THE EFFECT OF A CONSPECIFIC MODEL ON A CAPUCHIN MONKEY'S *(Cebus apella)* CHOICE

BETWEEN A CERTAIN, CONSISTENT FOOD OPTION AND A RISKY FOOD OPTION.

By

TEPHILLAH JEYARAJ

(Under the direction of Irwin S. Bernstein)

ABSTRACT

This study examined the effect of the choices of a conspecific model on the decision making process of capuchin monkeys *(Cebus apella)* in the context of risk. In Experiment 1, I tested seven monkeys on their preference between an option awarding a fixed amount of food at a consistent rate (i.e. a certain choice) and an option that awarded double or nothing half the time (i.e. a risky choice). I found that six of them preferred the consistent option. I predicted that they would be influenced to shift their choice to the risky option when they saw a conspecific model receive a higher payoff for picking the risky choice. I found that while the model seemed to distract some of the monkeys, most of them stayed with their baseline preferences. In Experiment 2, I tested them with novel food containers to rule out the effect of prior experience with the options on their choices, predicting that in the absence of personal experience or information regarding the options, the monkeys would follow the model's choice. The baiting contingency for the consistent and risky options was similar for the model and the subjects. Results were variable with some preferring the model's choice, some preferring the consistent choice, and some showing no preference between the choices. Predicting a stronger

effect of the model when the subjects saw him receive double the amount of food at a consistent rate, I tested the subjects using two more novel food containers (Experiment 3). Results were once again variable across individuals. I conclude that while there is evidence showing that capuchin monkeys attend to their own and a partner's outcomes, they do not appear to keep track of their outcomes, or a partner's outcomes, over a series of trials. They do however, seem to be distracted by the model. When faced with choices unfamiliar to them, some of them tend to follow the model's choice indicating that prior experience can interfere with the influence of a social model.

INDEX WORDS: Risk, Decision making, Social effect, Prior experience, Capuchin monkey

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DEDICATION

To Mum, Dad, Raja, and Preeda.

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CHAPTER 1

INTRODUCTION

Decision making in animals is generally studied in the context of foraging. During foraging, the animal can make decisions among several options regarding patch selection, specific foods to eat, when to leave a patch and travel routes.

An option is defined as being risky if the outcome of that choice is seen as less certain than another (adapted from von Neumann & Morgenstern, 1944; Rothschild & Stiglitz, 1970). When an individual makes a choice with an uncertain outcome, he can either gain something, or lose something already owned. Types of risky choices that do not involve loss on part of the individual involve uncertainty either in the quantity of reward gained or uncertainty in the time associated with receiving the reward. In experiments where quantity is manipulated, one option will guarantee a certain fixed amount of food while another will provide varying quantities of food. If the temporal variable is manipulated, then one option will offer food after a certain fixed time interval while another will produce food after variable time delays. If the chooser picks the variable options in these scenarios, he can not know exactly how much the next outcome will be or exactly after how long it will be until it is provided, respectively. The uncertainty involved in these last two outcomes makes them risky choices. In general, if the chooser picks one option more than the other, he is said to be 'risk-sensitive'; 'risk-prone' - if he picks the risky option more, 'risk-averse' - if he picks the certain option more. The existing literature shows that animals do exhibit risk sensitivity by showing preferences between

options whose outcomes differ in the degree of variance when the average gain is the same (Smallwood & Carter, 1996).

Another way of studying risk is by requiring the individual to 'invest' a resource already owned in an option with uncertain outcomes where the individual does not know whether he can gain something more valuable that what was 'invested' or incur a loss. Experimentally this type of risky behavior is studied using a trading paradigm to evaluate how an individual values a commodity already owned, and what the individual is willing to trade it for (Tversky & Kahneman, 1981; Lakshminarayanan, Chen & Santos, 2008). For the purpose of the present study, the focus was on the choice between two options that vary in the amount of food awarded in a probabilistic manner such that the net gain was the same.

One of the most popular approaches to the study of risk in animal decision-making is called Risk-sensitive theory (Kacelnik & Bateson, 1997). This is a normative approach which predicts how an organism should respond to risk to maximize its fitness. Specifically in the context of foraging, risk-sensitive foraging theory (Stephens, 1981; McNamara & Houston, 1987) predicts that whether or not the animal goes for the risky choice that is uncertain in terms of payoffs (can either offer much more food than the fixed food option, or a much less or even no food) is based on the animal's 'energy budget'. This in turn refers to whether or not the animal has met its energy requirements for survival. An animal on a positive energy budget has consumed enough food to survive whereas an animal on a negative energy budget has not met this requirement. According to risk-sensitive foraging theory, due to natural selection, individuals make riskier choices under a negative energy budget but safer choices under a positive energy budget (Mazur, 2004). When the animal has already met its energy

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requirement, it would be maladaptive to take risks which will have uncertain outcomes. When the animal has not met its energy requirement and faces survival issues, the safe choice might not provide enough food to meet the energy requirement while a riskier choice can potentially provide a big payoff. Thus, when the animal is on a negative energy budget, it is actually adaptive for the animal to pick foraging options with uncertain outcomes. For the most part, research with different species including birds such as the yellow-eyed junco, *Junco phaeonotus* (Caraco et al., 1980), tree shrews, *Sorex araneus* L. (Barnard & Brown, 1985), rats, *Rattus sp.* (Ito, Takatsuru & Saeki, 2000), stickleback fish, *Spinachia spinachia* (Croy & Hughes, 1991) and bumblebees, *Bombus sp.* (Cartar, 1991) support this model. There is however, evidence showing contrary results (Hastjarjo, Silberberg & Hursh, 1990) or showing no relation between energy budgets and risk-sensitivity (Battalio, Kagel & McDonald, 1985). It has been suggested that body weight might play a role in determining the animal's daily energy budget since smaller organisms might have a higher daily energy budget while larger animals that can store more energy, might have a smaller daily energy budget (Kacelnik & Bateson, 1996). Despite the varied results, this theory is currently the only theory on risk-sensitive decision making that includes the effect of energy budgets.

Another approach is a process model based on associative learning which focuses on how the animal acquires information regarding the available options. Animals have to first learn about the payoffs of different options and, in the laboratory, this is usually done by initially training them to understand the outcome of responding to specific stimuli. When animals pick an option by pressing a lever or pecking a button, for example, and the outcome of this choice is a fixed amount of food every time they select it, they are positively reinforced and are more

likely to make the same choice again. On the other hand, when the animal selects an option

that sometimes offers no food or sometimes a little food or sometimes a lot of food, i.e.

variable outcomes, the animal learns that the outcomes of this option are uncertain. When

both options are then offered simultaneously, the animal will choose the option which formed

the stronger stimulus-response association, in this instance, the fixed food option. Most

researchers interested in the role of associative learning on risky decision-making tend to either

focus on the temporal aspects of the reinforcers (such as whether the food is delivered

immediately or after variable time delays) or the temporal aspects in conjunction with amount

of food (i.e. a choice between a smaller quantity offered immediately or a larger quantity

offered later) (Kacelnik & Bateson, 1996).

