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Self-control assessments of capuchin monkeys with the rotating tray task and the accumulation task

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ABSTRACT

Recent studies of delay of gratification in capuchin monkeys using a rotating tray (RT) task have shown improved self-control performance in these animals in comparison to the accumulation (AC) task. In this study, we investigated whether this improvement resulted from the difference in methods between the rotating tray task and previous tests, or whether it was the result of greater overall experience with delay of gratification tasks. Experiment 1 produced similar performance levels by capuchins monkeys in the RT and AC tasks when identical reward and temporal parameters were used. Experiment 2 demonstrated a similar result using reward amounts that were more similar to previous AC experiments with these monkeys. In Experiment 3, monkeys performed multiple versions of the AC task with varied reward and temporal parameters. Their self-control behavior was found to be dependent on the overall delay to reward consumption, rather than the overall reward amount ultimately consumed. These findings indicate that these capuchin monkeys' self-control capacities were more likely to have improved across studies because of the greater experience they had with delay of gratification tasks. Experiment 4 and Experiment 5 tested new, task-naïve monkeys on both tasks, finding more limited evidence of self-control, and no evidence that one task was more beneficial than the other in promoting self-control. The results of this study suggest that future testing of this kind should focus on temporal parameters and reward magnitude parameters to establish accurate measures of delay of gratification capacity and development in this species and perhaps others.

1. Introduction

Sometimes waiting leads to better rewards than simply taking what one can have more immediately. The initial choice between waiting for later or acting now (called inter-temporal choice) and the ability to maintain that choice through a delay to a better reward (delay of gratification) are two aspects of what is called self-control. Without question, the ability to wait, and thus show greater self-control, can produce clear advantages in a number of circumstances ranging from dietary habits to financial wellbeing (e.g., Baumeister et al., 1994; Logue, 1988; Mischel, 2014). Studies that assessed children's self-control and then re-examined those children's lives years or decades later showed that better self-control exhibited when young predicted better objective outcomes much later in life (e.g., academic and social competence, Mischel, et al., 1988; physical health, economic, and criminality outcomes, Moffitt et al., 2011; coping ability, Shoda et al., 1990; mental health, Tangney et al., 2004).

Within the comparative literature, a number of tests have been designed to assess self-control. Some, like the inter-temporal choice task, require animals to make dichotomous smaller-sooner (or lesser-sooner) versus larger-later (or better-later) choices. In that case, choice of the larger-later option means animals are then committed to waiting out the delay interval (e.g., Ainslie, 1974; Berns et al., 2007; Logue, 1988; Tobin et al., 1993, 1996; Rachlin and Green, 1972; Stevens et al., 2005a; Stevens and Mühlhoff, 2012). Other tasks require animals to avoid immediate rewards for the sake of obtaining later, better ones, either through movements through space where the less preferred item is encountered first (e.g., Evans and Westergaard, 2006; Stevens et al., 2005b) or by

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keeping a lower preference item (rather than consuming it) through a delay in order to exchange it for a more preferred item at a later time (e.g., Beran et al., 2016; Dufour et al., 2007; Judge and Essler, 2013; Pelé et al., 2010, 2011; Ramseyer et al., 2006). In these tasks, subjects must avoid taking the less preferred but more immediate reward, which is always present and (presumably) always a temptation, so as to later obtain the better reward (e.g., Beran et al., 1999; Grosch and Neuringer, 1981).

In some cases, the immediate reward may even increase in value over time, but only so long as the animal refrains from consuming the reward(s), thus demonstrating delay maintenance. This test, called the accumulation task, was first used with human children (e.g., Toner and Smith, 1977) and was later adapted for use with nonhuman animals (Beran, 2002). Some species are quite successful with this task, particularly the great apes (Beran, 2002; Beran and Evans, 2006; Evans and Beran, 2007a; Parrish et al., 2014; Stevens et al., 2011). Other species such as monkeys (e.g., Anderson et al., 2010; Evans and Beran, 2007b) and African Grey Parrots (Vick et al., 2010; but see Koepke et al., 2015) do not maintain the same degree of delay maintenance that is shown by apes in the accumulation task.

One species that has been studied fairly extensively with self-control tests is the capuchin monkey. These monkeys are well known for their manipulation skills, and for showing some cognitive abilities that rival those seen in Old World monkeys and in great apes (quantity discrimination, Beran, 2008; representing serial order, D'Amato and Colombo, 1988; tool discrimination, Evans and Westergaard, 2004; numerical competence, Judge et al., 2005; classification, McGonigle et al., 2003; same/different classification, Wright and Katz, 2006). However, capuchin monkeys typically failed to show good self-control, including in the accumulation test, and even with extensive experience (Addessi et al., 2013; Evans et al., 2012; Paglieri et al., 2013). Thus, the capuchin monkey provides a good model for attempting to facilitate better self-control through manipulation of experience and task parameters that might help generate longer delay of gratification.

