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Gambling and Decision-Making Among Primates: The Primate Gambling Task

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GAMBLING AND DECISION-MAKING AMONG PRIMATES: THE PRIMATE GAMBLING TASK

by

DARBY PROCTOR

Under the Direction of Sarah F. Brosnan

ABSTRACT

Humans have a tendency to engage in economically irrational behaviors such as gambling, which typically leads to long-term financial losses. While there has been much research on human gambling behavior, relatively little work has been done to explore the evolutionary origins of this behavior. To examine the adaptive pressures that may have led to this seemingly irrational behavior in humans, nonhuman primates were tested to explore their reactions to gambling type scenarios. Several experiments based on traditional human economic experiments were adapted for use with a wider variety of primate species including chimpanzees and capuchin monkeys. This allowed for testing multiple species using similar methodologies in order to make more accurate comparisons of species abilities. This series of tasks helps to elucidate risky decision-making behavior in three primate species.

INDEX WORDS: Gambling, Nonhuman primates, Chimpanzee, Capuchin monkey, Iowa Gambling Task

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by

DARBY PROCTOR

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1 Introduction and Literature Review

> The gambler is apparently the last optimist; he is a creature totally unmoved by experience. His belief in ultimate success cannot be shattered by financial loss, however great. He did not win today? So what? Tomorrow will be lucky. He's lost again? It doesn't prove a thing; someday he's bound to win.
>
> *Edmund Bergler (1957)*

Gamblers make decisions that are often difficult to explain. This is because gambling decisions are often based on feelings, irrational thoughts, and a misunderstanding of odds rather than being based on the probability of earning a net profit (Bergler, 1957; Rogers, 1998). Due to these factors, gambling often leads to the economically irrational decision to keep gambling in spite of mounting losses. This phenomenon occurs worldwide, in a wide variety of settings and across cultures (see the following as examples: Bechara et al., 1997; Bechara, 2005; Hills et al., 2001; Blaszczynski & Silove 1995; Walker et al., 2005; Cotte 1997; Williams & Wood 2007; Malloy-Diniz et al., 2008). Why, then, are some people willing to risk it all for an economic windfall? Gambling is, in essence, a decision-making context where potential benefits must be weighed against the risk of engaging in the behavior. Understanding why emotional reactions overrule accurate cost/benefit analyses in certain risk scenarios may help to elucidate this seemingly irrational human behavior. For instance, it may be that there was an evolutionary benefit to having strong emotional reactions to possible winning scenarios, even if they appear irrational in some contexts (Frank, 1988; Rogers, 1998; Bechara et al., 1997; Bechara, 2005).

Studying other primate species may elucidate whether responses to risk scenarios serve some adaptive role that is not apparent when studying human gambling behavior in isolation. To elucidate the evolutionary basis of risky decision-making in gambling contexts, I conducted a phylogenetic analysis of risky decision-making in the primate lineage. This dissertation explores three specific research questions through the use of the Primate Gambling Task (PGT), a modified version of the Iowa Gambling Task (IGT; Bechara et al., 1997). The first is how nonhuman primates (NHPs) negotiate the conflict between potential immediate rewards and long-term payoffs in gambling situations. Second, I explored gambling decisions as a function of satiation levels in NHP populations, as behavioral ecology studies suggest that species' risk preferences may shift with their energetic demands. Third, since primates are social animals and gambling decisions in humans are often made in front of others (for instance, in casinos), I used a social gambling task to determine if NHPs make different types of decisions in a social context in which another individual was rewarded, but could not influence outcomes. Finally, I used another experimental economics game, the Ultimatum Game (UG), to explore how decision-making is affected if a partner could influence payouts for both individuals, as is the case in many human gambling scenarios. This series of comparative studies begins to answer some of the questions regarding the evolution of risky decision-making in gambling scenarios across the primates.

1.1 Why Study Nonhuman Primates?

Comparing multiple species of primates, including humans, can elucidate similarities and differences in behavior across those species. Critically, these comparisons allow the evolutionary function of a behavior to be elucidated. In other words, exploring similarities and differences can help us understand why a given behavior was beneficial and selected for in the evolutionary past. Similarities between species can occur for one of two reasons. First, animals may have some phylogenetic continuity with closely related species. That is, due to shared common ancestry, species may exhibit similar traits. For example, all primates have opposable thumbs because the ancestor of all living primates had opposable thumbs. However, other factors, such as environmental conditions, can also lead to similarities, which arise through convergent evolution.

Convergent evolution occurs when some selective pressure leads two species with dissimilar ancestries to develop similar traits. Complex eyes, for example, seem to have evolved many times in many different animal groups (Land & Nilsson, 2002). This is because sight is a useful tool for such activities as navigating the environment and acquiring food. Thus, primates and flies both have complex eyes, not because of shared ancestry, but because eyes are evolutionarily useful. Recognizing convergences can help in identifying which selective pressures encouraged a trait to evolve. It is important to understand the distinction between phylogenetic continuity and convergent evolution, as an understanding of whether common descent or common selective pressures led to the trait in question can help to elucidate the evolutionary function of a given behavior, as behavioral traits are subject to similar evolutionary influences as anatomical adaptations (Darwin, 1859).

While it is useful to study the evolution of behaviors across diverse animal groups, I chose to focus on primates due to their close evolutionary relationship with humans. Studying primates that are closely related to humans is useful to determine if a trait is due to common descent. Additionally, studying more distantly related primates helps understand what adaptive pressures may have led to either convergent evolution or species differences. Here, I compare humans to chimpanzees (*Pan troglodytes*) and capuchin monkeys (*Cebus spp*). Chimpanzees are of clear interest due to their close evolutionary relationship with humans, as they shared a common ancestor as recently as ~6 million years ago (Steiper & Young, 2006). Capuchins have been used in past research because of their convergences with chimpanzees and humans in the realm of cooperation and social behavior (de Waal & Davis, 2003), but they diverged from the ape lineage over 40 million years ago (Steiper & Young, 2006), allowing for a comparison of humans to a more distantly related primate. Thus, because of these similarities both of these nonhuman primate species were used in the series of PGT experiments.

1.2 What is Risk?

A critical component of any gambling scenario is risk. Gamblers must stake their own wealth in order to participate, even though the risk of losing their stake is higher than the probability of winning. The amount of risk involved in gambling often influences the potential payout, such that riskier bets pay out more in terms of value but the odds of winning are smaller. While most people have some inherent understanding of risk, it is useful to examine how the term is used in the extant literature. MacLean and colleagues (2012) point out that the definition of risk used in the animal and gambling literatures is somewhat different than the traditional economic definition of risk. In economics, risk typically refers to a decision between options with known probabilities (Knight, 1921; Luce & Raiffa, 1957), while ambiguity refers to a decision between options with unknown probabilities (Huettel et al., 2006; Rosati & Hare, 2011). However, animals are typically classified as either risk seeking or risk averse based on results of choice tasks in which they are given a choice between two options that both involve unknown probabilities of payouts (e.g., Kacelnik & Bateson, 1996; MacLean et al., 2012; Shafir, 2000). One option always contains a small, minimally variable reward, while the other option is typically much more variable, with different payouts on each choice. The average payouts of both options are held constant, so all that varies is the way the payoff is received. If animals chose the less variable reward they are classified as risk averse, while if they chose the more variable option they are classified as risk seeking.

However, in such choice tasks and in gambling scenarios there are components of both ambiguity and risk. Initially, participants are not aware of the probabilities involved in each option, so ambiguity dominates. But, risk becomes the dominant feature as probabilities become apparent over the course of the task. Here, I was less interested in ambiguous decision-making than strategic behavior during the course of interacting with variable reward structures. Thus, I followed the animal literature and used the term risk to refer the amount of variability in potential reward outcomes, even if initially the probabilities associated with that variability were unknown.

1.3 Why Gambling?

There are three main reasons why gambling is a useful topic to study. First, while we typically think about gambling in terms of casino-style games, the basic components of gambling apply to a much wider variety of contexts. In the most basic form, gambling can be defined as an "activity that involves an element of risk or chance whereby money or a valued object is either won or lost" (Ladouceur et al., 2000). Note that in this definition of gambling, ownership of the valued resource prior to the gamble is not required. Thus, when two individuals compete over a resource, the winning individual gains the resource, while the other individual has lost the potential benefit of that resource. In this view of gambling, situations such as food or mate competition are also types of gambling decisions. That is, when animals compete over a resource there is an element of risk, such as possible injury or forgoing other resources, which must be weighed against the probability of success.

Often, animals, including humans, make optimal decisions based on their assessment of these odds. Male red deer (*Cervus elaphus*), for example, most often avoid fights when they are likely to loose, but will fight when the potential benefits, such as mating access, are high (Clutton-Brock & Alba, 1979; Clutton-Brock et al., 1979). They use roar contests to assess the size of their competitor, as size is a fairly accurate predictor of who will win the fight. If an individual realizes through a roar contest that he is the smaller individual, the potential costs (e.g., injury or death) would likely outweigh the benefits of pursuing the conflict. Thus, red deer make fighting decisions based on fairly accurate assessments of their competitor. Studying other risk scenarios, such as gambling, can aid in elucidating the pattern of decisions that animals make in risky situations.

Second, studying gambling type behaviors across species can help determine what social and environmental pressures influence risky decision-making. For example, the social system of a species may influence how much risk they are willing to accept in mate acquisition and foraging decisions. It is probable that promiscuous species, such as chimpanzees, would tolerate greater risk for a mating opportunity, as there are fewer mating opportunities for males due to their dominance structure. In contrast, a pair-bonded species, such as gibbons or tamarins, may tolerate less risk, as there are, theoretically, enough mates for each individual. Similarly, species that live in large social groups may have a higher tolerance for risk in food acquisition relative to a solitary species due to within group competition. The environment can also influence foraging decisions, as species with less overall food availability, such as desert-living lemurs, may be more risk prone in order to find sufficient food relative to a species with more plentiful food resources. Comparing the decision-making patterns of a variety of species could aid in parsing what factors influence the evolution of risk-taking strategies.

The final reason that gambling is a particularly interesting area to study is that animals do not always accurately assess probabilities of success. One of the areas in which this is most apparent is in human gambling behavior, where accurate assessments of the probability of winning do not drive gambling decisions (Bergler, 1957; Rogers, 1998). Thus, gambling is an exemplar of when accurate cost/benefit analyses fail to influence behavior and can be used to assess when and why deviations from optimal strategies occur. Researching other primates' decisions in risky contexts may help to elucidate the evolutionary pressures that resulted in human gambling behaviors.

1.4 Gambling in Humans

Gambling has been studied extensively in human adults and there are entire journals devoted to the study of this topic (e.g., Journal of Gambling Studies, Journal of Gambling Issues, etc.). However, covering the entire range of human gambling behaviors is beyond the scope of this dissertation. Rather, the focus here is on the Iowa Gambling Task (IGT), which was the model for the PGT series of studies. In the IGT (Bechara et al., 1997), participants are given $2000 in facsimile money and are told to play the game with the goal of making as much money as possible. Participants are presented with four decks of cards and are free to choose a card from any deck. Each card will indicate a winning or losing amount. Unbeknownst to the subjects, two decks are arranged so that they are advantageous and lead to the most overall earnings ($4500), but have no large payouts on any one card. The other two decks are disadvantageous and lead to overall losses (negative $500), but include some very large payouts. However, they are more variable and also include more frequent and larger losses. The decks are set up such that participants cannot predict which individual card will have a payout or penalty, although they can develop strategies for interacting with the deck as a whole. However, selecting a advantageous deck does not necessarily indicate risk aversion because the advantageous decks also leads to the greatest overall earnings. One problem with this reward structure is that a person who was risk averse and a person motivated by maximizing their rewards would both select the advantageous decks. Thus, risk aversion and reward maximization strategies are confounded in this payout structure. However, it was not the intent of the IGT to parse these influences.

The initial study done with the IGT (Bechara et al., 1997) was conducted with typical adults as well as with patients with prefrontal damage and associated decision-making deficits. Bechara and colleagues explored whether decision-making in this gambling task was the result of overt reasoning or whether it was preceded by a preconscious state of knowledge. To test this, they measured galvanic skin conduction to assess any physiological evidence of responses during the IGT. Typical participants began to have skin conduction responses when they selected the disadvantageous decks and started avoiding them prior to being able to express that they had developed a choice strategy. Thus, while initially attracted to the potential of larger payouts on a trial-by-trial basis, typical participants rapidly developed a preference for the advantageous decks (see for example; Wood et al., 2005; Sevy et al., 2007; Bowman & Turnbull, 2003; Turnbull et al., 2005). However, despite this, in normal participants, approximately one-third could not inhibit their preference for a disadvantageous deck (Bechara & Damasio, 2002). Nonetheless, amongst patients with impaired decision-making abilities, virtually all continued to choose decks with high risk and low payout. This pattern holds true whether participants were playing for facsimile money or real money (Bowman & Turnbull, 2003).

Bechara and colleagues (1997; 2002) conclude that two separate processes occur in parallel during the IGT. First, participants develop a sensory representation that holds non-declarative knowledge, which is why skin conductance responses begin before participants are able to verbalize the payoff structure of the decks. Second, participants develop a strategy based on overt reasoning where they recall prior wins and losses and plan how to interact with the decks on subsequent trials. Thus, while strategies based on a more complex understanding of the task can and do develop, they are not a prerequisite for participants to respond to the contingencies of the task. This suggests that a similar task would be successful with NHPs, as individuals do not need to develop declarative knowledge about the decks, but instead may rely on feelings and impressions.

The IGT (Bechara et al., 1997) launched an entire literature of work using similar methodologies, including widespread use among human clinical populations. It has been used to study people suffering from schizophrenia (Sevy et al., 2007), obsessive-compulsive disorder (Whitney et al., 2004), Huntington's disease (Campbell et al., 2004), and substance abuse and dependence (Goldstein et al., 2007; Bechara & Martin, 2004; Martin et al., 2004), among others. The general findings indicate that these clinical populations are more prone to risk taking behaviors than typical adults. However, this literature is beyond the scope of this dissertation as I focus on typical populations of humans and NHPs.

1.5 Risky Decision-Making in Nonhumans

Gambling behaviors have been studied in a variety of species from pigeons to various species of primates. Although there are few studies specifically addressing the IGT in nonhumans (which is discussed in the following section), there are studies that address similar questions, albeit with different methodologies. In a meta-analysis of 59 studies on risky decision-making in relation to foraging (covering 28 species including mammals, insects, fish and birds), most animals were either consistently indifferent or averse to risk. However, at times, a single species (e.g., pigeons) was classified as having different risk preferences in different studies, with no clear indication of why this would occur.

A possible explanation for the lack of clear risk preferences in some animals is that the various methodologies used may be driving risk preferences (Kacelnik & Bateson, 1996). Many studies included in Kacelnik and Bateson’s meta-analysis confounded the issues of quantity of reward and access to rewards. For example, if a rat is given a choice of two feeders, one with a steady payoff and one with a risky payoff, and is given time to explore both, the rat will be indifferent to risk, as there is no cost to sampling both feeders. However, if the rat is only allowed one choice in a given time period, the rats tend to pick the less risky choice, indicating risk aversion (Roche et al., 1997). There are many other methodological differences that may also be driving factors in how risk preferences are instantiated (Shafir, 2000). Unfortunately, as all of those studies varied not only with respect to outcomes, but also methodologies, it is difficult to compare them with each other and to the existing literature on human risky decision-making.

Similarly, outcomes of decision-making studies that assess risk taking and risk aversion with NHPs are varied, with no coherent picture emerging as to how species' risk preferences are expressed. With regard to the nonhuman apes, chimpanzees and orangutans appear to be risk prone, while bonobos and gorillas appear to be more risk averse (Heilbronner et al., 2008; Haun et al., 2011). However, these studies differed in the degree of risk aversion/proneness shown by each species. Haun et al. (2011) reported that chimpanzees, bonobos, orangutans, and gorillas selected the risky option more than 50% of the time. In contrast, Heilbronner et al. (2008) found that bonobos only selected the risky option approximately 30% of the time. Similarly conflicting results were found in a number of primate species (Behar, 1961; Hayden & Platt, 2007; McCoy & Platt, 2005; Steelandt et al., 2011). It is possible that slight variations in methodology change these animals' responses to risk in choice tasks, a phenomenon known from other tasks in the animal literature (Brosnan et al., 2011). Thus, a task is needed that can be broadly applied to a variety of NHP species to enable cross species and cross study comparisons.

1.6 IGT in Nonhumans

Unfortunately, there has been little headway into testing the IGT in nonhumans (Potenza, 2009), although there are a few studies that address the IGT in rats and mice using paradigms similar to human experiments (Rivalan et al., 2009; Zeeb et al., 2009). For the typical studies, test enclosures were built with holes aligned on one wall, representing the decks of cards in the human experiments. The rodents had to select a hole by touching it with their nose. Rewards were then provided based on the payout structure of the hole. Another variant involved mazes with different paths leading to different reward outcomes, such that each maze path was equivalent to a deck of cards (van den Bos et al., 2006).

In all of these studies, most rodents successfully learned which options were most profitable and preferentially selected those options (van den Bos et al., 2006; Rivalan et al., 2009; Zeeb et al., 2009). The authors suggested the rats behaved similarly to humans, such that individuals were able to inhibit choosing the highly variable option in order to maximize rewards over the long-term. However, as in human IGTs, this design confounds risk aversion and reward maximization, as both strategies would result in the same decision-making pattern.

Moreover, while the majority of rats acted to maximize their long-term payoff, a minority systematically persisted in choosing the high variability option (Rivalan et al., 2009). The proportion of risk prone rats was similar to the proportion of humans who were risk prone in similar studies (~30%; Bechara & Damasio, 2002), suggesting that across species, risk aversion varies amongst individuals, and that there may be a percentage of individuals whose strategy diverges from the typical species' preference.

Additionally, Zeeb et al. (2009) found that while the most advantageous deck was the most preferred by rats, the second most preferred was the highest variability deck. Thus, like humans, rodents generally choose the low variability, high overall reward option, but some individuals are nonetheless temped by the high-variability option with the potential for large payouts on one trial. Unfortunately, studies with humans have not specified what deck was the second most preferred. It would be interesting to see if the majority of humans, like rats, are also tempted by the high-risk, high-payoff option. Again, this highlights the need to study multiple species with similar paradigms so that these types of comparisons are possible.

1.7 Challenges of Comparative Research

In comparative research, there are many concerns when adapting a methodology to be appropriate for multiple species. For example, some authors have pointed out that humans are often given unfair advantages when compared to nonhumans in experimental research (Boesch, 2007; 2010; de Waal et al., 2008). In particular, humans are typically given verbal instructions. This is a clear advantage when compared to other animals that cannot use language and so must interpret a task over the course of the experiment. Additionally, humans are tested with members of their own species, while animals are often tested by another species, and this may confer some advantage to humans. It is important to avoid giving any one species an advantage in comparative research because that could lead to inaccurate assertions of species differences when in reality they may be due to methodological variation. Thus, methodologies should be as similar as possible across species to have an accurate comparison of their abilities.

However, it would be equally inaccurate to test a species using a paradigm in which there was a minimal chance of success due to some characteristic of the species or their ecology (Rumbaugh, 1970). It can be necessary and appropriate to adjust a paradigm based on a species specific trait. As an example, monkeys are often trained to interact with computers for cognitive testing (e.g., Evans et al., 2008). The vast majority of monkeys do this by using their hands to manipulate the computer, similar to how humans use computers. However, lemurs, whose lineage split from monkeys and apes ~ 77 million years ago (Steiper & Young, 2006), are more reliant on their nose rather than their hands for interacting with the environment. Thus, when lemurs are asked to do computerized testing, they often manipulate the computer with their nose rather than their hands (e.g., Merritt et al., 2007). While lemurs and monkeys may interact with computers in different way (i.e., nose versus hands), the same experimental methods can be used with either response method. But, if lemurs were forced to use their hands like monkeys, there may have been performance differences that were attributed to species differences whereas in reality they were the result of a methodological advantage given to the monkeys.

There is, however, no consensus in the literature regarding what constitutes a species appropriate methodology. On one hand, methodologies need to be as similar as possible across species. Nevertheless, methodological changes may be needed to make a task species appropriate. Finding a balance between these competing needs can be challenging and there is often disagreement in the literature when different authors use varying methodologies to address the same question and arrive at different conclusions (Boesch, 2007; de Waal et al., 2008; Rumbaugh, 1970).

I designed the series of experiments in this dissertation using suggestions from Boesch (2007; 2010) regarding how to make experiments species appropriate and to avoid giving any species an advantage. First, I attempted to avoid designing tasks from an anthropocentric point of view. That is, I tried to design the tasks so they would be accessible to a broad range of primate species, not just humans. For example, the PGT experiments do not require any training. This means that I did not have to give detailed verbal instructions to humans. Instead, humans and NHPs alike had to interpret the task through the course of the experiment. Thus, no one species had an advantage due to a better understanding of the contingencies of the tasks. Additionally, I tested my tasks on multiple populations of a species when possible. Boesch (2010) suggested that due to the specialized cognitive training of some captive animals, they may not be representative of the species as a whole (Note that this is also an issue in human research which is primarily conducted in Western, educated, industrialized, rich, and democratic countries; Henrich et al., 2010). When possible, I used chimpanzees from two research facilities with very different rearing and testing experiences to get a broader representation of the abilities of these animals. Although it was not possible to remove all potential species advantages or confounds, these steps should have made my experiments better able to address species differences that were not due to methodological variation and not due to specific rearing or testing histories of the subjects.