Overall, theories of individual decision-making in the context of risk predict that animals

will prefer options that offer fixed food quantities over variable ones. However, a review of

non-human research including a variety of insect, fish, bird and mammal species (Kacelnik &

Bateson, 1996) reveals mixed results among the studies that tested response to variable

quantities. A majority report risk aversion, some find no preference and a few show that the

animals are risk prone. A recent example is a comparative study by Heilbronner et al. (2008)

that found that chimpanzees *(Pan troglodytes)* significantly preferred the risky option over the

fixed food option while bonobos (*Pan paniscus)* preferred the latter.

Research with non-human primates shows that the decision-making environment plays

an important role in the strategy adopted by the animals. Various factors in the environment,

and within the animal, can cause them to form and change their risk preferences. For example,

one factor that has been shown to change risk preference is how the outcomes are presented,

also known as framing effects. The existing human literature (Tversky & Kahneman, 1981) shows that people evaluate outcomes of choices based on a reference point and when an outcome is framed in the context of a loss in comparison to the expected outcome, people avoid selecting it, but if the same outcome is framed as a gain compared to a reference point, people are more willing to select it. They are thus, risk-averse to loss but risk-prone to gain. Chen, Lakshminarayanan, and Santos (2006) also demonstrated this in captive capuchin monkeys *(Cebus apella)* using a token-trading paradigm.

Another way in which the context can be manipulated is by introducing a social partner who is also selecting between two options - a fixed amount reward option and a variable one. With the social partner's choice acting as the potential reference point for the subject, one can see if the social partner has an effect on the subject's choice when the latter is presented with identical options. The existing animal literature testing risk theories using fixed and variable reinforcement schedules focuses more on predicting individual choice without much attention to the social context.

Researchers who are interested in social effects on risk-taking behavior seem to concentrate more on human decision making, specifically in the context of gambling behavior. Studies reveal that there is generally an increase in risk-taking behavior in a group setting, compared to when an individual is alone, due to the diffused feeling of responsibility (Wallach, Kogan & Bem, 1962). There is also research showing an increase in risk-taking when alone due to increased familiarization with the situation (Flanders & Thistlethwaite, 1967). The mixed results in these cases can be attributed to other variables including perception of control (Langer, 1975), personal efficacy (Bandura, 1977), and the level of confidence (Shields et al.,

2005) which have been found to determine whether a person makes risky choices when alone or in a group. Social processes such as competition and conformity can further confound these already variable findings.

To explore changes in individual risk preferences in variable social contexts, Zajonc et al. (1970) proposed the social facilitation hypothesis. They predicted that individuals in a group that makes risky decisions will themselves shift in a risky direction when alone, but if they are in a conservative group, they will shift in a conservative direction when acting alone.

Humans are able to deal with decisions involving risk when they are provided with information describing the probability of the outcomes as well as experience gained from repeated sampling of the options (Hertwig et al., 2004; Weber, Shafir & Blais, 2004). Animals however, rely on feedback from actual experience rather than verbal information. They may gain this information from personal trial-and-error learning. There is another way that individuals can learn about the outcomes, and that is through observation of others making decisions.

Fragaszy and Visalberghi (2004) discuss socially biased learning in monkeys as learning that occurs as a result of individual experience and exposure to others' behavior, and perhaps their outcomes, and not due to imitation (Visalberghi & Fragsazy, 1990). They review literature supporting this type of learning in the context of eating novel foods, using a new tool and solving a problem. An interesting comparison of capuchin monkeys *(Cebus apella)* and callitrichid monkeys *(Callithrix sp.* and *Saguinus sp.)* reveals that in addition to individual characteristics (motivation, prior and current experience), both physical contexts (substrates, accessibility) and social environment (such as social structure and social tolerance) play an

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important role in influencing whether or not efficient learning takes place. Thus, while socially biased learning may be a better explanation of learning in a social context, there is little information regarding decision making under risk. If a conspecific's choice was used as a reference point, or served as a model, this could bias the subject towards the same choice.

Brosnan and de Waal (2003) and Fletcher (2008) have demonstrated that capuchin monkeys *(C. apella)* are sensitive to the outcomes of the choices of others. This indicates that the monkeys are using the information regarding a conspecific's rewards in their own decision making processes. The present study investigated the conditions under which, subjects use such information, specifically in the context of deciding between a consistent and a risky reward option.

The existing literature on risk preferences shows that when choosing between outcomes that vary in the quantity of the food awarded, individuals tend to prefer fixed or consistent options over variable or risky options. I predicted that capuchin monkeys will also show a preference for the consistent option (Hypothesis-1), but when they see a conspecific model choose the risky option and receive a better reward than they did, then they will shift to the risky choice as well (Hypothesis-2).

Since prior experience or knowledge of the options influences decision making, the subject can gain sufficient experience through the course of the experiment, to potentially interfere with the social effect. In order to test the extent to which a monkey might rely on a social model in the absence of any personal experience, I tested the subjects with novel options in Experiment 2, predicting that the model will have a much stronger effect on the choices of the subject when observing the model is the initial source of information regarding the options

(Hypothesis-3). The outcomes of the options were identical to what the subject received in Experiment 1 but were presented under novel containers unfamiliar to the subjects. The model always picked the risky payoff and received two food items half the time. However, in the event that the subjects were attending to the model's inconsistent payoff rate and did not pick the model's choice, in Experiment 3, I increased the model's payoff to double the food at a consistent rate to see if monkeys unaffected in Experiment 2 would be more prone to following the model's choice in this condition.

CHAPTER 2

EXPERIMENT 1

Research shows that humans and animals are quite strongly averse to risk (when presented in the form of variable food amounts at a probabilistic rate) and prefer a fixed amount of food at a more consistent rate (Kacelnik & Bateson, 1996). However, I had hypothesized that animals which prefer the consistent choice when alone will switch to the risky choice only when they see a conspecific receive more food for choosing the risky option. This experiment tests that prediction.