We recently designed a task that might be more intuitive and easier for these monkeys to engage with, the rotating tray task (Bramlett et al., 2012). Capuchin monkeys successfully exhibited self-control in this test. One concern in previous assessments was that the prepotency of the visible food item might influence responding. In other words, a visible food item may elicit a prepotent response to take the food, even if doing so means that the larger-later item is never recovered. However, this is not due to a lack of self-control per se, as subjects may not have understood the nature of the task and simply responded to prepotent cues. Similarly, when presented with a smaller and larger item simultaneously, subjects might take the larger item without understanding that it is related to a longer delay (see Paglieri et al., 2013). To overcome these issues, we began by presenting monkeys with two food items that were at different spatial locations, but still simultaneously visible. One food item was nearer, and would move within reach more immediately, whereas the second started further away, but could be visually tracked throughout the trial as it moved closer to the monkey. In this way, the rotating tray task removed some of the prepotency issue as both options started at a distance rather than immediately within reach of the monkey and it removed the uncertainty about future availability of each food reward as both were visible and clearly part of the apparatus that the monkey could engage. At the same time, the rotating tray task, like the accumulation task, did require inhibition of reaching-and-taking responses because on trials in which self-control was required, the monkey had to allow the lower value reward to pass by in order to receive the more valuable reward. However, it also differed from the accumulation task in that after an item moved past a monkey, it again went out of reach. This allowed the monkey to attend more to the next item that approached, whereas the accumulation task always kept accumulated food items within reach of the subject, potentially requiring greater levels of sustained self-control in face of a growing reward set.

Our initial efforts with qualitatively different foods were successful, as the monkeys allowed a low-preference carrot piece to pass them by in order to obtain a banana slice (the more preferred food; Bramlett et al., 2012). Having demonstrated success with that variation, we then gave them different quantities of the same food type (banana). Some researchers have argued that quantitative reward differences are less likely to promote or sustain delay of gratification than qualitative differences (e.g., Hillemann et al., 2014), but in this case, many of the monkeys we tested also proved successful in waiting for the larger piece of food. In a follow-up study, we presented new conditions in which the food items were first shown to the monkeys and then placed into opaque containers rather than being visible throughout the trial (Perdue et al., 2015).

After these initial efforts to train and test capuchin monkeys with the rotating tray task, it was clear that these monkeys had become more proficient on that task than the accumulation task (e.g., Evans et al., 2012), but there was an order effect to consider, given that they were exposed to the rotating tray task after their experiences with the accumulation task. Thus, our first question in the present study was whether experience with the rotating tray task might have led to a generalized increase in self-control that would manifest in better performance with the accumulation task. In essence, we were interested in whether the monkeys might have become more self-controlled simply due to more experience in having to wait to get better rewards across different paradigms. To assess this in Experiment 1 and Experiment 2, we gave capuchin monkeys alternating sessions of each delay of gratification test, and then examined which of the two tests led to objectively better self-control. To do this, we carefully controlled the temporal parameters of both tests, and also the payouts for delay of gratification in both tests. We predicted that, although performance on the rotating tray task would exceed performance in the accumulation test, the monkeys might still show better performance in the accumulation task than they had shown in previous studies (Evans et al., 2012). Subsequent experiments assessed the extent to which performance had improved in these animals on the accumulation test and assessed their general levels of self-control compared to previous experiences. We also tested new, task-naïve monkeys with no experience on either self-control task to determine the relation of performance in these two tasks, and whether training and experience with one might scaffold performance on the other. Such results, if evident, could provide insights for interventions that would work to improve self-control in at-risk individuals or low self-control species.

2. Experiment 1

This experiment assessed whether capuchin monkeys were better at accumulating rewards when they could watch the reward progressing towards (and then past) them using the rotating tray task than in the accumulation task that involved rewards continuously being placed into an immediately-accessible food tray. We compared performance levels in terms of the number of items obtained with each task. We predicted, given past results with these animals, that the rotating tray task would produce better performance than the accumulation task because the maintenance of inhibition in the rotating tray task is required only while the reward passes by, and because attention can be focused elsewhere at this time (on the delayed, distant and better reward). The two tasks were otherwise identical in the sense that the accumulation of available food rewards increased in a manner that made it consistently more attractive to wait longer.

