

5-6-2014

Brown Capuchins (*Cebus apella*) Exhibit Self-Control On A Delay Of Gratification Food Exchange Task When Food Options Differ Qualitatively

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**Brown Capuchins (*Cebus apella*) Exhibit Self-control on a Delay of Gratification Food
Exchange Task when Food Options Differ Qualitatively**

by

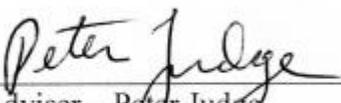
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A Proposal Submitted to the Honors Council

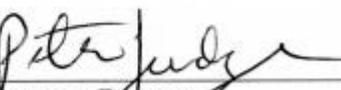
For Honors in Animal Behavior

May, 6, 2014

Approved by:



Adviser – Peter Judge



Program Director

Abstract

Self-control allows an individual to obtain a more preferred outcome by forgoing an immediate interest. Self-control is an advanced cognitive process because it involves the ability to weigh the costs and benefits of impulsive versus restrained behavior, determine the consequences of such behavior, and make decisions based on the most advantageous course of action. Self-control has been thoroughly explored in Old World primates, but less so in New World monkeys. There are many ways to test self-control abilities in non-human primates, including exchange tasks in which an animal must forgo an immediate, less preferred reward to receive a delayed, more preferred reward. I examined the self-control abilities of six capuchin monkeys using a task in which a monkey was given a less preferred food and was required to wait a delay interval to trade the fully intact less preferred food for a qualitatively higher, more preferred food. Partially eaten pieces of the less preferred food were not rewarded, and delay intervals increased on an individual basis based on performance. All six monkeys were successful in inhibiting impulsivity and trading a less preferred food for a more preferred food at the end of a delay interval. The maximum duration each subject postponed gratification instead of responding impulsively was considered their delay tolerance. This study was the first to show that monkeys could inhibit impulsivity in a delay of gratification food exchange task in which the immediate and delayed food options differed qualitatively and a partially eaten less preferred food was not rewarded with the more preferred food at the end of a delay interval. These results show that New World monkeys possess advanced cognitive abilities similar to those of Old World primates.

Introduction

Self-control and its opposite, impulsivity, are two cognitive processes commonly attributed to humans. Self-control is advantageous when it allows an individual to obtain a more preferred long term outcome by forsaking immediate interests (Beran & Evans, 2012). The ability to exhibit self-control to achieve future interests is considered an outcome of advanced cognition (Tobin, Logue, Chelonis, Ackerman, & May, 1996). Advanced cognitive processes can be classified as executive functions, which include cognitive processes such as reasoning, problem solving, response inhibition, and planning. Self-control is in this class of cognitive abilities as it includes weighing the costs and benefits of impulsive versus controlled behavior, determining risk or consequences of such behavior, and making decisions based on the most advantageous course of action. Choosing the most advantageous response also implies plasticity in behavior; for example, the ability to make quality and quantity judgments and decide the corresponding worth of inhibiting impulsivity to wait for the choice assigned the higher value.

Goal directed planning and using future interests to guide current behavior are not traits unique to humans (Evans, Beran, Paglieri, & Addessi, 2012). Many non-human primates also exhibit self-control, and apes and monkeys seem to have precursors to advanced executive functions that are also necessary to exhibit self-control (Tobin et al., 1996). This is not surprising considering the importance of the prefrontal cortex in controlling these processes in humans, and the neurological and phylogenetic similarities between human and non-human primates (Phillips & Sherwood, 2007 as cited in Addessi, Paglieri, & Focaroli, 2011; Tobin et al., 1996). The social intelligence hypothesis suggests that non-human primates may have evolved self-control along with the advanced cognitive abilities that allow for such behavior due to their ecology and social organization (Pelé, Dufour, Micheletta & Thierry, 2010). Although impulsivity is potentially

beneficial under particular circumstances such as when resources are limited, it is advantageous to exhibit self-control in the wild in instances where foregoing an immediate reward leads to a delayed but more preferred reward. Some examples include an animal waiting for fruit to ripen, a predator waiting to attack prey, a subordinate individual waiting to obtain food to avoid conflict, or an individual waiting for an optimal mating opportunity to arise.

The self-control abilities of Old World primates have been extensively researched and some studies have also explored this ability in New World monkeys (chimpanzees, *Pan troglodytes*: Beran & Evans 2006, 2009, 2012; Dufour, Pelé, Sterck, & Thierry, 2007; Evans et al., 2012; rhesus macaques, *Macaca mulatta*: Szalda-Petree, Craft, Martin, & Deditius-Island, 2004; tonkean macaques, *Macaca tonkeana*: Pelé, Micheletta, Uhlrich, Thierry, & Dufour, 2011; long-tailed macaques, *Macaca fascicularis*: Pelé et al., 2010; Tobin et al., 1996; brown capuchin monkeys, *Cebus apella*: Addressi et al., 2011; Bramlett, Perdue, Evans, & Beran, 2012; Drapier, Chauvin, Dufour, Uhlrich, & Thierry, 2005; Paglieri, Focaroli, Bramlett, Tierno, McIntyre, Addressi, Evans, & Beran, 2013; Ramseyer, Pelé, Dufour, Chauvin, & Thierry, 2006; Westergaard, Liv, Rocca, Cleveland, & Suomi, 2004). The capacity to inhibit impulsivity differs both between and within species. Inhibition of impulsivity is considered an enhanced cognitive skill, so showing self-control abilities in New World monkeys implies the presence of advanced cognitive abilities that correspond to self-control behavior in Old World primates and humans. Since Old World primates, especially chimpanzees, have shown high capacities for self-control, it is important to determine if New World monkeys have similar capacities and to determine the phylogenetic roots of self-control abilities. It is also important to determine the differences in delay tolerance between and within species to elucidate how different species and different individuals value certain items and what may cause this value to decrease over time. For

example, if feeding ecology plays a major role in self-control abilities, species that eat fruit and must wait for it to ripen may highly value an item at longer waiting periods compared with a species that eats insects and relies on impulsivity to catch their prey and may value an item less at longer waiting periods.

Delay of gratification tasks in which a subject must forego an immediately available reward in order to receive a delayed but more preferred reward are utilized most often to test the capacity for self-control. It is important to note that true self-control has two components. Inhibiting impulsivity to take the immediate reward is the first step, and the second step is maintaining this initial choice while waiting a delay period in its entirety before receiving the more preferred option. Measures of true self-control include an option to change a decision during the delay after choosing to forego an immediately available option (Paglieri et al., 2013). For this reason, procedures involving delay of gratification tasks are optimal because they involve the availability of the immediate reward throughout the entire session, requiring continuous inhibition of impulsivity for the duration of the delay.