METHOD

Subjects

Eight pair-housed adult male capuchin monkeys *(Cebus apella)* from the Primate Cognition & Behavior Laboratory at the University of Georgia participated in the experiment. Seven of them were the subjects (LE, XE, CH, MI, SO, XA and JO) while one (NI) was the conspecific model. All the monkeys were born and raised in captivity. Their average age at the time of testing was around 20 years. All of them were well experienced in working on various laboratory tasks designed to test their cognitive and motor capabilities. Although prior research (Addessi, Crescimbene & Visalberghi, 2008; Beran et al., 2008) shows that capuchin monkeys *(C. apella)* can visually discriminate between the different food quantities (1, 2 and 4 pieces), I tested my 7 subjects and confirmed this (Appendix B provides the testing procedure and results).

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Materials

Two large plastic Solo® cups of the same size but of different colors (red and blue) were inverted and used to hide the food (Kellogg's Cheerios®). They were placed on a platform (16.25 x 10.25 x 4.0 inches), which in turn was set up on a movable cart (23.6 x 15.7 x 30.5 inches). I pushed the cart up to the monkey's testing cage during trials. A rectangular opening (5.4 x 2.5 inches) allowed the monkey to reach out his arm and access the cart. Cardboard occluders were used to hide the platform from the monkey while the cups were being baited.

Procedure

I brought each subject to the testing room from his homeroom in a transport cage and let him into the testing cage to perform his trials. In conditions where the model was required, the conspecific was also brought from the homeroom in a similar manner. He was placed in a cage approximately four feet from the subject and facing the subject. Once testing was completed, the monkeys were taken back to their home cages.

Experimental design

<u>Pre-training</u>

Each subject was trained to displace an inverted cup to obtain the food underneath. The subject received 10 trials per cup and had both the red and blue cups each day. The blue cup (i.e. consistent choice) always contained one cheerio; the red cup (i.e. risky/variable choice) contained two cheerios half the time. The net gain for choosing either cup was the same. I

presented only one cup at a time. Each monkey did a total of 100 trials (over 10 days) for each

of the blue and red cups. The order of presentation of the cups each day was randomized.

While training the model, I baited the red cup with food and never the blue cup. The

subject did 10 trials of the red cup with food underneath 50 % of the time, followed by 10 trials

with the blue cup which was never be baited.

Subject-Alone condition (Baseline)

The subject was presented with both cups. The blue cup always covered one cheerio;

whether or not the red cup had food (2 cheerios) on a particular trial was randomly

determined, but it covered food 50% of the time. This was the reward contingency for the

subject throughout this experiment. Whenever the red cup concealed two cheerios, the

cheerios were always placed a half inch apart to be distinctly visible as two items when

revealed to the subject. In order to avoid a side bias, the placement of the cups on the left and

right sides was pseudo-randomized (i.e. a particular cup was not placed on the same side on

more than two consecutive trials). This was done to avoid a location bias. While the cups were

being baited, they were hidden from the monkey's view by the occluder. Once baited, the

screen was removed and the cart was pushed up against the monkey's cage. The monkey was

allowed to displace a cup and take the food reward. I ran each monkey on 10 trials every testing

day. I had 10 testing days per subject. All subjects' choices were recorded and this was taken as

their baseline performance.

<u>Model-Present condition</u> (Control)

I used this step to assess the effect of the mere presence of the model on the subject's preferences. In this condition, the model was present in the room in another cage facing the subject (Figure 1). The model did not work with the cups. The baiting procedure for the subject was similar to the way it was done in the baseline condition. The subject was also tested on choices identical to those presented in the baseline condition. Once again, the subject did 10 trials a day for every testing day (i.e. 10 days).

Figure 1 - The experimental setup in conditions that required the model.

Next, there were two test conditions requiring the active participation of the conspecific model (who had been previously trained to choose the risky choice or red cup, over the consistent option or blue cup). The amount of food received by the model when he picked the risky choice was varied: in one condition, the model received less food than the subject did, when he

picked the risky option (i.e. Model-gets-less), in the other condition, the model received more (i.e. Model-gets-more). Subjects that preferred the risky choice (red cup) initially or showed no preference, were first tested on the Model-gets-less condition, and then on the Model-gets-more condition. If the monkeys preferred the consistent option (blue cup) initially, they went directly to the Model-gets-more condition.

Model-gets-less condition

During testing, the red cup for the model was baited with only one cheerio on half of the trials presented which in turn was randomly determined. The blue cup was never baited as the model had been pretrained to avoid choosing that cup. The subject and the model were placed in testing cages facing each other with the cart in the middle, initially out of reach of both monkeys. During baiting, the cups were hidden from both monkeys using the cardboard occluders.

The occluders were removed and the cart was moved closer to the model. The model did 10 consecutive trials in each of which he chose the red cup and received one cheerio on half the trials. He therefore received a total of five cheerios over the 10 trials. After each trial, the cups were concealed and re-baited. I visually monitored the subject to see if he watched the model during these trials. Once the model finished 10 trials, the subject was given the choice between the red and blue cups for 10 consecutive trials. The baiting of the cups for the subject was similar to the baseline condition. All the subject's choices were recorded. This completed one testing session. Each subject did only one session every test day and had a total of 10 test days.

Model-gets-more condition

This condition was similar to the Model-gets-less condition, except that the model's choice (i.e. the red cup) was baited with four cheerios on 50% of the trials. He therefore received a total of 20 cheerios over 10 trials. Then the subject had 10 consecutive trials and his choices were recorded. Once again the subject's cups were baited as they had been done in the baseline condition. Each subject had 10 days of testing, resulting in 100 trials for this condition.

Model-picks-blue condition

On completing the Model-gets-less condition, if any of the subjects showed a preference for the risky choice, he was tested with the model that picked only the consistent choice (i.e. the blue cup). The model was trained prior to testing to pick the blue cup which revealed one cheerio when displaced. The rest of the testing procedure was similar to Model-gets-less and Model-gets-more conditions. The Model-picks-blue condition was done to see whether the subject was following the model's behavioral choice or was attending to the model's outcome. If the subject switched to the consistent option or blue cup I concluded that he was following the model's behavior and not outcome.

