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Do Monkeys Save the Best for Last? Examining Sequence Order Preference in Capuchin Monkeys

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Do Monkeys Save the Best for Last? Examining Sequence Order Preference in Capuchin
Monkeys

by

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Under the Direction of Sarah F. Brosnan, PhD

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ABSTRACT

Primate decision-making is often underlined by cognitive biases and how sequences are evaluated is no different. Human research shows the most salient parts of sequences are the peak and end affect experienced within them along with a preference for sequences with increasing value. However, inconsistent results from non-human primate studies deny the ability to determine if these biases are a primate-wide cognitive shorthand to quickly evaluate experiences, or if these primarily impact humans. This experiment builds on previous works and tests if tufted capuchin monkeys experience an end bias using a dichotomous manual task which allows them to choose between receiving a high reward sooner or later. Overall, capuchin monkeys preferred a higher reward at the start of a sequence, this effect only was strengthened when accounting for delay discounting. Rank and exposure to sequences were most often the best predictors for sequence preference, while sex never impacted choice.

INDEX WORDS: Peak-End, Sequence order, Bias, Preferences, Cognition, Capuchin monkeys

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2022

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DEDICATION

I dedicate this study to my parents, Luis E. Saldaña Leiva and Gracie C. Santisteban Fernandez, who without their undying love and support none of this would have been possible. I also dedicate this work to my brother Luis E. Saldaña Santisteban for providing guidance and being the first of our family to pave the way for others to achieve higher levels of learning in academia in the United States. Lastly, also dedicate this to my loyal canine companion, Beowulf, who over the last decade has not only provided comfort and happiness but also continuously pushes me to try and better understand animal behavior and cognition.

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1 INTRODUCTION

1.1 Rational Decision-Making Models and Failures

A classical view of economics centered around utility maximization theory relies on consumers making choices that, on average, will maximize their returns on a purchase or investment (Kahneman & Tversky, 1979). This concept assumes that decisions made by consumers are rational choices and thus allows for economic models which simplify decision-making based on maximizing profits. This creates straightforward supply-demand interactions between consumers and producers, which is useful for such models.

For instance, models based on utility maximization have been previously proposed to help predict consumer behavior when considering multiple travel prices. A rational consumer should equally weigh out all options within their travel plans and choose the option that equally balances price, time, and duration (or whatever other factors are important to the consumer; Golob & Beckmann, 1971). These models also extended beyond individualistic choice and are used to predict how companies respond to operational cost changes. For instance, when tax increases decrease the profit margins, a rational company has to decide whether to endure increased production costs (i.e. accepting decreased returns or lowering workers' wages) or pass the burden of the tax to consumers by increasing the price of goods being sold (Sebold, 1970).

Other non-fiscal applications of utility maximization theory aim to explain some of the decreases in road safety with increases in driving regulations (i.e., seatbelt mandates) such that the increased cost these regulations put on consumers causes them to overly rely on safety features to maximize their returns, which results in decreased safe driving behavior (Blomquist, 1986; Peltzman, 1975). A similar view was proposed to account for increases in child drug poisoning incidents with the introduction of mandated child-proof bottle caps, noting that parents

have begun to maximize their utility of increased safety features by decreasing safety practices, such as placing bottles outside of a child's reach, and overly relying on child-proof bottle caps to prevent access to dangerous substances (Viscusi, 1984).

Although utility maximization theory has proven useful at explaining rational behavior, a major criticism is its requirement for humans to always act as rational economic agents who are capable of making unbiased decisions derived from accurately predicting the outcomes of all presented choices (Kahneman & Thaler, 2006). Indeed, extensive research has shown that humans are far from consistent rational beings and are routinely affected by lapses in rational judgment and decision-making. A variety of factors such as personal experience, outcome perception, and heuristics collectively known as cognitive biases affect how we carry out our daily lives. Although these factors can add up and affect our decision-making in a variety of ways, the most relevant to this study occurs when decisions are based on incorrect evaluations of past events and experiences (Kahneman & Thaler, 2006). These misconceptions tend to create preferences against perceived unfavorable events, creating a bias against them. For example, such biases are often reported during retrospective evaluations of painful events; irrationally, humans perceive a shorter event with a constant level of pain as less favorable than the same event with an additional less painful ending, even though the latter has more total pain (Kahneman et al., 1993; Redelmeier et al., 2003; Redelmeier & Kahneman, 1996; Schreiber & Kahneman, 2000).

Biases like this one are important to understand for two reasons. First, they extend beyond laboratory experiments and theoretical frameworks into daily life, influencing decisions quite often for the worse. For instance, a review of cognitive biases and medical decision-making conducted by Blumenthal-Barby and Krieger (2014) reported that 64% of the studies analyzed (n

= 213) showed an effect of cognitive biases. Similarly, a secondary review of studies on medical decision-making by Saposnik et al. (2016) found evidence that cognitive biases affected diagnosis in anywhere from 36.5% to 77% of cases studied ($n = 114$) and played a role in therapeutic and management errors 71.4% of the time. Jeanguenat et al. (2017) reported in their review of cognitive biases and forensics that interpretations of DNA analysis are subject to different biases that call into question the reliability of results presented in court cases and hearings. Second, a more comprehensive understanding of how these biases express themselves helps distinguish between human-unique qualities and ones we more broadly share with other primates, with whom we share many biases and make irrational decisions.

However, while biases are important, they are not the only factor that influences decision-making; although Kahneman and Thaler (2006) did not discuss this, preferences are an additional way in which irrational decision-making can negatively impact outcomes. Our daily experiences and interactions, whether positive or negative, can affect different aspects of our decisions, such as what we do (e.g., cook dinner or go to a restaurant), whom we would like to spend our day with (e.g., a workmate or a friend from school), or where to go (e.g., an Italian or Korean restaurant). Preferences can help us decide between seemingly equal choices by injecting personal experiences in lieu of some aspects of rational thinking. Preference-based decisions undermine the view of the rational consumer, as they are inherently biased opinions that we form over time based on our interactions with people, objects, places, and other entities. Furthermore, even once we have created preferences towards events, they are not all-or-nothing but can vary over time (Druckman & Lupia, 2016; Lytle et al., 2000)

If preferences can play such a large role in decision-making, how do we create preferences for events that have different rewards, conditions, or values across time? For

instance, do we prefer a more valued outcome to occur at the beginning or do we save the best for last? There are at least two possibilities. First, while people have preferences for certain options, perhaps a rational consumer does not care where a preferable instance occurs in a sequence. Instead, that consumer might add up the value of all outcomes within a sequence and rate it based on its average value. While this idea would support decision-making models with rational players, most evidence suggests that humans do not behave this way. Instead, research has shown that once again we are susceptible to cognitive biases, but in a variety of ways.

Humans sometimes prefer sequences that increase in value (trend bias), and/or place a higher value on sequences that end in a positive event (end bias) and a higher value on sequences with larger peak values than ones that match in overall value but contain no peaks (peak bias) (Ariely, 1998; Chapman, 1996, 2000; Frank & Hutchens, 1993; Hsee et al., 1991; Hsee & Abelson, 1991; Kahneman et al., 1993; Loewenstein & Prelec, 1993; Loewenstein & Sicherman, 1991; Redelmeier & Kahneman, 1996; Ross & Simonson, 1991). These biases are collectively referred to as the peak-end effect, which is the topic of the current review.

1.2 The Peak-End Effect

Kahneman (2000) described the peak-end effect as a cognitive shortcut in which the perception of a past event is based around a representative moment, a “snapshot,” which contains a combination of some of the separate attributes experienced during an event. This snapshot is, however, not inclusive of *all* attributes but is based on an average between the most extreme affect experienced (*peak*) and the affect experienced towards the end (*end*) of the event (Kahneman, 2000). The average value favors events with both high peak and high end values over those lacking one or both features. Along with a preference for increasing trends, these two anchor points seem to be able to explain how humans develop irrational preferences when

comparing events that share overall equal average values, but vary in snapshot averages.

Although Kahneman and Thaler (2006) used retrospective evaluations of pain to validate the peak-end effect, not all preferences require active retrospective thinking to be formed.

Kahneman et al. (1993) reported the end effect in a study in which participants provided retrospective preferences of painful experiences. After immersing their hands in one of two cold-water baths (both initially lasting 60 seconds, but one continuing for another 30 seconds in slightly less cold water), participants preferred the longer-lasting experience. Similarly, colonoscopies that contained a one-minute “rest” period before ending were rated as more pleasant than those without rest and constant displeasure, even though the former increased the cumulative pain experienced (Redelmeier et al., 2003; Redelmeier & Kahneman, 1996).

Paradoxically, people also favor events with loud noises as less painful when a period of lower volume is added at the end (Schreiber & Kahneman, 2000). Additionally, adults more positively view receiving one highly rated movie over receiving both a highly rated movie and a lower-value one; children show the same effect with candy (Do et al., 2008), supporting the importance of the value present at the end of a sequence for positive as well as negative experiences.

The peak effect is exemplified by the preference for constant painful shock sequences over those where the maximum pain endured occurred in the middle, even when the net pain for both was equal (Ariely, 1998). Even more surprisingly, a difference in preference is not reported when the maximum pain occurred at the beginning of the sequence versus sequences with a constant pain level. Similarly, the peak bias extends beyond physical pain and includes emotional distress, as seen in arguing couples whose post-conflict affect is primarily dictated by negative peaks experienced during a fight (Sels et al., 2019). Notably, neither a positive peak nor end affect were predictors of post-conflict mood, which hints that the peak-end effect may not be

the only explanation for differences in behavior. Furthermore, both peak and end biases can combine and affect how likely someone will be to repeat a short unpleasant event, such as with inactive people and workouts (Hargreaves & Stych, 2013), or rate longer-lasting events, such as with tourists' evaluation of guided experiences (Kim & Kim, 2019). An important commonality across both peak and end bias studies is that they not only rely heavily on retrospective evaluations, but also on comparisons between sequences. The ability to ask participants for their thoughts on how pleasant an individual sequence was, seems to differ from how likely they were willing to repeat it when compared against other sequences. Therefore, it may be the case that the peak-end effect informs how likely we are to repeat an event, but not how we feel afterward.

Additionally, while the peak and end biases rely on individual affect points to influence sequence preferences, a third bias, the trend bias, accounts for our general preference for increasing values within a sequence. Research shows that humans prefer sequences that increase in value over decreasing ones, even when the net outcome is equal. For example, workers reliably prefer increases in salary over decreases, even when both earn them the same net gain (Hsee et al., 1991; Loewenstein & Sicherman, 1991). This trend bias extends into meals, for which humans prefer incrementally better tasting sequences over the reverse (Lau-Gesk, 2005) and pain, where a decreasing chronic headache is seen as more favorable over an increasing one (given that both reach the same max pain level; Chapman, 2000).