A common method to study self-control is an accumulation task (Anderson, Kuroshima, & Fujita, 2010; Beran & Evans, 2006, 2009; Evans & Beran, 2007; Evans et al., 2012; Paglieri et al., 2013; Pelé et al., 2010). In general, food items are piled up one by one in front of the animal with a certain delay period between the placement of each item, and the subject must refrain from reaching toward the pile. The amount of reward subjects receive depends on how long they wait to reach toward the pile, and the longer the subject waits to reach toward the pile, the more rewards accumulate. The moment the subject reaches for the pile, accumulation stops and the subject only receives the amount that has accumulated. Delaying gratification for the entire trial allows for maximum payoff of obtaining the largest reward possible and maximally inhibiting

impulsivity. Accumulation studies with chimpanzees show their capability to refrain from impulsive behavior to receive a more preferred outcome in the future (Beran & Evans 2006, 2009; Evans & Beran, 2007; Evans et al., 2012; Pelé et al., 2010). Chimpanzees can wait up to 11 minutes to receive all possible food items in an accumulation task, indicating longer delay maintenance of Old World primates (Beran & Evans, 2006), especially when compared with capuchin monkeys (Anderson et al., 2010; Evans et al., 2012; Paglieri et al., 2013) that can wait up to 10 seconds to receive all possible food items in an accumulation task (Evans et al., 2012).

Prior research has also explored self-control abilities by utilizing exchange tasks (Beran & Evans 2012; Drapier et al., 2005; Dufour et al., 2007; Pelé et al., 2010). Chimpanzees delay gratification when food options differ quantitatively, in which they forgo a smaller reward to receive a larger reward after a delay period ranging from a few seconds to four minutes (Dufour et al., 2007). Chimpanzees are able to interpret the size of the reward and the delay period and decide whether the reward is worth waiting the delay. Exchange tasks have also been used to study self-control in New World primates. Drapier et al. (2005) performed both quantitative and qualitative food exchange tasks with brown capuchins and found that capuchins were capable of comparing foods and traded a less preferred item for a more preferred item.

Delay maintenance tasks involve a choice between an immediate or delayed reward, and show the abilities of New World primates to postpone gratification when options differ quantitatively. Cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*) forgo two food pellets to receive six food pellets after a short delay, with marmosets waiting significantly longer delays than tamarins to receive the delayed greater quantity food reward (Stevens, Hallinan, & Hauser, 2005). Capuchins show higher delay tolerance than marmosets and tamarins, and will forgo two pieces of peanut to receive six pieces of peanut after

delays ranging from 40-145 seconds (Addessi et al., 2011). Brown capuchins will also wait at least 10 seconds to trade a smaller piece of cookie for a larger piece, and individuals exhibit longer delay capabilities such as 20 and 40 seconds based on the costs and benefits attributed to delay time versus reward size (Pelé et al., 2011). Capuchins are able to anticipate delay duration and determine whether or not to wait for the more preferred reward, and waiting duration increases with increasing reward size based on individual differences in the capacity to wait. Ramseyer et al. (2006) also tested the waiting abilities of capuchins when food choices differed quantitatively. All six subjects succeeded in waiting for the larger reward with a 5-second delay, and five subjects succeeded in waiting for the larger reward with a 10-second delay. However, when three subjects were tested with a 20-second delay, they only had about 25% success in waiting for the larger reward.

Since New World primates have shown high mental capacities and the ability to determine quantitative differences between items through accumulation, delay maintenance, and exchange tasks, it is important to further explore the ability to determine qualitative differences of items. In nature, it may be optimal to differentiate qualitative differences of food items in order to make strategic decisions in a constantly changing environment (Addessi, Mancini, Crescimbene, Ariely, & Visalberghi, 2010). Token exchange tasks reveal that monkeys do differentiate between items and develop preferences. When chimpanzees had the choice to eat an immediate food or select a token that could be exchanged later for a more preferred food, they chose the token option that led to the more preferred reward, even when the delay between exchanging a token and receiving food was three minutes (Beran & Evans 2012). When monkeys are required to trade back a token representing a food item that is available for exchange, they instead trade back a token that represents a more preferred food that is not

available for exchange (Brosnan & de Waal, 2004). They learn the relationships between each token and its corresponding reward, but may not exchange unless it is the more preferred reward that they can receive. Judge and Essler (2013) also explored self-control abilities in capuchin monkeys using a token exchange task. They found that when given a choice between a piece of food or a token that could be exchanged for a more preferred food, two of seven capuchin monkeys significantly chose the token that could be traded for the more preferred food instead of the immediate food option. Since token exchange tasks show monkeys are capable of attributing values, exchange tasks in general are a reliable way to test behavior using items of differing value, and monkeys should be able to exhibit self-control in exchange tests in which items differ qualitatively. Westergaard et al. (2004) showed that tufted capuchins were able to attribute values to food and tool items depending on the circumstances. The subjects had the choice to exchange a less preferred food for a more preferred food or for a metal bolt tool that could be used in a baited probing apparatus to extract syrup, an even higher preferred food. The preference of each exchange option changed based on whether the probing apparatus was baited with syrup. When a probing apparatus was baited with the most preferred food, the subjects assigned a higher preference to the probing tool option than the immediate food option. However, when the probing apparatus was not baited, the subjects assigned a higher preference to the immediately available more preferred food item than to the probing tool. This was the first time New World monkeys showed the capability to assess an object's value based on their current circumstances and make a decision to perform an exchange or not.

Some prior studies have explored self-control in New World primates utilizing delay of gratification in which barter choices differ qualitatively and have found various delay maintenance abilities (Bramlett et al., 2012; Drapier et al., 2005; Evans & Westergaard, 2006;

Ramseyer et al., 2006, Westergaard et al., 2004). For example, in Ramseyer et al. (2006), a capuchin had to hold a certain food item for a fixed duration of time, and then had the opportunity to exchange it with an experimenter for a more desired reward. Multiple experiments were carried out with the same subjects, including both qualitative and quantitative food exchanges. When foods differed in quality and partially nibbled items were accepted, subjects returned a less preferred food for a more preferred food at above 50% success rate when required to wait a delay of 10, 20, 40 and 80 seconds. However, accepting a partially eaten less preferred food item at the end of a delay period as a self-control response might not accurately reflect true self-control. When foods differed in quality and partially nibbled items were not accepted, three subjects did not succeed in the task and the other three subjects returned the less preferred food for the more preferred food at high success rates when required to wait a delay of 2, 5, and 10 seconds. Additionally, the less preferred food presented was monkey diet pellets which were available ad lib before the experiments began, which could bias the monkey's decision to prefer the alternative option. Experimenters also set fixed waiting durations (i.e. 2, 5, 10, 20, 40, and 80 seconds) which may not have adequately reflected natural abilities because they were previously assigned without taking individual differences in delay tolerance into consideration. To my knowledge, this was the only study that utilized a delay of gratification food exchange task in New World monkeys in which the food options differed qualitatively.