The sequence of conditions and the potential outcomes for each condition in this experiment is depicted as a flowchart in Figure 2.
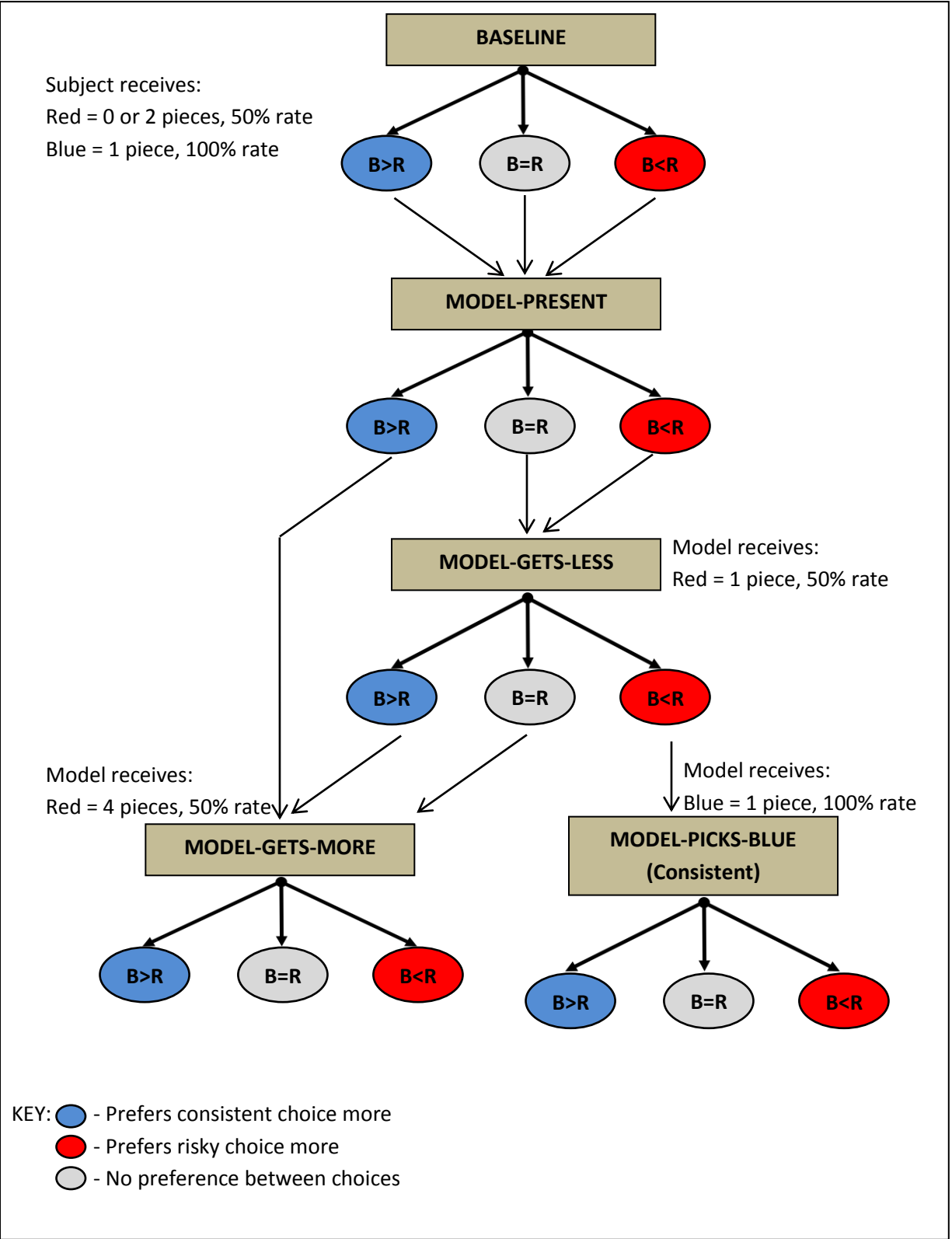
Figure 2 - The sequence of conditions and potential outcomes in Experiment 1.

Analysis

I used binomial tests to analyze cup preference within each condition and proportions tests to compare changes in cup preference across conditions. I tested statistical significance at an alpha of .05. I also applied a Bonferroni correction when multiple pair-wise comparisons were required.

RESULTS

When tested alone (i.e. Baseline), six of the seven subjects (LE, XE, MI, XA, CH & SO) significantly preferred the blue cup or the consistent choice (p<.05) whereas one subject (JO) showed a preference for the red cup or the risky choice.

In the mere presence of a model (i.e. Model-present condition), four (LE, XE, MI & XA) of the six continued their preference for the consistent choice. In the next phase, they went directly to the Model-gets-more condition. The other three (CH, SO & JO) did not show a significant preference between the two options when the model was merely present.

When tested on the Model-gets-less condition, these three monkeys each responded differently: one subject (CH) went back to his baseline preference for the consistent option, JO continued to not show a preference for either option while SO showed a significant preference for the risky option. Because of this preference, SO was tested on the Model-picks-blue condition where he again showed no significant preference between the cups.

Of the six monkeys which did the Model-gets-more condition, five of them (LE, XE, MI, XA & CH) significantly preferred the consistent choice while JO showed a preference for the risky choice. Table 1 presents the results of this experiment.

Table 1 – Preferences of the monkeys in Experiment 1.

Subject	Baseline			Model-Present			Model-gets-less			Model-gets-more			Model-picks-blue		
	Blue	Red	Sig.	Blue	Red	Sig.	Blue	Red	Sig.	Blue	Red	Sig.	Blue	Red	Sig.
LE	**81**	19	0.000	**85**	15	0.000				**97**	3	0.000			
XE	**64**	36	0.002	**62**	38	0.004				**72**	28	0.000			
MI	**84**	16	0.000	**84**	16	0.000				**70**	30	0.000			
XA	**75**	25	0.000	**84**	16	0.000				**90**	10	0.000			
CH	**61**	39	0.007	54	46	0.058	**55**	45	0.048	**64**	36	0.002			
SO	**60**	40	0.011	48	52	0.074	41	**59**	0.016				47	53	0.067
JO	43	**57**	0.030	48	52	0.074	50	50	0.080	45	**55**	0.048			

KEY:
- Indicates significant preference for consistent choice (Blue cup)
- Indicates significant preference for risky choice (Red cup)
- Indicates no significant preference between the choices
- Indicates the subject did not do this condition

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DISCUSSION

When alone, six of the seven monkeys performed as predicted in preferring the option awarding consistent food over the risky reward option. While in the presence of the model, three of the seven that showed a preference in baseline, failed to show a preference suggesting that the mere presence of the model distracted these monkeys. However, when the model also participated and made choices, the responses were varied: in the condition where the model got less food than the subject for the risky choice, out of the three that had been distracted by the mere presence of the model, one returned to his baseline preference, one changed preference but may have followed the model's behavior and not outcome, and the third continued to show no preference. In the condition where the model got more food than the subject for the risky choice, five of the six that preferred the consistent choice in baseline, continued to do so, while the one who had preferred the risky choice in baseline reverted to his original preference for the risky option.