Although peak, end, and trend biases are well documented, the role that humans' cognitive capabilities play in shaping perceptions of events (i.e., saving the best for last) remains unclear. Humans generally prefer decreasing negative results and increasingly positive ones and that these preferences can affect how we retrospectively rate our experiences. Additionally, the most salient points within an event are used as a shorthand to develop preferences. However, it is

unclear if trend, peak, and end biases are a function of cultural preference or are an innate evolutionarily developed heuristic that helps offset cognitive load. Basing the value of an event around only the most salient points (peak and end) could be a useful shortcut that is more efficient than keeping track of all points and creating an average. However, human populations provide some challenges regarding differences in cultural emphasis on value. What might be considered valuable in western industrialized nations may not reflect the values of other cultures.

Moreover, testing humans creates the challenge of providing adequate scales for factors that may differ between cultures. The previous studies mentioned relied on measurements that increased or decreased a participant's affect, but what if the reward payouts or pain experience within a sequence is not unanimously agreed upon across cultures? One way to avoid this problem is to study samples for which both cultural variations and cognitive capacity are minimized. Non-human primates constitute ideal candidates for studies that control some of these variables because they lack human culture and show less cognitive ability. Further, the use of non-human primate samples allows researchers to examine the peak-end effect as an evolved heuristic. Unfortunately, the results to date from studies with non-human primates show mixed results as to whether only humans show the peak-end effect.

1.3 Non-Human Primates and the Peak-End Effect

Similarities between primate species arise in one of two ways: homologous (traits present in all descendants of one common ancestor) and convergent evolution (similar traits independently developed by two distinct species). For example, the evolution of the general structures (ligaments and muscles) which allow for the human thumb's fine motor skills are homologous among primates (Diogo et al., 2012). In theory, the presence of these general structures among the hands and wrists of many primates suggests that the last common ancestor

must have also possessed them, as it would be unlikely for these characteristics to individually evolve across the various extant primate species. However, in some cases, unrelated lineages possess similar abilities through different means. Tool usage, for example, is widely reported among different capuchin monkey species (*Cebus [Sapajus] spp.*), in which individuals will choose and often carry a large rock (*hammer*) and place it on a secondary flat rock (*anvil*) that stabilizes a nut during impact, causing the nut to crack (de Moura, 2004; Falótico et al., 2019; Ottoni & Izar, 2008; Spagnoletti et al., 2011, 2012). Similarly, chimpanzees (*Pan troglodytes*) also have a long history of choosing specific hammers and anvils to crack nuts (Boesch & Boesch, 1983, 1984, 1990; Inoue-Nakamura & Matsuzawa, 1997; Morgan & Abwe, 2006; Sakura & Matsuzawa, 2010; Sumita et al., 1985), yet the lack of consistent tool usage among the species that lie phylogenetically between capuchins and chimpanzees points to a case of convergent evolution, in which tool usage has evolved separately in two distinct lineages. But why is it important to define between homologies and convergent traits?

Understanding the difference between homologies and convergent traits in primate behavior is a key reason that we use a comparative approach to determine the evolutionary history of behavior or cognitive mechanism (Smith et al., 2018). Given our general homologies as primates (i.e., sociality, group living, complex social structures, etc.), the question becomes whether primates more broadly still show these effects of preferences developed through trend, end, and peak biases. In other words, is this shorthand method generally used by many different primates to create preference in different contexts, such as pain avoidance or foraging strategies? If so, then it could be argued that these biases serve as an evolutionary homology among primates, perhaps due to shared cognitive architecture or some other widespread trait. Should the peak-end effect only be observed in some phylogenetically distant primate lineages, then it

suggests that it is instead a case of convergent evolution and has uniquely evolved multiple times. This would then raise interest as to how and why different evolutionary and social strategies selected for a cognitive shortcut that favor more rapidly developing preferences while others did not. If only humans show a peak-end effect, then it may be that human preferences developed via trend, end, and peak biases are a case of divergent evolution (when the descendant of a common ancestor evolves a unique characteristic not found in others), suggesting it is a specialization, raising questions of how and why it developed. Perhaps humans have evolved to rely on language and culture to determine preferences and values, or perhaps our highly cognitively demanding lives have led us to take shortcuts wherever possible to decrease the cognitive load which we experience.

Additionally, it is because of human characteristics such as language, culture, and higher cognition that primates make a great model to contextualize the peak-end effect. As previously mentioned, end biases are often tested using retrospective measurements of pain; however, the perception of pain has been reported to differ across cultures (Al-Harthy et al., 2016; Nayak et al., 2000; Rahim-Williams et al., 2012), emphasized in the need for increased cultural sensitivity during health care visits (Lasch, 2000). Peak biases are often tested using cultural norms such as aggression, whose expression varies across different countries (Archer, 2006), making it difficult to standardize what an average human might consider low, medium, and highly aggressive actions. Other measurements, such as self-perceived instances of pleasure/discomfort, can vary between cultures. For example, peak-end studies involving the perception of a couple's fight may be confounded by the different ways in which cultures perceive love and violence (Cala & Soriano-Ayala, 2021). These differences make it difficult to generalize studies that exclude a wide range of subjects to a broader population because what might be considered a salient peak

behavior (e.g., a heated argument) is not universal across cultures. Lastly, a monetary context is often used in trend bias studies (Hsee et al., 1991; Loewenstein & Sicherman, 1991), which can be problematic as income inequality is disproportional among White, Black, Asian, and Hispanic Americans (Intrator et al., 2016). Pouwels et al. (2008) found that income has a positive relationship with individual happiness and also life satisfaction, which can affect the context in which individuals evaluate their decisions. When comparing similar hypothetical incomes (e.g., increasing towards \$20,000 and decreasing to \$20,000), individuals with an actual higher income may undervalue the endpoint regardless of scaling trends and be indifferent towards an outcome, as both options secure them a severe reduction in pay. The benefit of testing non-human primates is that these confounds are largely avoided due to cultural, cognitive, and more importantly differences in language capacities and communication.

Non-human primates are often tested using food rewards and therefore lack the same confounds of using monetary rewards. Additionally, due to the practicalities of much human psychology research, subjects often participate in a low number of sessions (often just one in pain or invasive studies), while researchers working with captive non-human primates maintain access to their subjects for extended periods, allowing for more extensive follow-ups. This not only allows experimenters to lessen the impact that random choices/behaviors have on the results, but allows for greater dissection of individual aspects within a paradigm by re-testing the same individuals in follow-up studies. As previously discussed, human decision-making is a complex topic that is subject to different aspects that are susceptible to daily changes. Therefore, the answers provided in an experiment that samples human participants once can be more susceptible to sampling error or random biases, such as those induced by mood or other relative occurrences, whereas sampling non-human primates over time provides a better measure of their

general decision-making strategies because random effects (presumably) average out. Lastly, the presentation of the study and the framing of questions may impact human studies, but the lack of language helps ensure that studies with non-human primate populations avoid both the framing biases inherent in non-human studies and the reporting biases whereby we rely on what participants report as their goals rather than what they actually did.

Although studying non-human primates provides some benefits, other challenges remain. Easily quantifiable measurements, such as money, are especially helpful in determining sequence preference due to their scalar values and exact value. While the value of money between individuals may differ, relative increases and decreases (e.g., \$20 is twice as much as \$10) are more universal. This means that comparing sequences with specific ratios, such as increases in yearly salary, is more clearly defined as having a set or predictable trajectory than sequences that used food rewards (e.g., an increasing sequence that first gives out a piece of bell pepper, then cucumber, then a piece of apple, and lastly a grape). Furthermore, while some general food preference trends exist, these may vary between individuals such that what one considers a medium-value reward is seen as a low-value reward by another. Ultimately, even though a grape might be seen as a better reward than a piece of apple, there is not a set trading standard that between the two that resembles or is as clearly defined as changes in monetary value. The inability to communicate directly with participants can lead to a disconnect between what is being measured by experimenters and what the participants determine to be the question being asked. After all, testing human paradigms on non-human primates requires a carefully translated protocol to properly communicate the purpose of a task (e.g., choosing the sequence that they prefer) and to also maintain the adaptations between the tasks the same across multiple (Smith et al., 2018). However, even with stringent controls and parameters, it is not guaranteed that the

purpose of the task is always understood by the subjects or that they will not find work around. For example, if a monkey prefers a sequence with just a piece of grape over one with a piece of grape and apple over many trials, we may conclude that the apple piece has a negative value within its sequence. However, if this comparison did not have a proper intertrial interval which forced a time-out period, then it could also be the case that the monkey chose the sequence which allowed them to obtain another piece of grape soonest. In other words, by choosing the option that ended the trials the fastest, the monkey found a work around that avoided sequence preference testing and instead of comparing the apple to a time delay, it compared it to the grape in the next trial; this *selective value* effect has been noted in both monkeys and apes (Beran et al., 2009; Silberberg et al., 1998). Secondly, when testing more than one species, this issue only increases as we also run the risk that one species may interpret the task in their own unique way, which may differ from the purpose of the task. In addition to careful planning, an absence of language also means we cannot retrospectively ask monkeys about their experiences (a common methodology in human studies), but instead we must rely on frequency of choice to inform us of their preferences. Furthermore, some biases lend themselves to be more easily tested with language than without it (e.g., retrospective judgement and a peak bias). This methodological constraint leads some biases easier to test than others.

While end and trend biases have been tested using food rewards, as order and scaling of rewards can be more easily manipulated in experiments, peak biases as tested in humans often rely on retrospective judgment, which proves more difficult to assess in non-human primates. Therefore, not all peak-end effect studies with non-human primates include a peak bias condition. Furthermore, the consistent end and trend bias results from human studies, but not from studies of non-human primates, raise the question of how relevant these biases might be

across primates. Perhaps differences in our evolutionary histories have resulted in some of these being more useful for one species than the other, or perhaps the method in which we ask these questions remains too human-centric and requires further examination to clarify the unknowns.

Another challenge centers around *delay discounting* and the strong cost that it casts on rewards the later they come within sequences for non-human primates. A meta-analysis by Stevens (2014) regarding intertemporal choices in 13 non-human primates species seems to suggest that non-human primates, due to their lifespan and metabolic rate differences from humans, tend to perform more poorly with increases in waiting periods during intertemporal tasks (i.e., preferring higher value rewards sooner rather than later). It is, therefore, possible that delay discounting more readily affects non-human primates than humans, such that higher-value rewards more quickly lose their value the longer participants must wait to obtain them. Indeed, a review by Vanderveldt et al. (2016) concluded that while delay discounting takes effect in seconds for some animals, humans can and are willing to wait for relatively long periods (anywhere from minutes to months and even years) based on the type and value of the reward.