The purpose of the present study was to replicate the Ramseyer et al. (2006) study, but modify the procedures to provide a better test of self-control. In my design, brown capuchins were given a less preferred food and had to exchange it in its entirety to receive a qualitatively more preferred food in order to demonstrate their self-control capacity. Briefly, a subject was given a less preferred food item, required to wait a delay period, and then allowed the

opportunity to exchange the less preferred food for a more preferred food. Rather than use specific delay intervals as in Ramseyer et al. (2006), I increased duration of delay by one second on an individual basis when a subject successfully waited the duration of the current interval. The maximum duration of time a subject postponed gratification was considered their delay tolerance. I hypothesized that brown capuchins would trade back a less preferred food item for a qualitatively different more preferred food item after waiting a specific delay period. Based on previous studies, I predicted the capuchins would show some sort of waiting time, and if they did wait there would be individual variations in waiting time.

Prior research with chimpanzees has shown that distraction aids in inhibiting impulsivity and increasing delay tolerances (Beran & Evans, 2009; Evans & Beran, 2007). In an accumulation study, Evans and Beran (2007) presented the first experimental evidence that chimpanzees could cope with delayed gratification by utilizing certain strategies, such as playing with a toy, while allowing a greater amount of food to accumulate. In this study, a subject's self-control capability was directly related to their level of self distraction, indicating subjects purposely distracted themselves to avert their attention away from the accumulating reward and increase their delay maintenance ability. Chimpanzees also utilized a computer task as a distractor when the task was not required to receive the reward, possibly promoting greater self-control (Beran & Evans, 2009). The use of a distractor to enhance self-control abilities has never been shown in monkeys, and such a result would indicate behavioral and cognitive similarities with Old World primates in ability and strategy to prevent impulsive decisions. I hypothesized a distractor object would also allow delay tolerance to increase in New World monkeys. I predicted that introducing a metal clip to manipulate as a distraction during the waiting period would increase delay tolerance further than the delay tolerance reached without the clip present.

My study was the first to explore self-control abilities in capuchin monkeys utilizing a delay of gratification food exchange task in which the food options differed qualitatively and the delay period depended on individual progress in incremental delays, which accurately represented each individual's threshold. Not rewarding a returned partially eaten food item allowed for a more accurate representation of true self-control, and accurate delay measures based on individual progress allowed for more refined phylogenetic comparisons of capuchin delay tolerance to delay tolerances of other New World and Old World primate species.

Method

Subjects and Housing

The subjects were six tufted capuchin monkeys living in a socially housed colony of 17 monkeys in the Animal Behavior Laboratory at Bucknell University, Lewisburg, Pennsylvania. The colony was established in 2000 with six capuchins, and all other individuals were born and raised in the colony. The six individuals were chosen for testing because they previously experienced food and token exchange tasks with an experimenter, and exhibited differential food preferences. Subjects did not have prior experience with any type of delay task. Subjects included one adult male (DaVinci), and five adult females (DeAngela, Newton, Niko, Socrates, and Shroeder).

All monkeys were housed in an indoor enclosure consisting of plastic paneling, stainless steel wire caging, and multiple perches, shelves, and climbing structures to encourage natural movement. The entire enclosure contained 17 interconnecting compartments connected by doorways that the monkeys could freely move between, and the doorways could be closed off from outside the enclosure to separate monkeys for testing. Overhead tunnels also connected some compartments, and these could also be closed off with a divider to separate animals. Floors

of the enclosure were covered with wood shavings. Water was available ad libitum by means of water bottles throughout the caging, and enrichment items were continuously available.

Capuchins were fed in the morning and afternoon on a diet consisting of monkey biscuits and various fruits, vegetables, cereals, and other preferred foods. The project complied with Bucknell University IACUC guidelines and all USDA requirements.

Procedure

Testing sessions occurred once a day 4-6 times a week, with four subjects tested from October-December 2013 and two subjects tested from January-May 2014. The study consisted of a delay of gratification food exchange task in which a subject was given a lower-value food that could be exchanged for a size-matched higher-value food after a delay period. Based on previously established food preferences, a piece of cucumber was used as the less preferred food offered as the immediate reward for all six subjects, and a raisin was used as the more preferred food offered for exchange after the delay period for five subjects. Newton received a piece of banana chip as the more preferred food.

Each individual was isolated into one of the subcompartments in the indoor enclosure for a single session per day consisting of 10 trials per session. The subcompartment contained two closed off, interconnecting doorways that provided shelves on which the monkeys could jump. There were perches in the front and back of the compartment, and subjects were tested on the perch 1.13 m from the ground and 29 cm from the caging. The experimenter stood 28 cm from the caging. The first session was a control session in which there was no delay. The subject was offered the cucumber as the less preferred food, immediately followed by the opportunity to exchange it for the raisin or banana chip as the more preferred food. The signal of the opportunity for an exchange was the experimenter opening her right hand with palm facing up in

front of the testing compartment, giving the monkey an opportunity to place the cucumber in the experimenter's hand and exchange it for the more preferred food which was visible in her left hand approximately 28 cm from the cage. Subsequent sessions incorporated a delay, beginning with one second and increasing by one second on an individual basis when a subject's session contained at least nine out of 10 successful delay trials. The one second increment advance was utilized rather than longer intervals used in previous studies because the subjects were not experienced with delay maintenance tasks and increasing by smaller increments should more accurately assess individual variation in and the limits on self-control ability.

For each trial of the delay sessions, the experimenter stood in front of the testing compartment and held up a raisin or banana chip in her left hand and a piece of cucumber in her right hand. She offered the cucumber to the subject, closed her right hand for the length of the delay, then presented her right hand with palm facing up in front of the cage signifying an opportunity to trade. During the delay and the opportunity to trade, the more preferred food was still visible in the experimenter's left hand approximately 28 cm from the cage. If, after the delay, the subject traded back the entire cucumber piece without consuming any of it, the experimenter offered the subject the more preferred food. If, after the delay, the subject traded back a partial piece of cucumber or did not have anything left to trade when the experimenter offered her right hand, the experimenter did not offer the subject the more preferred food and stepped back from the cage. The experimenter did not reward partially eaten cucumber pieces because nibbling may not accurately represent self-control. All subsequent trials after the first began when the subject either finished consuming the more preferred food item, or approximately 10 seconds after the opportunity to trade was offered but the subject did not receive the more preferred food item. The outcome of each trial was classified into five

categories depending on whether the monkey ate portions of the less preferred food or returned the less preferred food (see Table 1). Subsequent sessions increased by one second on an individual basis when a subject's current session contained at least nine out of 10 successful delay trials. Sessions were video recorded for future reference.

When a subject remained at the same delay length without advancing for 10 consecutive sessions (100 trials), testing continued with a distractor object available to determine if the chance to occupy themselves with an object would aid in advancing to the next delay period and in increasing the individual's delay tolerance. At the beginning of each session, a familiar metal clip (Figure 1), which the monkeys have manipulated in the past, was hooked onto the cage approximately 29 cm from the perch and 1.15 m from the ground, and remained there for all 10 trials. The rest of the session was carried out exactly as before the distractor was introduced, as described above. When a subject remained at the same delay length without advancing for 10 consecutive sessions (100 trials) with the distractor present, testing ended for that subject.