CHAPTER 3

EXPERIMENT 2

Experience with the choices gained during training, baseline and model-present conditions may have been strong enough to interfere with any effect the model could have had in the first experiment. For example, four monkeys (LE, XE, MI & XA) continued to show a significant preference (p<.05) for the consistent choice or blue cup throughout Experiment 1. Research also shows that task familiarity or prior experience can influence whether or not humans will make riskier choices (Flanders & Thistlethwaite, 1967). I tested the monkeys with novel cups to rule out any possible effects of cup familiarity, thereby enabling me to test the prediction that in the absence of any information regarding the outcome of the options, the monkeys will follow the model's choice (Hypothesis-3).

METHOD

Subjects

The same seven subjects and model were used.

Materials

I used two novel containers of roughly the same size – a silver metal bowl and a yellow plastic cup. The containers were distinguishable on color, shape and texture, so that regardless of which cues the monkeys used, they could tell the options apart. The subjects had no prior experience with these containers in this decision making paradigm and did not know what

rewards if any, these inverted cups concealed. The rest of the apparatus was the same as used in the first experiment.

Procedure

The subject and model were brought from their homeroom in transport boxes to the testing room. The testing cages were set up as in the first experiment. The conspecific model was trained prior to testing to always choose the yellow plastic cup or the risky choice. It awarded two cheerios half the time. I used the silver metal bowl as the consistent option and it awarded one piece of food on every trial.

Once the subject and model were in cages facing each other with the cart in the middle, the cups were baited and first offered to the model for selection. He always picked the risky option and obtained any food concealed under the cup. Placement of the cups on the left-hand side or right-hand side of the platform was pseudo-randomized (similar to the first experiment), so also was the availability of food on the risky choices. I repeated the presentation of the options eight times to the model and visually monitored the subject to make sure he was watching the model. After the conspecific completed eight trials, the subject had a chance to make a selection. The baiting for the subject was identical to the baiting given to the model. This was the subject's first trial. The model was given four more trials after which the subject got one test trial and this was repeated until I had twenty trials from the subject. This was all done in one testing session.

On the next three consecutive days, I tested the subject by himself on the same cups with the same baiting contingency. This was done to see whether his pattern of choices after

testing with the model persisted when the latter was not present. The subject did 40 trials a day for a total of 120 trials over three days.

Analysis

I did binomial tests ($\alpha = 0.05$) to assess cup preference within each condition.

RESULTS

When tested with the model on the first day, four subjects (MI, SO, XA & JO) showed a significant preference (p<.05) for the risky choice (i.e. model's choice). XE showed a significant preference for the consistent choice whereas LE and CH did not significantly prefer one cup over the other.

When tested alone, XE retained his earlier preference for the consistent choice, and SO and MI retained their preference for the risky choice (p<.05). LE and CH now demonstrated a significant preference with LE choosing the risky option and CH, the consistent option. Two monkeys (XA and JO) shifted their preference from the risky choice to the consistent choice. The results of this experiment are presented in Table 2.

DISCUSSION

Experiment 2 used novel cups with a baiting contingency identical to the baseline condition of the first experiment: one cup was the consistent choice and always contained one cheerio while the other was the risky choice and contained no food half if the time or two cheerios half of the time. Results were variable across individuals. Some monkeys followed the

model's choice of the risky option even though they had shown a strong preference for the consistent choice in Experiment 1. Some reverted to their preference for the consistent choice in the absence of the model. Some showed no preference when tested with the model but either preferred the risky choice or the consistent option when tested alone. One subject remained unaffected by the model and persistent in his choice of the consistent option as he did in the first experiment. Overall, the results of this second experiment show that some monkeys do follow the model's choice when they have no prior experience or information regarding the choices.

Table 2 – Preferences of the monkeys in Experiment 2.

Subjects	With Model			Alone		
	Consist.	Risky	Sig.	Consist.	Risky	Sig.
LE	12	8	0.120	13	**107**	0.000
XE	**20**	0	0.000	**117**	3	0.000
MI	0	**20**	0.000	0	**120**	0.000
XA	7	**13**	0.001	**74**	46	0.003
CH	12	8	0.120	**77**	43	0.000
SO	0	**20**	0.000	0	**120**	0.000
JO	5	**15**	0.015	**70**	50	0.013

KEY: ☐ Indicates significant preference for consistent choice (Silver bowl)

☐ Indicates significant preference for risky choice (Yellow cup)

CHAPTER 4

EXPERIMENT 3

In order to make the model's reward more salient to the subject, I decided to increase the

payoff for the model's choice when the model selected that cup. I increased the rate of reward

to a 100% and doubled the quantity with 2 cheerios on every trial. I predicted that the monkeys

will be more likely to follow the model's choice when the model consistently received twice as

many food pieces as the subject did (Hypothesis-4).

METHOD

Subjects

      I used the same seven subjects and model.

Materials

      I used two more novel containers - a green plastic cup to represent the risky option and

a brown bowl to represent the consistent option. The rest of the apparatus was similar to the

previous experiments.

Procedure

      The baiting contingency for the model was different in this condition. The model was

trained to pick only a green cup which awarded two cheerios at a 100% rate. For the subject

however, the green cup represented the risky choice and awarded two cheerios on half of the

trials and or no food on half of the trials; the brown bowl represented the consistent choice and

always awarded one cheerio. The testing procedure and the number of trials were similar to what was done in the second experiment.

Analysis

I used binomial tests (α = .05) to assess cup preference within each condition.

RESULTS

When tested with the model, subjects LE, XE, SO and CH followed the model's cup choice even though it rewarded them with two cheerios only half the time. MI and XA significantly preferred the consistent choice over the model's choice. When tested alone, everyone persisted in their previous preferences (LE, XE, SO and CH still chose the risky choice, and MI and XA chose the consistent choice), except JO who had failed to show a preference when tested with the model but now preferred the consistent choice. Table 3 presents the data for this experiment.

DISCUSSION

I predicted that the model would have a stronger effect on the subjects when he got a bigger payoff at a consistent rate. The results varied across subjects. Two monkeys (CH & XE) in Experiment 2 which were not influenced by the model showed a significant preference for the risky choice in Experiment 3. Two subjects (LE and SO) once again followed the model as they had done in Experiment 2. Inexplicably, MI did not seem to be influenced by the model receiving a higher payoff even though he had followed the model's choice throughout the second experiment.

Three subjects (LE, CH & XE) had shown a significant preference for the consistent option in the baseline and model-gets-more conditions of Experiment 1 but picked the risky choice in Experiment 3. Lack of prior information or experience with the choices seemed to influence some of the monkeys to follow the model's choice regardless of previous preferences.