Of particular interest is how researchers have modified the IGT to be appropriate for nonhuman animals. In the IGT, cards may contain losses, which researchers take from the human's earnings. However, it is difficult to take earned rewards away from nonhuman animals. In an effort to simulate some type of penalty, van den Bos and colleagues (2006) used rewards treated with quinine (a bitter but edible substance) in the highly variable option. In contrast, Rivalan et al. (2009) and Zeeb et al. (2009) used time-out periods that varied in length depending on the selected option, with longer time-outs being associated with higher rewards and short time-outs with lower, but more consistent payouts.

However, changing the IGT in the manner described above results in potential confounds. For example, when using quinine treated rewards (van den Bos et al., 2006), the rewards varied both on quality and quantity. There are no IGT studies in humans that combine these reward factors. It is possible that variation in the quality of rewards could lead animals to make different choices than if only quantity was variable. Thus, van den Bos and colleagues' study may (or may not) be testing slightly different motivations in the rodents than in humans. If a similar task had been run with humans and performance was similar to a traditional IGT, confidence that this design was equivalent to the human literature would increase. Thus, testing nonhuman versions of tasks with humans is needed to make a more accurate species comparison.

1.8 The Primate Gambling Task

The Primate Gambling Task (Experiment 1, Chapter 2) was designed as a way to establish gambling behavior in chimpanzees, capuchin monkeys and humans, using a comparable method to a standard human gambling game, the IGT. The Primate Gambling Task, as well as the IGT, meet the definition of gambling defined above (Ladouceur et al., 2000), as they both involve decisions with an element of risk than can result in a win or a penalty or loss, making these methodologies a useful analog for gambling. I used a similar methodology with all three species in order to be able to directly compare the results among the different members of the primate lineage. Additionally, in Chapter 6, I discuss preliminary results of this task with human children.

Here, I used small stackable Tupperware type containers (118 mL Gladware mini-rounds) in place of decks of cards. Each "deck" of containers was opaque and visually distinct from the other deck. Rewards were hidden inside the containers, but some containers were left empty as a penalty. Participants selected a deck and were given the reward from the topmost container of that deck. I tested three conditions to better compare these results to the disparate methodologies that are present in both the human and nonhuman literatures. First, in the Equitable PGT (EPGT) condition, I used the standard payout model from the animal literature where average payouts of the low and high variability options led to the same overall quantity of rewards. In the PGT condition, I used the standard payoff structure from the IGT, in which the low variability option paid out more overall than the high variability option, but may have paid out less on individual trials. And finally, in the reverse PGT condition, I used a payout structure where the high variability deck led to the greatest overall rewards and thus risk aversion was in conflict with reward maximization. This allowed me to 1) compare human and nonhuman preferences on a traditional animal task, 2) compare human and nonhuman preferences on a traditional human task and, 3) determine if these choices were made to maximize payouts or to avoid (or seek) risk.

1.9 Hunger and Decision-Making

As discussed earlier, Kacelnik and Bateson (1996) classified most animals in their meta-analysis as risk averse or indifferent to risk. However, in some studies this preference varied depending on the animal's energy budget (Caraco, 1981; Caraco et al., 1980; Stephens, 1981). That is, depending on energy requirements sometimes it may be in an animal's best interest to opt for a riskier or more reliable food source depending on the ecology of the species in question. For example, juncos (a small bird) prefer a consistent reward to a variable one. However, in colder temperatures, where the birds need more energy than is typical to keep warm and food is less available, they prefer a highly variable food source, as a big payout is the only way for them to meet their energetic needs (Caraco, 1981). Yet, chimpanzees appear to have the opposite strategy, hunting (a risky prospect, as success is not certain) only when plentiful plant-based food sources are available (Gilby & Wrangham, 2007). This may occur because even if the hunt fails, the chimpanzees have enough energy resources to cope with potentially missing a meal and the energetic expenditures of the hunt. Thus, a species' ecology and the individual's current situation clearly impact risk preferences, but not always in the same way.

However, these examples were due to large-scale food availability, either deprivation or abundance. What is unknown is whether risk preferences vary as a function of more typical daily variation, such as short-term hunger and circadian rhythms. If so, these are potential confounds in any risk preference study. Thus, a micro level analysis of how these factors may influence risk preferences. Therefore, Experiment 2 (Chapter 3) builds on the findings from Experiment 1 to explore whether typical daily variations, in this case relative hunger levels or circadian rhythms, affect gambling decisions in NHPs. To do so, I retested the NHPs using the same methodology as in Experiment 1, but I tested them after the typical short-term hunger that results from fasting overnight, as is typical in diurnal animals (Anderson, 1998). This was presumably when the NHPs were the hungriest as their last meal was ~12 hours prior when they were fed their evening meal. I then compared these data to their performance in Experiment 1, where animals always had received food prior to testing (~20% of their daily caloric intake). This allowed me to test whether these animals' sensitivity to risk changed in response to a typical short-term fluctuation in their state (e.g., satiation). This may provide a more naturalistic understanding of how hunger, rather than a drastic reduction in food availability, alters animals' decision-making. No animal was ever food deprived for this study and received their typical caloric intake regardless of performance on this task. Humans were not included in this study as I could not manipulate their hunger.

1.10 Social Influences on Gambling Behavior

The majority of research on the IGT involves solitary subjects (Orford et al., 2010). However, humans outside of the laboratory typically gamble around or with other people. For example, in the U.S. in 2007 (the most recent year with available data), 65% of total gaming revenue came from casinos, which are inherently social (American Gaming Association, 2011). Unfortunately, statistics from other social gambling activities, such as racetrack betting, were not available, so the total percent of gaming that occurs in a social setting is unknown. Regardless, it appears that well over half of the legalized gambling in the U.S. takes place in social settings, which influences gambling behavior (Rockloff, 2010; Rockloff & Dyer, 2007; Rockloff et al., 2010).

Evidence of social influences in competitive situations can be traced to Triplett (1897), who found that participants in bicycle races performed at higher speeds when there were other participants racing with them compared to individual time trials, despite both being competitive events. This same phenomenon is seen in gamblers (Rockloff, 2010; Rockloff & Dyer, 2007; Rockloff et al., 2010). In studies with simulated electronic gambling machines where participants were told that there were other players in different rooms, players made more bets and lost more money (Rockloff & Dyer, 2007; Rockloff, 2010) compared to those who were not told that anyone else was playing. Crowds also influenced participants to make smaller bets but gamble longer (Rockloff et al., 2010), an effect more pronounced in people with gambling disorders (Rockloff, 2010). These studies indicate that social contexts increase the persistence of gambling and lead to greater long-term losses. While there are no studies on how social situations may affect gambling in NHPs, there is evidence that their strategic behavior can be influenced by the presence of other individuals (Bräuer et al., 2007; Brosnan et al., 2006; Brosnan et al., 2010; Hare et al., 2000; Hare et al., 2003; Hare et al., 2006; Hare & Tomasello 2004; Melis et al., 2006;).

Experiment 3 (Chapter 4) addressed whether the presence of conspecific peers affected humans' and NHPs' gambling decisions similarly to the behavioral changes seen in humans in typical gambling situations. For this, I used the same general design of the PGT with one modification. In this experiment, another member of their social group was given the reward from the deck the subject did not choose, in order to draw the subject's attention to the partner, prior to the subject being rewarded.

However, in the social PGT prepotent responses may influence decision-making more so than in solitary tasks, where other reward outcomes are unknown. That is, animals that see another individual receive a larger payoff than themselves may have a prepotent response to select that option on future trials, even if inhibiting that response would net them a larger overall reward (Lansbergen et al., 2007). Inhibiting such prepotent responses are particularly challenging for NHPs (Boysen & Bernston, 1995; Vlamings et al., 2006; Kralik et al., 2001; Silberberg & Fujita, 1996). In Experiments 1 and 2, animals could not see any reward except for the one they received, suggesting that prepotent responses were not driving choices. In contrast, in the social PGT, where a more direct comparison of rewards was possible, seeing another individual receive a larger payout may have altered the individuals' decision-making, even though the partner could not influence the reward distribution. In order to control for this effect, I also included a control condition where the rewards were removed, but there was no partner present.

1.11 The Ultimatum Game

Humans often gamble in situations where other individuals can and do influence their payouts, such as in poker. What is unclear is how NHPs, and chimpanzees in particular, respond to such contingencies. In the Ultimatum Game (UG), one individual (the proposer) can split a quantity of rewards in any way with another individual (the respondent). If the respondent accepts the offer, both players are rewarded, using the proposed split. If the respondent rejects the offer then neither player is rewarded. In other words, the UG is a simplified “bet” where the proposer has to decide whether to take the “safe” bet of an equal split of the reward, which is unlikely to be refused, or “gamble” that the partner will accept an unequal split, benefiting the proposer. Therefore, the difference between the UG and the social PGT is that the partner was able to influence reward distributions in the UG but cannot in the social PGT.

A previous UG was tested on chimpanzees, in which the animals had to wait 30 seconds in order to refuse to participate in a trial (Jensen et al., 2007). In that experiment, chimpanzees rarely refused the offer, a contrast to human results that led the authors to conclude that the chimpanzees were acting based on different motivations than humans. However, using a paradigm with humans that also included a delay in order to refuse, humans also rarely declined to participate (Smith & Silberberg, 2010). Thus, because of a slight methodological variation chimpanzee’s performance initially appeared different than humans, but once that methodological difference was controlled for, both species responded similarly to the task. These examples highlight the need to test nonhuman versions of tasks on human subjects, not just adapt human tasks to nonhumans. Without that type of control it is not clear whether performance on a given task was different because of a species difference or because of a methodological variation

In Chapter 4 (Experiment 5), I used a modified UG based on a token exchange paradigm to investigate this task in chimpanzees and human children. In this version of the UG I used tokens representing one of two offers, either an equal split of rewards or an unequal split favoring the proposer. The proposer picked one of these two offers and passed it to the respondent, who could either return it to the experimenter and be rewarded according to the proposed split, or not return the token indicating a refusal of the offer. Thus, the respondent had direct control over the rewards of the proposer, as in many human gambling games. Note that capuchin monkeys were not included in this experiment due to the complexities of the task, which included a number of controls that eliminated half of our chimpanzee population from being tested, suggesting the task would have been challenging for the monkeys.

1.12 Overview of this Dissertation

There are many unresolved questions with regard to gambling behavior and risky decision-making in the primate lineage. This dissertation was designed to begin addressing these questions through the use of a novel paradigm, the PGT, and a more established paradigm, the UG. Here, I used the PGT to address baseline gambling preferences in primates (Chapter 2), the effect of short-term hunger on gambling decisions (Chapter 3) and how social contexts influence gambling decisions (Chapter 4). Additionally, I used an experimental economics task, the UG, to further elucidate how peers can influence gambling decisions in chimpanzees (Chapter 5). Finally, I discussed the preliminary results of a PGT with children (Chapter 6). These comparative studies are particularly useful as multiple primate species were tested using similar paradigms, allowing for a more accurate comparison of gambling behavior in the primate lineage.

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2 The Primate Gambling Task

Humans have a propensity to engage in gambling activities, as evidenced by gaming revenue. For example, in Macau, Philippines, the largest gaming zone in the world, casino revenue was over $33 billion in 2011 (as a comparison, the Las Vegas strip had revenue of $6 billion; O'Keeffe, 2012). But, gambling is more than big business. There are also social issues that go along with gaming, such as problem gambling, which affects up to 5% of the population in some regions (Welte et al., 2002). Rogers (1998) reports that cognitively, decisions to gamble are often based on feelings, irrational thoughts, and a misunderstanding of odds rather than being based on probabilities of earning a net profit. Thus, humans often behave in economically irrational ways when faced with gambling decisions. That is, they act on feelings rather than what impartial logic would suggest as the optimal strategy to maximize their net gain. This leads to a conflict between the chance of an immediate payout from a bet and the long-term economic consequences (losses) of overall gambling behavior. This phenomenon is not unique to one population of humans, but occurs in a wide variety of settings and across cultures (see the following as examples: Bechara, 2005; Bechara et al., 1997; Blaszczynski & Silove, 1995; Cotte, 1997; Hills et al., 2001; Malloy-Diniz et al., 2008; Walker et al., 2005; Williams & Wood, 2007).

A critical question is why humans evolved to make seemingly irrational decisions in gambling contexts. Humans, as well as other animals, are faced with weighing costs, benefits, and risk in a variety of other contexts and often do make accurate assessments of risk and probabilities. Red deer (*Cervus elaphus*), for example, engage in roaring contests prior to physical aggression (Clutton-Brock & Albon, 1979; Clutton-Brock et al., 1979).

The sound of the roar is an honest indicator of the size of each animal. Since the larger deer is most likely to win, smaller deer often withdraw from the encounter as the risk of injury outweighs the benefit of winning the fight. Thus, they make an accurate assessment of their probability of being stronger than their rival.

Why, then, does the ability to accurately assess risk and probabilities fail in human gambling scenarios? Studying humans alone is insufficient to answer this question. Instead, a phylogenetic comparison of gambling behavior across the other primates is needed to understand what adaptive pressures may have led to the evolution of human gambling decisions. For instance, there may have been some evolutionary benefit to having strong emotional reactions to the mere possibility of some benefit even if the likelihood was low and the risk was high, such as an economic windfall or a particularly nutritious food source. It is also possible that emotional reactions represent rules of thumb that were, on average, beneficial, even if the outcomes were irrational in some situations or contexts (Bechara, 2005; Bechara et al., 1997; Frank, 1988; Rogers, 1998). Alternatively, it may be that risk-taking behavior is beneficial in some circumstances, such as acquiring mates, in which case gambling may be a side effect of this selective pressure. In order to explore the phylogeny of the behavior, we developed a methodology that can address gambling preferences in a variety of species, including humans, and be compared to the existing human literature.

One challenge to this was the wildly disparate methodologies and terminology between the literatures. These methodological issues are discussed below, but first a note is in order about terminology. The definition of risk used in the animal and gambling literature (e.g., MacLean et al., 2011; Bechar et al., 1997) is somewhat different than the traditional economic definition of risk. In the economic literature, ‘risk’ typically refers to a decision between options with known probabilities (Knight, 1921; Luce & Raiffa, 1957), while ‘ambiguity’ refers to a decision between options with unknown probabilities (Huettel et al., 2006; Rosati & Hare, 2011). However, animals are typically classified as either risk seeking or risk averse based on results of choice tasks in which they are given a choice between options that all include unknown probabilities of payouts, which economists would classify as ambiguity (MacLean et al., 2012). In such choice sessions, there are, ultimately, components of both ambiguity and risk. During initial trials, participants in these tasks are not aware of the probabilities involved in each option, so ambiguity dominates. But over the course of the session, risk becomes the dominant feature as probabilities become apparent. Here, there was less interest in the initial ambiguous decisions than in the longer term strategy for dealing with risk. Thus, in keeping with the animal and gambling literatures the term risk was used to refer to the level of variability in potential reward outcomes, including the possibility of not earning a reward, even when subjects may not have been fully aware of the probabilities of each outcome.

One common method for assessing gambling behavior in humans is the Iowa Gambling Task (IGT; Bechara et al., 1997). This task contains both an element of risk and the chance to win or lose, making it a useful analog to gambling as defined by Ladouceur et al. (2000). Bechara and colleagues developed the IGT to test decision-making in the context of gambling in both typical and clinical human populations. In their task, participants were given four decks of cards and $2000 dollars in fake money and asked to play the game with the goal of making as much money as possible.

Participants drew a card that contained either wins or losses. The decks differed in payoff structure, such that two decks resulted in net losses, but had some cards that gave high (and presumably tempting) payouts, while the other decks had no large payouts, but consistently led to larger net gains. Thus, these decks differed in both the variability of individual payouts *and* the overall payout. Participants could not predict which card would have a payout or penalty on individual trials, although they could develop strategies for interacting with the deck as a whole based on the average payouts of each deck.

Non-clinical, or typical, participants primarily formed a preference for the less variable, higher-payout deck, a finding that has been replicated in many populations (see for example; Bechara, 2005; Bowman & Turnbull, 2003; Kerr & Zelazo, 2004; Sevy et al., 2007; Turnbull et al., 2005; Wood et al., 2005). Importantly, participants initially formed these preferences without conscious awareness; they began to have skin conduction responses when they selected a deck that led to overall losses and began avoiding that deck prior to being able to articulate the structure of the game. Thus, people apparently developed a sensory representation that held non-declarative knowledge, prior to being able to verbalize their strategy (Bechara et al., 1997; Bechara & Damasio, 2002). While strategies based on a more complex understanding of the task can and do develop, they are not a prerequisite for participants to respond to the contingencies of the task. This suggests that a similar protocol would be successful with NHPs, as individuals do not need to develop declarative knowledge about the decks, but instead may be able to make stable choices based on feelings and impressions. However, because of the payout structure, the IGT does not parse whether participants acted to avoid risk or to maximize winnings, as both strategies would result in selecting the low variability, high reward deck. The animal literature on risk preferences illustrates potential methodologies that may allow researchers to distinguish between decisions made as a result of an aversion to risk and those made to maximize winnings.

Generally, in animal choice tasks, animals are given a choice between two options with the same average payoffs: one option is a low variability option that pays out small quantities of rewards, while the other option has more variability, including a chance of zero or negative payoffs (see for example: Kacelnik & Bateson, 1996; MacLean et al., 2012; Shafir, 2000). However, since the average payouts of both options are held constant in animal choice tasks and lead to the same quantity of rewards overall, all that varies is the way the payoff is received (i.e., a low or high variability reward distribution). If animals chose the less variable option they are classified as risk averse, while if they chose the more variable option they are classified as risk seeking. In this way, typical animal choice tasks assess risk at the level of the individual trial, but do not assess risk strategies when overall payouts vary.

Although the general method described above is common, the way those options are presented to animals across studies can vary dramatically. Differences in methodology are known to make a difference in subjects' responses, making it critical for comparisons between species to utilize methodologies that are as similar as is possible. These variations lead to conflicting reports of whether some species are risk prone or averse. For example, in a meta-analysis of 59 risk preference studies in nonhumans, with 28 species represented, the studies varied substantially in how they measured risk (Kacelnik & Bateson, 1996). Some studies used variability in the amount of rewards, others used time delays to the reward and some used both of these different risk scenarios simultaneously. When risk was measured by variability in the amount of rewards, animals were generally either risk averse or indifferent. However when risk was measured by delay to rewards, animals were "universally risk prone." Perhaps not surprisingly, utilizing different methodologies resulted in different risk preferences even within the same species.

This holds true both across species and in studies on nonhuman primates (NHP). For example, two studies assessed risk preferences in bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) using the same population of NHPs, and, in several cases, the same individuals, but found different risk preferences (Heilbronner et al., 2008; Haun et al., 2011). In a two choice task between a consistent number of grapes (low variability option) and a variable quantity of grapes (higher variability option), bonobos selected the low variability option ~70% of the time while chimpanzees selected the high variability option ~ 65% of the time (Heilbronner et al., 2008). Thus, bonobos were classified as risk averse and chimpanzees as risk prone. In contrast, in a study where chimpanzees and bonobos could chose between a small, visible piece of banana or a larger piece hidden in one of four locations, bonobos opted to gamble for the larger reward over 80% of the time and chimpanzees over 90% (unless the visible reward was at least 2/3 the size of the risky option, versus 1/6 or 1/3 the size of the larger reward; Haun et al, 2011). Thus, bonobos switched risk preferences between the two studies and chimpanzees became more risk seeking. The differences in methodology make it unclear whether the conflicting results of these studies are 1) due to the fact that the designs employed quantity judgments versus size judgments, 2) the apes' ability to track probabilities over two or five options, or 3) the apes' inability to inhibit preferences for a larger versus smaller piece of food. Similarly contrasting results between studies of the same species using disparate methodologies have been found in other primates (Behar, 1961; Hayden & Platt, 2007; McCoy & Platt, 2005; Steelandt et al., 2011).

We wanted to design a methodology that could be used as an analog of human gambling situations and across multiple primate species, including humans, to assess risk preferences in a uniform way to enable more accurate comparisons across species and studies. Here, we follow Ladouceur et al. (2000) and define gambling as an activity in which a valued resource can be gained or lost due to some risk or chance. Note that ownership of the valued resource prior to the gamble is not required. Thus, when two individuals compete over a resource, the winning individual gains the resource, while the other individual has lost the potential benefit of that resource.

Here, we present the Primate Gambling Task (PGT), which is based on a simplified IGT designed for human children (Kerr & Zelazo, 2004), as a methodology that can be used across multiple primate species and that disentangles the issues of risk preferences and reward maximization. To parse these two potentially competing strategies required three experimental conditions. First, in the PGT condition, we used the standard payoff structure from the human IGT literature, in which the low variability deck paid out more overall than the high variability deck, but could pay out less on individual trials. In the equitable PGT condition (EPGT), we used the standard payout model from the animal literature, in which average payouts of the low and high variability decks were the same and led to equivalent overall rewards. Finally, in the reverse PGT (RPGT) condition, the high variability deck had a higher overall payout than the low variability deck. This allowed us to fully disentangle risk from overall reward maximization.