Data Analysis

Subjects advanced by one second every time they achieved 90% or higher success in one session because nine out of 10 is statistically significant according to a binomial distribution ($p < .05$, two tail). Therefore, statistically significant self-control levels were determined by the longest waiting duration in which this criteria was achieved, both without and with the distractor available.

Results

All six subjects reached a maximum delay length for which they exchanged a lower preference food for a higher preference food and exhibited self-control, followed by 10 sessions (100 trials) in which four of the six subjects did not inhibit impulsivity at the next higher delay

time and therefore did not continue with this part of the study. Each of these four subjects then experienced at least 10 sessions (100 trials) during which they were given the opportunity to play with a distractor object in an attempt to encourage self-control at the next higher delay length at which they did not receive at least nine out of 10 Success (SCS) trials in any of 10 sessions without the distractor. Since self-control was exhibited up until the 10 sessions in which subjects acted impulsively without a distractor, a summary of performance percentages up until these 10 sessions can be found in Table 2. Information from the 10 sessions (100 trials) four of the six subjects remained at the same delay without exhibiting self-control and advancing to a greater delay tolerance, as well as information from the sessions involving the distractor was not included in Table 2 due to lack of self-control during these sessions. As of this writing, two subjects had not reached a threshold delay tolerance, so the maximum delay they reached by the end of this study was included in Table 2 as well as information from all of the trials which they experienced. Subjects also varied in the number of sessions required to achieve at least nine out of 10 successful trials and advance to the next delay period (Figure 2). Due to variability in performance across subjects, a general behavioral profile was summarized separately for each individual.

During his delay periods, DaVinci was the least mobile of all subjects. He simply sat on the perch holding the cucumber and waited for the delay to pass and the opportunity to trade. When he ceased inhibiting impulsivity after reaching his maximum 6-second delay tolerance, he almost always ate the cucumber right away, sometimes even attempting to take it from my hand with his mouth. He often jumped to the shelf in one of the interconnecting doorways after eating the cucumber, and seemingly did not pay attention when I offered to trade. On occasions when he dropped the cucumber it seemed as though he did so on purpose. During the 10 sessions with

the distractor, DaVinci mainly ignored the distractor. He occasionally touched it, but more often exhibited the same behavior patterns as when he acted impulsively without a distractor present in which he ate the cucumber right away and then jumped to the shelf in the doorway. He ate the cucumber on almost all 100 trials during which he ceased inhibiting impulsivity and did not advance to the next delay, yet throughout the experiment he was the least likely to nibble and only nibbled on four trials of the 240 trials without the distractor and on zero of the trials with the distractor. On two separate occasions when he ceased inhibiting impulsivity, I offered the opportunity to trade right away without a delay, and both times DaVinci ate the cucumber right away and ignored the raisin.

During a trial, DeAngela repeatedly moved back and forth on the vertical caging in an “S” pattern in which she would grab the cage upward to the right with her right hand and swivel her head towards that hand at the same time and then repeat this motion downward to the left while waiting the delay. Occasionally she remained motionless on the perch staring at something that was possibly distracting her. When she ceased inhibiting impulsivity after reaching her maximum 7-second delay tolerance, she mainly either responded with Nibble (NBL), or jumped to the shelf in one of the interconnecting doorways and ate the cucumber while not paying attention to my offer to trade. Sometimes she motioned to trade a nibbled piece, but took one last bite before actually trading it back to me. Other times she still had a piece of nibbled cucumber left when I offered to trade but continued to eat the entire cucumber rather than trade back the uneaten portion. She was also the most likely to throw the cucumber at me during the delay period. During the 10 sessions with the distractor, DeAngela played with it often before, during, and after the delay period. However, she still ate the cucumber right away, or took it to the shelf in the doorway to eat as before. On 94 of 100 trials during which the distractor was present,

DeAngela ate the cucumber. On two separate occasions when she ceased inhibiting impulsivity I offered the opportunity to trade right away without a delay, and she responded with NBL for one of them indicating she still knew she was supposed to trade the cucumber back, but EAT for the other opportunity.

While holding onto the cucumber and waiting the delay period, Socrates put her face right up to the caging and held onto the caging with both hands and one leg, with the other leg stretched back to the perch. She repeatedly reached for the raisin before taking the cucumber from my hand. Occasionally she behaved similarly to DeAngela in moving back and forth, and other times she behaved similarly to Newton (mentioned below) in reaching her hand holding the cucumber all the way out of the cage. Interestingly, Socrates smelled the cucumber often while waiting. When she ceased inhibiting impulsivity after reaching her maximum 9-second delay tolerance, she often banged the cucumber against a surface such as the wall, cage, perch, or even her own hand, and then ate the cucumber. Almost half of her impulsive trials were NBL. While acting impulsively, she often assumed the same position as when she was inhibiting impulsivity, but ate the cucumber instead of holding on to it and waiting. As before, she repeatedly reached for the raisin before taking the cucumber as well as after eating it. Socrates was the only monkey to increase delay tolerance by one second after the distractor was introduced therefore experiencing 12 sessions (120 trials) with the distractor rather than 10 sessions (100 trials), but did not interact with the distractor during the session that allowed her to advance to the next delay duration. In general, she only occasionally interacted with or smelled the distractor before eating the cucumber and between trials, but did not utilize it to increase delay tolerance further. On the two separate occasions when she was acting impulsively I offered the opportunity to trade

right away without a delay, and she responded with EAT both times, the second of which she motioned as if she was going to trade but then ate the cucumber instead.

Once given the cucumber, Newton would immediately stick her arm holding the cucumber as far out of the cage as possible while waiting. Sometimes she walked back and forth on the perch sticking her arm through random openings in the caging. She occasionally placed the cucumber into an opening in the perch and she would not have to hold it while waiting. When she ceased inhibiting impulsivity after reaching her maximum 13-second delay tolerance, she regularly took the cucumber and immediately jumped away with it, sometimes not even looking back at me when I offered to trade. She also periodically waited to start eating the cucumber and ate it slowly or only ate half and dropped the rest. She still reached for the banana chip after eating the cucumber indicating interest, and hit my hand when I offered to trade but she had nothing to exchange. During the 10 sessions with the distractor, Newton played with it during and after eating the cucumber, and played with the distractor the most out of all four monkeys that experienced sessions with the distractor. However, she continued to eat the cucumber despite manipulating the distractor clip and never advanced to the next delay period. On two separate occasions when she was acting impulsively I offered the opportunity to trade right away without a delay, and she responded with SCS both times.