Table 3 – Preferences of the monkeys in Experiment 3.

Subjects	With Model			Alone		
	Consist.	Risky	Sig.	Consist.	Risky	Sig.
LE	5	**15**	0.015	16	**104**	0.000
XE	1	**19**	0.000	6	**114**	0.000
MI	**20**	0	0.000	**75**	45	0.002
XA	**19**	1	0.000	**80**	40	0.000
CH	4	**16**	0.005	49	**71**	0.001
SO	3	**17**	0.000	0	**120**	0.000
JO	10	10	0.176	**78**	42	0.000
KEY:	▨ Indicates significant preference for risky choice (Green cup)					
	▨ Indicates significant preference for consistent choice (Brown bowl)					

CHAPTER 5

GENERAL DISCUSSION & CONCLUSIONS

The purpose of this study was to test the efficacy of a conspecific model in influencing capuchin monkeys to change their preference from a consistent or certain option to a risky one. I made four predictions. In accordance with the existing risk research, my first hypothesis predicted that, when alone, the monkeys would prefer the consistent reward option over the risky option. While this seemed to be the case with six of the seven subjects initially, once they had been exposed to the model, two subjects including the one which had preferred the risky choice showed a disruption of their preferences which persisted, even when the subjects were once again alone.

My second hypothesis predicted that the subjects would follow the model's choice when they saw the model receiving a higher payoff. The results however showed that all six monkeys in Experiment 1 persisted with their baseline preferences and appeared unaffected by the model in this condition (i.e. Model-gets-more).

Speculating that prior experience with the options could be a stronger influence on the subjects' choices than the effect of a social model, my second experiment tested the monkeys with novel cups and predicted that in the absence of information regarding the choices the monkeys will follow the model. The data revealed individual differences among the monkeys with four of the seven subjects being so influenced, two showing no preference and the last preferring the consistent reward.

In the third experiment, I expected that seeing the model receive a much higher payoff for a cup that they had no prior information about, would influence the subjects to follow the model. Once again I found four of the seven were influenced but these were the same four subjects who had been influenced in Experiment 2. Of the four which had been influenced in Experiment 2, two now preferred the consistent reward, one showed no preference and one followed the model. On the other hand, the two who showed no preference in Experiment 2 now followed the model, as did the only one who had chosen the consistent reward in Experiment 2.

Although all seven subjects were influenced by the model at some point, at no stage of the study did more than four of the seven subjects follow the model. The failure of the model to influence the subjects was not due to inattention of the monkeys to the model, as subjects were observed to be watching the model. The data also led to the conclusion that capuchin monkeys do not keep track of a conspecific's rewards over the course of a series of trials.

It also appears that the subjects may not be averaging their own rewards over a series of trials. On the other hand, other researchers (Beran et al., 2008) have shown that they are capable of not only judging quantity but also remembering how much food there was when it was no longer visible to them. The present study however, does not provide evidence that the monkeys were able to remember what the two options awarded, and how much food they each obtained over 10 trials in a testing day. All seven monkeys were able to clearly differentiate an option that provided a consistent reward from one that was inconsistent, and six monkeys preferred getting food on each trial, even if it was one piece, rather than no food at all.

Overall, it appears that capuchin monkeys are variable in their use of a conspecific's behavioral choices, and the outcomes of these choices, in their own decision making process. Their level of personal experience on the options seems to have some influence over whether or not the individual follows the choice of a conspecific. While they are able to respond to quantitative differences in the food items presented as well as the rate at which they are awarded, it appears they are less sensitive to the same specific variables when it comes to those of a conspecific partner, particularly over a series of trials.

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APPENDIX A

Review of the Literature

Decision making in animals is generally studied in the context of foraging. During foraging, the animal can be making decisions regarding patch selection specific foods to eat, when to leave a patch and travel routes (Stephens & Krebs, 1986). When making these decisions, there may be certain trade-offs that the animal might need to take into consideration such as energy costs and predation risks (Bednekoff, 2007). Social animals also forage in groups (Giraldeau & Caraco, 2000). This in turn complicates the factors to consider in making foraging decisions (Waite & Field, 2007). Furthermore, there is uncertainty in the natural environment and therefore animals choosing between foraging options need to be sensitive to potential risks.

Definitions & Theories

The concept of 'risk' is defined differently in the human decision-making literature than in the foraging literature. This is because decision-making was traditionally in the realm of economists who consider a 'risky' situation to be one where the individual knows the mathematical probabilities of the possible outcomes of the available choices (Knight, 1921). When the exact probabilities are unknown, the situation is considered to be an 'uncertain' one. When studying animals, this distinction between 'risk' and 'uncertainty' is more difficult to make as it is not easy to confirm that animals really understand the mathematical probabilities. Instead, we consider an option as being 'riskier', if the outcome of that choice is seen as less

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certain than another (adapted from von Neumann & Morgenstern, 1944; Rothschild & Stiglitz, 1970).

Generally, testing risk sensitivity in animals is done by having the animal choose between two options, one that awards fixed amounts of food (i.e. 'certain' choice) and another that awards variable amounts of food (i.e. 'risky' choice) (Kacelnik & Bateson, 1996). The options can also vary on the time delay to reinforcement: food awarded after fixed time intervals (i.e. 'certain' option) versus food awarded after variable time delays (i.e. 'risky' option) (Mazur, 2004; Lagorio & Hackenberg, 2010). Researchers also use options that vary on both the quantitative and temporal aspects by having the animal choose between an option that awards a fixed amount of food at a constant rate, and one that awards variable quantities after variable time intervals. These types of studies generally fall in the domain of temporal discounting, which deals with how animals make trade-offs between smaller, immediate payoffs and larger, delayed payoffs (Read, 2004; Beran & Evans, 2006; Hayden & Platt, 2007). Assessing risky decision-making in this manner is based on the associative learning process model. Animals learn about the payoffs of different options which, in the laboratory, are usually done by initially training them to understand the outcome of responding to specific stimuli.

While the above methods involve the decision-maker potentially gaining a reward, researchers also study risk in the context of losing a resource already owned where the individual is required to 'invest' in an option that may or may not result in a loss. Sometimes this may be a perceived loss and not a real one. Prospect theory discusses this type of decision-making under risk (Kahneman & Tversky, 1979) where individuals evaluate losses and gains relative to an arbitrary reference point, and weigh outcomes differently from their actual

probabilities. Thus, whether or not an individual will opt for the risky choice, does not depend on a consideration of the mathematical probabilities, but on a comparison of how much might be lost to what they originally expected to lose. Similar biases were seen in capuchin monkeys *(Cebus apella)* (Santos & Chen, 2010).