2.1. Method

2.1.1. Participants

Nine adult capuchin monkeys[1] (ages 9–18 years; 5 males, 4 females) participated in the experiment. These monkeys all were experienced in a variety of cognitive tasks (e.g., Agrillo et al., 2014; Beran et al., 2012, 2008; Beran and Parrish, 2012; Beran and Smith, 2011; Smith et al., 2012). One monkey, Nkima, had no previous experience in self-control tasks such as those used in the present study. All remaining monkeys had experience in computerized self-control tasks (Evans and Beran, 2014; Evans et al., 2014), as well as with the accumulation task (Addessi et al., 2013) and the rotating tray task (Bramlett et al., 2012; Perdue et al., 2015).

Each monkey voluntarily entered an individual test box attached to his/her enclosure for testing. Visual access to the remaining monkeys was maintained at all times. Water was available ad libitum, and the monkeys were otherwise maintained on their normal diet of fruits, vegetables, and protein sources independent of their performance on this task. All testing protocols complied with guidelines for working with nonhuman primates as established by protocols approved by the GSU Institutional Animal Care and Use Committee. GSU is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care.

2.1.2. Apparatus

The test boxes in which the monkeys worked measured 33 × 46 × 61 cm stainless steel mesh, and were suspended from a stainless steel mesh wall approximately 1 m above the floor. The front panel of these test boxes was interchangeable depending on the test conditions (see below). For the rotating tray task, this panel was made from solid, transparent Lexan except for a 4 cm diameter circle cut from the middle to allow monkeys to reach one hand out and toward the apparatus.

For the accumulation task, the front panel instead had a Plexiglas pan (25 × 6.5 cm) attached on the experimenter's side of the testing compartment at 14.5 cm from the bottom of the panel. The experimenter could either lock or unlock the pan by sliding a deadbolt, and when it was unlocked the subject could pull the pan into his or her side of the compartment to access any food items inside that pan (Fig. 1).

The rotating tray apparatus was an independent piece of equipment and was moved to the testing area during sessions. It consisted of an elevated revolving disk (38 cm in diameter) affixed to a rolling cart (Fig. 1). The disk was mounted on top of a rotation device that could be set to different rotation speeds. Attached to opposite ends of the disk were two small clear plastic cups into which food items could be placed.

The same apparatus was used during presentation of accumulation trials. In the accumulation task, however, it served as the bench on which the food items were placed before manual transfer by the experimenter into the pan attached to the monkeys' testing boxes (see below for details).

2.1.3. Design and procedure

Rotating Tray (RT) task. The apparatus was aligned with the monkey's test box so that the two transparent cups were perpendicular to the monkey's test box faceplate. The rotation device was set to revolve at 10 s per revolution, so that the first transparent

[1] Note that the tufted or brown capuchin formerly referred to as *Cebus apella* is now classified in a separate genus, *Sapajus apella.* See Alfaro et al. (2012a,b) for more information.

Table 1
Progression of trials in the rotating tray task and the accumulation task in Experiment 1.

Rotating Tray Task				Accumulation Task			
Forced Obs. Trial		Test Trial		Forced Obs. Trial		Test Trial	
Choice	Total	Choice	Total	Choice	Total	Choice	Total
Cup A	1	Cup A	1	Add 1	1	Add 1	1
Cup B	3	Cup B	3	Add 2	3	Add 2	3
Cup A + 5	6	Cup A + 5	6	Add 3	6	Add 3	6
Cup B + 9	12	Cup B + 9	12	Add 6	12	Add 6	12
Cup A + 14	20	Cup A + 14	20	Add 8	20	Add 8	20
		Cup B + 28	40			Add 20	40

Note: Looking down each column shows the successive choices that were available to the monkey in each task. In the forced observation trials, the monkeys could not take the food pellets until the final choice that gave them 20 pellets. For the test trials, there were six points at which the pellets could be taken.