We tested two species of NHPs, chimpanzees (*Pan troglodytes*) and capuchin monkeys (*Cebus apella*), as well as human adults (18 years old or older) on the Primate Gambling Task. We predicted that all three species would develop preferences for the low variability option in the PGT condition, as that option *both* minimized risk and maximized overall rewards. In the EPGT, we predicted that none of the three species would form preferences for one option over the other because although the options differed in the way rewards were distributed (high or low variability), the mean payouts of both options were equivalent and many animals appear indifferent to risk with this payout structure (Kacelnik & Bateson, 1996; Shafir, 2000). Finally, in the RPGT condition, when reward maximization and risk aversion were in conflict, we predicted that humans would be risk averse, as they are in many gambling tasks (e.g., Bechara et al., 1997). However, because of the disparate methodologies used in the nonhuman literature and the entanglement of these two strategies, we were unable to make directional predictions for NHPs.

2.1 Subjects

2.1.1 Human Subjects

We tested thirty undergraduate students (21 females, 9 males, age range: 18 to 26; mean age: 19.8) in the Learning and Development Laboratory at Georgia State University. Participants were recruited through an on-line recruitment system and received course credit in introductory psychology courses for participation. Participants could choose to withdraw at any time with no penalty and were debriefed after the experiment. The Institutional Review Board at Georgia State University approved all testing procedures.

2.1.2 Nonhuman Primate Subjects

We tested nine chimpanzees from two research centers (Yerkes National Primate Research Center Field Station (YFS): N = 6 females, age range = 19 to 39 years, mean age = 29.00 years; Language Research Center (LRC): N = 3, 1 female, 2 males, age range = 25 to 41 years, mean age = 35.00 years) and eight capuchin monkeys from the LRC (3 females, 5 males, age range = 7 to 22 years, mean age = 12.75 years). All primates were socially housed and received chow, fresh fruits and vegetables several times per day. All primates had *ad libitum* access to water and were never food deprived. At YFS the chimpanzees had access to large (over 500 m^2 or 41.7 m^2 per chimpanzee) outdoor enclosures with wooden climbing structures and enrichment devices as well as an indoor area with multiple rooms. These chimpanzees lived in social groups of 12 individuals. Chimpanzees at the LRC also had access to outdoor areas (288 m^2 or 72 m^2 per chimpanzee) with multiple story climbing towers and enrichment devices as well as an indoor area with multiple rooms. Similarly, capuchin monkeys lived in indoor/outdoor enclosures with six individuals in each of two groups (Group 1: 38.79 m^2 or 6.47 m^2 per monkey, Group 2: 39.29 m^2 or 6.55 m^2 per monkey).

Chimpanzees were tested alone in either their home enclosure (LRC) or in a testing facility adjacent to their home enclosure (YFS). Capuchin monkeys had previously been trained to voluntarily enter individual test chambers where they tested (see Evans et al., 2008). All primates could choose whether or not to enter the testing area and participate in the study. The Institutional Animal Care and Use Committee of each facility approved all procedures.

2.2 General Methods

Each species was tested with the same procedure except when a species appropriate adjustment (noted below) had to be made. In lieu of decks of cards, subjects chose between two “decks” of small (118 mL) stackable containers. Each deck consisted of fifty opaque containers with the same color and pattern (which differed between decks and conditions). The decks were presented in 5 stacks of 10 containers (See Figure 2.1). Each stack of containers was topped with an opaque lid, so that rewards were hidden from view. One deck was a “safe” deck that gave a minimally variable reward distribution (low variability option, LV). The other deck was a “risky” deck, in which the rewards were more variable and included both larger individual payoffs than the safe deck and low and zero payoffs (high variability option, HV; see Table 2.1). Note that in this context, ‘safe’ and ‘risky’ refer to the variability in reward presentation rather than the average payoffs associated with the decks. In the PGT and RPGT conditions these decks also varied on the overall quantity of rewards (highest overall rewards, HR; lowest overall rewards, LR).

Rewards were already present in the containers, so when a participant indicated their choice of a deck, the top container was picked up and the contents were immediately given to the participant. This resulted in immediate rewards, which are typically used in animal, but not human, studies (although see Brosnan et al., 2011; Brosnan, Beran & Wilson, 2011). The next trial began as soon as the participants finished processing the rewards (see below for rewards for each species).

Note that the payout structure differed from the typical human IGT as we changed it to involve smaller and larger gains, including payoffs of zero (i.e., empty containers), rather than wins and losses. We chose to use zero payouts rather than losses for two reasons. First, nonhuman primates generally eat any rewards they are given and will not return food items without sufficient motivation (Brosnan et al., 2008). Secondly, while it is possible for some species to accumulate rewards and be given them at the end of a task (Beran, 2002; Sousa & Matsuzawa, 2001), we felt that using that methodology would reduce the emotional valence of the rewards, a component of the game that allows typical humans to outperform clinical populations (Bechara et al., 1997; Bechara & Damasio, 2002). That is, NHPs may not have had the same responses to a task that delayed gratification until the end of the session rather than giving rewards after each trial.

We ran three conditions. The conditions varied only on the payout structures of each deck. In the PGT condition, the LV was also the HR deck and led to 50% more rewards than the HV, LR deck. Thus, the PGT condition most closely resembled the IGT from the human literature where the decks varied on *both* the payouts of individual trials and overall payoffs. In contrast, the equitable PGT (EPGT) condition most closely resembled animal choice tasks, such as those described in Kacelnik and Bateson (1996), where decks varied on individual payouts, but netted equivalent overall rewards. However, those two conditions alone were not sufficient to determine if an individual was risk averse/prone or acting to maximize overall rewards. For example, if an animal preferred the LV, HR deck in the PGT condition, which would net them the most overall rewards, and did not form a preference in the EPGT condition, where overall reward payouts were the same, we would not be able to distinguish between reward maximization and risk aversion. Therefore, we also ran a reverse PGT condition (RPGT). In the RPGT, the HV deck was also the HR netting 50% more rewards than the LV, LR, which is the opposite payout structure of the PGT condition (See Table 2.1 for payout structures). If an individual was motivated by increasing overall rewards, they should have preferred the HV, HR deck, while if they wished to avoid very low or zero payoffs, they should have preferred the LV, LR deck, despite its lower average payoff. Thus, combined with the other conditions, the RPGT allowed us to determine whether participants were acting to avoid risk or to increase winnings. See Table 2.2 for the potential strategies of risk aversion/proneness and reward maximization.

The decks of containers were randomized for presentation side as well as meaning. That is, for half of the participants one set of containers was the LV deck, while that same deck was the HV deck for the rest of the participants. Each deck was unique to one condition (i.e., pairs of differently colored/patterned decks were used in each of the three conditions).

2.2.1 Human methods

Humans indicated their choice by either pointing to or verbally indicating the deck. They were rewarded with facsimile money, as in Bechara et al. (1997). Even though adults were not tested with a valuable reward, previous work demonstrated that facsimile and real money yielded similar results on the IGT (Bowman & Turnbull, 2003).

After a selection was made, the researcher poured the rewards on the table in front of the participant, which they collected and stored in a bag after each trial. Humans were given one session of 40 trials and were tested in one condition. We chose to use different cohorts of humans in each condition (i.e., a between-subjects design) because we did not want to bias their decisions by running all three conditions in a row, as the NHP were only given one session per day (we could not bring human subjects back in to the laboratory on subsequent days).

2.2.2 NHP methods

Prior to being included in the study, NHPs had to pass quantity preference tests. This was essential because in the human IGT (Bechara et al., 1997) participants were told to maximize their rewards. Since we cannot instruct NHPs to do this, we needed to ensure that we could assume that the animals were acting with that motivation. Thus, the quantity preference tests demonstrated that the animals were sensitive to the quantity differences seen in the task and had a preference for the larger quantities, suggesting they had the same implicit preferences as humans prior to the task. To do this, NHPs were presented with a choice of two quantities and were given the quantity they selected. Two sessions of 10 trials for each of the following quantities were given: 6/3, 3/2 and 2/1, for a total of 6 sessions. They had to demonstrate a significant preference for the larger quantity in each set (15 out of 20 trials, Binomial Test, $p < 0.05$) to be included in the study. All animals successfully discriminated between these quantities. During testing, NHPs were given two sessions of 40 trials (80 total trials) in each condition and the order of conditions was counterbalanced to eliminate any order effects (i.e., a within-subjects design). No NHP was given more than one session per day.

2.2.2.1 Chimpanzees

Chimpanzees touched the tray in front of the stacks of containers to indicate a choice. If a chimpanzee touched the tray in front of both stacks simultaneously or touched a space that was not directly in front of a deck, the tray was removed and the trial was restarted. After a choice, the selected container was emptied into the chimpanzee's enclosure. Rewards were 1 cm^3 dried pieces of coconut.

2.2.2.1 Capuchin Monkeys

Special doors that allowed capuchin monkeys to reach for one deck, but blocked them from reaching towards both decks simultaneously, were fitted on their test enclosures (See Figure 2.1). This was necessary as capuchins had a tendency to repeatedly reach for both options simultaneously. The monkeys all had prior experience making a dichotomous choice using this method (Salwiczek et al., in revision). After a choice, the container was presented to the monkey and it was able to take the rewards (Bio-Serv® 45-mg, grain-based, banana-flavored, dustless precision pellets) directly out of the container.

During testing, we realized that the monkeys made their choices very quickly and did not appear to react to zero outcomes, possibly because there was little delay between their choices (Kacelnik & Bateson, 1996; Roche et al. 1997; Shafir, 2000). Rats in a similar two choice task with varying reward schedules were indifferent to variability when they could immediately start the next trial as there no penalty for a less optimal decision (Roche et al., 1997). However, when inter-trial intervals were used, the rats demonstrated a preference for the less variable option. Similarly, we suspected that the immediacy of the next trial was interfering with the monkey's motivation to track probabilities over time, as delays to choices increase the weight given to the amount of reward as compared to the temporal factor (Green et al., 1981; Green et al., 1994; Green & Myerson, 2004). Therefore, in Experiment 2, we re-ran the study with capuchin monkeys and included a 10 second inter-trial interval between each choice in an effort to increase the value placed on each decision. After a monkey was rewarded, the experimenter restricted access to the testing space by holding the choice doors closed (See Figure 2.1). After 10 seconds, the monkeys were free to make their next selection. All conditions were repeated, with two sessions for each condition. For Experiment 2, novel color/pattern combinations were used for each deck to prevent carryover of deck preferences from the original task. Results of both versions of the task are presented below.

2.3 Results

2.3.1 Humans

In the PGT condition, humans as a group significantly preferred the LV, HR deck (Binomial Test, $p < 0.001$), a finding consistent with performance on the IGT (Bechara et al., 1997). This suggests that the PGT and IGT test a similar phenomenon and justifies the comparison between performance on the PGT and traditional human IGTs. However, humans did not form a preference in either the EPGT (Binomial Test, $p = 0.121$) or the RPGT (Binomial Test, $p = 0.211$) conditions.

2.3.2 Chimpanzees

Like humans, chimpanzees as a group significantly preferred the LV, HR deck in the PGT condition (Binomial Test, < 0.001). However, unlike humans, chimpanzees also developed a significant preference for the LV deck in the EPGT (Binomial Test, $p < 0.001$). Again similarly to humans, they did not have a preference in the RPGT condition (Binomial Test, $p < 0.126$).

In addition to comparing the species as a whole, we conducted analyses at the individual level for the NHPs to see whether individual preferences were consistent across conditions. Three of the nine chimpanzees preferred the LV deck across each condition, suggesting that these individuals were more motivated by minimizing variability than maximizing their overall rewards. Two chimpanzees selected the HR deck whenever possible (i.e., in the PGT and RPGT conditions) and showed no preference in the EPGT, suggesting a reward maximization strategy. One chimpanzee preferred the LV deck in both the PGT and EPGT conditions, but did not have a preference in the RPGT condition. This suggests she may have avoided variability unless the payout was sufficiently high for her to alter that strategy. Finally, three chimpanzees did not form any consistent preferences across conditions, although they did form significant preferences in at least one condition. See Table 2.3 for individual preferences in each condition.

Interestingly, performance differences in the RPGT condition were correlated with the population of chimpanzees. In the RPGT, the LRC population significantly preferred the HV, HR deck (Binomial Test, $p < 0.001$) while the YFS population preferred the LV, LR deck (Binomial Test, $p < 0.001$) and this difference was significant (Kruskal-Wallis Test, $\chi^2 = 5.445$, $p = 0.02$). However, there were no performance differences in the PGT (Kruskal-Wallis Test, $\chi^2 = 2.864$, $p = 0.091$) or EPGT (Kruskal-Wallis Test, $\chi^2 = 0.067$, $p = 0.795$) conditions.

2.3.3 Capuchin Monkeys

One monkey had a significant side bias, choosing the deck on his left on 95% of all trials in all conditions, indicating that neither deck payouts nor the visual appearance of the decks were driving his choices. We therefore excluded him from all analyses. In Experiment 1, when capuchin monkeys started the next trial as soon as they finished eating their previous reward, they preferred the LV, HR deck in the PGT condition (Binomial Test, $p < 0.001$), as did humans and chimpanzees (See Table 2.2). And, like humans, they did not form preferences in the EPGT (Binomial Test, $p < 0.374$) nor the RPGT (Binomial Test, $p = 0.099$) conditions.

At the individual level, only two monkeys had a consistent preference across conditions. One individual preferred the HR whenever possible (PGT & RPGT) but did not form a preference in the EPGT, suggesting a reward maximization strategy. The other individual preferred the LV option whenever there was also a difference in the overall quantity of rewards (PGT & RPGT) but had no preference when overall payouts were equivalent (EPGT), possibly suggesting a mild aversion to risk. Three individuals developed a preference in one condition but not in the others, making their strategy uninterpretable. The remaining two monkeys did not develop a preference in any condition. See Table 2.3 for individual preferences.

In Experiment 2, when a 10 second inter-trial interval was included (Table 2.3), capuchin monkeys again demonstrated a significant preference for the LV, HR deck in the PGT condition (Binomial Test, $p < 0.001$). However, their preference was stronger in Experiment 2 compared to Experiment 1 (McNemar Test, $\chi^2 = 6.2$, $p = 0.013$). As found previously, no preference was formed in the EPGT (Binomial Test, $p = 0.422$) and this was not significantly different than their performance in Experiment 1 (McNemar Test, $\chi^2 = 1.6$, $p = 0.213$). They did, however, exhibit a significant preference for the HV, HR deck in the RPGT condition (Binomial Test, $p < 0.001$) and this was significantly different from their performance in Experiment 1 (McNemar Test, $\chi^2 = 93.1$, $p < 0.001$). This suggests that increasing the time delay between trials increased the value the monkeys placed on each choice.

At the individual level, four monkeys maximized their overall rewards, showing a preference for the HR deck whenever possible (PGT & RPGT), regardless of the amount of variability. An additional monkey showed this same pattern but was not significant in the PGT condition, although there was a trend in this direction (Binomial Test, $p = 0.09$). Two monkeys only showed a significant preference in one condition and thus their strategy was unclear. See Table 2.4 for individual preferences in each condition of Experiment 2. Thus, twice as many monkeys demonstrated a statistically significant strategy when a 10 second inter-trial interval was included.

2.4 Discussion

We used a version of a common human gambling assessment tool, the Iowa Gambling Task (IGT; Bechara et al., 1997), to investigate risk preferences across monkeys, apes, and humans. We included three conditions, one consistent with the payoff structure of the IGT and two additional conditions to disambiguate risk preferences (i.e., variability of reward distribution) from reward maximization (i.e., overall average payoffs). In the PGT condition, humans, chimpanzees and capuchin monkeys (in both Experiment 1 and 2) selected the low variability, high reward option as expected. Thus, when a single option both maximized rewards and minimized variability, all three primate species selected that option, as do humans in the IGT (Bechara et al., 1997). When overall payouts of both options were held constant (EPGT), as in typical animal choice tasks, the subjects only had a choice about how they received their rewards (i.e., through a low or high variability reward distribution). Humans and capuchin monkeys (in both experiments) were indifferent while chimpanzees preferred a minimally variable reward delivery schedule, suggesting that only chimpanzees were sensitive to risk in this condition. Finally, when reward maximization and risk aversion were in conflict because the high variability option was also the most profitable (RPGT), humans, chimpanzees (see below for discussion of differences within chimpanzees) and capuchin monkeys (in Experiment 1) did not form any preference. However, chimpanzees varied between populations, and, in Experiment 2, where a 10 second inter-trial interval was introduced, capuchin monkeys preferred the deck with the highest overall payout whenever possible (PGT & RPGT), suggesting that this strategy in which variability and reward maximization were in conflict induced the most variable responses.

Humans showed no clear strategy in the RPGT, neither maximizing their rewards nor avoiding risk. The reason for this is unclear. One possibility is that they may have recognized the payoff structure, as they did in the PGT, but risk aversion may have inhibited them from preferring the highest overall payout option. They may not have been able to rely on the "gut feelings" that led to advantageous performance on IGT tasks (Bechara et al., 1997; Bechara & Damasio, 2002) due to the conflict of these emotional responses and their cognitive assessment of probabilities (Loewenstein et al., 2001).

Alternatively, our results may have been inconclusive because of differing risk preferences within the human population. Approximately 30% of the human population is risk prone (Bechara & Damasio, 2002) and this may be what we captured in our results. In other words, individual differences of risk preferences may have driven different people to engage in either a risk aversion/proneness or reward maximization strategy, similar to the differences between chimpanzees. If this is the case, then both groups would have responded similarly in the PGT, leading to our significant finding, but would have diverged in the RPGT, leading to a non-significant result (and reward maximizers would have shown no preference at all in the EPGT). We were not able to explore this hypothesis further as we tested humans in a between-subjects design. It is also possible that sex differences may have accounted for the variation as males gamble more frequently than females (Welte et al., 2002), although there were not a sufficient number of males in each condition to assess this. However, both individual and sex differences are an area that we feel deserves further study.

Like humans, chimpanzees as a group did not develop a preference in the RPGT. However, unlike humans, and supporting our above hypothesis explaining the humans' results, we were able to analyze individual results across conditions and found differences in behavior that were correlated with where the subjects were housed. Specifically, the chimpanzees at the YFS avoided risk, showing a consistent preference for options that minimized variability across conditions regardless of the overall payouts of each deck. However, LRC chimpanzees switched from a risk aversion strategy in the EPGT to a reward maximization strategy in the RPGT, despite the increased variability.

One possibility for this difference in behavior is that the rearing and experimental histories of the animals influenced their performance (Boesch, 2010). YFS chimpanzees have been used extensively in behavioral research, (e.g., Horner et al. 2010; Whiten et al., 2005; de Waal & Aureli, 1999), but have received relatively less exposure to cognitive tasks and have not received explicit cognitive training. In contrast, the LRC chimpanzees were raised in a human enriched environment, and two of the three chimpanzees tested at the LRC were trained in symbolic communication (Rumbaugh, 1977). Perhaps most critically, all LRC chimpanzees were tested extensively on cognitive tasks. In particular, they were experienced with quantity judgment tasks (Beran, 2001; Beran, 2009; Beran et al., 2008a; Evans et al., 2010; Beran, 2010; Beran et al., 2011a; 2011b; Beran, 2012). It is possible that their past experience comparing quantities and probabilities, sometimes over long time delays, may have influenced their tendency to maximize rewards when reward maximization was in conflict with risk aversion. That is, because of their proven ability to discriminate quantities over time, they may have been more able to delay gratification on an individual trial in order to increase their longer term (i.e., overall) rewards. Note that all chimpanzees passed the quantity preference tests, indicating that this was not an artifact of a difference in the ability to discriminate between different quantities.

We do note that the percent of risk prone chimpanzees, at 33%, was similar to the percent of risk prone humans found in the Bechara studies (30%; Bechara & Damasio, 2002) and rats in an IGT type experiment (30%; Rivalan et al., 2009). Thus, it is possible that the difference between groups is an artifact of a chance difference in behavior that appears non-randomly distributed. However, given the almost perfect correlation we instead think that the individuals' experience may have influenced their risk preferences, something that should be investigated in more detail in both chimpanzees and humans. These population differences highlight the need to test multiple populations of a species whenever possible (Brosnan et al., 2011).