These previous reviews indicate that delay discounting wait times are related to not only the evolutionary trajectory and niche that species' possess, but also partially correlate with life expectancy and metabolic rates, such that primates and other animals with lower life expectancies and those with high metabolic rates show shorter wait times (Stevens, 2014; Vanderveldt et al., 2016). Presumably, both shorter life expectancies and higher metabolic rates favor shorter wait times (and, therefore, faster decisions) because an individual may not be alive at the time in which a payoff occurs (end bias here may not be an evolutionary viable strategy, as the later portion of an event is not guaranteed) and to maintain the higher needs for homeostasis, respectively. Therefore, it is feasible to expect humans to possess the ability to wait for a higher

reward at the end of a sequence since they are not as susceptible to its value discounting over time as other smaller primates may be.

Thus far, there have been three studies of the peak end effect in primates (see Table 1). In one study, three rhesus macaques (*Macaca mulatta*), like humans, showed two aspects of the peak-end effect: trend and end biases (Blanchard et al., 2014). The researchers used a computerized dual-choice task that utilized gaze shift to assess monkey preferences. First, a control sequence that either increased or decreased the quantity of reward dispensed (juice) was presented; reward sequences were made up of different individual quantities of juice (in mL), such as [1-2-3-4-6] for increasing, [6-4-3-2-1] for decreasing, or [3.2-3.2-3.2-3.2-3.2] for a flat sequence. The monkeys showed a preference for sequences that ended in larger rewards (trend bias) as well as a preference for flat sequences over ones that began with a high juice content but decreased as the sequences progressed, showing an aversion to decreasing trends. A follow up condition compared primarily flat sequences that varied their location of a single large high peak: [8-2-2-2-2], [2-8-2-2-2], [2-2-8-2-2], [2-2-2-8-2] and [2-2-2-2-8]. The macaques' preferences mirrored the peak's position within the sequence, favoring an end peak over all other sequences, with a start peak being the least valued one. The addition of a smaller final reward [2-2-2-8-1] to the most preferred sequence from the previous condition created an aversion in the monkeys, who showed a preference for increasing sequences that either contained no smaller reward [2-2-2-8] or included a delay (d, five seconds) in place of an additional reward [2-2-2-8-d] (end bias). The results of the end and trend sequences align with what is known about human studies. However, when asked to choose between a sequence with a sharp middle peak ([2-2-8-2-2]) and ones with less contrasting peak ([2-3-5-3-2] and [2-4-4-4-2]), the monkeys preferred the flatter

sequence. This contrasts with human studies and peak biases, although as mentioned this could be a result of different types of delivered rewards and experiences.

Table 1: Overview of the differences and similarities between peak-end studies done with non-human primates.

	Blanchard et al. (2014)	Xu et al. (2011)	Egan Brad et al. (2016)
Task	Computer Task	Manual Task	Manual Task
General Methods	Two-choice task between baseline and comparator sequences which used eye gaze to determine sequence preferences	Two-choice cup selection task between sequences containing high (HVR) and low value (LVR) food rewards, as well as time delays, which determined sequence preference	Two-choice token trading task that determined preference between food rewards each with different reward values coated onto a lop rod-like biscuit
Training	Yes	No	No
Delay Discounting	Yes	Yes	No
Peak Bias	Not observed	Not tested	Observed in half of participants
End Bias	Observed	Opposite observed (Start bias)	Observed in half of participants
Trend Bias	Observed	Not tested	Not tested

However, in a different study three other rhesus macaques (T, H, and P) showed a preference for receiving a higher-valued reward (A: grape) first over a low-value reward (B: half of a sugar snap pea or green bean), and they failed to show an end effect in a study with five different food preference manual tasks (Xu et al., 2011). All monkeys showed a significant preference for receiving the $A \rightarrow B$ sequence over $B \rightarrow A$. Two follow-up experiments assessed the value of the low-value reward by comparing $A \rightarrow B$ to $A \rightarrow []$ ($[]$ = five seconds) and then $B \rightarrow A$ to $[] \rightarrow A$ to see if B had a positive or negative effect on the order choice. Here, if B had a positive value, then options with both rewards would be preferred, no value should result in

indifference between choices, and a negative value should show a preference for A alone, similar to what has been observed in humans (Do et al., 2008). However, the results were mixed, with only monkey H preferring the options with both rewards, monkey P preferring $A \rightarrow B$ and $[] \rightarrow A$, and monkey T preferring $B \rightarrow A$ and having no preference in the other comparison. The inconsistent patterns among the macaques hinted that perhaps a selective-value effect occurred under some contexts for some individuals but not others and highlights once again that primates are rarely perfect rational decision-makers.

Xu et al. (2011) performed a subsequent experiment that retested food preferences with different rewards (high value: mini marshmallow, low-value: one Cheerio®), in which monkeys H and T maintained a preference for $A \rightarrow B$ while P flipped to $B \rightarrow A$. This was used to then test if order truly mattered, similar in theory to the end bias test from Blanchard et al. (2014), or if the monkeys preferred the high-value food first. The final experiment compared a preference for either $[] \rightarrow A \rightarrow B$ or $B \rightarrow A \rightarrow []$ and found that monkeys P and H preferred the former while monkey T showed no preference. It is possible that T gave no value to the lower food reward and therefore seemed to not have a preference for an order of rewards because the higher value target maintained its location, as in some chimpanzee studies (Beran et al., 2009). This stands in contrast to the end bias found by Blanchard et al. (2014) and human studies, and instead show a preference for start bias in these three rhesus macaques, who initially all preferred the higher reward first in the $A \rightarrow B$ and $B \rightarrow A$ sequence comparison. This preference was also seen when Xu et al. (2011) attempted to control for delay discounting in the last experiment, in which two monkeys chose to obtain the high-value reward first even when it meant enduring a time delay with no reward.

Adding to the confusion, Egan Brad et al. (2016) reported an end bias in two out of four capuchin monkeys (*Cebus [Sapajus] apella*). Similarly to Xu et al. (2011), the monkeys were first asked to establish a food preference for either receiving the frosting-covered end of a long, stick-shaped cookie (a Japanese Pocky biscuit; high-value reward) or the non-frosted side (low-value reward) first. Much like Blanchard et al.'s (2014) and humans, half of the capuchins showed a preference for the low-value reward first (~76% and 71% of the time), favoring an end bias, while the others did not show a significant preference. A follow-up experiment changed the options, and the monkeys chose between receiving a biscuit that was only frosted in the middle (i.e., peak bias) and a biscuit whose first 2/3rds was covered in frosting equal to the amount in the peak biscuit. Importantly, this ensured that no matter the choice an equal amount of frosting was acquired. The same monkeys that showed an end bias in the first experiment also showed a peak bias, choosing the middle-frosted biscuit approximately 72% and 66% of the time, while the remainder showed no preference. Given that capuchin monkeys were also included in Stevens (2014) and are subject to delay discounting, thus it would be expected that they would favor a start bias. This should have resulted in a preference for the frosting to be consumed first during experiment one and for the more consistently covered biscuit in experiment two. However, only half of the participants showed these preferences, making it difficult to generalize these findings to capuchins overall and to support the findings by Blanchard et al. (2014) that other non-human primates show the peak-end effect.

These three empirical studies vary widely in their methods and rewards, making it difficult to compare them, see Table 1. Both macaque studies, Xu et al. (2011) and Blanchard et al. (2014), used different reward types, making it difficult to compare as it is unknown whether rhesus macaques similarly treat quantity discrimination between liquids to that of rewards for

which the quantities can easily be seen in advance. Whereas Xu et al. (2011) and Egan Brad et al. (2016) tested pre-existing preferences (i.e., food preferences) using manual tasks, Blanchard et al. (2014) used a computerized task and based their preferences on first teaching the monkeys the value of possible payouts during a training phase.

Lastly, only two studies tackle the issue of delay discounting by including delays within their payouts to assess the weight of the highest-valued reward. Blanchard et al. (2014) weighed the highest value reward (8 mL) in two different methods: once against lower-valued rewards (e.g., [8-2-2-2-2], [2-2-8-2-2], [2-2-2-2-8]) and in a separate occasion to no rewards (i.e., [8-0-0-0-0], [0-0-8-0-0], and [0-0-0-0-8]). In both instances delay discounting was not observed, as the macaques chose to receive the highest value reward at the end significantly more than all other options. Furthermore, this serves to remind us of the comparison of the end peak sequence ([2-2-2-2-8]) sequence to those with a small reward [2-2-2-8-1] or a five-second time delay [2-2-2-8-0] and the lack of a significant difference there. The lack of preference could show that the macaques may not be assessing time between trials as notable enough to matter, therefore, the effects of delay discounting may not be as impactful and could require some more fine-tuning.

Xu et al. (2011) attempted to assess delay discounting differently, by comparing the position of the high-value reward in high first ([] \rightarrow A \rightarrow B) and low first (B \rightarrow A \rightarrow []) sequences that contained a time delay. The mixed final results favoring a start bias contrast with Blanchard et al.'s (2014) uniform findings favoring an end bias. Yet, the large individual differences shown by Xu et al.'s macaques during their assessment of the low-value reward within sequence value, impedes our ability to understand how the macaques assessed this last comparison. Similarly, we cannot speculate how Blanchard et al.'s (2014) macaques assessed all parts of their sequences as the study lacked a direct comparison between a low-value reward to

no reward across their different conditions to see if it was positive, negative, or had no value. If Blanchard et al. (2014) had included such a control and had their macaques preferred sequences with the low-value rewards over no rewards, then it would have made a remarkably strong case supporting an end bias. Not only would it have given a within sequence value to the low-value reward, but it would have shown that the Blanchard et al. (2014) macaques attended the entire sequence and not just the peak and end portions. Importantly, these low-reward vs no reward comparisons also allow for comparisons between macaques and humans, who are known to preference a sequence with only one high-value reward over one that also had a low-value one (Do et al., 2008). Showing that both species are cognitively aware of the low-value reward's presence, but choosing against it, would strongly support a more phylogenetic peak-end effect.

Careful control of time extends beyond controls and involves intertrial intervals. Given that in some instances rhesus macaques have been able to wait 30 and up to 120 seconds to receive a more valuable reward (Evans et al., 2014; Evans & Beran, 2007), the importance of adequate time intervals is crucial at separating sequence preference from reward maximization. Too small of a gap between trials may lead to monkeys basing their choices on how fast they can reach the next trial to earn a favorable reward and away from the point of the study, in this case sequence comparisons. Since Egan Brad et al. (2016) did not include the length of time in-between trials nor the average time which capuchin monkeys took to eat their rewards, we cannot include them in this comparison. However, Blanchard et al. (2014) and Xu et al. (2011) reported their overall trial lengths and their intertrial intervals for their delay discounting comparisons. Xu et al.'s (2011) macaques spent a total of 23 seconds per trial: five seconds for the initial delay, five seconds while eating the high-value reward, five seconds eating the low-value reward, and then an eight-second intertrial interval. Blanchard et al.'s (2014) macaques spent a total of 26

seconds per trial: five seconds per delay (total of 20 seconds), five seconds to drink the juice reward, and then a one second intertrial interval. Although both studies have different time intervals for rewards and intertrial periods, they both present a new trial to their subject every 23 to 26 seconds. The similarity of overall trial length can be used to determine how effective time intervals were at preventing the macaques from trying to maximize how fast they obtained a high-value reward. Since the overall trial length for both studies falls well within the time length which macaques are capable of waiting for a larger later reward, it cannot be ruled out that they could have tried to cheat the purpose of the experiments. Increasing the time intervals of the rewards and delay may be one method of solving this issue. However, increasing these by too much can lead to greater effects of delay discounting further clouding the results. A second way is to increase the intertrial interval. This would allow the rewards within a sequence to not experience too much of a discounted value while also clearly separating individual trials. Additionally, this might also cause the macaques to be more cautious with their choices since they would have to sit and wait for a significant period of downtime between trials.