cup would take 2.5 s to be directly in front of the monkey, and the second transparent cup would take 7.5 s to be directly in front of the monkey. One 94 mg banana-flavored pellet was placed in the first cup (Cup A) and 3 of the same type of pellets were placed in the second cup (Cup B). The apparatus was turned on and began to rotate the first cup toward the monkey. If the monkey did not take the food item from the cup, and it reached the opposite side from which it started (i.e. the original location of Cup B), five additional pellets were added to Cup A, bringing the total pellets in that cup to six (whereas only three pellets remained in Cup B now approaching the monkey). If Cup B also reached its original position without the pellets being taken by the monkey, nine more pellets were added, bringing the total for Cup B to 12 pellets (compared to the six pellets in Cup A now approaching the monkey). This method continued in the same manner for a total of 4.5 total revolutions of the tray or until the monkey reached out and consumed the contents of a cup, with pellets added as outlined in Table 1. The dependent measure was the set of pellets finally taken by the monkey, with a range of scores from 1 (first cup taken, with one pellet) to 6 (last cup taken, with 40 pellets). We chose these increasingly larger numbers of items to be added at each point in a trial to ensure that, throughout the trial, the two quantities would be discriminable to the monkeys (i.e., the monkeys could discriminate that the later set to come was always larger than the more immediate set). Previous work with this species in our laboratory has indicated that quantities with these numerical differences and ratios were easily discriminable (see Beran et al., 2008; Evans et al., 2009).

Each session began with a trial in which the animal was forced to experience what would happen if they waited. In this trial, the presentation was as outlined above (see Table 1) but with the tray apparatus out of reach of the monkey. After all pellets were added, the tray stopped rotating when Cup A (containing 20 pellets) was in front of the monkey and then the cart was pushed forward so that the monkey could take those items. Two test trials, in each of which the full 40 pellets could potentially be earned, were then given to the monkey to complete the test session. The total duration that a monkey had to wait for a successful trial (waiting for the 40 pellets) was 45 s.

Accumulation (AC) task. In this task, the experimenter manually transferred pellets into the pan every five seconds so that the monkey experienced the same increasing escalation in reward size across time as in the RT task. Accumulation of pellets continued until the monkey pulled the pan in and consumed the pellets. To match the values of each discrete choice option in the RT task, pellets were added at each accumulation point in the AC task as outlined in Table 1. Again, each session started with a forced observation trial in which the pan was locked and could not be opened by the monkey. This was done so that the monkey experienced the

Fig. 1. The experimental apparatus. The rotating tray task (left image) involved the presentation of items from cups placed at the back of the apparatus into the two clear containers on the opposite sides of the larger white tray. That tray rotated so that those containers came into reach of the monkey one at a time. The accumulation task (right image) involved presentation of items into the central tray in the clear faceplate at the front of the testing box. Items continued to be added by the experimenter until the monkey pulled that tray toward itself so that it could access and eat the items inside the pan.

Table 2
The mean number of additions to the set (maximum = 6.0) that was consumed by each monkey in each task, and for each trial within sessions of Experiment 1.

	Rotating Tray Task		Accumulation Task	
	Trial 1	Trial 2	Trial 1	Trial 2
Gabe	2.6 (2,4,2,2,3)	2.4 (1,2,2,2,5)	4.4 (1,4,6,5,6)	3.6 (1,4,6,6,1)
Gambit	1.0 (1,1,1,1,1)	1.0 (1,1,1,1,1)	1.0 (1,1,1,1,1)	1.0 (1,1,1,1,1)
Griffin	3.8 (2,4,4,4,5)	4.0 (2,3,4,5,6)	4.0 (3,2,4,5,6)	4.2 (1,3,5,6,6)
Liam	5.0 (5,5,4,6,5)	4.2 (4,4,2,6,5)	6.0 (6,6,6,6,6)	5.8 (5,6,6,6,6)
Lily	4.4 (2,3,5,6,6)	4.8 (3,3,6,6,6)	5.0 (1,6,6,6,6)	6.0 (6,6,6,6,6)
Logan	3.8 (2,4,3,5,5)	4.4 (4,4,3,5,6)	6.0 (6,6,6,6,6)	6.0 (6,6,6,6,6)
Nala	2.8 (3,3,2,3,3)	3.6 (2,2,2,6,6)	2.2 (1,2,4,3,1)	2.6 (3,1,3,3,3)
Nkima	1.0 (1,1,1,1,1)	1.0 (1,1,1,1,1)	1.0 (1,1,1,1,1)	1.0 (1,1,1,1,1)
Wren	4.8 (4,5,3,6,6)	5.2 (4,5,5,6,6)	3.8 (2,3,2,6,6)	6.0 (6,6,6,6,6)

Note: The numbers in parentheses are the individual trial data for each monkey in each trial number within each task.

temporal and quantitative effects of waiting to consume all of the pellets. This forced observation trial was followed by two test trials.

In both tasks, a timer was set for 120 s at the onset of a trial and this was the total trial duration no matter how many pellets were obtained by the monkey. This ensured that there was no benefit to taking fewer pellets in order to speed up the presentation of the next trial. Only one task was presented to a monkey on a given day, with a randomly determined order across sessions. As noted, one forced observation trial and two test trials were given in each session. Each monkey completed five sessions for each task, for a total of 10 test trials within each task.