Our findings with chimpanzees contrast to those of Heilbronner et al. (2008) and Haun et al. (2011), who both found that chimpanzees were risk prone, although to different degrees. However, Heilbronner and colleagues used a payoff structure with little variability in the "risky" option. Because of this structure, selecting the more variable choice resulted in either one or seven grapes, with equal probability, while the other option always resulted in four grapes. The relatively high probability of getting the maximum payout (50%) may have influenced the chimpanzees to select the risky option. In contrast, in the current study, when overall rewards were equal, on any one trial the animals had a 20% chance of getting the maximum payout if they chose the high variability deck. Thus, the risky option in our study involved higher chances of earning a small reward or not being rewarded at all, which may have increased the animals' sensitivity to risk. Haun et al. (2011), on the other hand, did not include a condition with equal payouts and thus confounded the strategies of reward maximization and risk aversion/proneness, as is typical in the animal literature. That is, when faced with a decision to gamble for a larger reward or accept a smaller reward, two factors varied; both the overall size of the reward and the probability of finding the reward. Therefore, a strategy of reward maximization may appear to be risk proneness or vice versa. The three conditions used in the PGT allowed us to disentangle these two strategies.

In Experiment 1, capuchin monkeys, like humans, only formed a preference in the PGT condition. Despite this group level preference, we were surprised that only two monkeys developed interpretable strategies, as they too, had prior experience with quantity discrimination tasks (Beran, 2008; Beran et al., 2008b), although their performance was not as robust as chimpanzees. One explanation for this behavior is that the monkeys were able to move on to the next trial immediately following a losing trial and possibly be rewarded. Thus, there may have been minimal motivation to track probabilities over time as choices were not as valuable due to the immediacy of the next potential reward (Green et al., 1981; Green et al., 1994; Green & Myerson, 2004).

To test this, we ran an additional experiment (Experiment 2) with the monkeys where we added a 10 second inter-trial interval and risk preferences, or lack thereof, were more apparent. In this experiment, four of seven monkeys developed a consistent strategy across conditions, preferring the highest payout deck regardless of variability (PGT & RPGT). However, this finding could also be the result of more exposure to the task, as the monkeys received twice as many sessions as the chimpanzees and four times as many as the humans due to our inclusion of Experiment 2. Thus, while our results suggest that capuchin monkeys may be insensitive to risk, this should be confirmed in future studies. Additionally, while we did not re-test humans or chimpanzees using longer ITIs, this is a logical next step for future research.

The selective pressures that led to human gambling behavior appear to have evolved after New World monkeys diverged from the human lineage. Capuchin monkeys, at least in Experiment 2, were the only species that maximized their rewards whenever possible. This may suggest that capuchin monkeys do not have the same degree of emotional reactions to zero outcomes as the apes and instead *do* rely on accurate probability assessments. However, it is unclear what environmental or social pressures may have led to this difference. It is possible that having emotional reactions are more beneficial in apes due to the complexity of their social structure. That is, apes may be more use to relying on emotions to guide their daily interactions with members of their social group, which may have carried over into other contexts, such as gambling decisions. Alternatively, reactions to this type of risk scenario may be too costly for capuchin monkeys in terms of foraging decisions, as they have to consume food more frequently due to their faster metabolism and smaller energy stores, as compared to chimpanzees. However, these are only two of the many possible explanations for this difference.

To fully elucidate the pressures that led to the evolution of gambling behaviors in primates, a wider variety of species must be tested. We would expect that species would have different ways of interacting with risk based on their social behavior and ecology. For example, group living primates may have a higher tolerance for risk due to within group competition (e.g., for mates and food) compared to pair-bonded or solitary species that compete with fewer conspecifics. Thus, factors such as the species' social structure, mating system, and environment (e.g., food availability), may explain some differences in risk preferences, although these possible influences need to be researched further.

The PGT was designed to be well suited for a variety of primate species. This is important because the literature currently has no standard methodology in which to establish a species' risk preference or with which to compare risk preferences across species. Thus, different studies, sometimes using the same animals, arrive at different conclusions about a species' risk preferences. This, in turn, makes comparing risk preferences across species challenging. Using the PGT as a standardized test for risk preferences would help alleviate these issues and lead to a more accurate understanding of a species' risk preferences as well as allow more accurate species comparisons. We encourage other researchers to similarly standardize methodologies in other species, primate and non-primate, in order further elucidate the evolutionary origins of these decision-making patterns.

Figure 2.1: Arrangement and Presentation of Decks

A capuchin monkey reaches for a deck of containers using specially designed doors. When the monkey opened one door, the other one closed. This prevented the monkeys from trying to select both decks simultaneously.

Decks were presented to the subjects in 5 stacks of 10 containers. Note that there were 10 more containers in each deck than was necessary to complete 40 trials. This was so it never appeared to the subjects that they were nearing the end of the task, even if they preferentially selected from one deck. The presentation of the decks was identical across species, including humans.

Table 2.1: Sample Reward Distribution by Condition

	PGT		Equal PGT		Reverse PGT	
Trial	LVHR	HVLR	LV	HV	LVLR	HVHR
1	3	3	3	1	2	0
2	3	0	3	6	2	6
3	2	1	2	0	1	0
4	3	6	3	3	2	0
5	2	0	2	2	1	6
6	3	0	3	1	2	6
7	2	1	2	1	1	0
8	3	0	3	6	2	6
9	2	1	2	3	1	0
10	2	1	2	2	1	6
Average Payout	2.5	1.3	2.5	2.5	1.5	3
Net Payout	25	13	25	25	15	30
Chance of Zero	0%	40%	0%	10%	0%	50%

We tested three conditions with varying payout schedules. In the PGT condition, subjects could choose between a low variability, high reward option (LVHR) and a high variability, low reward option (HVLR). In the EPGT, overall payouts were equivalent so the choice was between low or high variability (LV or HV) reward distributions. In the RPGT, subjects had a choice between a high variability, high reward option (HVHR) and a low variability, low reward option (LVLR). Testing these conditions allowed us to disentangle the issues of risk and reward maximization. Randomized versions of these distributions were used for each block of ten trials. NHP were given two sessions of 40 trials each, with different randomization orders in each session. Humans received one session of 40 trials.

Table 2.2: Potential Strategies in the Primate Gambling Task

Stategy	PGT	EPGT	RPGT	Decision rule
Perfectly Averse	LVHR	LV	LVLR	Always avoid risk
Perfectly Prone	HVLR	HV	HVHR	Always seek risk
Perfectly Max	LVHR	None	HVHR	Always maximize rewards
Slightly Averse	LVHR	None	LVLR	Avoid risk, but indifferent when overall payouts are equivalent
	LVHR	LV	HVHR	Avoid risk as long as it also maximizes rewards
Slightly Prone	HVLR	None	HVHR	Seek risk, but indifferent when overall payouts are equivalent
	LVHR	HV	HVHR	Seek risk as long as it also maximizes rewards

The payout structure in this task can vary based on two dimensions: the amount of variability (high or low variability; HV, LV) in the reward distribution and the overall payouts of each option (highest or lowest overall rewards; HR, LR). In the PGT condition, subjects chose between a LVHR option and a HVLR option. In the EPGT, overall payouts were equivalent so the only decision was between a LV or HV payout schedule. Finally, in the RPGT, the choice was between a HVHR option and a LVLR option. Thus, the PGT is able to disentangle risk preferences, or variability, from reward maximization.

Table 2.3: Individual Results by Condition in Experiment 1

Chimpanzees	Population	PGT	EPGT	RPGT
Lana	LRC	66.3% LVHR*	55.0% LV	67.5% HVHR*
Mercury	LRC	57.5% LVHR	97.5% LV*	67.5% HVHR*
Sherman	LRC	65.0% LVHR*	56.3% LV	65.0% HVHR*
Barbie	YFS	57.5% LVHR	59.7% HV	73.8% LVLR*
Ericka	YFS	81.1% LVHR*	73.8% LV*	52.5% HVHR
Georgia	YFS	80.0% LVHR*	62.5% LV*	65.0% LVLR*
Katie	YFS	87.5% LVHR*	50.0% -	57.5% HVHR
Missy	YFS	77.5% LVHR*	62.5% LV*	71.3% LVLR*
Rita	YFS	80.0% LVHR*	65.0% LV*	76.3% LVLR*
Total		71.8% LVHR*	62.1% LV*	53.4% LVLR

Capuchins	Population	PGT	EPGT	RPGT
Drella	LRC	62.5% LVHR*	52.5% LV	55.0% LVLR
Gabe	LRC	58.8% LVHR	98.7% HV*	53.8% HVHR
Liam	LRC	52.5% LVHR	71.3% LV*	51.2% HVHR
Lily	LRC	75.0% LVHR*	53.8% LV	98.8% LVLR*
Logan	LRC	55.0% LVHR	52.5% LV	50.0% -
Nala	LRC	62.5% HVLR	52.5% LV	50.0% -
Wren	LRC	62.5% LVHR*	52.5% LV	73.7% HVHR*
Total		57.7% LVHR*	50.2% LV	53.1% LVLR

Humans	Population	PGT	EPGT	RPGT
1	GSU	87.5% LVHR*	70.0% LV*	72.5% HVHR*
2	GSU	87.5% LVHR*	57.5% LV	100.0% LVLR*
3	GSU	57.5% LVHR*	50.0% -	85.0% HVHR*
4	GSU	50.0% -	57.5% LV	68.0% HVHR*
5	GSU	57.5% LVHR	55.0% LV	60.0% LVLR
6	GSU	50.0% -	50.0% -	65.0% HVHR
7	GSU	50.0% -	50.0% -	50.0% -
8	GSU	52.5% HVLR	50.0% -	50.0% -
9	GSU	50.0% -	50.0% -	50.0% -
10	GSU	62.5% LVHR	50.0% -	52.5% HVHR
Total		59.3% LVHR*	54.0% LV	53.30% HVHR

* Binomial Test, $p < 0.05$

The percent indicated is their dominant strategy. Note that each cell for humans represents a unique participant.

Table 2.4: Individual Performance by Condition of Capuchin Monkeys in Experiment 2

Capuchins	Population	PGT	EPGT	RPGT
Drella	LRC	58.8% HVHR	66.3% HV*	56.3% LVLR
Gabe	LRC	82.5% LVHR*	60.0% LV	91.3% HVHR*
Liam	LRC	68.8% LVHR*	58.8% LV	87.5% HVHR*
Lily	LRC	67.5% LVHR*	43.8% HV	51.3% LVLR
Logan	LRC	66.3% LVHR*	60.0% LV	78.8% HVHR*
Nala	LRC	65.0% LVHR*	48.8% HV	63.8% HVHR*
Wren	LRC	60.0% LVLR	50.0% LV	95.0% HVHR*
Total		64.5% LVHR*	52.5% LV	72.7% HVHR*

This table shows the significant preferences (Binomial Test, $p < 0.05$) exhibited by capuchin monkeys when a 10 second inter-trial interval was added. Using a 10 second inter-trial interval increased performance on this task as compared to the version with no inter-trial interval (Table 2.2). Note that Wren trended toward the LVHR in the PGT condition, but was not significant (Binomial Test, $p = 0.09$).

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3 The Effect of Satiation on Risk Preferences

Studies from behavioral ecology suggest that, with respect to foraging strategies, animals should alter their typical risk preferences depending on a number of factors, including food availability, ease of finding food and level of satiation (Barnard & Brown, 1985; Caraco, 1981; Caraco et al., 1980; Caraco et al., 1990; Stephens, 1981). Theoretically, the ecology and current energy requirements of the species should dictate optimal risk taking behaviors. In particular, animals may vary in predictable ways depending upon whether a large food source is needed for immediate survival, or represents a gamble that may be less optimal if sufficient calories can be acquired more reliably. For example, juncos (*Junco hyemalis*, a small bird) prefer a consistent food reward (Caraco, 1981) unless exposed to cold such that only a large food bonanza would supply sufficient calories to survive the night (Caraco et al., 1990). Thus, under typical conditions juncos are risk averse, but they switch to a risk prone strategy under extreme circumstances.

On the other hand, chimpanzees (*Pan troglodytes*) seem to be risk prone only when there are sufficient other food sources. They hunt, a risky prospect as success is uncertain, only when backup food resources are available (Gilby & Wrangham, 2007; Watts & Mitani, 2002; Uehara, 1997). However, these cases represent the extremes of food availability. What remains largely unknown is how sensitive risk preferences are in response to more typical variations, such as short-term hunger, circadian rhythms and metabolism. It is important to understand the flexibility of risk preferences under a variety of conditions, not just in response to food availability extremes, to understand the dynamic decision-making processes of animals.

For this study, we were interested in whether captive, diurnal, non-food deprived primates would alter their risk preferences in response to the typical short-term hunger that results from fasting overnight. Diurnal animals, including humans, generally sleep at night and engage in sustenance activities during the day, and thus do not typically eat at night (Anderson, 1998; de Castro, 2001). Individuals who follow this sleep pattern often consume food shortly after waking. In humans, people eat because of the lack of energy content in their stomach, which is self-reported as hunger and varies throughout the day (de Castro & Elmore, 1988). Due to the physiological similarities between humans' and other primates' digestive systems (Lambert, 1998), we can infer that hunger is also the motivating factor for morning food intake in nonhuman primates (NHP).

Eating patterns can affect cognitive functioning in a number of ways. Human children who typically eat breakfast have increased academic performance such as better memory (e.g., retrieving answers to a test) relative to those that do not eat breakfast (for a review see Rampersaud et al., 2005). Food deprivation (in nonhumans) can also change behavior (e.g., Caraco, 1981; 1990) and often leads to decreased performance on cognitive tasks (e.g., Barnes et al., 1966; Bruce, 1941). However, these performance changes are the result of long-term food availability, not daily fluctuations. What remains largely unknown is how typical daily fluctuations, like hunger, affect primates' performance on cognitive tasks generally, and risk preferences in particular. This is an important area to explore as most of the cognitive literature regarding primates fails to control for, or discuss, these types of variables. Thus, our understanding of risk preferences may not be fully elucidated because of the possible influence of short-term factors on risk preferences.

We tested two diurnal primates, chimpanzees and capuchin monkeys (*Cebus apella*) that were never food deprived, to determine the sensitivity of risk preferences to standard overnight hunger. Here, we use the term risk to refer to the amount of variation and potential for no payout in a two choice task. Under typical laboratory conditions, chimpanzees appeared to be risk averse unless the riskiest option resulted in significantly more food overall (Proctor et al., in prep). When they were asked to choose between a reward distribution that varied only in the way rewards were distributed (a low variability option, with consistent rewards versus a high variability option, relatively larger and smaller rewards as well as no payoffs) and not the overall quantity of rewards, chimpanzees were risk averse and preferred the low variability reward delivery schedule. When the low variability option also led to the highest overall payouts, the chimpanzees behaved to maximize overall rewards and minimize risk. However, when the high variability option also led to the highest overall payout, chimpanzees diverged in their preferences, with some maximizing rewards and some minimizing risk. Importantly for our study, the chimpanzees tested in the current study universally switched their strategy to maximizing their rewards, thus this is the baseline assumption we will use in the current analysis (See Table 3.3, Proctor et al., in prep).

Capuchin monkeys, on the other hand, appeared insensitive to risk (see also Steelandt et al. 2011). That is, when capuchins had a choice between the high overall rewards versus low variability, they always selected the highest overall reward option, regardless of the variability. But, when their choice varied only on the way the rewards were distributed (low or high variability), they did not form a preference. Note that in the previous study (Proctor et al., in prep), capuchin monkeys were tested both with and without a 10 second inter-trial interval. However, here we only tested them with a 10 second inter-trial interval and thus only compare the results of that version of the task. See Table 3.1 and 3.3 for a summary of the conditions tested and the associated decision-making strategies.

Using three different payoff structures is useful because it disentangles whether subjects respond to risk or overall payouts. Here, we used the same methodology as in Proctor et al. (in prep), but tested the nonhuman primates (NHP) prior to their morning feeding, after they had fasted overnight for approximately 12 hours. However, while we focus here on hunger, it is important to note that hunger is confounded with circadian rhythms, and possibly other factors, such as metabolic rates. As this study was designed to see if risk preferences varied as a function of daily fluctuations, we did not attempt to dissociate these variables. We focused on hunger levels because those could be manipulated in known ways (but we do acknowledge that one of these other factors may be driving our results). Additionally, testing prior to the animals' morning feeding should have mimicked morning hunger levels that wild NHP would experience in concert with any other factors, such as circadian rhythms or metabolic rates. Thus, this approach provides a naturalistic understanding of how typical daily fluctuations, rather than artificial food restriction, alters animals' decision-making strategies.

We hypothesized that relative hunger levels would influence risk preferences in chimpanzees but not capuchin monkeys. In the wild, chimpanzees seem to alter their foraging strategies based on food availability (Gilby & Wrangham, 2007), suggesting they would be sensitive to food distributions when hungry. However, we did not expect to see drastic shifts in risk preferences like those seen in other animals that were food deprived to the point of starvation (Caraco, 1981; 1990), as these subjects never had any atypical energetic deficits as a result of their performance in this task. Thus, we predicted that chimpanzees would continue to prefer low variability reward distributions unless the high variability distribution also led to the highest overall payout (Proctor et al., in prep), but that their sensitivity to risk would decrease, and they would be more willing to gamble for a large payout on an individual trial when they were hungry. We did not predict any change in capuchin monkeys' risk preferences because they were more motivated by food maximization in previous studies using a similar methodology (Proctor et al., in prep) and were not sensitive to risk in another food choice task (Steelandt et al., 2011). We therefore predicted this pattern would continue, as maximizing overall rewards would presumably sate their hunger the most rapidly.

3.1 Subjects

We tested three chimpanzees (female = 1, male = 2, age range = 25 to 41, mean age = 35.00) and seven capuchin monkeys (female = 3, male = 5, age range = 7 to 22, mean age = 12.43) from the Language Research Center at Georgia State University. The NHP were socially housed in large indoor/outdoor enclosures. Chimpanzees had access to outdoor areas with multiple story climbing towers and an indoor area with multiple rooms (288 m^2 or 72 m^2 per chimpanzee). Similarly, capuchin monkeys lived in indoor/outdoor enclosures with six individuals in each of two groups (Group 1: 38.79 m^2 or 6.47 m^2 per monkey, Group 2: 39.29 m^2 or 6.55 m^2 per monkey). All animals were fed a diet of chow, fresh fruits and vegetables that they received multiple times per day. All animals had *ad libitum* access to water and were never food deprived for the purposes of testing, including this study (we compared their responses during times of normal food peaks and valleys, such as prior to or after their morning feeding). Subjects were tested individually in their home enclosure (chimpanzees) or a voluntarily entered testing chamber (capuchins; Evans et al., 2008). The Institutional Animal Care and Use Committee of Georgia State University approved this research.

3.2 Methods

We used a variation of the PGT as presented in Proctor et al. (in prep). Participants were presented with sets of small (118 mL), stackable containers. Each set was opaque and visually distinct, varying on both color and pattern. Animals were presented with two novel sets in each of three conditions (these sets also differed from those used in Proctor et al, in prep). There was always a low variability option that paid out a small, minimally variable quantity of rewards and a high variability option that could pay out a large amount, but could also pay out smaller amounts or not contain any rewards. Rewards (1 cm^3 pieces of dried coconut for chimpanzees and Bio-Serv® 45-mg, grain-based, banana-flavored, dustless precision pellets for capuchins) were loaded into the containers according to the payoff schedule for each condition (See Table 3.2).

The sets were presented to the animals on a table in front of their enclosure. Chimpanzees indicated which option they wanted by touching the table in front of that option. If a touch was made that was not directly in front of one of the sets, the table was pulled away and the trial restarted. Capuchin monkeys used a specially designed door system that allowed them to select only one set at a time (Salwiczek et al., in revision; Proctor et al., in prep). This was necessary because of the monkeys' tendency to reach for both decks simultaneously, a problem not encountered with chimpanzees. Once an animal made a selection, the experimenter gave the reward in the topmost container to the animal and placed the empty container out of view of the subject. For chimpanzees, the next trial started as soon as they had finished eating. With capuchin monkeys, a 10 second inter-trial interval was used as that was previously shown to increase the number of individuals who form an interpretable strategy in this task (Proctor et al., in prep). Sets were counterbalanced for both side and meaning. That is, for half of the animals one set of containers was the high variability option and for the others it was the low variability option. We counterbalanced the side on which each option was presented. Animals were given two sessions of 40 trials (80 trials total) on two separate days for each condition.

As in Proctor et al. (in prep), we tested three conditions: the PGT condition, the Equitable PGT condition (EPGT) and the Reverse PGT (RPGT). The order in which the animals received the conditions was counterbalanced to minimize any affect of experience. In these conditions the sets maintained their type (low or high variability) but the overall payoffs varied (highest or lowest overall payout; See Table 3.2 for payout structures of each condition). In the PGT condition, the low variability option paid out 50% more than the high variability option. In the EPGT condition, both sets paid the same amount overall, as in typical animal choice tasks (see for example Kacelnik & Bateson, 1996; MacLean, 2012; Shafir, 2000). Finally, in the RPGT condition the high variability option also resulted in the highest overall payout, which was 50% more than the low variability option. This allowed us to disentangle whether these decisions were driven by overall reward maximization or a risk preference. See 3.1 for a summary of these conditions.

All animals were tested first thing in the morning, prior to receiving any other food. This was presumably when the animals were most hungry, as their last meal was the previous evening and they had thus fasted for approximately 12 hours. We then compared these results to those of Proctor et al. (in prep) when the animals had always been given food prior to testing, either for their morning feeding or during other experiments (~ 20% of their daily caloric intake). This allowed us to assess the effect of short-term hunger on risk preferences. It should be noted that all animals completed the sated condition in Proctor et al. (in prep) prior to being tested after they had fasted overnight. Thus, there may have been an effect of experience. However, we needed to determine whether the PGT could accurately assess risk preferences prior to introducing any potentially confounding variables.