Regarding the last of the non-human primate peak-end studies, Egan Brad et al. (2016) contained no instance of employing a time delay or other method to account for delay discounting in their procedures. This makes it difficult to assess if the “later” end portion of the sequence was later enough to justify a true preference for “saving the best for last.” Without this control, we cannot know if the capuchins registered that eating a favored reward at the end came at a cost; if there is not cost associated with the positions then it is difficult to validate the sequence order matter. This might explain in part why half of the participants showed no preference throughout their conditions.

The differences among these studies make it challenging to assess the role these three biases have on decision-making and preferences. While some hint toward trend and end biases, the lack of consistent preferences across studies for sequences that have clear reward values balanced through careful positioning and usage of time intervals, highlights that more work remains to be conducted. Furthermore, all three studies had very small sample sizes, with a total of ten participants across the studies: three different individuals per macaque study and four capuchin monkeys. Therefore, a simple manual task that tests pre-existing preferences to minimize potential external confounds (such as training conditions, novelty effects, and complex computer interactions) and that incorporates tests of sequence preferences, the within sequence value of a lower-value reward, controls for delay discounting, and increases the intertrial interval to penalize shortcuts more greatly would be beneficial in addressing some of the previously discussed issues.

1.4 Examining Capuchin Sequence Order Preferences

For this study, I tested 11 capuchin monkeys (2 males), to determine how the order of rewards in a sequence can affect the preferences developed for each choice. Capuchin monkeys were chosen because, like humans, they are primates that live in large social groups containing complex hierarchies (Fragaszy et al., 2004; Jack et al., 2011). Capuchin monkeys possess a large brain-to-body size ratio (Stephan et al., 1988) and share numerous behavioral traits with humans, such as high tolerance towards others (de Waal & Brosnan, 2006), inequity sensitivity (Brosnan & de Waal, 2003; Talbot et al., 2018; van Wolkenten et al., 2007), cooperation in both wild (Baldovino & Di Bitetti, 2008; Crofoot et al., 2011; de Waal, 2000; Di Bitetti, 1997; Perry et al., 2003; Perry & Rose, 1994; Sargeant et al., 2015; Wheeler, 2008) and captive (Brosnan et al., 2010; de Waal & Berger, 2000; de Waal & Davis, 2003; Mendres & de Waal, 2000)

environments, and mirror human performance, such as by finding the Nash equilibrium, in some economic games (Smith et al., 2019), and tool usage (de A. Moura, 2004; Falótico et al., 2019; Ottoni & Izar, 2008; Spagnoletti et al., 2011, 2012). Also, like humans, capuchin monkeys fall prey to different cognitive biases (Parrish et al., 2015; Watzek & Brosnan, 2020) and make irrational choices (Watzek et al., 2018; Watzek & Brosnan, 2018). This combination of complex social living structures and similar cognitive biases allowed us to test for the presence of the peak-end effect and how it might be impacted by social and biological factors. Furthermore, it allowed us to try and help decipher if the peak-end effect, and our human preference to “save the best for last,” can be more generally categorized as a homologous or a convergent trait among primates.

This study used methods that closely resemble those in Xu et al. (2011), as their approach provided a test that partially relied on pre-determined food preferences and a manual touch-based task with solid, quantifiable food rewards. In this manner, not only is a comparison of effects across two species more easily carried out, but it provides participants with a simple manual task that sidesteps the more complex interactions of computerized testing as well as novelty biases and training effects. Due to only using two kinds of food rewards, this testing could only measure if capuchin monkeys show an end bias and could partially test a trends bias (preference sequences that increase in value). Whether capuchin monkeys show a peak effect may be an interesting question, but one that is not within the scope of this study. However, it should be examined under similar parameters in the future.

I first determined food preferences to establish a high and lower-value reward for each monkey. I then provided the participants with a baseline dichotomous choice between getting the higher value reward first (*high-low*) or last (*low-high*) to determine order preference. If capuchin

monkeys are similar to humans and are end biased, a preference for low-high should be clear across participants. Then, two additional testing conditions were presented to the monkeys to determine if the lower-value food adds a positive, negative, or no value to a sequence. The first of these additional conditions compared an end delay sequence (*high-delay*) to the high-low baseline sequence, while the other compared a start delay (*delay-high*) to the low-high baseline sequence to obtain the true value of the lower-value reward. Importantly, the delay was equal to the time given to the monkeys to eat a food reward, ten seconds, to keep all trials equal in time length regardless of condition. To assess if a true preference for an order was shown, I tested a final condition that reran the baseline conditions with a time delay added to the beginning of each sequence (*delay-high-low* and *delay-low-high*). Adding an initial delay decrease the overall value of the higher valued reward in these sequences, when compared to the baseline version. Therefore, if capuchin monkeys had a true preference for the most positive experience at the end of a sequence, an end bias, they would prefer the delay-low-high sequence, even if it means that the high-value reward came at a higher discounted rate. See Figure 1 for a visual representation of these conditions.

Baseline	A	B	ITI	
	B	A	ITI	
Low vs Delay 1	A	B	ITI	
	A	-	ITI	
Low vs Delay 2	B	A	ITI	
	-	A	ITI	
Discounting	-	A	B	ITI*
	-	B	A	ITI*

Figure 1: Visual representation of testing conditions. A represents a high-value reward, B a low-value reward, and “-“ a 10-second time delay. ITI was equal to 40 seconds while ITI equaled 30 seconds.*

If capuchin monkeys showed an end bias as humans do, they would show an initial food preference for the low-high sequence in the initial baseline test. If capuchin monkeys assigned a value to the low-value reward, then they would prefer the options which contained both rewards over one with the high value reward and then the delay, as these options provided a higher quantity of rewards and possessed no time penalty, because they are equal in duration to the options with the added time delay (i.e., follow up trials occur at approximately equal times). Lastly, if capuchin monkeys truly preferred to save the best for last, then they should favor the option which presented a time delay, then a low value reward, and finally a high value reward other, even the last reward came at a higher discounted cost.

2 EXPERIMENT

2.1 Introduction

Far from perfect rational decision-makers, humans often base their decisions on concepts that appear irrational, that is, appear to go against their immediate best interests (Kahneman &

Tversky, 1979). This goes against the concept of utility maximization, which states that humans should operate to maximize profits (Golob & Beckmann, 1971), however, we often fall short of utility maximization due to various cognitive biases which can sway our opinions or decisions (Haselton et al., 2015). Cognitive biases not only affect our perception of how we interact with the world but can also affect how we evaluate it. To give one example, Kahneman and Thaler (2006) argued that humans do not evaluate sequences as either an overall mean value or based on all instances within a sequence. Instead, we assign a sequence a set value based on a “snapshot,” which is based on the highest and ending affective points within a sequence, in what is known as the peak-end effect.

The peak-end effect has been used to explain a paradoxical preference for longer-lasting painful procedures as long as they ended on a decreased pain level, which is explained by an end bias (Kahneman et al., 1993; Redelmeier et al., 2003; Redelmeier & Kahneman, 1996; Schreiber & Kahneman, 2000). For example, some people prefer sequences with constant pain levels over those with lower constant pain that contains a sharp increase in the middle of the event, even though both sequences provided the same net pain (Ariely, 1998), explained by a peak bias. Alongside our preference for sequences that increase in value (Chapman, 2000; Hsee et al., 1991; Lau-Gesk, 2005; Loewenstein & Sicherman, 1991), known as a trend bias, the peak-end effect has been used as an explanation in fields as diverse as tourist experience (Kim & Kim, 2019), movie experience (Do et al., 2008), physical activities (Hargreaves & Stych, 2013) and even relationship counseling (Sels et al., 2019), but it is unknown what the full extent of the peak-end effect is. In particular, we do not know whether this bias is unique to humans, or whether it has evolved as a cognitive shortcut. If it is the latter, other species may also show the peak-end effect.

One way of addressing these questions is to use a comparative approach (Smith et al., 2018). That is, if other primates also show peak, end, and trend biases, then it may be reasonable to conclude that we as primates more broadly develop sequence preferences in similar manners. However, if only humans show these biases, then perhaps the peak-end effect is a unique shortcut that we have developed. Thus far, only a handful of studies have been carried out with non-human primates and their conflicting results have only muddied our understanding of how sequence preferences between primate species relate to one another.

In one study, three rhesus macaques (*Macaca mulatta*), like humans, showed a trend and end bias (Blanchard et al., 2014). The researchers used a computerized dual-choice task that utilized gaze shift to assess monkey preferences. Importantly, monkeys were asked to make a choice between increasing ([1-2-3-4-6]) and decreasing sequences ([6-4-3-2-1]) that dispensed a juice reward (in mL) or a flat sequence (e.g., [3.2-3.2-3.2-3.2-3.2]) of equal value that resulted in a trend bias, or a preference for increasing sequences. A follow-up condition placed a high peak along a flat sequence, starting in the left most position (8-2-2-2-2]) and shifting one spot to the right until its located at the end ([2-2-2-2-8]). The monkeys' preference for ending on a high peak once again showed an end bias. Additionally, a condition aimed at delay discounting (an effect that explains how rewards lose value the longer they take to be obtained) assessed if it was the delay imposed by the location of the high-value reward that dictated the monkeys' preferences. When comparing a sequence made up of five second delays and a high value reward in the beginning ([8-delay-delay-delay-deal]), middle ([delay-delay-8-delay-deal]), or end ([delay-delay-delay-deal-8]), macaques overall preferred the end peak sequence. This suggests that, surprisingly, even with a the more discounted value of being last, the high-value reward was still preferred at the end. This contradicts what is expected from non-human primates given that

their lower life spans and higher metabolisms should make them more susceptible to delay discounting (Stevens, 2014). Lastly, when comparing the end peak sequence to one that had a small reward ([2-2-2-2-8-1]) and a five second delay ([2-2-2-2-8-delay]), the monkeys showed an aversion for the ending small reward, thus, supporting the presence of an end bias.