2.2. Results

Table 2 presents the results of the experiment for each monkey. We conducted a 3-way repeated measures ANOVA with task (RT or AC), Session Number (1–5) and Trial Within Session (1st trial or 2nd trial) to analyze the results. The outcome of the analysis indicated that there was no main effect of task, $F(1, 8) = 3.34$, $p = 0.11$, $\eta p^2 = 0.30$ and no main effect of trial number within session, $F(1, 8) = 1.46$, $p = 0.26$, $\eta p^2 = 0.15$. There was a main effect of session, $F(4, 32) = 8.73$, $p < 0.001$, $\eta p^2 = 0.52$. There were no two-way interactions, all $F < 3.40$, $p > 0.07$. There was not a three-way interaction, $F(4, 32) = 2.26$, $p = 0.085$, $\eta p^2 = 0.22$.

The main effect of session reflected improved performance across sessions in both tasks, and was confirmed by a significant test of within-subjects contrast for linear fit, $F(1, 8) = 13.76$, $p = 0.006$, $\eta p^2 = 0.63$. In the RT task, the average number of added sets in the two combined trials from Session 1 to Session 5 was 4.89, 6.11, 5.67, 8.00, and 8.56. In the AC task, the average number of added sets in the two combined trials from Session 1 to Session 5 was 5.78, 7.22, 8.44, 8.89, and 8.33.

2.3. Discussion

We predicted that, as a group, capuchin monkeys would perform better in the RT task than in the AC task given past performance. However, this was not true. There were large individual differences across monkeys in how well they performed, ranging from two very poorly performing monkeys (Gambit and Nkima, who never showed any self-control and always took the first reward immediately in both tasks) to those monkeys who came closer to gaining the majority of food items on trials in both tasks (e.g., Liam, Lily, and Wren). These results suggested that these monkeys had improved in their accumulation abilities compared to previous efforts with that task, perhaps as a result of their exposure (and success) with the rotating tray in the previous experiment (Bramlett et al., 2012). However, it also was clear that performance in both of these tasks improved as a function of the number of sessions completed, and this argued for experience playing a role in performance in both tasks. A more direct comparison of this hypothesis was one of the goals of later experiments in this study.

One of the major differences between Experiment 1 and past tests with these animals to assess self-control was the use of increasingly larger additions of items to the sets within a trial. Past experiments with the accumulation task had used only a one-at-a-time method for accumulating items within reach of the monkey, so it was possible that the better performance of monkeys in Experiment 1 was the result of the escalation in the amount of items added each time within a trial. This would be analogous to humans' preference for compound interest compared to simple interest accumulation of savings. To assess this, in Experiment 2 we increased the available items only one at a time, to see if the equivalent performance in each task would occur in that situation.

3. Experiment 2

3.1. Method

3.1.1. Participants

The same nine capuchin monkeys from Experiment 1 participated in this experiment.

3.1.2. Apparatus

The apparatus was the same as in Experiment 1.

3.1.3. Design and procedure

In this experiment, food increments were adjusted for the RT and AC tasks. For the RT task, a series of six small, transparent cups were placed below the rotating tray in view of the monkey. Two pellets were placed in five of the cups, and one pellet was placed in the sixth cup. The one-pellet cup was then shown to the monkey, and its contents dumped into a tray affixed to the rotating tray labeled Cup A. Two pellets were then shown to the monkey and placed in a tray labeled Cup B, and then the rotating apparatus began to move. For each revolution the tray made, two pellets were placed into the cup passing its closest point to the researcher (the cup that had just passed by the monkey). At any given time, there was only a one pellet difference between the two cups. This pattern was repeated three times for Cup A and Cup B with a maximum of five and six pellets, respectively, if the contents were not consumed during the full trial duration. After the final pellets were added, making the comparison five items versus six items, no more food was added although the tray would continue to rotate until the monkey took one of the sets.

As in Experiment 1, each session began with a forced observation trial where the rotating tray was placed out of reach of the monkey until the maximum number of pellets (five and six) was in the two cups. At that point, the side of the rotating cart containing Cup B was put within reach of the monkey who was allowed to reach out, take, and consume its contents. This was followed by two test trials that ended whenever a monkey would reach out and consume the contents of a cup.