Schroeder and Niko had the highest delay tolerance of all monkeys with 35 and 30 seconds, respectively, and did not reach a period of ceasing inhibition of impulsivity or criteria to introduce a distractor for the duration of the experiment. They both often required more than one session to advance to the next delay length. Schroeder and Niko both responded with NBL often, with Niko nibbling the most out of all six subjects. Niko put the cucumber in her mouth on the majority of trials, but did not eat it. Niko walked back and forth on the perch while waiting the

delay and appeared to be very aware of what was going on around her and regularly looked all around. Often during the trials Niko ate the cucumber, she attempted to trade something else that she retrieved from the floor of the compartment. Schroeder was similar to Socrates in grabbing the caging with all four limbs and tail and in banging the cucumber on the wall when she ate it, and to Newton in sticking her arm out as far as possible. Schroeder was unique in that she put her head to the cage and bit it, and also took the cucumber while hanging upside down on the caging. Frequently, when Schroeder ate the cucumber she had the opportunity to trade part of it but chose to continue eating instead. Interestingly, when she traded me back the cucumber she was hesitant and placed it in my hand very slowly. Because she was doing well and the project was ending, when Schroeder was successful at a 30 second delay, I increased the delay interval by five seconds.

Discussion

The results support my hypothesis that brown capuchins will trade back a less preferred food item for a qualitatively different more preferred food item after waiting a delay period, and these results were comparable with previous studies. All monkeys showed some degree of self-control and refrained from eating the less preferred food. The maximum delay tolerance reached was the maximum duration of time a subject postponed gratification instead of responding impulsively. The highest tolerances should be considered with caution because on some trials it seemed as if the animal would have waited longer if I had not given them an opportunity to trade at the scheduled exchange time. For example, on some trials, it seemed as though DaVinci would have continued sitting still, DeAngela would have continued moving back and forth in her “S” pattern, Socrates would have continued holding onto the cage or sticking her arm out, and Newton would have continued holding her arm out of the cage, had I waited longer than their

individual delay length to present the opportunity to trade. It is interesting that most subjects exhibited the same behavior when acting impulsivity as they did when exhibiting self-control, such as moving back and forth or sticking their arm out of the caging. Responding with the same behaviors but without reaching criteria to increase to the next delay length further evidenced that the subjects knew what inhibiting impulsivity entailed but no longer wanted to participate in waiting a delay. This was made even clearer by the fact that while or after eating the cucumber, most of the monkeys jumped to the shelf in one of the interconnecting doorways and did not pay attention to my offer to trade. Lack of completing the exchange task is what ultimately determined the delay tolerances for the four subjects who reached criteria to cease testing. Perhaps in the wild the more often an organism must forgo an immediate reward for a delayed reward the less likely they are to continue doing so. This may also represent temporal discounting in which the expectations of receiving a reward decrease the longer an individual must wait to receive the reward, and as the expectation of receiving the reward decreases the value of the reward itself decreases. Pelé et al. (2011) also described similar temporal discounting with subjects' self-control responses over time. Newton had a high percentage of successful trials overall. It is interesting to note that of the six individuals tested, Newton was the lowest ranking. Lower ranking individuals may have to inhibit impulsivity longer or more often than higher ranking individuals in situations such as obtaining food or mates in order to avoid conflict. In nature it is advantageous for subordinates to decide how long it is worth waiting for a feeding or mating opportunity to avoid aggressive interactions with higher-ranking individuals (Evans et al., 2012; Pelé et al., 2010). However, there did not seem to be a strong rank effect based on the performances of the other subjects.

Shroeder and Niko did not reach a maximum delay tolerance and instead continued to exhibit self-control throughout the experiment. The delay tolerances they obtained by the end of the study provide excellent evidence of the advanced self-control abilities of capuchin monkeys, as well as evidence of the advanced cognitive abilities required to exhibit self-control.

Other research also found variability in species and individual waiting capacities (Anderson et al., 2010; Drapier et al., 2005; Paglieri et al., 2013; Ramseyer et al., 2006; Stevens et al., Hauser 2005). Capuchins waited 10 seconds for maximum reward in an accumulation task (Evans et al., 2012), 5, 10, and 15 seconds for a more preferred reward on a revolving disc (Bramlett et al., 2012), and at least 10 seconds with some waiting 20 and 40 seconds in a quantitative food exchange task (Pelé et al., 2011). To my knowledge, Ramseyer et al. (2006) is the only other study that tested delay tolerances of capuchin monkeys using an exchange task in which foods differed qualitatively. When nibbling was accepted, all six subjects had high return percentages when required to wait 10, 20, 40, and 80 seconds, though return percentage decreased as delay duration increased. However, when nibbling was not accepted, three of six subjects did not succeed in the task and the other three subjects returned the less preferred food for the more preferred food at high success rates of 90.3, 88.9, and 60.4 percent when required to wait a delay of 2, 5, or 10 seconds, respectively (Ramseyer et al., 2006). In the current study, I did not accept nibbling from the beginning and all six of my subjects had high success rates, with three of my subjects surpassing these previous findings. Therefore, the maximum delay tolerances in the current study as represented in Table 2 are comparable with prior studies, as well as exceed some of these prior tolerances by using a different methodology to test self-control capacities. My subjects were also comparable to long-tailed macaques that wait 20 to 80 seconds in a quantitative food exchange task (Pelé et al., 2010), to rhesus macaques that wait six

seconds for a delayed reward (Szalda-Petree et al., 2004), and to tonkean macaques that wait 20 to 80 seconds in a quantitative food exchange task depending on delayed reward size (Pelé et al., 2011).

The individual patterns of behavior exhibited during the waiting period represented individual mechanisms for inhibiting impulsivity and exhibiting self-control. Moving around or looking around could have been a means of keeping oneself busy while waiting the delay. Holding the cucumber as far out of the cage as possible may have been a means of keeping the temptation at a distance and showing readiness and willingness to exchange it for the more preferred reward. Placing the cucumber somewhere other than their hands such as an opening in the perch or their mouth may have been a strategy to avoid eating the cucumber by hiding it. This may not seem as logical for the act of putting the cucumber in their mouth because there it is more easily accessible than in their hand, but this was a common behavior and has been shown in other studies as well (Drapier et al., 2005). Smelling and banging the cucumber against surfaces as Socrates did, or hanging upside down from the caging as Schroeder did may be other forms of self-distraction to endure the delay. A very interesting behavior was that Schroeder was very hesitant to place the cucumber in my hand, as if she was not sure she would receive the raisin if she chose to give up the cucumber. This behavior may have been evidence of decision making, risk taking, and weighing the costs and benefits of giving up an immediate reward.

Although exchanging a nibbled piece of cucumber did not lead to the more preferred reward, all subjects responded with NBL at least sometimes, some subjects much more often than others (Table 2). Nibbling the less preferred food but still trading it back in an attempt to receive the more preferred food could represent a way to maximize gains. The subject may have known they must trade the cucumber to receive the more preferred reward, but took a bite of the

cucumber first so they consume as much food as possible. This explanation was further supported by the trials in which a subject was about to trade a nibbled piece of cucumber, but took another bite before exchanging the smallest piece possible. Drapier et al. (2005) performed a food exchange task with brown capuchins and found that the majority of subjects nibbled the food item before exchanging. When nibbled pieces were no longer accepted, four of six subjects ceased to exchange. Individuals may maximize gains by nibbling and returning the smallest possible piece, when nibbled pieces are acceptable for exchange (Drapier et al., 2005).