However, in a different two-choice manual study three other rhesus macaques showed a preference for receiving a higher-valued reward (A) first over a low-value reward (B), and they failed to show an end effect in a manual task using food preferences (Xu et al., 2011). In a finding opposite the human literature and Blanchard et al.'s (2014) findings, all monkeys showed a start bias, or a preference for receiving the $A \rightarrow B$ sequence. However, two follow-up experiments cast doubt whether the monkeys attended the lower-value reward or perhaps rather ignored it all together. The first of these conditions compared an $A \rightarrow B$ sequence to $A \rightarrow []$ ($[] =$ five seconds) and the second a $B \rightarrow A$ sequence to $[] \rightarrow A$. Presumably, a positive B value should be reflected in a preference for sequences with both rewards, while a negative value would be shown as an aversion to these sequences. Importantly, a negative B value would mirror what is observed in humans, who prefer sequences with only a high-value reward over those with both a high- and low-value one (Do et al., 2008). However, the results of these conditions were mixed as the inconsistent patterns among the macaques hinted that perhaps the high-value reward's presence eclipsed the value of the lower one, a selective-value effect, under some context for some individuals but not others.

Xu et al. (2011) then used a final experiment to then test if order truly mattered, similar in theory to the end bias test from Blanchard et al. (2014), or if the monkeys preferred the high-value food first. The final experiment aimed to use delay discounting and compared a preference for either a $[] \rightarrow A \rightarrow B$ or a $B \rightarrow A \rightarrow []$. If a true start bias was present, then the monkeys

would prefer the high-low sequence that starts with a time delay over a low-high sequence that ends in a delay. Two of the three macaques maintained their original preference for receiving the best first and preferred the first sequence while the third showed no preference. It is possible that one monkey gave no value to the lower food reward and therefore seemed to not have a preference for an order of rewards because the higher value target maintained its location, as in some chimpanzee studies (Beran et al., 2009). This stands in contrast to the end bias found by Blanchard et al. (2014) and human studies, and instead show that twice a preference for a start bias was seen in rhesus macaques.

In a third study, a two-choice manual task, Egan Brad et al. (2016) reported an end bias in two out of four brown-tufted capuchin monkeys (*Cebus [Sapajus] apella*). Similarly to Xu et al. (2011), the experimenters first established the monkeys' baseline sequence preference for either receiving a high-value reward (the frosting-covered end of a long stick-shaped cookie: a Japanese Pocky biscuit) or a low-value reward first (the non-frosted side) first. Favoring an end bias, and much like Blanchard et al. (2014) and human studies, half of the capuchins showed a preference for the low-value reward first, while the others did not show a preference. A follow-up peak bias experiment changed the options to choosing between a biscuit that was only frosted in the middle and one whose first 2/3rds was covered in frosting equal to the amount in the peak biscuit. This ensured that no matter the choice an equal amount of frosting was acquired so the preference made was not based on quantity but rather order. The same two end biased monkeys also showed a peak bias, choosing the middle-frosted biscuit, while the other two again showed no preference. Much like macaques, capuchin monkeys should still be more greatly affected by delay discounting than humans (Stevens, 2014; Vanderveldt et al., 2016) which should have resulted in a preference for the frosting to be consumed first during experiment one (start bias)

and for the more consistently covered biscuit in experiment two. However, it's difficult to generalize these findings to capuchins in general or corroborate them to those from Blanchard et al. (2014) because only half of the participants showed these preferences support a peak-end effect in non-human primates.

These three empirical studies vary widely in their methods and rewards, making it difficult to compare them, see Table 1 for a summary of the three studies. Both macaque studies, Xu et al. (2011) and Blanchard et al. (2014) used different reward types, making it difficult to compare as it is unknown whether rhesus macaques similarly treat quantity discrimination between liquids to that of rewards for which the quantities can easily be seen in advance. While both Xu et al. (2011) and Egan Brad et al. (2016) tested pre-existing preferences (i.e., food preferences) using manual tasks, Blanchard et al. (2014) used a computerized task and based their preferences on first teaching the monkeys the value of possible payouts during a training phase.

Lastly, since delay discounting is expected to impact non-human primates more than humans, time intervals are used commonly in tasks to try to prevent participants from incorrectly assessing the purpose task. However, only Xu et al. (2011) and Blanchard et al. (2014) reported specific time durations for their conditions. Although total trial lengths were similar (23 and 26 seconds, respectively), the time intervals for the rewards, delays, and intertrial periods were inconsistent between studies. Given the importance of how time can affect the value of a reward, these methodological differences were likely one of the causes of why each study reported different results.

The differences among these studies make it challenging to assess the role these three biases have in decision-making and preferences. While some hint toward trend and end biases,

the lack of consistent preferences across studies for sequences that have clear reward values, highlights that more work remains to be conducted. Furthermore, all three studies had very small sample sizes, with a total of ten participants across the studies: three different individuals per macaque study and four capuchin monkeys. Therefore, a simple manual task that tests pre-existing preferences to minimize potential external confounds, and that not only tests sequence preferences, but also the within sequence value of a lower-value reward, would be beneficial in addressing some of the previously discussed issues. Therefore, I chose to partially replicate the methodology used by Xu et al. (2011), adjusting the delay discounting controls, and test some aspects of the peak-end effect while also evaluating the within-sequence value of the lower-value rewards. To contrast Xu et al.'s (2011) work with rhesus macaques, I tested brown tufted capuchin monkeys to compare results across two different primate classifications, catarrhines for rhesus macaques and platyrrhines for the brown-tufted capuchin monkeys.

For this, I tested four different conditions, the first of which established a baseline preference for either a high-low or a low-high sequence. Then, I included two conditions with an added ten-second time delay (the time equal to eating one food reward), so the monkeys could choose from a high-low or a high-time delay sequence and then between a low-high or a time delay-high sequence. Lastly, I reran the original baseline comparison with an added initial time delay to compare a delay-high-low sequence to a delay-low-high one.

If capuchin monkeys also “save the best for last” then they should prefer the low-high sequence as humans do in the baseline condition. If capuchin assign a positive within sequence value to the lower-value food reward, then a preference for the sequence with two rewards over one should be observed and the opposite for a negative value; no preference between sequences would be indicative of having no additional value. Lastly, a true preference for a high-value last

would be seen if the monkeys preferred a delay-low-high sequence over the delay-high-low one, as the high-value reward comes at a more discounted value due to its location within the sequence.

2.2 Methods

2.2.1 Participants

I tested 11 capuchin monkeys housed at Georgia State University's (GSU) Language Research Center. All participants had been mother-reared in captivity and lived in typical social groupings, each with a dedicated indoor room and large outdoor yard filled with enrichment material (e.g., climbing ladders, swing sets, tunnels, ropes, toys). Each group's outdoor yard was open except during inclement weather or required maintenance. The participants lived in one of three mixed-sex groups. All groups contained individuals from various adult age categories ranging from young adults to geriatric individuals. Additionally, all participants have lived in typical social groupings for their entire lives.

Each group's outside enclosure contained access to both shaded and non-shaded regions with ground and climbing structures. When outside, all participants had auditory contact with each other and visual access to at least one other group. Indoors, one group shared a room with another group of monkeys who were not included in this study and so have visual and auditory access to them. At no point did any individuals have direct contact with non-group members.

Water was always accessible, even during testing, and was never limited except for veterinary purposes or hormone sample collection. Food was provided to all participants multiple times per day in the form of primate chow, vegetables, and fruits, regardless of testing participation, and all received additional food rewards for any testing they chose to complete. Participants' health and well-being were monitored daily by researchers as well as GSU

Department of Animal Resources (DAR) employees, including veterinary care as needed. All testing was entirely voluntary, with subjects choosing to enter test boxes attached to the indoor section of their home enclosure if they wished to participate. Subjects were never deprived of food, water, treats, outdoor access, or social contact to motivate testing.

Participants were regularly monitored, and their social behavior/group structure was observed during individual focal observations (Reilly & Brosnan, 2022). These provide up-to-date accounts of each group's network through social behavior-related activities and states such as grooming, aggression, and proximity. These social networks were then used to provide relative hierarchical rankings, as capuchins do not have strictly linear relationships. In addition, life history data such as age, sex, and rearing method were available to researchers (all subjects were mother reared except a couple of our older subjects who were born in other facilities for whom rearing data was not always known).

For testing, participants were previously trained to voluntarily separate from their groups into single testing boxes (23 $\frac{3}{4}$ x 13 $\frac{3}{4}$ x 20 cm) for cognitive and behavioral testing. During this time, they did not have physical contact with their group mates but maintained auditory and visual contact with other group members. All research at the LRC is non-invasive. GSU's Language Research Center is a fully accredited institution by the Association for Assessment and Accreditation of Laboratory Animal Care, and all protocols were approved by GSU's Institutional Animal Care and Use Committee (IACUC; A20018 to Sarah Brosnan) and were in accordance with the guidelines for animal research used by the Association for the Study of Animal Behaviour and the Animal Behavior Society.

2.2.2 *Materials*

To test the monkeys without interference from other group members, all testing sessions were conducted while participants were in their individual test boxes. Testing was done using a manual apparatus that contained the different sequence options. The apparatus consisted of a rectangular platform upon which two “cups” were placed that represent one of two possible sequences. Each cup was made up of two 2-inch polyvinyl chloride (PVC) pipe headcovers spaced 25.5 cm apart from each other and attached to the platform via a small 1-inch metal hinge. The platform itself was a black PVC board (68.5 x 46 cm). Each PVC pipe head cover represented a choice; the covers were colored differently across each testing condition (individual color sets are listed below in Figure 2), taking into account the fact that many capuchin monkeys are red-green dichromats (Gomes, 2002). On every occasion, one of the two cups were additionally painted using a pattern to help the monkeys distinguish between each option. The rewards for each option varied based on testing conditions and options and included different combinations of an apple cube (1 x 1 x 1 cm), grape cube (1 x 1 x 1 cm), and a time delay (10 seconds, determined to be equal to the time needed for a monkey to eat either of the food rewards). Testing sessions were recorded using either a Sony camcorder or an iPhone 12 pro max (non-cloud linked) to verify all results collected and for assessment of inter-observer reliability.