In the AC task, a series of six small, transparent cups again were placed on the Rotating Tray apparatus in view of the monkey. These cups were then each filled with a single banana pellet. The researcher then placed the pellet in the first cup into the pan. The researcher continued to add pellets one by one into the pan until either six pellets were added or the monkey began consuming the pellets in the pan. Each session began with a forced observation trial in which the pan was locked outwards, thereby not allowing the monkey to access the pan's contents, and all six pellets were accumulated. This was followed by two test trials that ended when the monkey began to consume the pellets in the pan.

In both tasks, a timer was set for 120 s at the onset of a trial and this was the total trial duration no matter how many pellets were obtained by the monkey. This ensured that there was no benefit to taking fewer pellets in order to speed up the presentation of the next trial. Only one task was presented to a monkey on a given day, with randomly determined order across sessions. As noted, one forced observation trial and two test trials were given in each session. Each monkey completed five sessions in each task, for a total of 10 test trials in each task.

Table 3
The mean number of additions to the set (maximum = 6.0) that was consumed by each monkey in each task, for each trial within sessions of Experiment 2.

	Rotating Tray Task		Accumulation Task	
	Trial 1	Trial 2	Trial 1	Trial 2
Gabe	5.6	3.8	5.2	5.0
Gambit	1.0	1.0	1.0	1.0
Griffin	1.0	1.0	1.0	1.0
Liam	4.2	4.2	6.0	5.8
Lily	5.2	4.8	2.0	5.0
Logan	4.6	4.8	6.0	6.0
Nala	5.8	6.0	2.0	2.4
Nkima	1.0	1.0	1.0	1.2
Wren	5.8	6.0	5.4	6.0

3.2. Results

Table 3 presents the results for individual monkeys. We conducted a 3-way repeated measures ANOVA with task (RT or AC), Session Number (1–5) and Trial Within Session (1st trial or 2nd trial) to analyze the results. The outcome of the analysis indicated that there was no main effect of task, $F(1, 8) = 0.16$, $p = 0.70$, $\eta p^2 = 0.02$, no main effect of trial number within session, $F(1, 8) = 0.38$, $p = 0.55$, $\eta p^2 = 0.05$, and no main effect of session, $F(1.58, 12.63) = 3.91$, $p = 0.055$, $\eta p^2 = 0.33$ (note that the assumption of sphericity was violated, and so the Greenhouse-Geisser correction was used). There were no two-way interactions, all $F < 2.32$, $p > 0.16$. There was not a three-way interaction, $F(4, 32) = 1.26$, $p = 0.31$, $\eta p^2 = 0.14$.

In the RT task, the average number of added sets in the two combined trials from Session 1 to Session 5 was 8.22, 6.67, 7.78, 6.33, and 8.11. In the AC task, the average number of added sets in the two combined trials from Session 1 to Session 5 was 7.22, 7.33, 7.11, 6.00, and 7.33. Finally, we correlated the overall mean performance in each task (collapsing across Trial 1 and Trial 2) for each monkey, to provide an assessment of how similar performance in the two tasks was for these monkeys. That correlation was statistically significant, $r(7) = 0.73$, $p = 0.013$.

3.3. Discussion

The aim of this experiment was to assess whether or not the better performance of the monkeys in Experiment 1 compared to performances in past experiments with the accumulation task was the result of the escalation in the amounts added each time within a trial. Interestingly, the single item-by-item increase in the present experiment resulted in the monkeys' performances remaining roughly the same as at the end of Experiment 1. Most monkeys also did equally well (or equally poorly) in both tasks, suggesting that the two tasks tap into the same potential inhibitory mechanism that underlies delay of gratification. However, stronger support for this claim requires testing more animals so that one could look at more than simply correlations in performance in a fairly small sample. That said, the present results do indicate that the accumulation task and the rotating tray task are equally viable as tests of animal self-control, at least among capuchin monkeys, even if they do not tap into identical mechanisms for supporting such self-control.

We again saw that performance was as good on the accumulation task as it was on the rotating tray task, despite our predictions, and despite our past data from these same animals suggesting performance was enhanced for the rotating tray task. This suggested that we should re-evaluate the general capacities of these monkeys for the AC task relative to their past performances, to document more directly the improvements they might have made with time and experience. Past research efforts with these monkeys using the

AC task used a different food type (raisins) that was much more preferred than the banana-flavored pellets in Experiment 1 and Experiment 2; therefore, we first sought to determine whether the proficiency seen with the AC task by some of these monkeys was motivationally-driven and whether it would continue even with a much more preferred food item that accumulated. Thus, we continued the study using only the AC task to document the present capacities of these monkeys to engage that task for higher preference items.