3.3 Results

In the overnight-fasting condition, chimpanzees significantly preferred the options that had the overall highest payoff, regardless of risk (high or low variability), in both the PGT condition (Binomial Test, $p < 0.001$) and the RPGT condition (Binomial Test, $p < 0.001$). They did not, however, develop a preference in the EPGT condition (Binomial Test, $p = 0.061$; see Table 3.4). Thus, the overall pattern of results was similar to the PGT and RPGT of Proctor et al., (in prep), but not in the EPGT condition.

While the overall pattern of choices, regardless of when they were fed, was similar in the PGT condition, there was a significant difference between the two (McNemar Test: $\chi^2 = 5.750$, $p = 0.016$). That is, while the chimpanzees' preference in both conditions was for the low variability option, they selected the high variability option less often after fasting overnight compared to when they had eaten before the task. In the EPGT, they increased their frequency of choices for the high variability option after fasting (McNemar Test: $\chi^2 = 32.640$, $p < 0.001$), which resulted in no overall preference being formed. In the RPGT, chimpanzees preferred the high variability, highest payout option regardless of relative hunger levels (McNemar Test, $\chi^2 = 0.137$, $p = 0.712$).

Capuchin monkeys in the PGT condition did not form a preference after fasting overnight, although there was a trend to prefer the low variability, high reward option (Binomial Test, $p = 0.07$), as they did after receiving food. They, too, did not form a preference in the EPGT (Binomial Test, $p = 0.22$), but did form a preference for the high variability, high reward option in the RPGT. Comparing capuchins' performance after fasting overnight to their performance when tested after eating, there were significant differences in the PGT and RPGT conditions, but not in the EPGT (McNemar Test, $\chi^2 = 3.124$, $p = 0.077$). In the PGT condition, the monkeys more often chose the high variability option after fasting (McNemar Test, $\chi^2 = 12.760$, $p < 0.001$). However, in the RPGT, where the high variability option also led to the highest overall rewards but had a greater chance of not paying out, the monkeys selected more from the low variability option after fasting (McNemar Test, $\chi^2 = 16.504$, $p < 0.001$). See Tables 3.3 and 3.4.

3.4 Discussion

We explored whether risk preferences in primates varied as a function of typical daily fluctuations, focusing on relative hunger levels. Both chimpanzees and capuchin monkeys altered at least some of their risk preferences after fasting overnight, although this was expressed in different ways. After fasting, chimpanzees increased their preference for the risk, as defined by the variability of reward distribution, when overall payouts were equivalent (EPGT). This change presumably occurred because of the potential for a large payout on an individual trial, which would be more valuable when a NHP had not eaten in the previous 12 hours. Thus, chimpanzees increased their sensitivity to the variability of payoffs at the individual trial level despite the fact that these were well fed subjects who had experienced no food deprivation other than the species-typical overnight fast. Under other payoff structures (PGT and RPGT), chimpanzees showed the same pattern of preferences for reward maximization. Additionally, in the PGT condition their preference for increasing rewards was stronger after fasting. Thus, daily fluctuations in satiation level, and perhaps circadian rhythms, can alter chimpanzees' performance in a risky decision-making task.

Capuchin monkeys also showed a trend towards increasing their preference for variability in the PGT condition after fasting overnight, although they did not demonstrate an overall preference for either option (previously they preferred the low variability, high reward option). In contrast to this, in the RPGT, they decreased their tolerance for variability in the reward distribution when the high payoff option had a high probability of not being rewarded, even though this option also led to the highest overall payouts. The reason for this is unclear. One possibility is that hunger caused the capuchins to become more sensitive to the probability of not earning a reward, which was 40%, or 32 trials out of 80, in the high variability option of the PGT and 50%, or 40 trials out of 80, in the high variability option of the RPGT (See Table 3.2). That is, capuchins may have been more willing to gamble on a large payout in the PGT condition when there was less risk, but less likely to maximize payouts in the RPGT condition because of the higher probability of receiving nothing. This, too, could have been the result of hunger levels, as it was potentially more aversive to not be rewarded when they were presumably the most hungry. However, the difference between a 40% and 50% chance of not being rewarded seems minimal over this number of trials, and in typical circumstances capuchins struggle to discriminate quantity differences of this ratio (Evans et al., 2009). We therefore find it doubtful that their decisions changed based on the relative chance of not being rewarded. Risk preferences in capuchin monkeys should be further researched to determine why their strategies changed in these ways.

Interestingly, our finding that chimpanzees increase their tolerance for risk in the EPGT (although not in the PGT or RPGT) when they were (presumably) hungry seems to conflict with the theory that chimpanzees increase hunting behavior when there are sufficient fall back food sources (Gilby & Wrangham, 2007). However, there is a significant difference between morning hunger in captive chimpanzees and food availability in the wild, which makes these studies difficult to compare. It may be that, because hunting requires significant energy expenditures, it is not motivated strictly by energy budgets or nutritional needs (Gilby & Wrangham, 2007; Speth, 2010) and may be primarily used to facilitate social relationships (Gomes & Boesch, 2009; McGrew, 2001; Mitani & Watts, 2001; Nishida et al., 1992; Stanford, 1996; 1999; 2001; Watts & Mitani, 2002). Thus, hunting decisions may not be based solely on an energetic cost/benefit analysis, in which case risk preferences seen in other foraging decisions may play a minimal role in hunting behavior. It is also possible that because the risk of being unsuccessful in a hunt is much greater than the risk of not earning a reward in the current task, their risk preferences alter depending upon those probabilities. More research on hunting behavior is needed to further elucidate why chimpanzees hunt and how risk preferences may or may not factor into their decisions.

These results indicate that primate strategies for interacting with risk are not static, even when the animals being tested are in captivity and will not have any discernible energetic deficits as a result of their decisions. This may help explain why reported risk preferences in animals vary across studies (Kacelnik & Bateson, 1996; Shafir, 2000). Not only do studies vary widely on methodology but animals also are often tested under different conditions, such as food deprivation, satiation levels, and time of day. These findings highlight the importance of controlling for typical daily variations in NHPs, such as relative hunger level, circadian rhythms, and possibly other factors such as metabolism, when researching risk preferences.

Table 3.1: Summary of Conditions and Possible Risk Strategies

Stategy	PGT	EPGT	RPGT	Decision rule
Perfectly Averse	LVHR	LV	LVLR	Always avoid risk
Perfectly Prone	HVLR	HV	HVHR	Always seek risk
Perfectly Max	LVHR	None	HVHR	Always maximize rewards
Slightly Averse	LVHR	None	LVLR	Avoid risk, but indifferent when overall payouts are equivalent
	LVHR	LV	HVHR	Avoid risk as long as it also maximizes rewards
Slightly Prone	HVLR	None	HVHR	Seek risk, but indifferent when overall payouts are equivalent
	LVHR	HV	HVHR	Seek risk as long as it also maximizes rewards

The payout structure in this task can vary based on two dimensions: the amount of variability (high or low variability; HV, LV) in the reward distribution and the overall payouts of each option (highest or lowest overall rewards; HR, LR). In the PGT condition, subjects chose between a LVHR option and a HVLR option. In the EPGT, overall payouts were equivalent so the only decision was between a LV or HV payout schedule. Finally, in the RPGT, the choice was between a HVHR option and a LVLR option. Thus, the PGT is able to disentangle risk preferences, or variability, from reward maximization.

Table 3.2: Sample Reward Distribution by Condition

	PGT		Equal PGT		Reverse PGT	
Trial	LVHR	HVLR	LV	HV	LVLR	HVHR
1	3	3	3	1	2	0
2	3	0	3	6	2	6
3	2	1	2	0	1	0
4	3	6	3	3	2	0
5	2	0	2	2	1	6
6	3	0	3	1	2	6
7	2	1	2	1	1	0
8	3	0	3	6	2	6
9	2	1	2	3	1	0
10	2	1	2	2	1	6
Average Payout	2.5	1.3	2.5	2.5	1.5	3
Net Payout	25	13	25	25	15	30
Chance of Zero	0%	40%	0%	10%	0%	50%

Randomized versions of these distributions were used for each block of ten trials. NHP were given two sessions of 40 trials per condition, with different randomization orders in each session and trial block.

Table 3.3: Summary of Findings

	Chimpanzees		Capuchin Monkeys	
	After Feeding	After Fasting	After Feeding	After Fasting
PGT	62.9% LVHR	72.9% LVHR*	64.5% LVHR	53.9% HVLR*
EPGT	69.6% LV	56.3% HV*	52.5% LV	52.7% HV
RPGT	66.7% HVHR	68.8% HVHR	72.7% HVHR	61.0% HVHR*

* Significant change between conditions. McNemar Exact Test, $p < 0.05$

This table shows the overall pattern of choices in each condition for each species as a group.

Table 3.4: Individual Performance After Eating and After Fasting Overnight

	PGT		EPGT		RPGT	
Chimpanzees	After Feeding	After Fasting	After Feeding	After Fasting	After Feeding	After Fasting
Lana	66.3% LVHR*	95.0% LVHR*	55.0% LV	100.0% HV*	67.5% HVHR*	52.5% HVHR
Sherman	65.0% LVHR*	51.2% LVHR	56.3% LV	65.0% LV*	65.0% HVHR*	87.5% HVHR*
Mercury	57.5% LVHR	72.5% LVHR*	97.5% LV*	66.3% LV*	67.5% HVHR*	66.3% HVHR*
Group	62.9% LVHR*	72.9% LVHR*	69.6% LV*	56.3% HV	66.7% HVHR*	68.8% HVHR*

	PGT		EPGT		RPGT	
Capuchins	After Feeding	After Fasting	After Feeding	After Fasting	After Feeding	After Fasting
Drella	58.8% HVLR	60.0% LVHR	66.2% HV*	56.3% HV	56.3% LVLR	57.5% HVHR
Gabe	82.5% LVHR*	60.0% LVHR	67.5% LV*	56.3% HV	91.3% HVHR*	57.5% HVHR
Liam	68.8% LVHR*	56.3% HVLR	58.8% LV	62.5% LV*	87.5% HVHR*	53.8% LVLR
Lily	67.5% LVHR*	50.0%	51.2% HV	60.0% HV	51.2% LVLR	57.5% HVHR
Logan	66.3% LVHR*	60.0% HVLR	60.0% LV	52.5% HV	78.8% HVHR*	62.5% HVHR*
Nala	65.0% LVHR*	67.5% LVHR*	51.2% HV	51.2% LV	63.8% HVHR*	67.5% HVHR*
Wren	60% LVHR	56.3% LVHR	50.0%	57.5% HV	95.0% HVHR*	75% HVHR*
Group	64.5% LVHR*	53.9% LVHR	52.5% LV	52.7% HV	72.7% HVHR*	61.0% HVHR*

* Significant preference, Binomial Test, $p < 0.05$

In the PGT condition, subjects could choose either the low variability, highest overall reward payout option (LVHR) or the high variability, lowest overall reward payout option (HVLR). In the EPGT, subjects make a choice between the way rewards were distributed (LV or HV), as overall rewards were equivalent. The reward structure of the RPGT is opposite of the PGT. Subjects could chose from a high variability, highest overall reward payout option (HVHR) and a low variability, lowest overall reward payout option (LVLR).

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4 The Social Primate Gambling Task

Animals are constantly faced with decisions between a relatively safe choice and a riskier one. For example, which of two food sources should a chimpanzee select? These types of decisions become even more complex when they occur in a social situation. Which food source should the same chimpanzee access if one food source is also visible to a dominant individual while another food source is not? In primates, including humans, it is well documented that behavior and decision-making change in the presence of other individuals (e.g., capuchin monkeys: Pollick et al., 2005; tamarins: Roush & Snowden, 2000; chimpanzees: Slocombe & Zuberbühler, 2007; Hare et al., 2001; bonobos: Clay et al., 2011; humans: Triplett, 1898; Rockloff, 2010; Rockloff & Dyer, 2007; Rockloff et al., 2010). Often, decisions that are made in social contexts differ for good reasons. For example, in the food competition task referenced above, subordinate chimpanzees behaved differently based on which food items a dominant individual could see (Hare et al., 2001). That is, when two food items were presented, both of which were visible to the subordinate but only one was visible to the dominant individual, the subordinate chose the food hidden from the dominant, minimizing competition. This decision was presumably made to avoid an aggressive encounter or the risk of losing both foods altogether. Thus, the individual's strategy changed due to the social pressures of the situation. Str

However, primates, including humans, also change their behavior in social contexts in ways that appear irrational. For example, the Asch conformity studies (Asch, 1951; 1955; 1956) showed that some people would give an obviously incorrect answer to a simple visual matching task if everyone else in the room gave the (same) incorrect answer. Chimpanzees (*Pan troglodytes*) showed similar conformity effects in social learning tasks, copying a preferred trained model over another individual (Horner et al., 2010) and conforming to a model's behavior even when doing so resulted in a less preferred reward (Hopper et al., 2011). In these cases there were apparently no benefits, in terms of rewards, from conforming to group norms, and in the latter case, subjects actually paid a cost to conform. The consistent presence of such behavior across species and contexts indicates that social factors contribute potentially strong influences to patterns of decision-making in primates.

Another area in which humans make seemingly irrational decisions in social contexts is gambling, where cues given by other individuals impact their decisions (Rockloff & Dyer, 2007). Humans most frequently gamble in social contexts, such as casinos (American Gaming Association, 2011), and simply being in the presence of others leads people to make more bets and gamble longer (Rockloff, 2010; Rockloff & Dyer, 2007; Rockloff et al., 2010). In studies with simulated electronic gambling machines, where participants were told there were other players in different rooms, players made more bets and lost more money compared to individuals who were not told that anyone else was playing (Rockloff & Dyer, 2007; Rockloff, 2010). In a simulated crowd, participants made smaller bets but continued to gamble longer and had larger monetary losses compared to those who gambled alone (Rockloff et al., 2010). This effect has also been seen in children (Hardoon & Derevensky, 2001). Notably, people with gambling disorders exhibited this type of audience effect even when other individuals were not engaged in gambling or attending to the gambler (Rockloff, 2010).

There are several theoretical explanations for why people may respond this way. The presence of other individuals can create an adverse affective state (Green, 1991; Zajonc, 1965) and may lead to a fear of public failure or motivation to outperform others (Triplett, 1897; Rockloff & Dyer, 2007). When gambling, these feelings may result in increased gambling behavior in spite of mounting losses because people do not want to appear to be “losers”

(Rockloff & Dyer, 2007). Additionally, gambling decisions are often based on salient environmental cues (Kahneman & Tversky 1979), which, as social primates, are often the winnings of other gamblers (Rockloff & Dyer, 2007). Gamblers view their potential losses more critically when other people are perceived to be winning and increase their gambling behavior and associated economic losses. Conspecifics are also distracting. This distraction may cause the gambler's ability to focus on the task to be impaired, leading to decreased performance (Green, 1991) and incorrect assessments of losses over time (Rockloff & Dyer, 2007). Thus, a variety of proximate mechanisms lead to increased gambling behavior in social situations. However, the ultimate reasons that led to the evolution of these behaviors in humans remain unclear. This is an important area of research as understanding the basis for such seemingly irrational decision-making could have significant implications for social problems that arise because of gambling and for treatments of pathological gamblers.

One way to clarify how and why social gambling behavior evolved in humans is through phylogenetic comparisons with other primates. Examining nonhuman primate (NHP) responses to similar situations will help elucidate the adaptive pressures that may have led to the evolution of this seemingly irrational behavior in humans. Here, we tested humans, chimpanzees (*Pan troglodytes*), and capuchin monkeys (*Cebus apella*) with a social gambling task, a variant of the Primate Gambling Task (PGT; Proctor et al., in prep), to determine if similar changes in gambling behavior occurred when NHPs were tested alone or with a conspecific partner.

In typical gambling studies with humans, anonymous partners are used for social aspects of tasks (e.g., Rockloff & Dyer, 2007) in order to simulate crowds and audiences similar to the strangers who would be present if gambling in a casino. However, we could not test NHPs with strangers due to the high risk of aggression, so the social component of the experiment involved known members of their social group. To keep the social dynamics consistent across species, we tested humans with individuals with whom they had a prior relationship. Thus, in all species, individuals brought their existing social relationship into the testing environment, a feature that may influence their performance (Brown, 1987; Homans, 1961; Kelley & Thibaut, 1978; Schino & Aureli, 2009).

We hypothesized that both humans and chimpanzees would alter their behavior when tested with a known conspecific. As they are known to do in other, similar tasks (e.g., Rockloff, 2010; Rockloff & Dyer, 2007, Rockloff et al., 2010), we predicted humans would increase their risky choices when a conspecific was involved in the task, although we were unable to form a direction prediction about how a friend, as opposed to an anonymous stranger, would affect the results. We similarly predicted that chimpanzees would increase their risky choices with a partner, based both on the human literature as well as their known problems inhibiting prepotent responses. Prepotent responses are reactions to an event driven by some immediate reinforcement (e.g., food) or by a previously associated reinforcer (Lansbergen et al., 2007). That is, subjects who see another individual receive a larger payoff than they receive may have a prepotent response to select that option on future trials, even if inhibiting that response would net them a larger overall reward. Chimpanzees, in particular, have difficulty inhibiting their preference for larger food quantities in such situations (Boysen & Bernston, 1995; Vlamings et al., 2006; Silberberg & Fujita, 1996). However, prepotent responses can be overcome by masking rewards or by using symbolic representations, which enables the NHP to switch their attention from the reward to the task solution (Boysen & Bernston, 1995; Vlamings et al., 2006). In previous studies using the PGT paradigm (Proctor et al., in prep), subjects could not see any reward except the one they received, and even then they only saw the other possibility after having made the first choice, suggesting that prepotent responses were not driving their choices. In contrast, in the social PGT, where a more direct comparison of rewards was possible, seeing another individual receive a larger payout may have altered the subjects' decisions.

With respect to capuchin monkeys, we were unable to make a directional prediction because of the conflicting evidence in the existing literature. In previous studies using the PGT methodology, capuchin monkeys' responses indicated a motivation to increase their overall rewards, and they showed no evidence of having a preference for, or aversion to, the amount of variability involved (Proctor et al., in prep). That is, under a variety of conditions the monkeys were more influenced by the overall quantity of rewards rather than the amount of variability in each choice. However, it is equally likely that social factors would affect their behavior, as it does in other contexts (Di Bitetti, 2005; Gros-Louis, 2004; Pollick et al., 2005).

4.1 Subjects

4.1.1 NHP Subjects

We tested six chimpanzees from two research facilities (Language Research Center (LRC): female = 1, male = 2; Yerkes National Primate Research Center Field Station (YFS): female = 3; age range = 19 to 41, mean age = 29.8) and seven capuchin monkeys (LRC: female = 3, male = 4, age range = 7 to 22, mean age = 12.75). Both species were socially housed in mixed sex groups. Chimpanzees at the LRC had access to outdoor areas with multiple story climbing towers and enrichment devices as well as an indoor area with multiple rooms (288 m^2 or 72 m^2 per chimpanzee). At the YFS, the chimpanzees had access to large (over 500 m^2 or 41.7 m^2 per chimpanzee) outdoor enclosures with wooden climbing structures and enrichment devices as well as an indoor area with multiple rooms. Similarly, capuchin monkeys lived in indoor/outdoor enclosures with six individuals in each of two groups (Group 1: 38.79 m^2 or 6.47 m^2 per monkey, Group 2: 39.29 m^2 or 6.55 m^2 per monkey).

Subjects were tested either in their home enclosure (LRC chimpanzees) or a testing area (YFS chimpanzees & capuchin monkeys). Chimpanzees were called by name and could choose whether to participate. Capuchin monkeys were previously trained to voluntarily enter their testing enclosures (Evans et al., 2008). All animals received primate chow and fresh fruits and vegetables several times per day with *ad libitum* access to water. No animals were food deprived in this study. The Institutional Animal Care and Use Committee of each institution approved this research.

4.1.2 Human Subjects

We tested twenty undergraduate students (female = 14, male = 6, mean age = 21.55, age range: 18 – 28) at Georgia State University, all of whom received course credit for participation. Ten subjects were tested in the partner absent condition (female = 6, male = 4, mean age = 21.44, age range: 18-28). For the partner present condition, the remaining ten subjects (female = 8, male = 2, mean age = 21.3, age range: 18-28) were instructed to bring a friend with them, who then served as their partner. All participants, including partners, could stop the test at any point. The Institutional Review Board of Georgia State University approved this research.