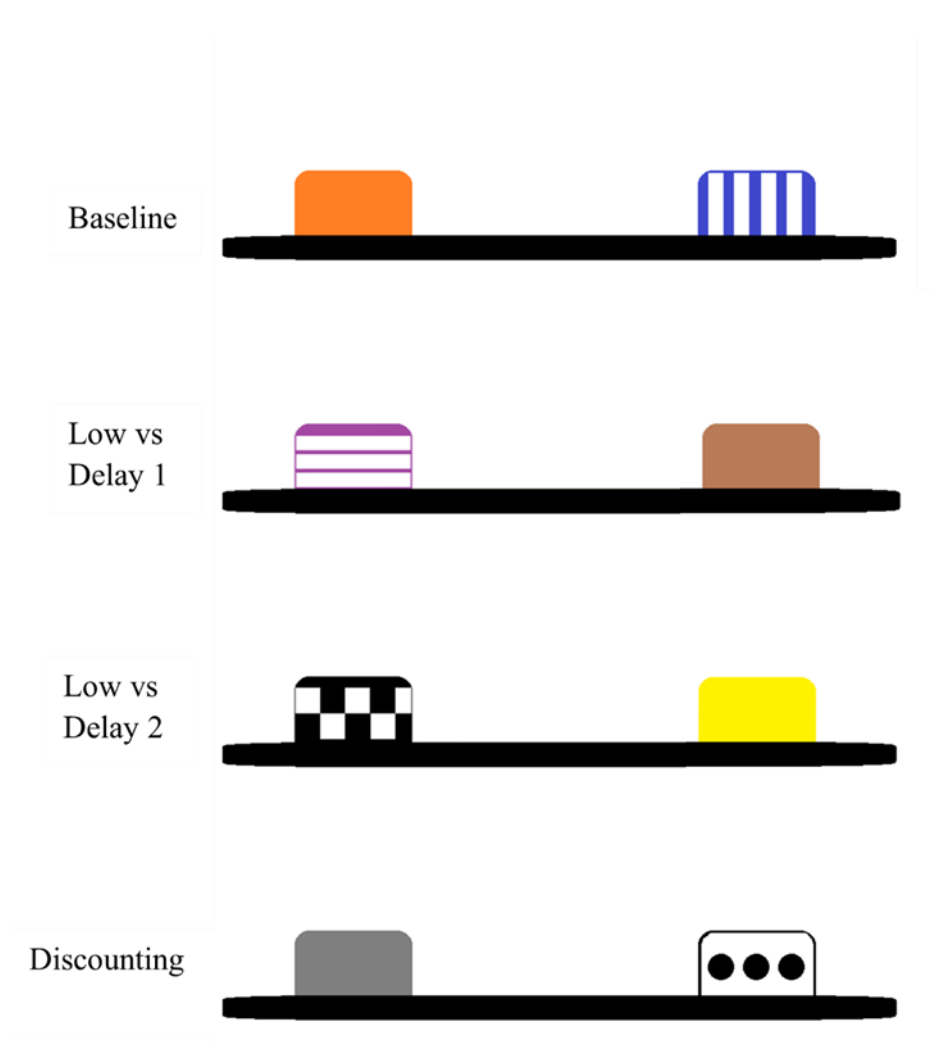


Figure 2: Individual cup colors and patterns used to test monkey sequence preferences.

2.2.3 General Procedures

For this experiment, all participating monkeys underwent two sessions (16 trials each) of a simple two-choice food preference test between an apple cube (lower-value reward) and a grape cube (high-value reward) to verify their preferences. Each monkey was presented with the option to choose one of the rewards from a PVC board, at which point the other one was taken away. The passing criterion was set at choosing one item on at least 13 out of 16 trials for the two consecutive sessions (total of 28 out of 32). Monkeys that did not pass the criterion were not included in this study.

After passing the initial food preference portion, all monkeys completed four different conditions in the same order (Baseline, Low vs Delay 1, Low vs Delay 2, and Discounting). Each condition was made up of six sessions, and each session was made up of 16 trials. Of these, four were exposure trials, in which only one sequence was made available to the monkey to familiarize them with the reward payouts, and the following 12 trials were experimental trials containing both sequence options. During the experimental trials, the experimenter loaded the appropriate payout beneath the color/patterned cups on top of the testing apparatus and then proceeded to cover them. The loaded apparatus was then placed within reach of the monkey, who could choose from one of the options. After a choice was made, the apparatus was removed, the cups were flipped open in view of the monkey, and the appropriate reward sequence and intertrial intervals were given out (see below for further details regarding each condition). This procedure was continued until all trials for a session were completed. All testing sessions were videotaped. Data was recorded live and a secondary coder, blind to the hypothesis and predictions of the study, coded 20% of sessions to obtain interrater reliability.

Note that the monkeys had previously completed baseline testing with an older design of this study that lacked both timed blocks for each reward and an intertrial interval. Additionally, four subjects were midway through the low vs delay 1 condition as well. This design was eliminated when I realized that the capuchins could simply choose the high-delay sequence in the low vs delay 1 condition to obtain a high reward faster as there was no set intertrial interval that prevented them from maximizing how fast they obtained high value rewards. For completeness and to decrease the potential of a selective-value effect affecting the data collected, all 11 monkeys reran all previously completed sessions and conditions under the new methodology described.

2.2.3.1 *Baseline*

This initial condition tested whether monkeys had any preference between receiving a high-value reward first or last by presenting the monkeys with the option to choose between a high-value reward followed by a low-value reward (high-low) or a low-value reward followed by a high-value reward (low-high). The first part of the sequence was placed closest to the monkey on the rectangular tray, with each subsequent component of the sequence placed further away. Overall, each trial only lasted 60 seconds, made up of 10 seconds per choice/reward followed by a 40 second intertrial interval.

2.2.3.2 *Low vs Delay 1 and Low vs Delay 2*

The low vs delay 1 condition assessed if the low-value reward had a positive value when received after a high-value reward. The low vs delay 2 assessed the value when received before the high-value reward. For the low vs delay 1 condition, the monkeys chose between a high-value reward followed by a time delay of 10 seconds (high-delay) and a high-value reward followed by a low-value reward sequence (high-low). For the low vs delay 2 condition, monkeys chose between a low-value reward followed by a high-value reward sequence (low-high) and a time delay followed by high-value reward sequence (delay-high). An empty space similar in size to that of an apple cube was used to visually represent the time delay on the apparatus. Overall trial length and intertrial interval remained the same as in the baseline condition.

2.2.3.3 *Discounting*

This final condition tested whether adding a delay to the baseline sequences affected whether monkeys chose to receive a high-value reward sooner in the sequence or later at a higher discounted value. For this, the monkeys were presented with a 10 second time delay-high-low (delay-high-low) sequence and a 10 second time delay-low-high (delay-low-high) one. Reward

positions followed the same order as in previous conditions, with the time delay being closest to the monkey spatially on the apparatus. Overall trial length and time per choice/reward remained the same as in previous conditions, with only the intertrial interval decreasing to 30 seconds to maintain the trial length at 60 seconds.

2.2.4 Analysis

Due to the varying reward outcomes in the different sequences offered, I could not directly compare proportions across conditions but had to compare them within. Monkey sequence preferences within a condition were determined using a paired samples t-test comparing mean sequence choice rather than total choice count. Changes over time were assessed using a binomial logistic regression model with sequence choice as the outcome variable and session number, sex, and ranking as predictors in each of the four testing conditions. Due to the number of males tested ($n = 2$, both high ranking), the potential for confounding the effects of sex and rank was present. Therefore, I checked variance inflation factors for all predictors to help inform how much collinearity was present among them. Additionally, I also ran a separate regression with sex excluded from the predicting variables. A chi-square test was used to assess if these models differed from a null model with no predictor. If appropriate, paired sample t tests were also used to determine potential differences in sequence preference within sex and rank for each condition. Lastly, a trail was considered failed if the monkeys did not interact with the apparatus for two minutes while a session was considered failed if three failed trials occurred in row. However, neither of these occurred by the conclusion of the study.

3 RESULTS

3.1 Baseline

Monkeys preferred to receive the high-value reward first ($t(154) = 5.32, p < .001$; Figure 3: top left). Although the initial logistic regression ($\chi^2(4, N = 936) = 9.86, p = .043$) showed no effect of sex or session, it did show that middle-ranked individuals were approximately two times more like to choose the high-low option than higher-ranking individuals ($p = .023$). Surprisingly, when I tested the assumption of collinearity among our variables, we found no evidence for multicollinearity (Sex, Tolerance = .59, VIF = 1.69; Rank, Tolerance = .59, VIF = 1.69; Session, Tolerance = 1, VIF = 1). However, when I excluded sex as a predicting variable, the model ($\chi^2(3, N = 936) = 9.22, p = .027$) showed that both lower- ($p = .003$) and middle-ranking ($p = .001$) monkeys now were 0.41 and 0.5, respectively, more likely to choose a low-high sequence than high-ranking monkeys. When I examined ranking preferences, I saw that high-ranking individuals preferred starting their sequences with a high-value reward ($t(34) = -3.00, p = .005$), while middle- ($t(58) = 4.03, p < .001$) and lower-ranked monkeys ($t(58) = 7.30, p < .001$) both favored receiving their high-reward last (high-low sequence; see Figure 4). Given that the high rank category was predominantly male (there was one high ranking female), we chose to use only rank, and not sex, as a factor in future analyses.

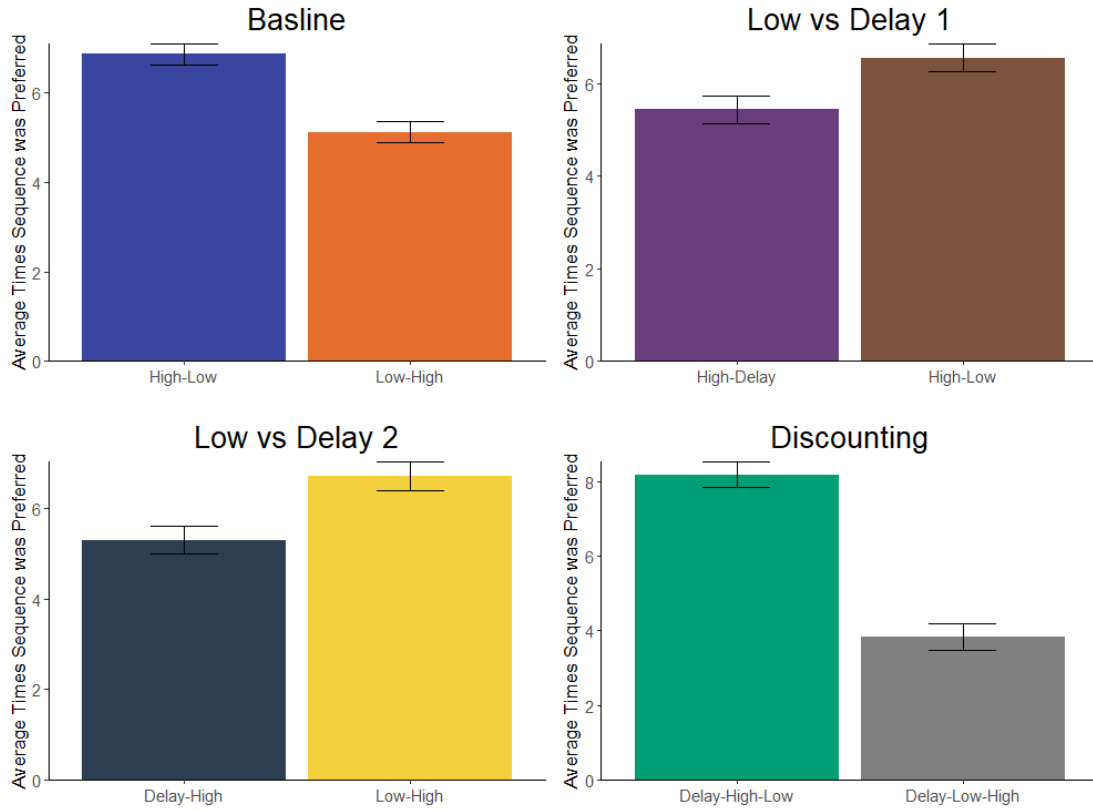


Figure 3: Average times monkeys preferred a sequence within a session separated by condition. Error bars represent standard errors.