4. Experiment 3

Experiment 3 was designed to assess the temporal and quantitative limits at which the monkeys were no longer willing/able to delay gratification of the accumulating reward, despite prior experience with both the rotating tray task and accumulation task (Experiments 1 and 2). We manipulated the rate at which the raisins were dispensed and the maximum number of potential rewards available to be accumulated. Through four phases, the monkeys were given trials with up to 20 raisins that accumulated at a rate of 2 s per raisin (Phase 1), or 4 s per raisins (Phase 2) or up to 50 raisins that accumulated at a rate of 5 s per raisin (Phase 3) or at 2 s per raisin (Phase 4). The resulting data allowed us to assess the monkeys' performance levels in terms of the number of food items obtained per trial and the length of time each individual waited before consuming any raisins and terminating the accumulation. We also could compare the resulting performance of the monkeys in this test to their own previous performances before experiencing the rotating tray task when they were given highly similar accumulation tests in terms of these accumulation rates and maximum numbers of items (Evans et al., 2012). This allowed us to see whether their overall delay of gratification capacity had improved.

4.1. Method

4.1.1. Participants

The nine capuchin monkeys from Experiment 1 and Experiment 2 participated in the first two phases of Experiment 3. Three subjects (1 male – Nkima, 2 females – Gambit and Nala) were not included in Phase 3 and Phase 4 due to their low performance in the prior phases.

4.1.2. Apparatus

All phases of Experiment 3 were AC tasks; therefore, the interchangeable faceplate used was the panel with a Plexiglas pan. The RT apparatus described in Experiment 1 was used as a bench on which the transparent cups were lined up for each trial of all conditions. Each cup was baited with one raisin which would be manually transferred by the experimenter into the Plexiglas pan during a trial. The number of baited cups was phase dependent (see below). The bench was approximately 8 cm away from the front of the faceplate, allowing the baited cups to remain visible but out of the monkeys' reach.

4.1.3. Design and procedure

Phase 1 consisted of 10 sessions per monkey, with only one session performed per day. In each session, one forced observation trial was followed by two test trials. Before each trial began, 20 baited cups were lined up on the rotating tray apparatus (10 on the top shelf and 10 on the rotating platform). Standing to the left of the rotating tray apparatus, the experimenter manually transferred one raisin at a time into the pan. Each raisin was dispensed every two seconds so that the monkey experienced the same increasing escalation in reward amount across time. After each raisin was transferred into the pan, the emptied cups were discarded into a large bowl that rested on the lower shelf of the rotating tray apparatus. Accumulation of raisins continued until all 20 raisins had been dispensed or the monkey pulled the pan inward and began to consume the raisins. Each trial lasted 120 s, regardless of when the accumulation was terminated. This allowed for a minimum of 80 s at the end of each accumulation for the monkey to consume any accumulated raisins that were obtained. The number of raisins accumulated per trial was recorded.

Phase 2 also consisted of 10 sessions per monkey, each comprised of one forced observation trial followed by two test trials. Twenty baited cups were lined up on the rotating tray for each trial (10 on the top shelf and 10 on the rotating platform). Compared to Phase 1, the raisin dispensing rate was slowed as the experimenter manually transferred one raisin into the pan every four seconds (instead of every two seconds as in Phase 1). Accumulation of raisins continued until all 20 raisins had been dispensed or the monkey pulled the pan inward and began to consume the raisins. Each trial was 160 s long, regardless of when the accumulation ended, allowing for a minimum of 80 s at the end of each accumulation for the monkey to consume the accumulated raisins. The number of raisins accumulated per trial was recorded.

Phase 3 consisted of only five sessions, and this phase, along with Phase 4, was not presented to Nala, Nkima, or Gambit given their lack of any strong evidence of delay of gratification in Phase 1 or Phase 2. Due to the other subjects' familiarity with the accumulation task, and to avoid satiation, each session consisted of only one test trial. The forced observation trial and second test trial were eliminated. In this condition, 50 cups, each baited with one raisin, were lined up on the rotating tray apparatus (25 on the top shelf and 25 on the rotating platform). The experimenter manually transferred one raisin into the pan every five seconds so that the monkey experienced the same increasing escalation in reward size across time. Accumulation of raisins continued until all 50 raisins were dispensed into the pan or the monkey pulled the pan inward and began to consume the raisins. The number of raisins accumulated per trial was recorded.

Phase 4 also consisted of five sessions, with one test trial per session. There was no forced observation trial. In Phase 4 the experimenter transferred one raisin into the pan every two seconds instead of every five seconds. This modification allowed us to better discriminate whether the average accumulation threshold was temporally or quantitatively based. All other parameters of Phase 4 remained consistent with those of Phase 3.