4.2 General Methods

We used a modified version of the Primate Gambling Task (Proctor et al., in prep) to test whether the presence or absence of a partner would alter gambling behavior. In both the partner present and partner absent conditions, participants were presented with two sets of small, stackable Tupperware-type containers (Gladware Mini-Rounds; 118 ml) in which rewards had previously been hidden. Each set was opaque and visually distinct, varying in both color and pattern (both also varied from previous versions of the task; Chapters 2 & 3). Subjects were free to choose from either set. One set, the low variability option (LV), always paid a small, minimally variable, quantity of rewards and led to the greatest quantity of rewards overall. The high variability option (HV) was more variable and included both payouts that were larger and smaller than the safe option, as well as empty containers. Overall, the LV led to 50% more rewards than the HV. Thus, the sets varied both on the way the payouts were received and the average payouts (Table 4.1) similar to the PGT condition from previous studies (Chapters 2 & 3). After subjects made their selection, the experimenter first gave the non-chosen option either to a partner (partner present condition) or placed it into an opaque container placed in the same location as a partner would have been (partner absent condition). This allowed us to control for both a reaction to seeing rewards removed and to seeing the rewards moved to a particular location. Following this, the experimenter gave the subject their chosen reward. Rewarding the partner first maximized the chances of the subject noticing what happened to the unselected reward by moving it prior to giving them their reward. This process was repeated 40 times in the session. See below for species specific details.

4.2.1 NHP methods

NHPs were given four sessions each, two sessions of 40 trials in each condition (80 total trials/condition), with a maximum of one session per day. The order in which participants received each condition was randomized for each species so that half the subjects were tested in the partner absent condition first, while the remaining animals were tested with the partner present condition first. Rewards consisted of 1 cm^3 pieces of dried coconut for chimpanzees and Bio-Serv® 45-mg, grain-based, banana-flavored, dustless precision pellets for capuchins.

The sets were presented to the NHP on a table in front of their enclosure. For chimpanzees, the table was pulled away between each trial. Chimpanzees indicated which set they wanted to choose for a trial by touching the table in front it. If the chimpanzees touched in front of both decks simultaneously or made a touch that was not directly in front of a set, the trial was restarted. Capuchin monkeys used a specially designed door system that allowed them to select from one set, but not both (Salwiczek et al., in revision; Proctor et al., in prep). This was necessary as the monkeys tended to reach for both sets simultaneously and thus the experimenter was unable to interpret their choices. The doors were closed in between each trial to prevent access to the sets. For chimpanzees, the next trial started as soon as they had finished eating. With capuchin monkeys, a 10 second inter-trial interval was used, as this had previously been shown to improve their performance on the task (Proctor et al., in prep).

At the YFS, all chimpanzees were tested with the same 30-year-old female who was not otherwise involved in the experiment. We chose this individual because she had a neutral relationship (i.e., she was neither significantly affiliative nor significantly avoidant) with all the test subjects over the past two years of behavioral observations. This controlled for the quality of the relationship. At the LRC, there was no individual that had a neutral relationship with all the test subjects. We paired both of the males with a 26-year-old female who was not otherwise involved in the task. However, she had an agonistic relationship with the female test subject. We therefore paired that female with a 38-year-old-male in order to avoid a potential confound due to the strained relationship between the females.

We tested all of the adult capuchin monkeys at the LRC and therefore could not use an individual who was not involved in the experiment. We therefore paired individuals based on sex and relative rank. Our pairs were a 1) a 15- and a 20- year-old male, 2) a 9- and a 7- year-old male, 3) a 10- and a 15- year-old female and 4) a 14-year-old alpha male and a 10-year-old alpha female. These pairs were tested in both directions. That is, the subject would become the partner and vice versa, but only after a condition was completed in its entirety.

4.2.2 Human methods

Humans were given one session of 40 trials and separate cohorts were used for each condition. Human testing was between subjects rather than within subjects as we did not want to bias the results by giving humans two conditions in a row, and we were unable to bring participants back to the laboratory on a separate day. Participants sat at a table across from the experimenter and were rewarded with facsimile quarters. Note that previous studies on gambling tasks in humans showed that performance did not change depending upon whether they used real or facsimile money (Bowman & Turnbull, 2003). Subjects could either gesture or verbally state which set of containers they chose. The non-chosen reward was placed into an opaque container situated away from the subject and in front of the partner.

4.3 Results

Chimpanzees selected the HV option significantly more when alone than with a partner (McNemar Test: $\chi^2 = 5.082$, $p = 0.024$), even though they preferred the LV in both conditions (Binomial Test: partner absent, $p < 0.001$; partner present, $p < 0.001$).

Capuchin monkeys showed no difference in choice behavior dependent upon the presence or absence of a partner (McNemar Test: $\chi^2 = 4.954$, $p = 0.207$) and, similarly to chimpanzees, preferred the LV option in both conditions (Binomial Test: partner absent, $p = 0.016$; partner present, $p < 0.001$).

Humans did not alter their risk preferences as a function of whether or not a partner was present (McNemar Test: $\chi^2 = 0.006$, $p = 0.941$) and, like the other species, they preferred the LV option in both conditions (Binomial Test: partner absent, $p < 0.001$; partner present, $p < 0.001$).

However, these overall results hide a pattern in the data that indicates an experience effect in chimpanzees and capuchin monkeys. Despite the small number of sessions and trials, chimpanzees developed strategies for interacting with the first condition they received, but failed to do so in the second condition they received (Binomial Test: first condition, $p < 0.001$; second condition, $p = 0.254$; this difference was significant: McNemar Test: $\chi^2 =87.823$, $p < 0.001$). That is, in the first condition they received they showed a preference for the LV option, whereas in the second condition their performance did not differ from chance. This held true regardless of whether the first condition was the partner absent or partner present condition, indicating that experience was likely far more influential than the condition itself. Capuchin monkeys showed the opposite pattern and did not form a preference in the first condition they encountered (Binomial Test: $p = 0.057$), although there was a trend to prefer the LV. They did, however, develop a significant preference for the LV in the second condition they encountered (Binomial Test: $p < 0.001$; this difference was significant: McNemar Test: $\chi^2 = 13.488$, $p < 0.001$). Again, this was independent of which condition was experienced first or second. Note that we could not analyze this in humans as each subject received only a single condition.

This was unexpected as no experience effects were detected in two previous studies using a similar methodology with similar counterbalancing (Chapters 2 & 3). Therefore, to control for experience we ran a secondary analysis using a between subjects design. For this, we looked only at the first condition and compared the performance of the individuals who received the partner absent condition first to the individuals that received the partner present condition first. In neither species did we find differences in their performance based on the presence or absence of a partner (Kruskal-Wallis Test: chimpanzees, $\chi^2 = 0.429$, $p = 0.513$; capuchin monkeys, $\chi^2 = 0.125$, $p = 0.724$). Given the clear experience effects, we believe these results are more accurate than the within-subjects analyses and use them for the remainder of the analyses.

At the individual level, two of three chimpanzees, one of four capuchin monkeys, and four of 10 humans had a significant preference for the LV in the partner absent condition (Binomial Test: $p < 0.005$) and an additional monkey (Nala) showed a trend for this same preference (Binomial Test, $p = 0.057$). All three chimpanzees tested in the partner present condition significantly preferred the LV (Binomial Test: $p < 0.001$) as did one of three capuchin monkeys (Binomial Test: $p = 0.033$) and five of 10 humans (Binomial Test: $p < 0.05$). One human in the partner present condition had a significant preference for the HV option (Binomial Test: $p = 0.017$). No NHPs, regardless of condition, preferred the HV option. See Table 4.2.

4.4 Discussion

In the current study, we explored how the social context affected the decision-making of capuchin monkeys, chimpanzees, and humans in a gambling task. However, contrary to previous findings with humans (Rockloff, 2010; Rockloff et al., 2010; Rockloff & Dyer, 2007), none of the primates tested here, including humans, showed evidence of changing their gambling behavior when a conspecific was present. In fact, our only significant finding was an experience effect in the nonhuman primates that was independent of condition (humans were not tested in a within-subjects design and so this could not be assessed). While we cannot ascertain why this occurred, in particular given the lack of a similar effect in previous studies of this task in these species, we consider these results further below.

There are several factors that may have influenced these findings. First, unlike previous studies in humans (Rockloff, 2010; Rockloff et al., 2010; Rockloff & Dyer, 2007), our partners were individuals with whom the subjects had a prior relationship. Although we expected humans to gamble more with someone they knew, as they do in front of strangers, it may be that humans who have a prior relationship are less sensitive to the winnings of the other person (Brown, 1987; Homans, 1961; Kelley & Thibaut, 1978). They may not have had the same emotional reactions they would have with strangers, such as fear of failure, competitiveness and the desire to display economic fitness (Green, 1991; Rockloff & Dyer, 2007; Triplett, 1897; Zajonc, 1965). This could explain why their decisions did not vary as a function of social context.

Another difference between the current study and previous work is that in our study, the partner was an active participant in the interaction (although they could not influence the outcome) rather than simply being present. We originally designed the study in this way to draw attention to the presence of the partner, particularly for the NHPs, for whom other individuals are often present during testing procedures. However, because partners were rewarded, subjects may have viewed them as direct competitors, which could have affected their strategy differently than does the presence of completely uninvolved individuals. This possibility deserves further study to determine if previously established relationships influence gambling behavior differently than do strangers and how both relationship types may be differently affected in uninvolved versus involved (and potentially competitive) situations.

Additionally, unlike computerized gambling studies (Rockloff, 2010; Rockloff et al., 2010; Rockloff & Dyer, 2007), the experimenter ran the task and so, by necessity, was also present for all three species' testing. This may have added another social variable, as subjects were not only with another participant, but were also interacting with the experimenter. In humans in particular, subjects may have made decisions because of some perceived expectation of the experimenter (Orne, 1962; Pierce, 1908).

Another unexpected finding was the significant effect of experience shown by NHPs. This was particularly surprising, as other studies using similar methodologies did not show this effect, despite including more sessions and conditions than were utilized here (Proctor et al., in prep). It is unclear which feature of the experiment would have caused this change. One possible factor was the way rewards were handled in this study as compared to previous PGT experiments. In the current study, we removed the rewards that were not selected and thus the subjects did not have a chance to earn those rewards on subsequent trials. However, in previous PGT tests the non-chosen rewards remained present and hence were options for future choices. Moreover, these non-chosen rewards were not seen at the time of the choice, perhaps making them less salient. Finally, in the current study there was a longer time interval between choosing a stack and receiving the reward, as the partner (or empty container) first had to be rewarded. Unfortunately, there was no way to distinguish these possibilities using the current data.

More research needs to be conducted to understand risky decision-making in social contexts with NHPs and humans in order to elucidate the evolution of these types of decisions. While the current study failed to find any social effects of gambling behavior in NHPs, other evidence on behavioral changes in NHPs (e.g., Pollick et al., 2005; Roush & Snowden, 2000; Slocombe & Zuberbühler, 2007; Hare et al., 2001; Clay et al., 2011) and humans (e.g., Green, 1991; Rockloff & Dyer, 2007; Triplett, 1897; Zajonc, 1965) suggest this may be a fruitful area for future study.

Table 4.1: Payout Structure

Trial	LV	HV
1	3	3
2	3	0
3	2	1
4	3	6
5	2	0
6	3	0
7	2	1
8	3	0
9	2	1
10	2	1
Average Payout	2.5	1.3
Net Payout	25	13

The low variability option (LV) always paid a consistent, although variable, reward. On any one trial, the high variability option (HV) could payout more than the LV, but also included smaller payouts as well as no rewards. The LV led to the greatest overall rewards.

Table 4.2: Individual Binomial Results of the First Condition

Chimpanzees	Condition	Choice
Katie	PA	56.3% LV
Lana	PA	92.5% LV*
Missy	PA	76.3% LV*
Georgia	PP	70.0% LV*
Mercury	PP	98.8% LV*
Sherman	PP	81.3% LV*

Capuchins	Condition	Choice
Gabe	PA	57.5% HV
Liam	PA	99.6% HV
Logan	PA	72.5% LV*
Nala	PA	61.3% LV
Drella	PP	52.5% HV
Lily	PP	62.5% LV*
Wren	PP	51.3% LV

Humans	Condition	Choice
1	PA	67.5% LV*
2	PA	50.0% -
3	PA	57.5% HV
4	PA	67.5% LV
5	PA	92.5% LV*
6	PA	52.5% LV
7	PA	65.0% LV
8	PA	77.5% LV*
9	PA	52.5% LV
10	PA	67.5% LV*
11	PP	70.0% LV*
12	PP	72.5% LV*
13	PP	50.0% -
14	PP	75.0% LV*
15	PP	57.5% LV
16	PP	85.0% LV*
17	PP	55.0% LV
18	PP	65.0% LV
19	PP	70.0% HV*
20	PP	80.0% LV*

* Significant preference, Binomial Test, $p < 0.05$.

Due to the effect of experience across conditions, we only present the individual data for the first condition that each individual received, either the partner absent (PA) or partner present (PP) condition. Only one individual, a human, showed a significant preference for the high variability option (HV).

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5 Chimpanzees Play the Ultimatum Game

Humans often make decisions that seem irrational from an economic perspective. That is, they engage in behaviors that may actually decrease their absolute wealth. One explanation for this pattern of behavior is that humans are not only concerned with their own rewards, but also the rewards of others (Fehr & Schmidt, 1999). Human reactions to reward distributions have been extensively studied through the use of experimental economics tasks, in particular the Ultimatum Game (UG; Guth et al., 1982; Camerer & Thaler, 1995; Camerer & Lowenstein, 2004). In the UG, one individual (the Proposer) can split a quantity of money with another individual (the Respondent). If the Respondent accepts the offer, both players are rewarded using the proposed split. If the Respondent rejects the offer then neither player is rewarded (Guth et al., 1982). People in Western cultures typically offer around 50% of the available money (Guth, 1995; Camerer & Thaler, 1995; Camerer & Lowenstein, 2004), even in one-shot games that lack any future interaction, presumably because they anticipate refusals of unfair offers. Although cultural norms of fairness vary substantially, in all study populations to date Proposers go against their own short-term interests in offering the partner more than the minimum portion of the money, presumably to avoid losing it all (Heinrich et al., 2001).

As much recent work has shown, nonhuman primates resemble humans in their decisions about cooperation and reward division, particularly in relation to the issue of (in)equity (Brosnan et al., 2005; 2011; Jones & Brosnan, 2008; Brosnan & de Waal, 2003; van Wolkenten et al., 2007; Melis et al., 2009; Bullinger et al., 2011). However, it is not clear how they react to situations in which a peer can influence outcomes in a social task, such as in the UG. In contrast to the human tendency to split rewards equally, a previous study found our closest relative, the chimpanzee, to be self-interested: Proposers offered the smallest possible amount and

Respondents accepting everything (Jensen et al., 2007a). However, the methodology deviated substantially from the typical human UG and it was unclear if the apes fully understood the task (Brosnan, 2008; Visalberghi & Anderson, 2008). Moreover, when humans were subjected to the same methodology as the apes, they produced the same self-interested behavior (Smith & Silberberg, 2010). These results do not contradict the thesis, therefore, of shared economic decision-making mechanisms in humans and other primates.

It would make biological and ecological sense for chimpanzees to be sensitive to unequal outcomes. They routinely cooperate, for instance by collaboratively hunting and sharing the catch (Boesch, 1994), and engage in reciprocal exchange, possibly suggesting mental scorekeeping (de Waal, 1997; Gomes & Boesch, 2007). Moreover, the ability to recognize and be sensitive to unequal outcomes would help them in establishing optimal partnerships (Brosnan, 2011). Chimpanzees are sensitive to unequal outcomes in experiments, refusing to participate when a partner earns a better reward for equal effort (Brosnan et al., 2005; 2010). Chimpanzees additionally pay attention to intent, reacting more negatively to a partner deliberately stealing their food rather than obtaining the food from a human experimenter (Jensen et al., 2007b; Tomasello, et al., 2005). They also show "targeted helping," which requires recognition of the other's needs and goals (de Waal, 2008; Yamamoto et al., 2012).

However, cooperation does not occur to the same degree in all situations (e.g., Gilby, 2006) and chimpanzees do not always respond to inequity (Bräuer et al., 2006; 2009), perhaps based on factors such as sex (Brosnan et al., 2010), social relationship (Brosnan et al., 2005), and experimental methodology (reviewed by Brosnan, 2011). Despite passing control tests to verify understanding, chimpanzees may not always interpret experimental designs the way human experimenters intended. Thus, different methodologies may yield dramatically different results

(Horner et al., 2011). For this reason, we developed a paradigm making use of token exchange, a well-established procedure with nonhuman primates that requires no apparatus and, based on previous results, appears to be intuitive to the subjects (e.g., Brosnan et al., 2005; Horner et al., 2011; de Waal et al., 2008; Brosnan & de Waal, 2005; Brosnan & Beran, 2009; Talbot et al., 2011; Dufour et al., 2009; Pele et al., 2009; Addessi & Rossi, 2011). Additionally, a number of controls were included to ensure that all of the chimpanzees responded to the contingencies of the task. Several individuals had to be excluded because they were unable to pass these controls (See SOM). This limited our sample size, but also increased the validity of the results as we were reasonably certain that the chimpanzees understood the task.

The purpose of our study was to investigate chimpanzees' sensitivity to the possibility that their partner could affect outcomes. This sensitivity would be reflected in them making similar responses to humans in the UG. Proposers were presented with a choice of two tokens, one of which represented an equal reward distribution and the other an unequal distribution favoring the proposer. Respondents could either accept the token offer from the other by returning it to the experimenter or reject the offer by not returning it. This methodology allowed us to explore whether Respondents were sensitive to unequal distributions (i.e., refuse unequal offers) and whether the Proposers themselves were sensitive to potential rejections (i.e., by altering their choice dependent on their partner's refusals). To verify that any behaviors were truly similar to those of humans, and not the result of paradigmatic differences, we tested human children in the same way by having them work with other children in their preschool class.

5.1 General Method

Prior to testing, individuals were trained on the contingencies of the task. See SOM for the training details of each species. After training, the two subjects were brought into the testing environment. The Proposer was presented with a choice of two differently colored tokens, each representing a different offer. One token represented an equal split of the 6 pieces of reward (3:3) while the other token favored the Proposer at a 5:1 ratio. The Proposer selected a token and passed it to the Respondent. The Respondent could either return the token to the experimenter, thus accepting the offer, or refuse to return the token, hence rejecting the offer. If the token was returned, both individuals were given the proposed split of the reward. If the Respondent failed to return a token for 30 seconds, no rewards were distributed (note that this never occurred in either species). See Figure 5.1 for the experimental setup. Choices in the UG were then compared to choices in a simple preference test, without the need for Respondent collaboration, to specifically determine whether offers varied if the partner lacked control over the reward distribution.

In the preference tests, the partner was a naïve group member who was not otherwise involved in the experiment. We used an untrained individual to decrease the likelihood of behavioral responses to the subject's token choice, which may have influenced offers. When the Proposer selected a token it was immediately returned to the experimenter and, as in the UG, the rewards were divided according to the selected offer and both the Proposer and the naïve individual were rewarded. Unlike with chimpanzees, we were able to test children only on a single day. Thus to avoid confounds, preference tests were done on a separate cohort of children (for details see SOM).

One goal of this study was to test chimpanzees and children using similar methodologies in order to avoid species biases and to ensure that in this particular procedure the humans responded as anticipated based on other UG designs. To keep the tests as similar as possible, children were tested with a peer from their social group (e.g., their preschool class) using an exchange procedure learned with limited verbal instruction. We also gave them repeated UG trials, in case the repetition changed behavior (most UG experiments with adults use only a single trial, called a one-shot game).

5.2 Chimpanzee Results

Despite initial preferences for the selfish token (binomial tests; all $p < 0.05$; See Table 5.1 for exact p-values), all four chimpanzee Proposers more often chose the equitable token in the UG condition compared to the individual preference test (Exact McNemar's test: See Table 5.1, Figure 5.2). Comparing choices to 50% chance, two of the four Proposers also significantly preferred the equitable token in the UG (binomial tests; See Table 5.1, Figure 5.2). During the UG, no Respondent ever refused to return an offer.

Thus, chimpanzees, like humans in previous studies, chose a more equitable split of rewards in the UG, as compared to their baseline preference when their partner had no recourse. This preference was apparently spontaneous, occurring without any refusals by the partner and within a small number of trials, making it difficult to ascribe it to learning during the experiment itself. Moreover, this preference was consistent, with all four individuals showing the same behavioral change. Thus, we find that chimpanzee Proposers changed their behavior between two conditions that were identical except for the degree of control given to the recipient. Like humans, chimpanzees respond with equitable offers in the UG.

5.3 Children Results

Similarly to chimpanzees, children preferred the selfish token in the preference tests (group level binomial p=0.045, two-tailed). However, while children showed no significant preference in the UG condition (group level binomial p=0.38, two tailed), as predicted by previous research (Murnighan & Saxon, 1998; Harbaugh et al., 2003), children were more selfish in the preference test than in the UG (Mann-Whitney U, N1=10, N2=10, p=0.044, one-tailed; See Figure 5.2). As with chimpanzees, no child ever refused to return an offer. Thus, children also changed their preferences in the UG, despite the absence of refusals by recipients. This result is not only similar to how the chimpanzees made decisions, but is also the typical pattern in other UG studies on children (Murnighan & Saxon, 1998; Harbaugh et al., 2003).