Another popular approach to the study of risk in animal decision-making is called Risk-sensitive theory (Kacelnik & Bateson, 1997). This is a normative approach which predicts how an organism should respond to risk to maximize its fitness. Specifically in the context of foraging, risk-sensitive foraging theory (Stephens, 1981; McNamara & Houston, 1987) predicts that whether or not the animal goes for the risky foraging option is based on the animal's daily energy requirements or 'energy budget' (Mazur, 2004). When the animal has failed to meet its daily energy quota and survival is an issue, it should choose the risky option which might pay-off in a big way. For the most part, research with different species including birds such as the yellow-eyed junco, *Junco phaeonotus* (Caraco et al., 1980), tree shrews, *Sorex araneus* L. (Barnard & Brown, 1985), rats, *Rattus sp*. (Ito, Takatsuru & Saeki, 2000), stickleback fish, *Spinachia spinachia* (Croy & Hughes, 1991) and bumblebees, *Bombus sp.* (Cartar, 1991) support this model. There is however, evidence showing contrary results (Hastjarjo, Silberberg & Hursh, 1990) or showing no relation between energy budgets and risk-sensitivity (Battalio, Kagel & McDonald, 1985). It has been suggested that body weight might play a role in determining the animal's daily energy budget since smaller organisms might have a higher daily energy budget while larger animals that can store more energy, might have a smaller daily energy budget (Kacelnik & Bateson, 1996). The quality of the animal's diet can also determine the strategy adopted by the animal. Gilby and Wrangham (2007) found that wild chimpanzees *(Pan*

troglodytes) were risk-averse when feeding on plant material and risk-prone when hunting colobus monkeys.

The present review focuses more on studies where animals make decisions between options that vary in the amount of food awarded in a probabilistic manner such that the net gain is the same.

<u>Individual decision making patterns in animals</u>

Theories of individual decision-making in the context of risk predict that humans will generally prefer options that offer fixed food quantities over variable ones. However, a review of non-human research including a variety of insect, fish, bird and mammal species (Kacelnik & Bateson, 1996) reveals mixed results among the studies that tested response to variable quantities. A majority report risk aversion, some find no preference and a few show that the animals are risk prone.

A recent example is a comparative study by Heilbronner et al., (2008) who tested captive chimpanzees *(Pan troglodytes)* and bonobos *(Pan paniscus)* in their preference between a fixed option that always awarded 4 pieces of food and a risky option that awarded either 1 piece or 7 pieces of food with equal probability. They found that the chimps significantly preferred the risky option over the fixed food option while the bonobos preferred the latter more. Tokuno and Tanaka (2007) tested 17 common marmosets *(Callithrix jacchus)* on a gambling task that required them to choose between a constant reward option (3 grains of sugar-coated rice) and a risky reward option (0 or 6 grains half the time). They found individual differences in the preferences of the marmosets with seven being risk-aversive, five being risk

prone and the other five showing a side preference. McCoy and Platt (2005) found that the two

rhesus macaques *(Macaca mulatta)* they tested on a gambling task involving consistent and

variable amounts of fluid rewards preferred the risky choice more. An earlier study (Behar,

1961) found that rhesus monkeys showed risk-aversion. Thus, among the non-human primates,

there does not appear to be much support for species-typical patterns regarding individual

decision-making under risk.

<u>Role of the decision-making context in risk preference</u>

Framing effects:

An example of a contextual factor that has been shown to change risk preference is how

the outcomes are presented, also known as framing effects. The existing human literature

shows that people evaluate outcomes of choices based on a reference point and when an

outcome is framed in the context of a loss in comparison to the expected outcome, people

avoid selecting it but if the same outcome is framed as a gain compared to a reference point,

people are more willing to select it. They are thus, risk-averse to loss but risk-prone to gain.

Tversky and Kahneman (1981) demonstrated this by having people hypothetically choose

between two ways of fighting a disease – if they picked one method there was chance of losing

lives but if they chose the other, they had a chance of saving the same number of lives.

Although the probability of loss was identical to the probability of gain, people distinctly opted

for the second method which "saved" lives. Similar preferences were demonstrated by Marsh

and Kacelnik (2002) in European starlings *(Sturnus vulgaris)* and by Chen, Lakshminarayanan,

and Santos (2006) in captive capuchin monkeys *(Cebus apella).* Chen et al., (2006) used a token-

trading paradigm to test the monkeys. A subject could trade his token for apple pieces with one

of two experimenters who both displayed the food that would be offered to the monkey. This

displayed food served as the reference point for the subject. One experimenter always

displayed one apple piece and if given the token would award the monkey the one piece or add

a second bonus piece. The other experimenter always displayed two apple pieces but would

award both pieces or visibly remove one and award only one piece. Overall the two

experimenters offered food at a 50% rate of one or two pieces but the monkeys significantly

preferred to trade with the first experimenter. The interpretation is that comparing to the

reference point they did not perceive themselves as experiencing a 'loss'. If anything they

perceived themselves as receiving a 'gain'.

Social effects:

        Researchers who are interested in social effects on risk-taking behavior seem to

concentrate more on human decision making, specifically in the context of gambling behavior.

Studies reveal that there is generally an increase in risk-taking behavior in a group setting,

compared to when an individual is alone. An example is the study by Wallach, Kogan and Bem

(1962, 1964) which found that individuals who discussed the options in a group, showed risky

shifts due to a diffused feeling of responsibility. There is also research that showed an increase

in risk-taking when alone due to familiarization with the situation, which in turn led to better

comprehension of the options (Bateson, 1966; Flanders & Thistlethwaite, 1967). The mixed

results in these cases can be attributed to other variables including perception of control

(Langer, 1975), personal efficacy (Bandura, 1977), and the level of confidence (Shields et al.,

2005), which have been found to determine whether a person makes riskier choices when alone or in a group (Ladouceur, Tourigny & Mayrand, 1986). Social processes such as competition and conformity (Dindo, Whiten & de Waal, 2009) can potentially confound these already variable findings. More recently, Hardoon and Derevensky (2001) demonstrated the effect of peer-pressure on gambling behavior in children.

