberberg, A., Ruggiero, A. M., & Suomi, S. J. (2006). Capuchin monkeys, inequity aversion, and the frustration effect. *Journal of Comparative Psychology, 120*(1), 67-73.
- Rose, L. M. (1997). Vertebrate predation and food-sharing in *Cebus* and *Pan*. *International Journal of Primatology, 18*(5), 727-765.
- Rosenthal, R. (1963). On the social psychology of the psychological experiment: 1,2 The experimenter's hypothesis as unintended determinant of experimental results. *American Scientist, 51*(2), 268-283.
- Rosenthal, R., & Fode, K. L. (1963). The effect of experimenter bias on the performance of the albino rat. *Behavioral Science, 8*, 183-189.
- Rosenthal, R., & Halas, E. S. (1962). Experimenter effect in the study of invertebrate behavior. *Psychological Reports, 11*(1), 251-256.
- Russel, P. A. (1973). Relationships between exploratory behavior and fear: a review. *British Journal of Psychology, 64*, 417-433.

- Russell, Y. I., Call, J., & Dunbar, R. I. M. (2008). Image scoring in great apes. *Behavioural processes*, 78(1), 108-111.
- Sanfey, A. G., Rilling, J. K., Aronson, J. A., Nystrom, L. E., & Cohen, J. D. (2003). The neural basis of economic decision-making in the ultimatum game. *Science*, 300(5626), 1755-1758.
- Schmitt, V., Schloegl, C., & Fischer, J. (2014). Seeing the experimenter influences the response to pointing cues in long-tailed macaques. *PloS one*, 9(3), e91348.
- Sheskin, M., Ashayeri, K., Skerry, A., & Santos, L. R. (2013). Capuchin monkeys (*Cebus apella*) fail to show inequality aversion in a no-cost situation. *Evolution and Human Behavior*, 35, 80-88.
- 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(3), 505–509.
- Silk, J. B., Brosnan, S. F., Vonk, J., Henrich, J., Povinelli, D. J., Richardson, A. S., Lambeth, S. P., Mascaró, J., & Schapiro, S. J. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. *Nature*, 437(7063), 1357-1359.
- Sommer, R. (1965). Further studies of small group ecology. *Sociometry*, 337-348.
- Sommer, R. (1967). Small group ecology. *Psychological Bulletin*, 67(2), 145-152.
- Subiaul, F., Vonk, J., Okamoto-Barth, S., & Barth, J. (2008). Do chimpanzees learn reputation by observation? Evidence from direct and indirect experience with generous and selfish strangers. *Animal Cognition*, 11(4), 611-623.
- Takimoto, A., & Fujita, K. (2011). I acknowledge your help: Capuchin monkeys' sensitivity to others' labor. *Animal Cognition*, 14, 715–725.

- 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*(2), 249-261.
- Talbot, C. F., Freeman, H. D., Williams, L. E., & Brosnan, S. F. (2011). Squirrel monkeys' response to inequitable outcomes indicates a behavioural convergence within the primates. *Biology letters*, *7*(5), 680-682.
- Talbot, C. F., Parrish, A. E., Essler, J., Leverett, K., Paukner, A., Brosnan, S. F. (in prep). Dissecting the inequity response in capuchin monkeys (*Cebus apella*) .
- Tinklepaugh, O. L. (1928). An experimental study of representative factors in monkeys. *Journal of Comparative Psychology; Journal of Comparative Psychology*, *8*(3), 197-236.
- Tuytens, F. A. M., de Graaf, S., Heerkens, J. L. T., Jacobs, L., Nalon, E., Ott, S., Stadig, L., Van Laer, E., Ampe, B. (2014). Observer bias in animal behaviour research: can we believe what we score, if we score what we believe? *Animal Behaviour*, *90*, 273-280.
- Van Wolkenten, M., Brosnan, S. F., & de Waal, F. B. M. (2007). Inequity responses of monkeys modified by effort. *Proceedings of the National Academy of Sciences*, *104*(47), 18854-18859.
- Wascher, C. A. F., & Bugnyar, T. (2013). Behavioral responses to inequity in reward distribution and working effort in crows and ravens. *PLoS ONE*, *8*(2), e56885.
- Wiesenfeld, B. M., Swann, W. B., Brockner, J., & Bartel, C. A. (2007). Is more fairness always preferred? Self-esteem moderates reactions to procedural justice. *Academy of Management Journal*, *50*(5), 1235-1253.
- Wood, J. N., Glynn, D. D., Phillips, B. C., & Hauser, M. D. (2007). The perception of rational, goal-directed action in nonhuman primates. *Science*, *317*(5843), 1402-1405.

APPENDICES

Appendix A

Summary of pairs' performances across studies. Sessions were always run to completion, so all measures of trials completed are out of 60 trials. Study 1 includes the number of trials completed on the inequity task and number of joystick touches for pairs that completed 0 of the 60 trials. Study 2 includes whether pairs passed Chicken Game criterion (completing two full sessions of 200 trials within two hours on two separate days); if pairs passed criterion, the number of trials completed on the subsequent inequity task is indicated (as well as the number of joystick touches for subjects that completed 0 of 60 trials). Study 3 includes the average number of trials completed over four sessions (criterion required an average of 20 trials), and the average number of trials completed over 8 sessions for the two pairs that completed the study. An asterisk indicates that the session was terminated early, based on only two sessions of 60 trials. Study 4 includes whether pairs passed the Chicken Game criterion (completing at least 10 trials in 10 minutes) and the number of trials completed in the subsequent inequity task for individuals that passed criterion. Study 5 includes the average number of trials completed over the 8 sessions for the two pairs that completed the study.

| Pair | Study 1 | | Study 2 | | | Study 3 | | Study 4 | Study 5 |
|-------------------|--------------------------|--|--------------------------------|--|--|--|--|--|---|
| | # trials completed (/60) | # times joystick touched (for sessions with 0/60 trials completed) | Passed Chicken Game criterion? | # trials completed for inequity task (/60) | # times joystick touched (for sessions with 0/60 trials completed) | Passed criterion? (avg. of 20 responses over 4 sessions) | Avg. # trials completed over 8 sessions (for 2 pairs that completed study) | Passed Chicken Game criterion?; # trials completed for inequity task (/60) | Avg. # of trials completed over 8 sessions (for 2 pairs that completed study) |
| Gambit Nkima | 19; 12 24; 11 | --- --- | Yes (within 6 sessions) | 9; 55 28; 26 | --- --- | Yes; 41.5 Yes; 32.75 | 43.5 26.9 | --- | --- |
| Wren Lily | 4 26 | --- --- | No | --- | --- | --- | --- | --- | --- |
| Liam Logan | 14; 60 14; 0 | --- 0 | No | --- | --- | --- | --- | --- | --- |
| Drella Griffin | 54; 31 0; 0 | --- 5; 0 | Yes (within 3 sessions) | 59; 27 0; 0 | --- 6; 0 | --- | --- | --- | --- |
| Gabe Nala | 0; 0 0; 50 | 0; 1 0 | Yes (within 3 sessions) | 0; 0; 0 35; 4; 60 | 3; 0; 0 --- | --- | --- | --- | --- |
| Liam Nala | --- | --- | --- | --- | --- | No; 1.5* Yes; 37* | --- | No | 45 46.6 |
| Wren Drella | --- | --- | --- | --- | --- | Yes; 22.8 Yes; 39.5 | 28.5 38.9 | --- | --- |
| Widget Lily | --- | --- | --- | --- | --- | Yes; 29.5 No; 5.75 | --- | Yes; 31 Yes; 5 | 45 16.6 |