5.4 General Discussion

Chimpanzees were similarly sensitive to the contingencies of the Ultimatum Game (UG) as human children. Although in a choice task both species preferred a "selfish" offer that brought the majority of rewards to themselves as compared to a passive partner (chimpanzees) or when alone (children), in the UG condition, in which their partner was affected by their choice, they switched their preference to the more equitable distribution. Thus, we demonstrated that chimpanzees, like humans, change their distribution preference in the same setting (i.e., paired with a conspecific from their social group) dependent on how their behavior affects a partner and how that partner may affect the outcome. Of those two possibilities, we do not know which one is more important. In fact, the chimpanzees showed a stronger shift in preference than the children. It is unclear if this reflects a stronger response in chimpanzees or that it may be explained by the lower level of training in children (training differences are a common confound in the comparative literature; Inoue & Matsuzawa, 2007; Cook & Wilson, 2010).

It is important to note that in neither the chimpanzees nor the children were there ever refusals, possibly because refusals were defined as the participant not returning the offer to the experimenter for 30 seconds. In experimental contexts, inaction may be sufficiently aversive to prevent refusals from occurring (Smith & Silberberg, 2010). However, we cannot rule out that the Proposers were pre-emptively responding to the potential for refusals, even if these never materialized. In fact, adult humans, who typically offer 50% of the rewards, usually are given only a single choice during the experiment (e.g., a one-shot game), so they have not been punished in the experimental context for making an inequitable decision, either. They were responding to the potential of refusal. Both chimpanzees and humans have prior experience with inequitable outcomes, which may make them more sensitive to the possibility of punishment in this task. Alternatively, because cooperation was needed to gain rewards, it is possible that Proposers were more generous because they were doing something with the Respondent. Thus, the cooperative nature of the task may also have increased equitable offers.

We cannot rule out the possibility that the Respondent's behavior, rather than the potential for refusals, influenced the offers made by the Proposer. Even though they were rare (too rare for quantitative analysis), communicative interactions by Respondents to Proposers did occur in both children and chimpanzees. Children Respondents sometimes made verbal comments about the reward distribution such as, "you got more than me," and, "I want more stickers." In chimpanzees, Respondents sometimes directed aggressive behaviors toward the Proposer, but Proposers never directed aggression at Respondents. For example, in the chimpanzee pair of MS-RT, five instances of aggression were recorded. Three instances involved

RT (Respondent) spitting water at MS (Proposer). The other two instances involved RT hitting the mesh barrier between them as MS was about to pass a token. Although we found no relation between offers made and aggressive behavior in the chimpanzees, it is possible these negative reactions sufficed to influence the Proposer. In both children and chimpanzees the Respondent's behavior may have cued the Proposer that either an aggressive response or a refusal was possible. We think this possibility deserves to be explored further in future research to elucidate the extent of chimpanzee's sensitivity to the behavior of others.

Table 5.1: Chimpanzee Choices of Equitable Token by Pair

Pair	Preference Test	UG
KT-GA	13% *	58% †
LA-SH	0% *	71% *†
MS-RT	17% *	67%†
SH-LA	14% *	92%*†

* Denotes significant difference from chance; Binomial Test $p<0.05$

† Denotes significant change from preference test to UG; McNemar's Test $p<0.05$

All chimpanzee pairs had a significant change from the preference test. Additionally, two pairs were significantly different than chance in the UG.

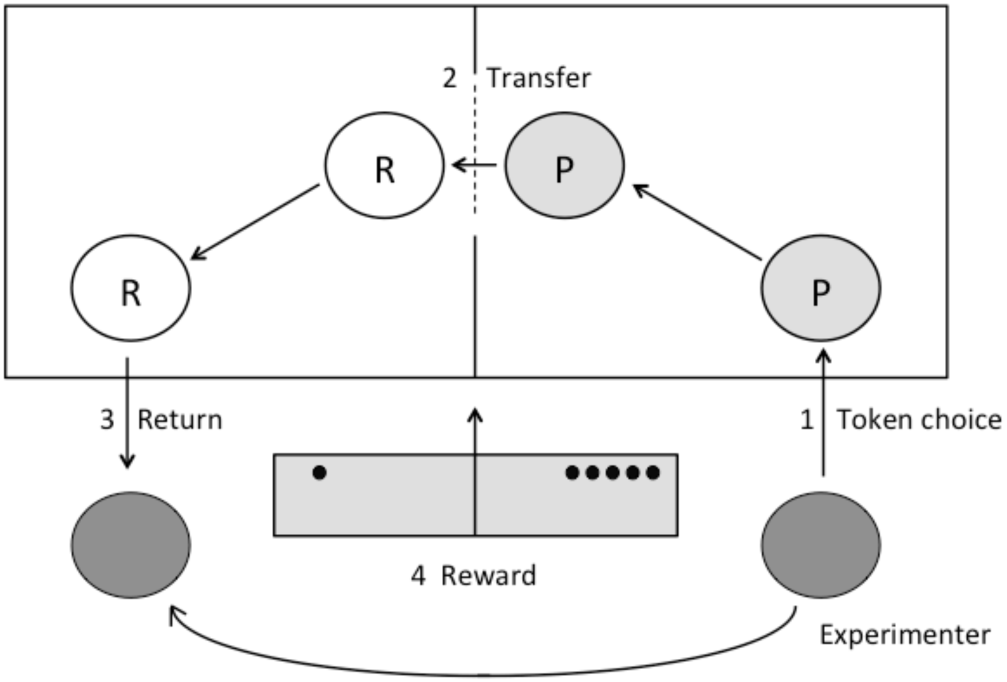
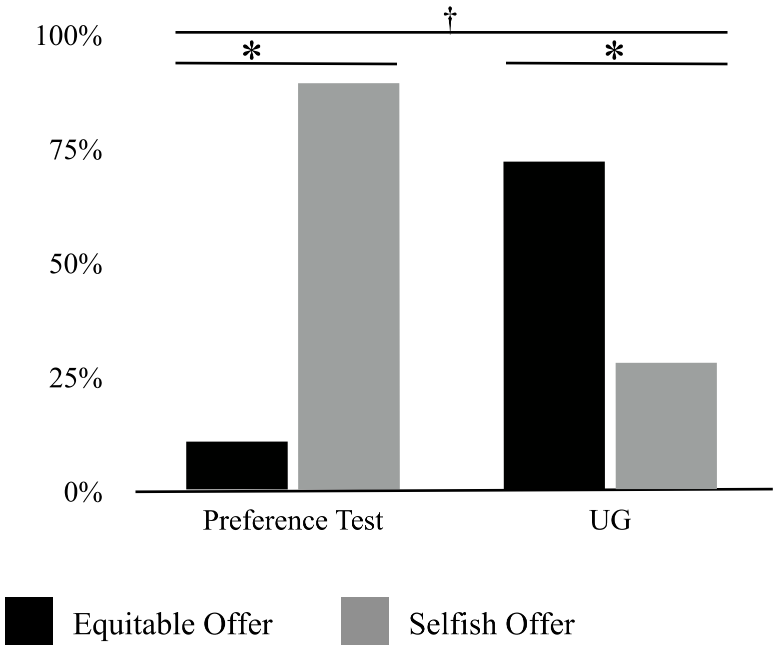


Figure 5.1: Experimental setup for the chimpanzees. 1) Subject pairs were presented with a choice of two tokens. One represented an equal split of the rewards and the other an unequal split favoring the Proposer (P). The Proposer was free to select either token. 2) The Proposer passed the selected token to the Respondent (R) through a mesh panel. 3) The Respondent could either return the token to the Experimenter to accept the offer or not return the token for 30 seconds to refuse. 4) The rewards were visibly divided on a tray in front of the chimpanzees according to the token selected. Here, the dots represent an unequal distribution of rewards in favor of the Proposer. The tray was pushed within reach of the chimpanzees so they could collect their rewards. Note that the experimental setup for children was similar, except a commercially available baby gate was used to separate the participants and the Experimenter.



* Denotes significant difference between equitable and selfish offer;
Binomial Test $p<0.05$
† Denotes significant change from Preference Test to UG; McNemar's Test $p<0.05$

Figure 5.2: Total Percentage of Offers Selected by Chimpanzees. Chimpanzees were presented with two different tokens representing either an equitable or selfish (favoring the proposer) offer. We compared their choices in a preference test, where the partner was naïve and passive to the UG where the partner could affect reward outcomes for both individuals. Although chimpanzees preferred the selfish offer during the preference test, they significantly changed their preferences towards the equitable offer in the UG condition. See Table 5.1 for offer selections by each pair of chimpanzees.

5.5 References and Notes

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5.8 Supplemental Materials

5.8.1 Chimpanzee Methods

We tested 6 adult chimpanzees (*Pan troglodytes*) from two research facilities (N=4 females from the Yerkes National Primate Research Center Field Station in Atlanta, GA; YFS; N=2, one male and one female from the Language Research Center at Georgia State University in Atlanta, GA; LRC). An additional 4 YFS chimpanzees failed to pass pretesting and were excluded from the study. All animals were socially housed and had access to both indoor and outdoor enclosures. At all sites, chimpanzees were fed a diet of chow and fresh fruits and vegetables in addition to any food they earned during testing. Water was available *ad libitum*. No animals were food or water deprived for this study. The Institutional Animal Care and Use Committee of the animals' respective institutions approved all research.

5.8.1.2 Pretesting

Prior to testing, chimpanzees were required to pass a number of controls. These controls were important to be sure that they understood the contingencies of the game. To be included in the study, chimpanzees had to 1) be able to pass a token to another chimpanzee, 2) have no initial preference for the tokens, 3) be able to discriminate between the reward quantities, 4) have exposure to what the offer meant for each position by using a naïve chimpanzee as a partner and 5) pass a final token preference where they preferred the offer that rewarded them the most (indicating an understanding of the token values).

First, chimpanzees were required to pass a token into an adjoining enclosure. This was an essential step, as the methodology required them to pass or receive tokens from another individual. Chimpanzees were placed in two adjacent testing rooms separated by a mesh panel that allowed full visual and auditory contact as well as limited tactile contact (e.g., limited grooming). All the chimpanzees involved in the experiment had prior experience passing a token to a human outside of their area. However, only the chimpanzees from the LRC had prior experience passing items between chimpanzee enclosures (Brosnan & Beran 2009). We therefore had to train the chimpanzees at YFS to pass tokens to an adjacent enclosure.

To train this behavior, an experimenter sat in the enclosure adjacent to the chimpanzee. The experimenter outside of the enclosures handed a token to the chimpanzee. The second experimenter then attracted the attention of the chimpanzee through vocalizations and gestures. If the chimpanzee passed the token to the second experimenter, they were rewarded with a banana slice by the second experimenter. After 10 successful passes the second experimenter began returning the token to the first experimenter, outside of the enclosure. The first experimenter then rewarded both the chimpanzee and the second experimenter with a slice of banana. After chimpanzees completed 10 consecutive passes on two separate days, they were considered trained. YFS chimpanzees were given up to four sessions of 20 minutes per day to accomplish this. The YFS chimpanzees found this more challenging than we anticipated, based on the ease with which the LRC chimpanzees had previously learned the task, and three YFS chimpanzees were unable to pass this stage. All remaining chimpanzees successfully transferred the token to another chimpanzee within two sessions of 20 minutes per day.

Next, chimpanzees had to pass an initial preference test with the tokens that represented offers. This was done to ensure that no chimpanzee had a bias toward one token before training occurred. We presented these tokens on a tray to the chimpanzee, who could then touch either token. As soon as one token was touched, the tray was removed and the tokens counterbalanced for the next trial. Each chimpanzee was given 1 session of 12 trials. No rewards were given for either token during this test to avoid reinforcement for either token. No individual had a greater than 75% preference for either token (average preference for preferred token = 6.625 out of 12).

Chimpanzees were next tested on whether they could discriminate between the quantities to which they could be exposed to in the experiment. We utilized six pieces of a high-quality food item (~1cm thick banana slices) as the pot that was to be split. The two offers that the chimpanzees were able to make in this limited form game were distributions of 3/3 or 5/1 (in favor of the proposer). Thus, animals in the proposer role received preference tests on the quantities of 5 versus 1 and 5 versus 3. Animals in the receiver role received preference tests on the quantities of 5 versus 1 and 3 versus 1. Animals passed the preference test if they selected the larger quantity on at least 18 trials out of two 12-trial sessions given on different days (binomial test, $p \leq 0.02$). Animals were given up to 10 sessions to reach this criterion. The LRC chimpanzees, who had extensive prior experience in numerical judgment (e.g., Beran 2009; Evans et al. 2010), all passed this pretest. One YFS chimpanzee was not able to pass this test.

Finally, chimpanzees (LRC = 2; YFS = 4) were given exposure to the offers the tokens represented. To train the chimpanzees on the offers, each chimpanzee was paired with a ‘foil’ partner chimpanzee. This was a chimpanzee who was not used in the experiment, who was naïve to the conditions of the task, and who did not participate in the training trials except as a passive recipient. As in the UG, the six rewards were lined up together on a tray in front of the chimpanzees. The subject chimpanzee was given a choice of two tokens to return to the experimenter (they did not pass the offer to the foil chimpanzee). The rewards were then divided according to the offer indicated by the chosen token and presented to the chimpanzees. Chimpanzees had to demonstrate a preference of at least 18 of 24 choices (binomial test, $p \leq 0.02$: See Table S1 for individual data) in two consecutive sessions for the offer that rewarded them the most. Subjects were given 12 trials a day for up to 10 days; LRC chimpanzees passed this pretest more quickly than the YFS chimpanzees, taking an average of 2.5 sessions compared to 6.75 sessions.

5.8.1.3 Test Procedure

During the test phase, all six rewards were lined up on a tray in front of the participants. To reduce location biases, tokens were presented on a vertical pegboard with eight token locations; token location was determined using random numbers. Proposers could choose either of the two offers, then they had to pass the offer to their partner. If the partner did not return the offer to the experimenter within 30 seconds, it was counted as a refusal, although this behavior was not trained and, given the long wait required, was unlikely (in fact, no refusals occurred during testing). After the offer was received, the experimenter divided the rewards according to the offer and moved each collection to the appropriate individual's side of the tray. The tray was moved adjacent to the chimpanzee enclosure and the chimpanzees could eat freely. The next trial began as soon as both chimpanzees finished eating. Chimpanzees received two test sessions of 12 trials each on two different days (24 total trials).

All test sessions were recorded on a digital video camera and later coded by a coder who was not involved with the experiment and was blind to the conditions and hypotheses. Inter-rater reliability was obtained for 20% of the sessions. Inter-rater reliability for offer choice and whether the offer was returned to the experimenter was 100% (Cohen's $\kappa=1$, $p<0.001$).

5.8.2. Human Methods

Twenty children from two preschools in the southeastern United States (N=20, 9 males, 11 females; age range: 2-7 years; mean age: 3.8 years; SEM: 0.36) were tested with other individuals from their class in the UG task. We were allowed to test these children for only a single test session, and so could not perform the preference test on a different day. To avoid the possibility that the exposure to rewards in one task would affect responses in the other, performed immediately subsequently, ten children were separately brought into a laboratory at Georgia State University to determine what reward distribution was preferred when they were alone (7 females, 3 males; age range: 3-4 years; mean age: 3.8 years; SEM: 0.13). This was similar to the token preference test in chimpanzees and allowed us to get group preferences without the potential bias of previous exposure. For all testing, children were seated on the opposite side of a commercial baby-gate from the experimenter, to mimic the separation between subjects and experimenter seen in chimpanzees.

5.8.2.2 Pretesting

All children were trained on the tokens and associated offers immediately prior to the experiment. The Proposer was given a token representing one of the two offers. Rewards (stickers) were laid out in front of the barrier so that the children could see, but not reach them. Children were instructed to pass the selected offer to their partner around the barrier. The partner could then return the offer to the experimenter. To indicate to the child that they could return the offer, the experimenter extended her hand palm up toward the child (a similar gesture was used to indicate the possibility of exchange with chimpanzee responders). No verbal instructions were used to get subjects to return the offer. The children were then rewarded according the offer returned. Children received a total of four forced-choice trials, two for each offer.

During training the experimenter talked to the children, in order to build rapport. However, besides the limited instructions given, the experimenter did not talk about the task (See Appendix 1). If the children asked the experimenter a direct question about the task, the experimenter would respond by saying, “What do you think?” or shrugging her shoulders.

5.8.2.3 Preference Test

Children participating in the preference test condition were tested at a laboratory at Georgia State University. Training and testing procedures were similar to those used in the UG, although with two differences, due to their being tested alone. During both training and the preference test, children returned the offer directly to the experimenter. They were rewarded with the selected offer as in the UG, but the portion of the reward that would have gone to a partner was removed from the testing area. Thus, the preference test was similar to the individual preference test given to chimpanzees, with the exception that in the chimpanzee tests, there was always a naïve conspecific partner present.

5.8.2.4 Test Procedure

The test procedure was identical to the training protocol, except that both tokens were presented to the Proposer. That child could then choose which offer to select. If a child tried to take both tokens, they were removed and replaced while the experimenter said "which one?" The Proposer passed the token to the Respondent, who could return the token to the experimenter. If the token was returned, the children were rewarded according to the offer represented by the returned token. Children were given one session of eight trials.

All test sessions were recorded on a digital video camera and later coded by a coder who was not involved with the experiment and was blind to the conditions and hypotheses. Inter-rater reliability was obtained for 20% of the sessions. Inter-rater reliability for token choice and whether the token was returned to the experimenter was 100% (Cohen's $\kappa=1$, $p<0.001$). One-tailed p-values were used based on our prediction that children would behave similarly to previous studies (Murnighan & Saxon, 1998; Harbaugh et al., 2003).

Table 5.8.1: Chimpanzee Performance on Quantity Preference Tests

Proposers	5 versus 1	5 versus 3
KT	23/24*	21/24*
MS	24/24*	23/24*
SH	22/24*	24/24*
LA	24/24*	23/24*

Respondents	5 versus 1	3 versus 1
Rita	24/24*	20/24*
Georgia	21/24*	21/24*
Sherman	22/24*	24/24*
Lana	24/24*	23/24*

* Denotes significant difference from chance; Binomial Test $p<0.01$

All chimpanzees that were tested passed pre-tested demonstrating that they could discriminate between quantities and preferred the token worth the larger quantity in a non-UG context (i.e., when there were not consequences for such a choice).

6 Children and the Primate Gambling Task

In addition to adult humans, I was interested in exploring how young children would respond to the Primate Gambling Task. Children's cognitive abilities are often used as comparisons with NHPs (see as examples: Warneken et al. 2006; Horner & Whiten 2005; Herrmann et al. 2010) and should have been able to use their "gut feelings" to navigate the task, as do adults (Bechara et al., 1997). However, unlike the vast literature on the Iowa Gambling Task (IGT) in adults (e.g., Bechara et al., 1997; Bechara & Damasio, 2002; Bowman & Turnbull, 2003), there has been relatively little research done on children's responses to this gambling scenario and those results are conflicting (Crone & van der Molen, 2004; 2007; Bunch et al., 2007; Garon & Moore, 2004; Kerr & Zelazo, 2004).

In children's versions of IGTs, performance was highly variable. Older children typically outperform younger children (Kerr & Zelazo, 2004; Garon & Moore, 2004), a pattern which continues through adolescence (Hooper et al. 2004; Crone & van der Molen, 2004; 2007). This is contentious, however, as several researchers report that some 3-year-olds can complete the task (Kerr & Zelazo, 2004; Garon & Moore 2004; Bunch et al., 2007), while other studies report that older participants (6-9 year-olds) perform similarly on this task to patients with an impaired ventromedial prefrontal cortex (Crone & van der, Molen 2004; 2007).

I originally thought that much of this contention was due to methodological variation, as the Crone and van der Molen (2004; 2007) task varied significantly from other children's tasks. In their version of the IGT, the stimuli were displayed on a computer screen, rather than the tangible decks of cards utilized in other studies and in adult versions of the IGT (Bechara et al., 1997). Secondly, the task was a prosocial one. Their version of the game featured a donkey that the children were instructed to help rather than gaining rewards themselves (Hungry Donkey

Task). The children could select one of four doors for the donkey to open. Behind the doors were either rewards or losses, in apples, for the donkey. The article did not mention any tangible reward for the participants, suggesting that they had minimal incentive to maximize payoffs. I believed that because of the lack of tangible rewards for the children, the Crone and van der Molen studies may not have been testing the same emotional responses as the other studies. In addition, their studies utilized four options, and young children may not yet have the ability to track probabilities over four decks (Bunch et al., 2007). I anticipated that making the task more similar to those of Kerr and Zelazo (2004), Garon and Moore (2004) and Bunch et al. (2007), would result in better performance by 4 year-old children, which I would then be able to compare to the NHPs.

6.1 Methods

To address this, I tested 20 4-year-old children (9 female, 11 male) in the Learning and Development Laboratory at Georgia State University. Children were brought to the lab by their parents. Prior to the experiment I obtained informed consent from the parent and tacit consent from the child. After playing with the child for several minutes to establish rapport, I asked them if they wanted to play a game with me. The child and I then entered the testing room. Parents also came into the room but sat behind the child to minimize any potential cueing by the parent.