To assess the role of social facilitation in decision making, Zajonc et al. (1970) explored changes in individual risk preferences in various contexts. After establishing an initial baseline preference for each subject when alone, they tested the effect of 1) the mere presence of an audience, 2) a co-actor whose choices were not revealed to the subject, and 3) a co-actor whose choice was revealed to the subject. They found that when alone, subjects preferred to select the more conservative choice which seemed to increase in the mere presence of the co-actor or when the subject was not knowledgeable of the co-actor's choice. They did find that the subjects tended to be more risk-prone when they knew the co-actor had made risky choices. The differences however varied from being statistically significant to not being so, making it difficult to attribute the results solely to social facilitation. The authors tested a fourth condition where the individual had to make a decision as part of a group to study the interactive effects of conformity or imitation and social facilitation. Their results showed that these processes do not sufficiently explain exactly how the group changes an individual's choice preference for risk. The existing animal literature demonstrates socially facilitated food consumption in various species (Harlow & Yudin, 1933; Tolman, 1964; Forkman, 1991; Addessi

& Visalberghi, 2001). However, there does not appear to be much evidence regarding socially facilitated behavior in the context of decision-making under risk.

Humans are able to deal with decisions involving risk when they are provided with information describing the probability of the outcomes as well as experience gained from repeated sampling of the options (Hertwig et al., 2004; Weber, Shafir & Blais, 2004). Animals however, rely on feedback from actual experience rather than verbal information. They may gain this information from personal trial-and-error learning. There is another way that individuals learn about the outcomes, and that is through the observation of others making risky decisions.

The current animal literature provides various examples of observational learning in a variety of species (see Pallaud, 1984). Laland (2004) and Kendal, Coolen and Laland (2009) explore different contexts under which animals use copying from others as an adaptive social learning strategy. They suggest that animals should copy others when acquiring the information on their own is too costly (like under the risk of predation), they should copy when they themselves lack prior knowledge, or when their prior experience is unreliable or outdated. Other researchers have shown that animals can copy a social model, even when no food rewards are involved. For example, Bonnie and de Waal (2007) showed that capuchin monkeys *(C. apella)* are capable of copying a conspecific model's choice when neither the subject nor the model received a food reward.

Fragaszy and Visalberghi (2004) discuss socially biased learning in monkeys as learning

that occurs not due to imitation (Visalberghi & Fragsazy, 1990), but as a result of individual

experience and exposure to others' behavior, and perhaps their outcomes. They compare

capuchin *(C. apella)* and callitrichid monkeys *(Callithrix sp.* and *Saguinus sp.)*, and find that in

addition to individual characteristics (motivation, prior and current experience), both physical

contexts (substrates, accessibility) and social environment (such as social structure and social

tolerance) play an important role in influencing whether or not efficient learning takes place.

Overall, the current literature on social learning in animals, particularly non-human

primates tends to focus on learning in the context of food consumption, using a new tool or

solving a problem, rather than on the effect of the social context on decision-making involving

risky options. A majority of the research seems focused on differentiating the different

processes of social learning that take place such as determining whether the animals are

learning through stimulus or local enhancement, imitation, social facilitation, or observational

learning (Galef, 1988).

Sensitivity to outcomes:

Finally, research requiring the subjects to make choices in social contexts supports the

fact that non-human primates, including capuchin monkeys, are sensitive to the outcomes of

others' choices as well as their own. For example, Brosnan and de Waal (2003) showed that

capuchin monkeys *(C. apella)* rejected a food reward that was qualitatively lower when they

saw a conspecific receive a more valuable one. They concluded that the monkeys were

exhibiting inequity aversion. Fletcher (2008) further demonstrated that the monkeys were

averse to inequity that was disadvantageous to them by preferring equitable outcomes (which awarded themselves and a social partner the same food) over inequitable outcomes. While these studies show that capuchin monkeys are capable of distinguishing between qualitatively different rewards, other research shows that these monkeys are also capable of discriminating between various quantities (Addessi et al., 2008). Beran et al. (2008) further demonstrated that the monkeys were also able to remember the quantities of food they had been shown and pick the larger option even when the options were no longer visible. Brannon (2005a, 2005b) provides a more comprehensive review of the numerical abilities of animals.

The evidence indicating that animals monitor their own and others' rewards makes it possible to test capuchin monkeys to see if they make use of the information they acquire from a social partner regarding his outcomes in their own decision-making process.

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APPENDIX B

Quantity Discrimination Tests

Even though there is evidence to show that capuchin monkeys can visually discriminate between varying quantities of food items presented to them (Addessi et al., 2008; Beran et al., 2008), we wanted to confirm that our subjects at the Primate Cognition and Behavior Laboratory (University of Georgia) were able to clearly discriminate between 1, 2 and 4 pieces of food by choosing the larger quantity when they were presented in pairs – 1 vs. 2 pieces and 2 vs. 4 pieces.

METHOD

Subjects

Eight adult male capuchin monkeys, pair-housed at the Primate Laboratory at the University of Georgia were tested. They were born and raised in captivity, and were experienced on various cognitive and motor tasks.

Materials

A wooden board (18 x 8 inches) divided in the middle with a 6 inch high wood partition was used to offer the food to the monkeys. Kellogg's Frootloops® cereal was used as the food reward. The Frootloops were sorted out by color to avoid any biases based on this cue. A cardboard occluder was used to hide the wooden board during baiting.

Procedure

The monkeys were tested in their home cages separated from their cage-mate by metal cage dividers. One monkey was tested at a time. The experimenter stood in front of the subject and offered a choice between two different quantities of food. They were placed approximately 12 inches apart on the wooden board, on either side of the partition. This set up was used in order to prevent the monkeys from simultaneously accessing both food choices. The monkeys were also given 2-3 seconds to view both choices before they made their selection. They were allowed only one selection per trial. The placement of the food was randomized between the left and right sides of the partition.

The ratios used were 1 vs. 2 pieces, and 2 vs. 4 pieces. Each ratio represented a condition and the monkeys progressed through them one at a time. Each monkey was run on 30 trials per ratio. On each trial, we recorded whether or not the monkey chose the larger quantity of food.

Analysis

To reach criterion, they had to pick the larger quantity on 70% or more of the trials. The overall percentage of choice of the larger quantity was calculated for the 30 trials, and taken as the monkey's score on this condition.

RESULTS

All eight subjects achieved criterion by choosing the larger food quantity. Table 4 presents the percentage of choice of the larger quantity for each of the two ratios.

Table 4 – The percentage of choice of the larger quantity.

SUBJECT	1 vs. 2	2 vs. 4
LE	90	90
NI	70	97
MI	85	97
SO	80	83
CH	80	80
XE	90	83
JO	90	83
XA	100	93

CONCLUSION

We confirmed that all the monkeys could visually discriminate between 1 piece of food and 2 pieces, and also between 2 and 4 pieces of food.

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