It is also possible both NBL and EAT responses occurred as a means of occupying themselves rather than because the subject actually desired to consume the less preferred food. For example, Newton sometimes waited to start eating the cucumber and ate it slowly, or only ate half and dropped the rest, as if she was only eating it because she was occupying herself while waiting the delay.

Other impulsive responses seemed to occur out of frustration. For example, purposely dropping the cucumber or throwing it at me implied a subject no longer wished to hold onto the cucumber and endure the delay. Hitting my hand when I offered the opportunity to trade but the subject had nothing left to trade also implied frustration with the task and with not receiving the more preferred reward, as evidenced by reaching for the more preferred option after hitting my hand. Not trading a nibbled piece of cucumber when the opportunity to trade arose and instead continuing to eat it could also be an act of frustration with waiting the delay. In addition to frustration, the monkeys often seemed anxious. Moving around a lot while waiting the delay as DeAngela, Socrates, and Niko did, scratching often as DaVinci and Niko did, or continuously sticking their arm out of the cage as Socrates, Newton, and Schroeder did all represent behaviors that may occur due to anxiety (Maestriperi, Schino, Aureli, & Troisi, 1992). Frustration and

anxiety could be signs of their anticipation of receiving the more preferred food item and continuously reevaluating if their decision to inhibit impulsivity was the most advantageous (Maestripieri et al., 1992).

When four of the six subjects ceased exhibiting self-control, they seemed to understand what a self-control response entailed as evidenced by NBL responses or reaching for the more preferred food, but they simply lost interest in participating in the self-control test. It was interesting to see the responses of each individual when I offered the two trials without a delay. DaVinci ate the cucumber both times, indicating he stopped participating in the task since he would not perform a simple exchange. Socrates also ate the cucumber both times, but motioned that she was going to trade indicating that she knew she should trade it to receive the raisin but decided not to exchange. DeAngela ate the cucumber one of the times, but returned a nibbled piece the other time indicating she was still aware of the necessity of exchanging the cucumber. Newton traded the cucumber both times and received the banana chip, indicating she knew she had to give the cucumber back to receive the reward, so her impulsive responses represented lack of desire to wait the delay. Unwillingness to exchange when the delay was removed implies more of a cessation of participating in the exchange task rather than a straight-forward cessation of inhibiting impulsivity resulting in maximum delay tolerances.

Feeding ecology and social organization may play a role in individual or species differences in delay tolerance and self-control abilities (Addessi et al., 2011; Amici, Aureli, & Call, 2008; Anderson et al., 2010; Stevens et al., 2005). Self-control might be especially important for highly impulsive species such as brown capuchins since it has implications for success in the wild. In a social society like that of capuchins, individuals might be faced with decisions in which they must exhibit self-control in order to achieve a future goal, and many

fitness benefits in the wild require waiting a delay until gratification is received. For example, in many altruistic situations an individual might not receive a reciprocal benefit until much later, but they should still perform an act for another due to the possibility of receiving a reward in return at some point in the future (Dufour et al., 2007). The ability to assess values, make decisions that optimize gains, and determine if a delay is worth the wait will lead to adaptive choices that benefit fitness in a constantly changing environment, as well as aid in avoiding costly risks.

This study was the first to test the role of a distractor object in potentially enhancing delay tolerance in a New World primate species. My hypothesis that a subject's delay tolerance would increase when a distractor metal clip was introduced was not supported. All four subjects who experienced distractor sessions did not utilize it as an object to distract themselves. The result is interesting considering their behavior during waiting before the distractor was introduced appeared to be implemented as distractions during the delay period. The subjects either ignored the clip, or played with it before, during, or after consuming the cucumber. Although Socrates did increase her tolerance by one second on a session including the distractor clip, lack of interaction with the distractor during this session indicated it was not distracting herself by playing with the clip that allowed her to advance. I do not think that these results show that a distractor does not aid in inhibiting impulsivity further. It is possible that the distractor failed to encourage longer delay tolerances because it was not an object the monkeys were interested in interacting with, even though it is a familiar object they have been observed manipulating in the past. Also, each of the four monkeys who experienced sessions with the distractor had already begun strong patterns of ceasing to inhibit impulsivity for 10 sessions without the distractor. This leads me to conclude that the subjects had already reached the

maximum delay tolerance during which they were willing to participate with the exchange task, and so introducing the distractor did not have an effect because the subjects had already ceased participating with the exchange task in general. It should also be noted that although the distractor object did not aid in advancing to the next delay interval, each monkey still had individual strategies for distracting themselves during the delay, as described above, that allowed them to reach their self-control tolerances. Future studies should test the effect of a distractor on enhancing delay tolerances in capuchin monkeys and other New World species when the subjects are still performing the exchange task.

This study is the first to utilize a delay of gratification food exchange task in which food options differ qualitatively to show self-control abilities in capuchin monkeys based on individual progress in incremental delays. Capuchins are able to attribute values and inhibit impulsivity by utilizing the cognitive abilities required to exhibit self-control, such as weighing costs and benefits, determining risk, and planning and reasoning to make the most advantageous decisions based on individual circumstances. Showing these self-control abilities in New World monkeys implies similar advanced cognition to those observed in Old World primates and humans. These abilities are advantageous in natural settings in which it is favorable to forgo an immediate reward to receive a delayed but more preferred or advantageous reward. Future research should continue to explore the delay tolerance thresholds and self-control abilities in New World monkeys using different methodologies to elucidate the presence of advanced cognitive abilities in New World monkeys that coincide with those of Old World primates and humans.

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Table 1

Trial Outcomes

Outcome (Code)	Description
Success (SCS)	The subject held onto the cucumber without consuming any portion of it, waited the delay, placed the cucumber back in the experimenter's hand, and received the raisin or banana chip.
Nibble-Fail (NBL)	The subject consumed a portion of the cucumber while waiting the delay, traded back the unconsumed portion, and did not receive the raisin or banana chip.
Throw (THROW)	The subject threw the cucumber at the experimenter during the delay period, and did not receive the raisin or banana chip.
Drop (DRP)	The subject dropped the cucumber out of the cage (or inside the cage without retrieving it) during the delay period, and did not receive the raisin or banana chip.
Eat (EAT)	The subject either consumed all of the cucumber or consumed a portion of the cucumber without trading the unconsumed portion upon the opportunity to trade, and did not receive the raisin or banana chip.