Children were then given a brief quantity discrimination task. Two quantities of stickers were presented to the child and they were asked which quantity had more stickers. This was repeated three times for the quantities of 6/3, 3/2, and 2/1. The side the larger quantity was on was randomized to control for possible side biases. All children were tested regardless of whether they correctly discriminated these quantities. Because performance in the IGT can be guided by “gut feelings” (Bechara et al., 1997), I thought that children who did not pass the quantity preference test might still have been able to develop a strategy in this task.

I intended to give children the same number of trials in a session as adults and NHPs. However, the first three children we tested stopped the task prior to 40 trials. We therefore reduced the number of trials to 30, which allowed all children to complete the full number of trials. Rewards for children were small stickers. Like the other species tested (Chapter 2), the decks were presented to children on a table and they were free to select either deck. After making a selection, the topmost container was removed and the stickers were poured out in front of the child, who then placed them in a bag to take home with them. This process was repeated until the end of the session. Children or their parent could stop the test at anytime, although this never occurred once the number of trials was reduced. As with adults, children were given one session of one condition so that completing multiple conditions in a row did not bias their results. I tested the same three conditions used elsewhere (Chapter 2).

6.2 Results

As a group, no significant preferences were formed for either the low or high variability deck in any of the conditions (Binomial Test: PGT, n = 7, *p* = 0.836; EPGT, n = 7, *p* = 0.062; RPGT, n = 6, *p* = 0.879), although there was a trend to prefer the safe option in the EPGT.

However, six children failed the quantity preference test prior to the start of the task. Excluding the individuals that failed the preference test, the sample was reduced to 14 subjects (PGT, n = 4; EPGT, n = 5; RPGT, n = 5). These subjects showed a significant preference for the high variability option in the PGT (Binomial Test, *p* = 0.001), but no preference in the EPGT (Binomial Test, *p* = 0.369) or RPGT (Binomial Test, *p* = 0.369).

6.3 Discussion

As a group, children did not distinguish between the various payout schedules used in the PGT. This is likely for a combination of reasons including the small sample size, failure to distinguish between the quantities encountered and the use of inappropriate rewards. Despite these limitations (discussed below), the individuals who correctly distinguished the quantities in the preference test showed a preference for the riskier option in the PGT condition. That is, when overall reward maximization and risk aversion would result in a strategy of choosing the low variability, high reward option, the children appeared risk prone and preferentially selected the high variability, low reward option, which is contrary to the typical IGT findings, but supports the existing hypothesis that young children perform similarly on this task to clinical adult populations (Crone & van der Molen 2004; 2007).

However, there are several limitations to the study. First, of the 20 children I tested, six of them failed to pass the brief quantity preference test administered prior to testing. As with NHP, I wanted to ensure that the children could discriminate between the quantities they would encounter in the test. The most difficult quantity for them to distinguish was between two and three stickers, with four children incorrectly selecting two stickers. Two children selected one sticker over two (including one child who also incorrectly selected two over three) and one child incorrectly picked three over six stickers. I tested these children in spite of failing the preference test in hopes they could rely on the “gut feeling” for selecting decks that Bechara et al. (1997) discussed. However, I suspect that these 4-year-olds were too young to be sensitive to the quantity differences used here, as evidenced by 30% of my sample failing this test. Thus, testing older children may have led to more robust results. Additionally, if the children were having difficulties discriminating between the quantities, it seems unlikely that they were able to track reward probabilities across multiple trials. This may be similar to how 6-9 year-olds were not able to track probabilities in some tasks (Crone & van der Molen, 2004; 2007).

Second, I believe stickers were not equivalent to the rewards used in other studies or species (Kerr & Zelazo, 2004; Garon & Moore, 2004; Bunch et al., 2007; Chapter 2). In other IGT tasks with children (Kerr & Zelazo, 2004; Garon & Moore, 2004; Bunch et al., 2007), rewards were consumable food items, such as small candies. I elected to use stickers rather than food items because of the challenges of 1) finding a food item that would be consumable by members of the diverse Atlanta community (e.g., Kosher, lactose free, gluten free, etc.) and 2) that all children would be motivated to work to earn. Stickers have been used with success in other tests with children (Chapter 5; Horner & Whiten, 2005), although those tasks did not explicitly test children's sensitivity to a wide variety of quantities. However, in the PGT, I think stickers were not equivalent to either the food rewards used with NHPs or the facsimile money used with adults. In both of those cases, the rewards had some intrinsic value and more was clearly better. However, with children, stickers seemed so exciting to the children that they were pleased to get *any* quantity. This may have made them insensitive to getting relatively more or less stickers on a single trial. Similarly, because children are routinely rewarded with one sticker as an indicator of accomplishment (e.g., getting a single sticker for good performance in school), multiple stickers may not lead to increased positive outcomes in the same way that earning more money would in the adult version of the task. Thus, stickers may not have provided the children with sufficient motivation to develop a strategy in this task, particularly after several trials when they had already earned a number of stickers. Thus, in my opinion, stickers may be problematic in this type of test and further studies are needed to elucidate children's responses to gambling tasks.

The children's Primate Gambling Task as it was presented failed to clarify any of the discrepancies about children's performance on the IGT. There are many manipulations that may have added clarity to this study, such as testing a wider age range and manipulating the type of rewards. The original purpose in testing children was to compare their performance on this task to that of NHPs. However, because of the variability in the existing literature as well as the challenges with the current methodology, I elected to focus my time on adults, whose responses to the IGT are consistent across studies and methodologies (e.g., Bechara et al., 1997; Bechara & Damasio, 2002; Bowman & Turnbull, 2003). Until I knew more about adult reactions to the Primate Gambling Task, it would have been challenging to put children's reactions into a larger context within the human literature, much less to compare them to other primate species. However, I believe children's reactions to gambling scenarios are an area that deserves further study to see if there are any developmental changes in response to risky scenarios.

6.4 References

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7 Conclusion

> The roulette table pays nobody except him that keeps it. Nevertheless a passion for gaming is common, though a passion for keeping roulette tables is unknown.
>
> *George Bernard Shaw (1903)*

Great thinkers from Aristotle to the founder of modern macroeconomics, John Maynard Keynes, have pondered the enigma that is human gambling behavior. However, relatively little work has explored the evolutionary roots of these decision-making patterns. Gambling is a form of decision-making in which potential gains and the risk of losses are in conflict. Gambling, is, in essence, the result of making risky decisions. One of the aims of this dissertation was to explore risky decision-making patterns in NHPs in a way that would be comparable to the extensive literature on human gambling behavior to elucidate the evolutionary origins of this behavior. Here, I modified a classic human gambling experiment, the Iowa Gambling Task (IGT; Bechara et al., 1997), to be widely applicable to a variety of primate species. The resulting Primate Gambling Task proved a useful method for determining strategies of interacting with risk in gambling-type scenario. Additionally, I addressed whether risk preferences would change based on relative hunger levels and whether conspecifics would alter those preferences both when they could and could not influence reward outcomes.

7.1 Why the Primate Gambling Task is Useful

One of the challenges in interpreting risk preferences and making cross-species comparisons is that methods vary widely, lead to conflicting results, and potential strategies are often confounded (Kacelnik & Bateson, 1996; Shafir, 2000). The Primate Gambling Task combines the different reward structures of the human and animal literatures as well as disentangles risk preferences from reward maximization strategies, resulting in a methodology that can more accurately assess risk preferences. The primary methodological improvement was the inclusion of a number of different payout structures that varied on two factors: risk and overall rewards. Risk was manipulated by changing the amount of variability in the reward distribution and the overall rewards were manipulated by making the different options lead to different overall payouts. Because of these two factors, I was able to disentangle strategies when 1) the low variability option also led to the highest overall payout (similar to the IGT; Bechara et al., 1997), 2) the overall rewards were equivalent but the way those rewards were distributed varied (similar to animal foraging tasks; e.g., Kacelnik & Bateson, 1996), and 3) when the high variability option also led to the highest overall payout (which is not typically investigated in either the human or nonhuman literature). Structuring the payouts in this manner allowed me to disentangle whether the subjects were engaging in a risk aversion/proneness strategy or whether they acted to maximize their rewards, independent of risk. Additionally, using a similar design across species allowed for more accurate species comparisons.

6.2 Risk Preferences of Humans, Chimpanzees, and Capuchin Monkeys

A critical feature of this dissertation was the ability to compare human performance on the IGT to NHP performance on the Primate Gambling Task. Humans and NHPs are often compared to each other, but on the basis of experiments that have key methodological differences (cf., Boesch, 2010; Jensen et al., 2007 compared to Smith & Silberberg, 2010; Inoue & Matsuzawa, 2007 compared to Cook & Wilson, 2010). Therefore, I wanted to verify that humans would perform similarly on the IGT and the PGT, in order to verify this novel methodology. Indeed, human responses were similar across methodologies (Chapter 2).

However, unlike the typical human finding (Bechara et al., 1997; Bechara & Damasio, 2002; Bechara, 2005), when humans were tested using a more traditional payoff structure from the animal literature, where overall payouts were equivalent, they were insensitive to risk, as are many other animal species (Kacelnik & Bateson, 1996; Shafir, 2000). This is partially due to the fact that the different literatures measure different things (i.e., when payouts differ only on the reward distribution or when both the reward distribution and overall rewards vary), but call both of them "risk." This leads to differences in outcomes that are typically interpreted as differences between the species when, in fact they are due to differences in methodology. Furthermore, this suggests that a species whose risk aversion is well documented (e.g., Arrow, 1965; Bernoulli, 1738; Binswanger, 1980; Harrison, 1989; Pratt, 1964), may appear insensitive to risk with the typical animal reward structure, indicating that measuring risk solely based on the variability of the reward distribution is insufficient to fully elucidate risk preferences. However, human reactions to these different reward structures should be explored further to understand why their reactions differed than what would be expected using a risk averse strategy.

In contrast, chimpanzees' reactions to the different payout schedules were largely consistent. Chimpanzees were the only species tested that were sufficiently risk averse to prefer the low variability reward distribution even when overall payouts were equivalent. Under all of the conditions tested, at least some chimpanzees were risk averse and preferred the low variability reward distribution regardless of overall payouts. However, there was also variability in the chimpanzees' behavior. A subset of individuals, those from the LRC, deviated from a risk aversion strategy (i.e., choosing the less variable option) and maximized their rewards when the highest overall payout also had the most risk. The most parsimonious explanation for this population difference is that the LRC chimpanzees have much more experience with quantity discrimination, and this type of cognitive training influences performance (Boesch, 2010). For example, while both groups passed quantity preference tests, it took the YFS chimpanzees longer to do so (Chapter 5), suggesting the LRC chimpanzees' prior experience allowed them to, at least initially, outperform the YFS chimpanzees.

This difference raises the question of which population is more representative of chimpanzees as a species. I think that YFS chimpanzees may be more representative of what a 'typical' chimpanzee *would* do, while the LRC chimpanzees are better able to answer questions regarding what chimpanzees are *capable* of with extensive training. While the LRC chimpanzees have much more experience with quantity discrimination, they most often make these decisions in isolated testing contexts. In contrast, YFS chimpanzees are frequently fed as a group, which suggests they may also need to factor in social issues while weighing food acquisition options. As chimpanzees in the wild would also have to discriminate quantities within a social context, the YFS chimpanzees may be more representative of how a wild chimpanzee would behave. However, both of these groups add to our understanding of chimpanzees because they address the questions of cognitive abilities (LRC) and behavioral responses (YFS). We note, though, that care should be taken when extending results from one type of chimpanzee population to the rest of the species depending upon whether the question is about chimpanzee behavior or chimpanzee abilities.

Interpreting capuchin monkeys' behavior was the most challenging. Initially, their performance was similar to humans. However, because of the lack of a time delay between their choices, I felt as if their decisions may not have been representative of a strategy for dealing with risk (Roche et al., 1997). Therefore, I added a longer inter-trial interval for the monkeys. Using this inter-trial interval, four of seven monkeys formed the same preference to maximize overall rewards across conditions, making their results more reliable. However, this manipulation was not done with the other species. In humans, I used a between-subjects design and we could not, therefore, track performance across sessions to determine an individual's strategy. In regards to chimpanzees, they seemed sensitive to the reward distributions without using an inter-trial interval as six of nine individuals developed a strategy, in contrast to two of seven capuchin monkeys. However, it is possible that using a longer inter-trial interval would also increase performance (i.e., form a strategy) in humans and chimpanzees. This is an area that warrants further research.

7.3 Are Risk Preferences Static?

In addition to confounds that are present in the risk preference studies discussed above, there are other factors that can influence animals' preferences. Perhaps the most obvious is food availability (e.g., Caraco, 1980; 1981; Gilby & Wrangham, 2007; Kacelnik & Bateson, 1996). However, what has been largely ignored is whether risk preferences shift due to short-term fluctuations in factors including an individual's satiation level and the current social climate. These are important variables to explore in order to fully elucidate the range of risk preferences that animals exhibit. To address this, I tested two modifications of the Primate Gambling Task in which I manipulated satiation level and whether a not a partner was present during the experiment.

First, to address whether short-term hunger would alter the NHPs risk preferences I re-ran the Primate Gambling Task, but tested the animals prior to their morning feeding. This was presumably when they were the most hungry, as their last meal was the previous evening. I then compared these results to those of Chapter 2, where the NHPs had always received ~20% of their daily caloric intake prior to testing. Short-term hunger did influence risk preferences in both chimpanzees and capuchin monkeys (Chapter 3). Unsurprisingly, as these were well fed captive animals, these fluctuations did not result in a complete reversal of the risk preferences. However, we did find that both chimpanzees and capuchin monkeys became more sensitive to the amount of variability within each payoff option. Chimpanzees increased their preference for risk even when that did not necessarily lead to larger overall rewards. Capuchin monkeys changed their preference for risk, but in different ways depending on the reward structure, which will require more research to elucidate. Nevertheless, these types of potential fluctuations should be controlled for in future studies to ensure that findings are not being solely driven by hunger or satiation.

Satiation clearly influences how animals make foraging-type decisions, but it is not the only factor that can frequently vary. Primates are highly social animals in which group members can influence behavior in the short-term depending upon the social context (Pollick et al., 2005; Roush & Snowden, 2000; Slocombe & Zuberbühler, 2007; Hare et al., 2001; Clay et al., 2011; Triplett, 1898). In particular, humans gamble longer and have greater losses when gambling occurs in a social setting (Rockloff, 2010; Rockloff & Dyer, 2007; Rockloff et al., 2010). To explore whether this same phenomenon was exhibited in NHPs, I ran a social version of the Primate Gambling Task in which a passive partner was present (Chapter 4). To draw attention to the partner, they were rewarded with the option the subject did not choose. These results were compared to performance when the reward they did not choose was removed and placed in an opaque container. I did not, however, find an effect of social context in gambling behavior.

Instead, there was a strong influence of experience such that chimpanzees did not form a preference in the second condition they were exposed to (partner absent or partner present) while capuchin monkeys only developed a preference in the second condition they encountered. This experience effect was not seen in any of the other experiments using the Primate Gambling Task. Thus, it seems the NHPs changed their responses due to some variable besides the presence or absence of a partner, although why this occurred is not clear, there are several possibilities that may explain these results.

First, the partner may have been viewed as a competitor since they were being rewarded even though they had no role in the task. Thus, the task may not have measured the type of audience effects seen in humans. Second, the NHPs may have been responding to the non-chosen rewards being removed. This could have been because, unlike other iterations of the Primate Gambling Task, non-chosen rewards were available on subsequent trials. Thus, in the social task, the animals may have viewed the removed rewards as losses rather than potential future rewards. Finally, because the partner had no role (besides eating) the subjects may not have been aware that they were part of the experiment. Other research (Talbot et al., 2011; Chapter 5) indicates that conspecifics may be less salient or less important when they are not actively involved in a process to gain a reward. These possibilities need to be further researched to elucidate performance in the social Primate Gambling Task.

In contrast, in Chapter 5, I explored how chimpanzees would alter their decision-making process when a conspecific was directly involved in the task and could influence the subject's rewards. To do so, I used a typical human experimental task, the Ultimatum Game (UG) where subjects were faced with the decision to gamble that their partner would accept an unequal reward distribution favoring the subject, or make the safe bet and offer an equal split of the rewards. The social partner could potentially reject unfair offers, in which case neither the partner nor the subject would be rewarded. I compared their performance in the UG to performance when a social partner was rewarded according to the reward distribution, but could not reject offers. In the UG, chimpanzees made more equitable offers compared to when the partner could not influence reward distributions, as is typical in human UG experiments (Guth et al., 1997; Guth, 1995, Camerer & Thaler, 1995; Camerer & Lowenstein, 2004).

It is possible that, as in the Primate Gambling Task, chimpanzees were risk averse to the possibility of not being rewarded and therefore preferred the equitable reward distribution. It is also possible that communication between the chimpanzees played a role. There were some, although too few for quantitative analysis, interactions between the partners and subjects that may have influenced their choices. Again, more research needs to be done to elucidate why the chimpanzees changed their behavior.

Despite the lack of support from the social Primate Gambling Task (Chapter 4), it seems that in certain contexts chimpanzees' preferences can be altered because of conspecifics (Chapter 5; Slocombe & Zuberbühler, 2007; Hare et al., 2001), although the mechanisms behind and the extent of that influence are unclear and warrant further research. Thus, both satiation level and conspecifics may influence NHPs decisions in gambling type scenarios. This is important for researchers to keep in mind in order to eliminate potential confounds in the assessment of risk preferences.

7.4 Future Directions

There are several extensions to this research that I am interested in pursuing. First, there may be sex differences in risk preferences among males and females, as there are in human gamblers (Grant & Kim, 2002; Welte et al., 2002). This may be suggested by the findings of Chapter 2, in which male chimpanzees may have been more likely to change from a risk aversion strategy when the highest variability option also led to the greatest overall payout. Unfortunately, the only two males from my sample were from the LRC and there were noted population level effects. Thus, although the female at the LRC showed the same pattern as the males, population and sex are currently confounded, and even if they were not, a larger sample is needed to further explore whether sex differences in risky decision-making are present in chimpanzees. This may be important if different adaptive pressures led males to be more risk prone than females.

I am also curious about my finding that capuchins are not sensitive to risk. I believe my findings are fairly clear, but I am hesitant to conclude they are uniformly indifferent to risk across varying contexts. It seems, at some point, that risk indifference would lead to negative outcomes. For example, a completely risk indifferent capuchin would, theoretically, attempt to get fruit from a tree regardless of whether or not a predator was in the tree. Thus, some level of risk aversion seems necessary for all animals. For that reason, I am currently working on a follow up study using a computerized gambling paradigm to see if this indifference to risk is replicable in a different context. Hopefully, the results presented here combined with those future results will elucidate whether capuchin monkeys are truly insensitive to risk.

Finally, while this dissertation contributes to a better understanding of risk preferences in humans, chimpanzees and capuchin monkeys, there is much more variation in the primate lineage than is present in the few species tested here which warrant research. This is necessary in order to test different hypotheses about which environmental factors were important in the evolution of risk preferences. A quick assessment indicates that risk could be affected by a species' social system, and in particular their mating system, foraging behavior, predation pressure, and body size, just to name a few. Given the sex difference in gambling behavior between male and female humans – which indicates that males take more risks gambling– I am interested in exploring the degree to which mate competition affected gambling behavior. I did not find sex differences in the current dissertation study, which may indicate that mating pressure is not the answer (i.e., one would anticipate that males, especially male chimpanzees, would have been selected to be risk prone given the winner-take-all style of mating). However, this could be better assessed by expanding this research to other primates with different social structures, such as pair bonded gibbons or tamarins. If mating behavior has influenced risk taking in males, we would expect to see far fewer differences in behavior between males and females in pair-bonded than promiscuous species, as the females in pair-bonded species are competing more for good quality males (at least in principle). Similarly, in female dominated primates, such as ring-tailed lemurs (although see MacLean et al., 2012 for risk preferences in lemurs) and bonobos, the mating behavior hypothesis would predict that females should be *more* risk prone than males.

Of course, mating preferences are not the only possibility. Still within the realm of mating, it is possible that risk is a sexually selected trait, and that in species with more "winner-take-all" mating strategies in which only a few individuals get to mate (at least amongst the males), there would be more selection for showy behavior that may be risky than in other species that have other competitive mating strategies (e.g. hamadryas baboons). Further, there is good evidence that feeding ecology may play a role. For instance, in callithrichids, gum eaters, who have to wait extended periods of time for the exudate from the trees, are far more willing to delay gratification than are insectivores, who must move rapidly (Stevens et al., 2005). It may be that feeding ecology plays a role in specifically risky situations as well. Predation pressure may also be important, as species with higher rates of predation pressure may be less likely to take risks than those with lower levels, due to the higher risk of becoming someone's prey.

In short, while this dissertation represents a starting point, far more research is needed to fully understand risk preferences, and in particular those that cause individuals to behave in maladaptive ways, such as in gambling. What this research does provide is a standardized way in which to assess risk preferences broadly across numerous species. With this tool in hand, we can now begin to address questions about the evolution of gambling behavior, as well as the social and ecological pressures that may have influenced some individuals or species to be more risk seeking than others. With this knowledge, we will hopefully form a better understanding about gambling behavior and how it can be addressed among humans.

7.5 References

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