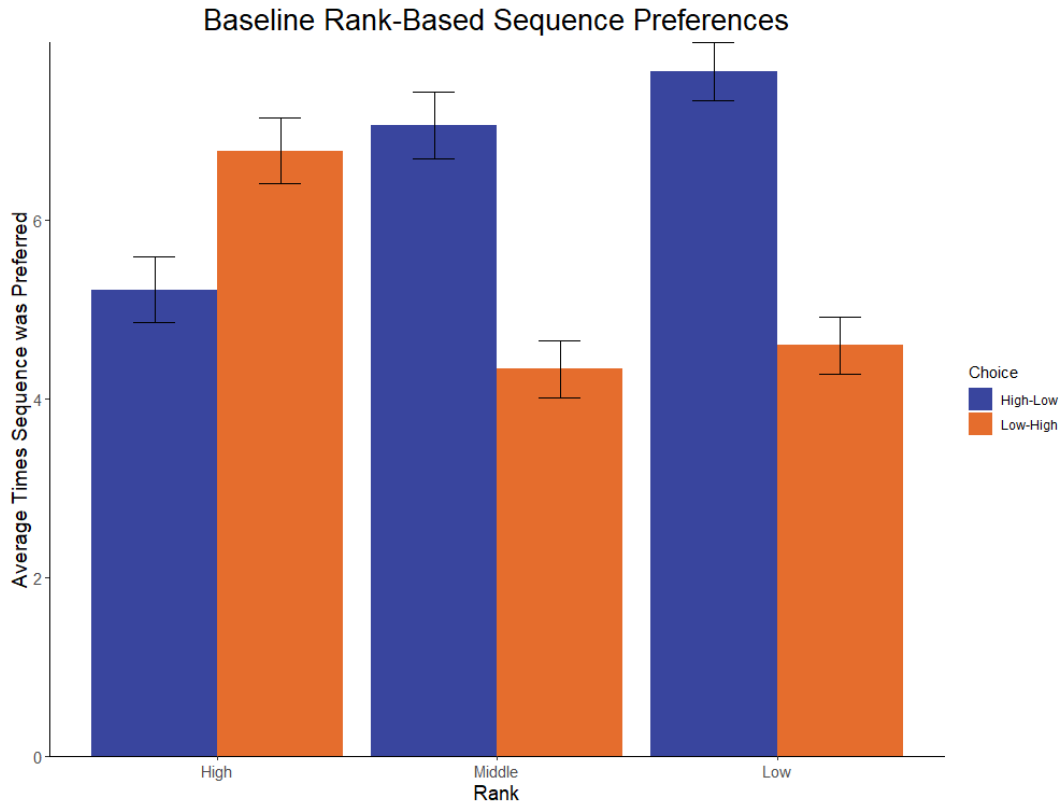


Figure 4: Average times a sequence was preferred by high-, middle-, and low-ranking monkeys in the baseline condition. High ranking monkeys preferred receiving a high-value reward first while low- and middle-ranking monkeys preferred it at the end. Error bars represent standard errors.

3.2 Low vs Delay 1

In the first delay comparison condition, monkeys preferred ($t(152) = 3.40, p = .001$; Figure 3: top-right) to receive the two reward sequence (high-low) over one containing just a high-value reward (high-delay). The removal of sex as a predictor from the second regression model ($\chi^2(3, N = 924) = 7.90, p = .048$) showed that monkeys were more likely to choose the high-low sequence as they completed more sequences ($p = .008$), see Figure 5. Once again, when I tested for multicollinearity in the initial model, I found no evidence for it (Sex, Tolerance = .59,

VIF = 1.69; Rank, Tolerance = .59, VIF = 1.69; Session, Tolerance = 1, VIF = 1).

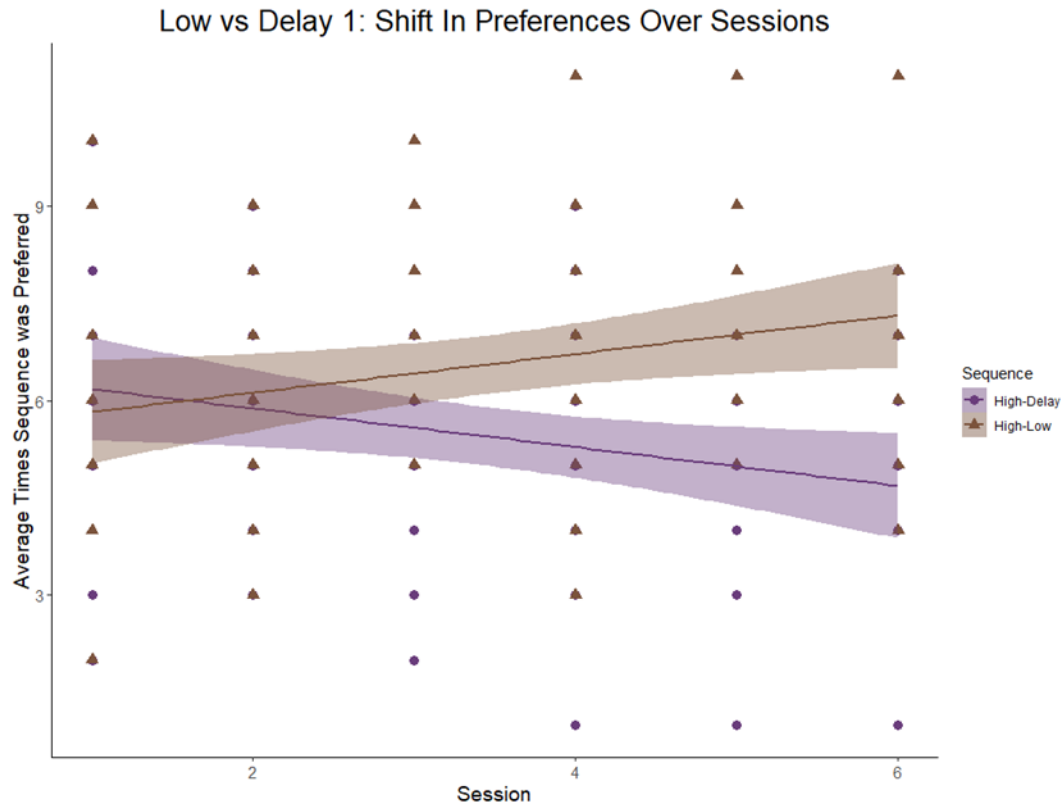


Figure 5: Individual changes in sequence preference across the low vs delay 1 condition. While initially there was not a clear preference between the sequences, as monkeys completed more sessions, they preferred a sequence with two rewards over just one.

3.3 Low vs Delay 2

Monkeys once again preferred ($t(128) = -3.24, p = .002$; Figure 3: bottom-left) a two-reward sequence (low-high) over one that gave only one high-value reward (delay-high).

However, neither regression model identified sex, rank, or session as contributing factors to their preferences.

3.4 Discounting

Lastly, capuchin monkeys repeated their baseline preference to receive a high-value reward sooner rather than later, and this time preferred ($t(105.90) = 10.74, p < .001$; Figure 3:

bottom right) a delay-high-low sequence over a delay-low-high one. Due to no high-ranking female having completed the final condition, I could not run a regression model with sex as a predicting variable. However, a model without sex ($\chi^2(3, N = 648) = 23.65, p < .001$) showed that as monkeys completed more sessions, they were more likely to prefer a higher reward sooner ($p < .001$; Figure 6). When I tested for multicollinearity in the first model, I once more found no evidence supporting overlap from variables (Sex, Tolerance = .43, VIF = 2.33; Rank, Tolerance = .43, VIF = 1.69; Session, Tolerance = 1, VIF = 1).

To measure the impact that delay discounting had on rank sequence preferences, I also compared baseline and discounting preferences for a higher sooner sequence. High-ranking monkeys switched their preference from a higher later (low-high) sequence in the baseline condition to receiving a higher sooner (delay-high-low) one in the discounting condition. This was a nearly 58% increase which was reflected by an almost 41% drop in preferences for saving the best for last. Both middle- and low-ranking monkeys maintain their higher sooner preferences from their baseline performance with both showing a roughly 27% and 6% increase for higher sooner sequences and a 31% and 18% decrease for saving the best for last, respectively (See Figure 7).

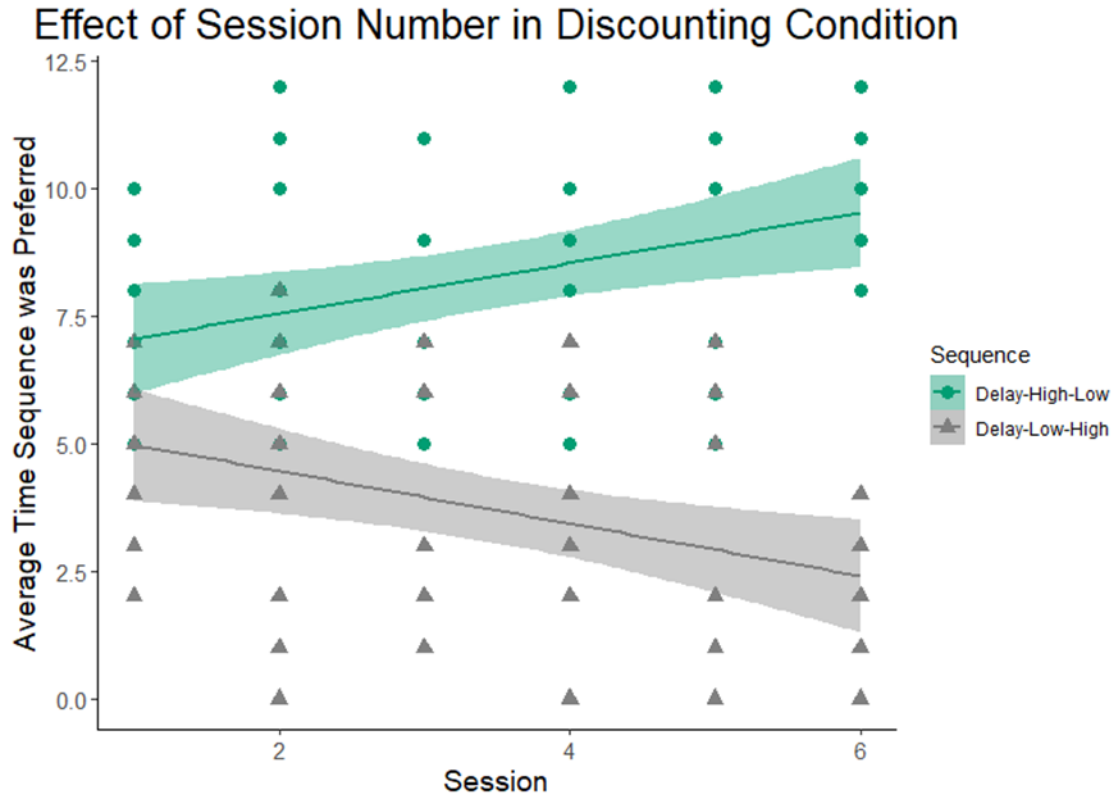


Figure 6: Individual changes in sequence preferences as sessions progress during the discounting condition. As the sessions progressed, the preference for a higher sooner sequence became greater.