Table 2

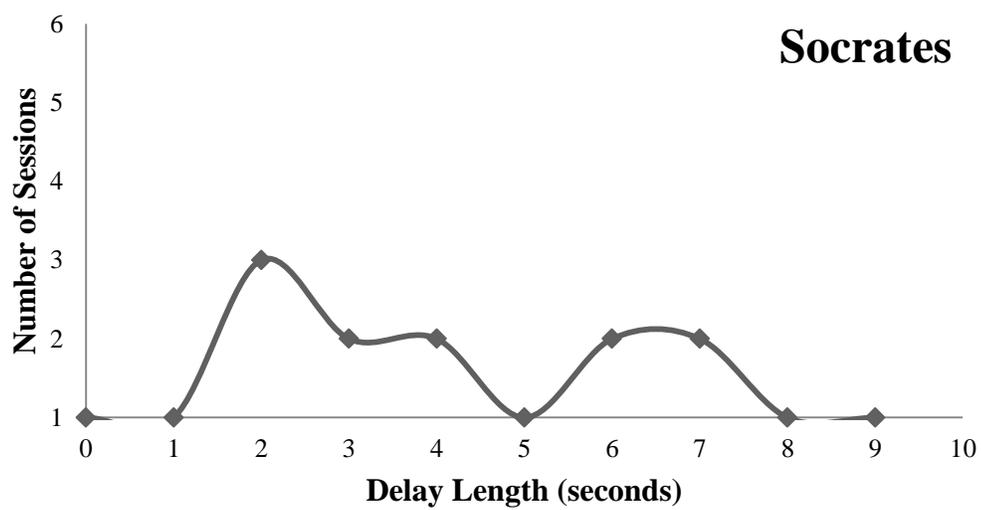
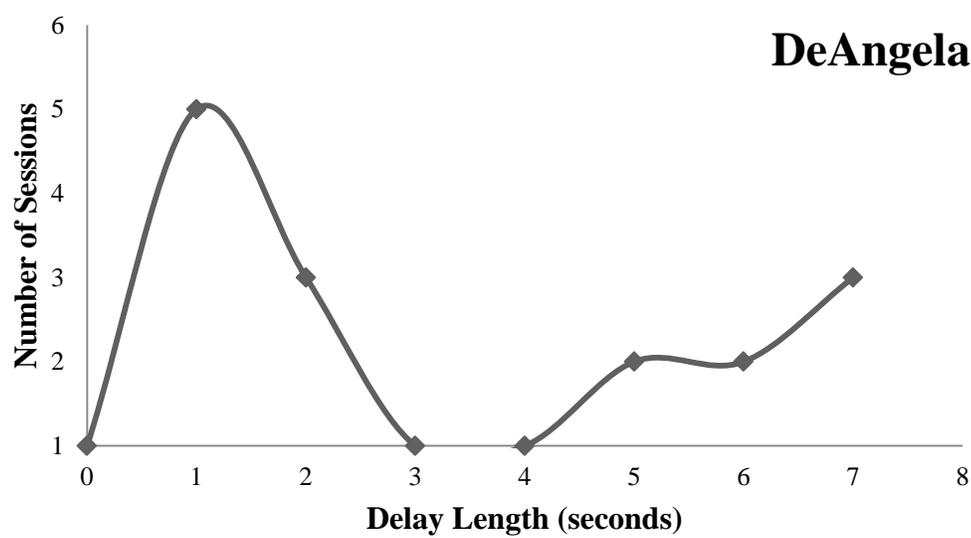
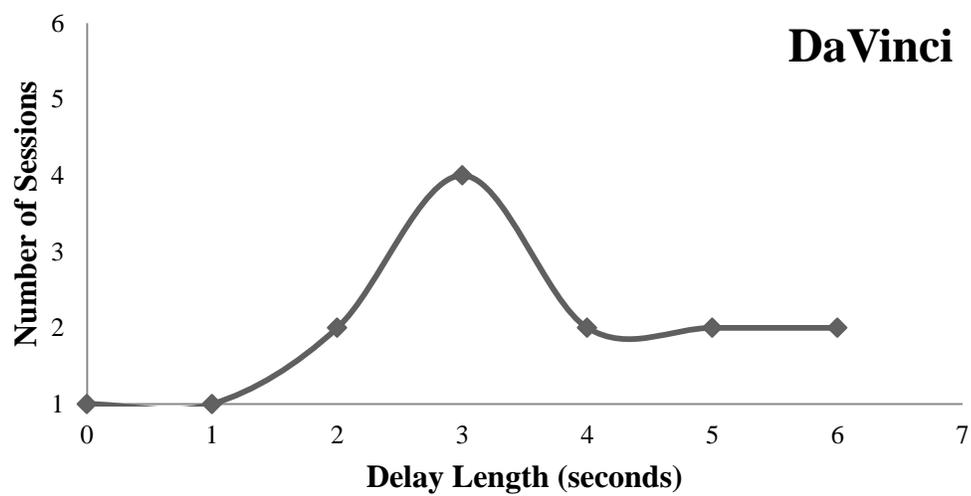
Summary of Behavioral Performance

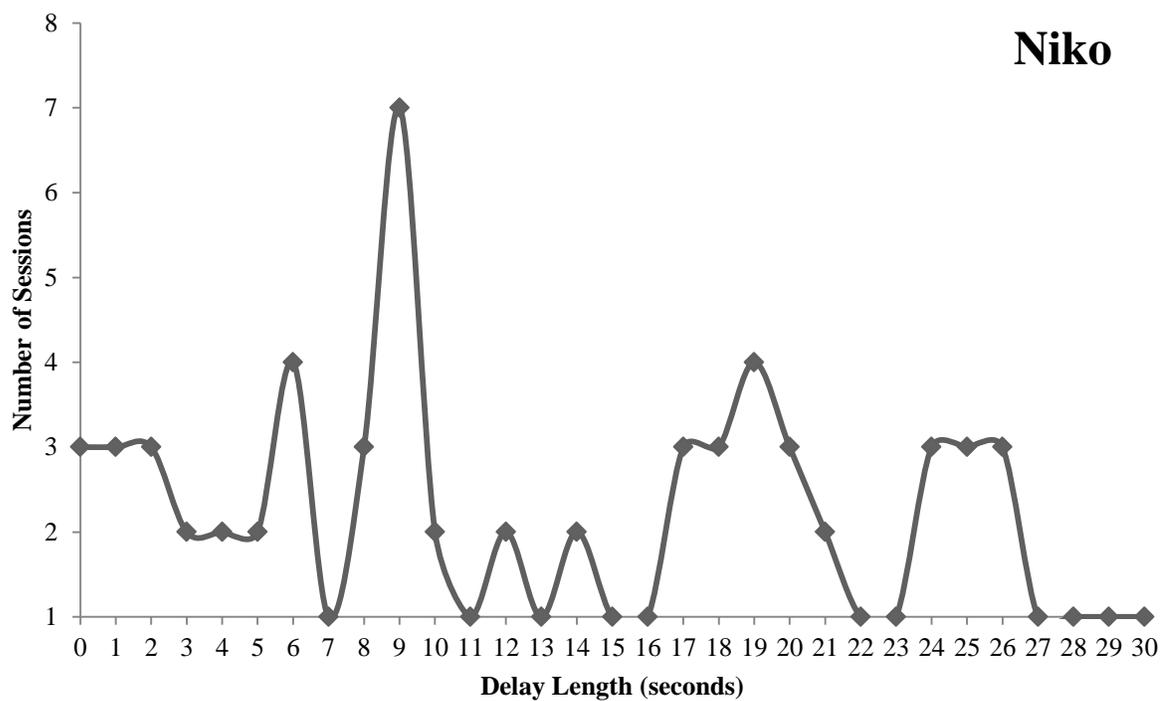
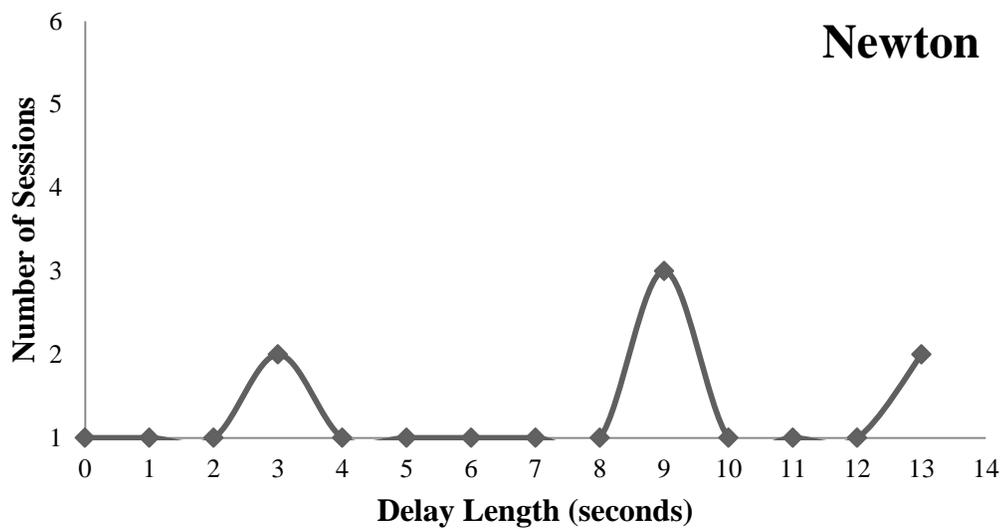
Subject	% SCS	% FAIL	% NBL FAIL	% NBL TOTAL	MAX DELAY
DaVinci	79.3	20.7	13.8	2.9	6 sec
DeAngela	64.4	35.6	23.4	8.3	7 sec
Socrates	85.0	15.0	45.8	6.9	9 sec
Newton	89.4	10.6	31.6	3.3	13 sec
Niko	72.2	27.8	46.1	12.8	30 sec
Shroeder	65.4	34.6	32.9	11.4	35 sec

Note. % SCS was the percentage of total trials each individual experienced in which the response was SCS and the individual received the more preferred reward. % FAIL was the percentage of total trials each individual experienced in which the response was NBL, THROW, DRP, or EAT, as described in Table 1, and the individual did not receive the more preferred reward. % NBL FAIL was the percentage of the failed trials for which the failed response was NBL. EAT, DRP, and THROW made up the rest of the failed trials. However, the DRP and THROW responses did not occur frequently enough across subjects to be included in this table. % NBL TOTAL was the percentage of NBL responses out of all trials included. The total number of trials included in these data included those up to the maximum delay tolerance for each subject, during which each subject successfully exhibited self-control. Subsequent trials involving the next higher delay period for which a subject did not exhibit self-control capacity and ceased inhibiting impulsivity, as well as those involving the distractor were not included in this table.



Figure 1. Distractor metal clip used on subsequent trials after DaVinci, DeAngela, Socrates, and Newton did not reach criteria to advance to the next delay length for 100 trials.





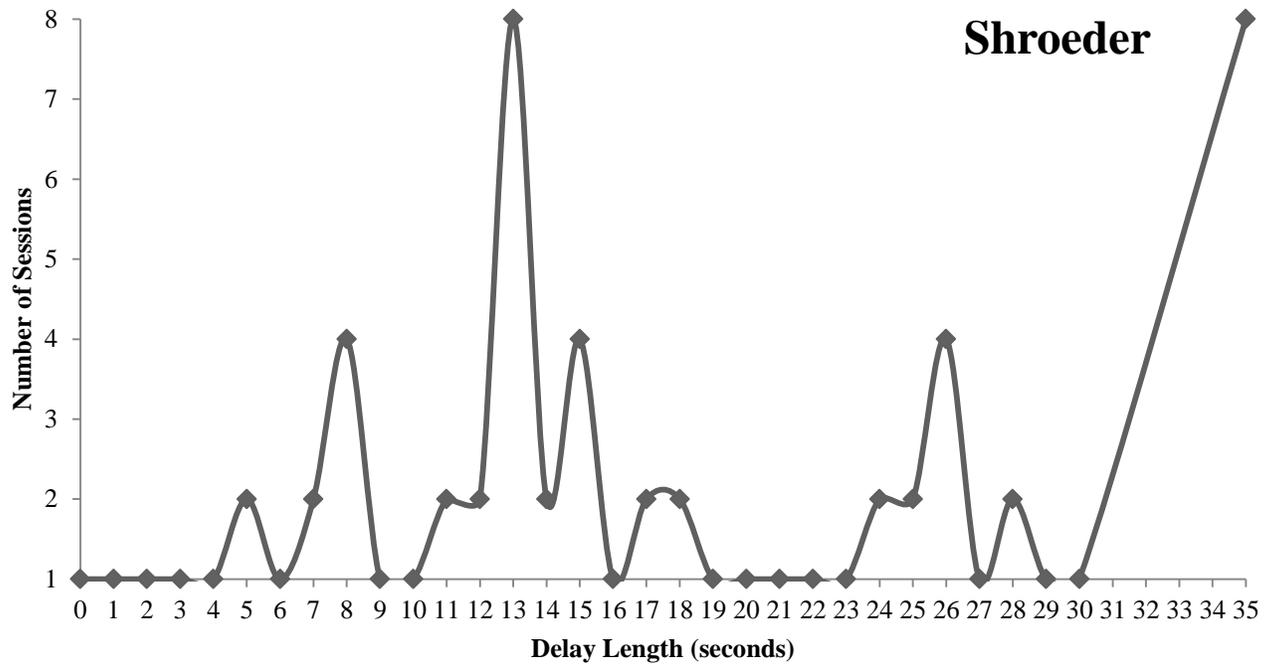


Figure 2. Number of sessions each individual experienced a delay length before receiving 90% or greater successful trials and advancing to the next highest delay. The point where a line ends represented the longest delay length for which a subject received 90% or greater successful trials out of 10, and this length was considered a subject's delay tolerance. The line stops because an individual experienced 10 ten-trial sessions without at least nine out of 10 successful trials at the next delay length.