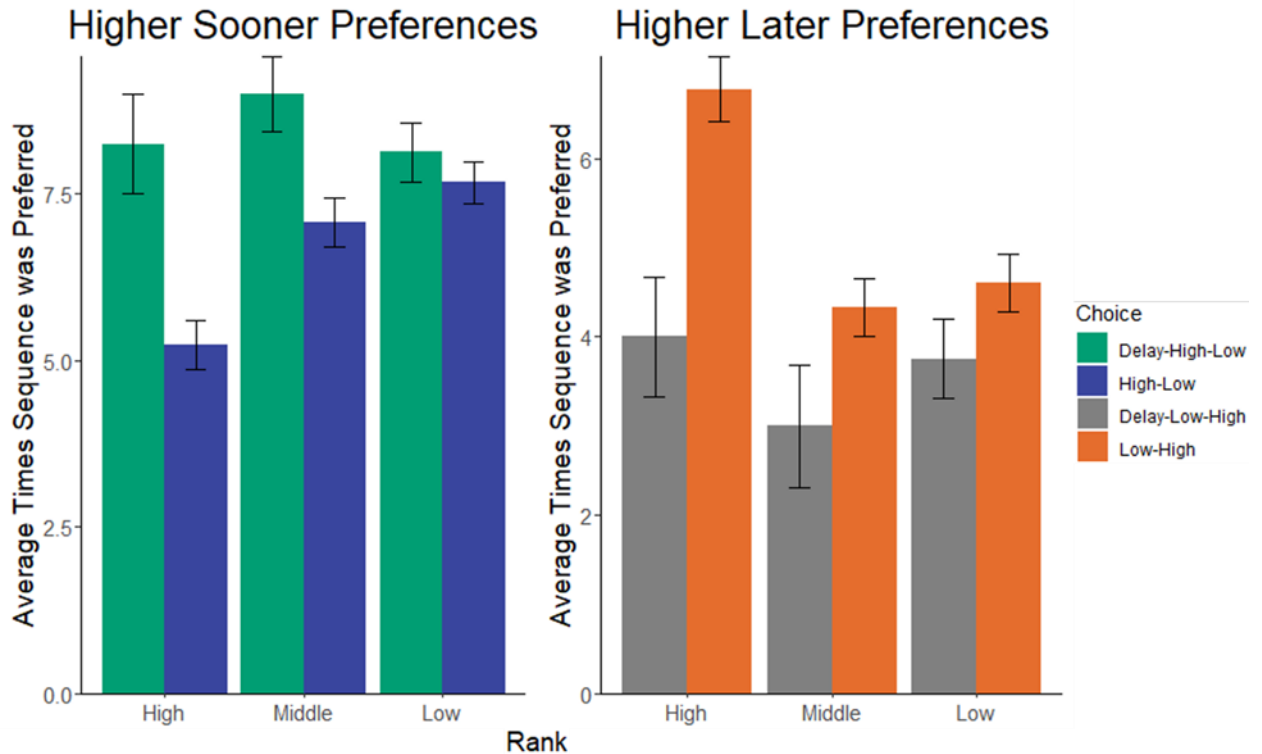


Figure 7: Average times either a higher sooner or higher later sequences was preferred during the baseline and discounting conditions. Notably, high-ranking monkeys switched their preference from the baseline condition where they preferred to receive a high-value reward at the end of the sequence. Error bars represent standard errors.

4 DISCUSSION

Cognitive biases can often underly human decision making, and one question that arises is to what degree these irrational preferences are the result of evolutionary pressures. To test this, I focused on the formation of sequence preferences and explored the peak-end effect in capuchin monkeys. Overall, most capuchin monkeys showed a start bias and did not save the best for last. Instead, they chose to consume higher-valued rewards sooner rather than later. Notably, their preferences seem to be most often influenced by their social standing and only sometimes by their familiarity with the reward sequences. Sex was never a predictor of preference, however, due to the small sample of males ($N = 2$, both high-ranking), I was unable to differentiate

between how much rank and sex account for the monkeys' behavior and am not completely confident that there would be no effect of sex in a larger sample. Therefore, while my results do suggest that monkeys form consistent preferences, the results do not support the peak-end effect as a cognitive shortcut found broadly among primates, but instead suggests it is either an adaptation seen in specific socioecological contexts or a more uniquely human feature.

Whereas only the baseline preferences of middle- and low-ranking monkeys reflected the findings by Xu et al. (2011), the results from the discounting condition showed that even high-ranking individuals preferred to receive the higher-value reward sooner when forced to endure a greater time delay (an almost 44% increase from their baseline preference, see Figure 7). By placing the grape cube later in the sequence, I was able to show the extent to which delay discounting can affect capuchin monkeys; while high-ranking individuals were willing to wait to receive a high-value reward last in the baseline condition, the initial 10 second delay in the discounting condition decreased the value of the grape cube so steeply that saving the best for last was no longer a favorable option. Additionally, I saw a steep incline in preferences for the delay-high-low sequence as monkeys completed more sessions, showing that the more familiar individuals became with the reward payouts, the less they chose to save the best for last. This roughly 41% increase in preference for a higher sooner sequence also supports previous meta-analysis negatively correlating life span and metabolic rates to intertemporal task performance in non-human primates and that shorter time spans affect non-humans primates more so than humans (Stevens, 2014; Vanderveldt et al., 2016).

Even though I observed a clear delay discounting effect, I was unable to define the within sequence value of the apple cube. While there was an overall preference for sequences with two rewards over one in both the low vs delay 1 and 2 conditions these preferences were so close to

chance that it was hard to determine a concrete value. However, in the low vs delay 1 condition, I determined that the longer monkeys were exposed to the reward sequences, the more they showed a preference for the high-low sequence. By the end of all the low vs delay 1 sessions, the monkeys showed an almost 19% increase preference for the high-low sequence compared to the first session. It could be that the monkeys initially displayed a selective value effect and did not care what came second in a sequence that rewarded them with a high-value food first. Instead, they eventually figured out the difference in payouts between their options and began to favor the high-low sequence over the high-delay one. However, it is unclear as to why this was not repeated for the low vs delay 2 condition, in which the high-value reward came second to either a time delay or a low-value one. One explanation for this could be that since the low-value reward and time delay came first in their respective sequences, the monkeys were forced to pay attention to their presence therefore increasing their saliency. This in turn meant that more sessions were not needed to adequately compare the sequences and determine a preference. Another explanation could be that by the time the monkeys started the low vs delay 2 condition, they had simply adjusted their preferences to reflect the missing second reward within the sequence (the time delay), as it was only just introduced in the previous low vs delay 1 condition. Therefore, the increase in preference for the high-low sequence could be the result of the monkeys learning that sequences can have either one or two food rewards, which is why I did not see this same effect in the later low vs delay 2 condition. Even with this change of preferences over sessions, I primarily saw that individual differences greatly affected monkey preferences due to the lack of consistent predictive power within the models or predicting variables. Similarly, Xu et al. (2011) also reported these inconsistencies during their versions of the two low vs delay conditions. This

hints that perhaps something different than sex and rank may be affecting their evaluation of the lower value parts of sequences.

Although I only tested two high-ranking males, the analysis showed no collinearity among the predicting variables of sex, rank, and session. Yet, the very small number of males, both of whom were the respective alpha males of their groups, does not fully rule out the possibility that sex and rank were effectively confounded. Studies with wild and semi-wild (free ranging with food subsidized) capuchin monkeys showed that high ranking-group members overall fed more than subordinates due to more often winning aggressive food-related bouts (Ferreira et al., 2006, 2008; Janson, 1985, 1988). Furthermore, an analysis of locomotion around food sources, foraging patterns, and dominance rankings showed that all high-rank individuals, and not just males, were also more readily able to meet their daily caloric intakes due to increased foraging and decreased locomotion times (Ferreira et al., 2008). These studies crucially made the distinction that access and aggression to food was primarily based on rank and age, rather than sex alone. However, one study previously reported 96% of wild female-female aggression to be food related (Izar, 2004), and both semi-wild and wild females to be less likely to form coalitions to defend feeding sites than males (Ferreira et al., 2008; Izar, 2004). These studies primarily suggest that sex is a secondary predictor of both access and consumption of food, therefore, it is unlikely that sex played a role in how capuchins broadly determine food preferences. What I saw instead was that rank and age were more likely contributing factors for food-related preferences since these more often determine its accessibility. This would also explain why in the baseline condition middle- and low-ranking monkeys preferred the high-low sequence in these studies, when they were momentarily separated from their higher-ranking group members. While this temporary separation provided them the access to high-value food

rewards, it might still be in their best interest to eat the higher reward sooner as normally they would be in danger of losing it to higher-ranking group members. In other words, saving the best for last is a bad strategy when access to a high-value reward is not guaranteed.

Largely, it seems that saving the best for last is a strategy only used by higher-ranking monkeys due to their increased accessibility to food, and even then not used all of the time. These results partially support Xu et al.'s (2011) conclusions, but contradict Blanchard et al. (2014) and Egan Brad et al.'s (2016) support of the peak-end effect as a broad primate cognitive shortcut. It could be that the similar methodology used by both Xu et al. (2011) and the present study resulted in both measuring something other than sequence preference and evaluations in non-human primates. However, Egan Brad et al. (2016) also reported large variability within their finding as only two out of four monkeys showed a peak and end bias. The lack of consistent results across and within studies hints that as of now there is no clear consensus on whether only humans show a peak-end effect or if it is a trait shared more broadly by primates. The inconsistencies also highlight the need for further exploration of how non-human primates develop sequence preferences and how they evaluate the individual components within a reward sequence, not to mention how social and biological factors affect sequence preferences and under which circumstances non-human primates might save the best for last.

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