4.2. Results

4.2.1. Phase 1

In this phase, monkeys received up to 20 raisins at 2 s intervals. We conducted a 2-way repeated measures ANOVA with Session Number (1–10) and Trial Within Session (first trial or second trial) to analyze the results. The outcome of the analysis indicated that there was no main effect of trial number within session, $F(1, 8) = 0.16$, $p = 0.70$, $\eta p^2 = 0.02$, no main effect of session, $F(9, 72) = 1.59$, $p = 0.14$, $\eta p^2 = 0.17$, and no interaction, $F(9, 72) = 1.34$, $p = 0.23$, $\eta p^2 = 0.14$. Fig. 2a presents the number of items obtained (out of 40 possible) for each session and each monkey. There was individual variability, with some monkeys obtaining nearly all items on all trials (Lily and Wren), some obtaining most items on most trials (Liam and Logan), some obtaining very few items (Nkima and Gambit) and some in the middle (Gabe, Nala, and Griffin).

Next, we compared the performance of the seven capuchins (Gabe, Griffin, Liam, Logan, Lily, Nala, and Wren) that had performed the 20-item accumulation test in Evans et al. (2012) with their performance here to see if it had improved. The group was significantly better at the accumulation test in the present phase

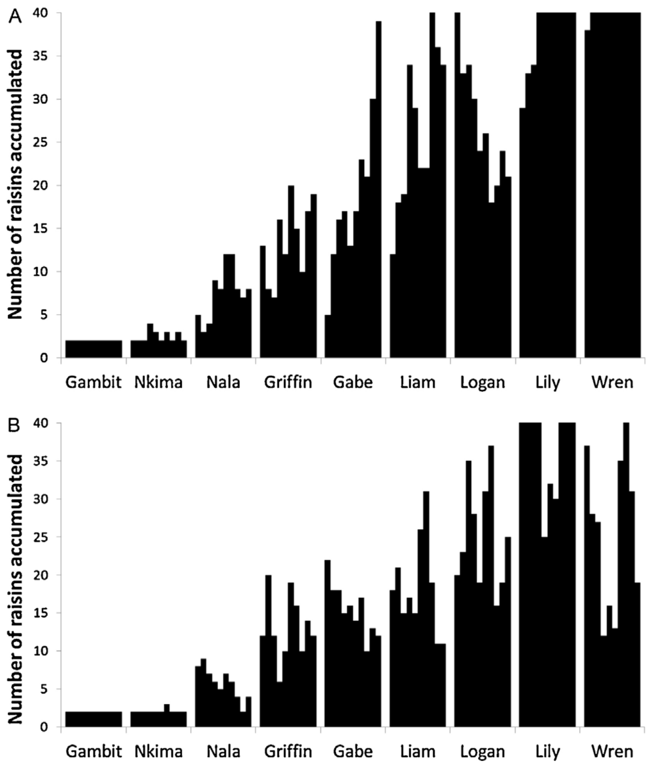

Fig. 2. Total number of items obtained (out of 40) for each monkey in each accumulation session in Phase 1 (panel A) and Phase 2 (panel B) of Experiment 3. In Phase 1 trials, monkeys could receive up to 20 raisins at 2 s intervals. In Phase 2 trials, monkeys could receive up to 20 raisins at 4 s intervals.

Table 4
Comparison of monkey performance in Evans et al. (2012) and the Experiment 3 trials with the Accumulation Task.

	Mean Number Obtained 20 items, 2-s interval			Mean Number Obtained 50 items, 2-s interval		
	Evans et al.	Phase 1	% Gain	Evans et al.	Phase 4	% Gain
Gabe	3.90	9.65	147%	5.38	16.2	201%
Griffin	3.20	6.85	114%	3.50	8.2	134%
Liam	6.00	13.80	130%	9.88	20.2	104%
Lily	14.60	18.80	29%	8.13	50.0	515%
Logan	9.70	13.50	39%	6.88	24.4	255%
Nala	2.30	3.80	65%	NA	NA	NA
Wren	9.70	19.90	105%	10.94	21.0	92%

Note: This table only includes the individuals tested in the current study and the Evans et al. (2012) study. Monkey Nala was not included in Phases 3 and 4 (50 items) in the current study due to her low performance levels in Phases 1 and 2.

(M = 12.32; SD = 5.95) than in the previous experiment (M = 7.06; SD = 4.46), $t(6)$ = 4.78, p = 0.003. And, every monkey improved, showing increases that ranged from 29% improvement to 147% improvement in the present experiment (see Table 4).

4.2.2. Phase 2

In this phase, monkeys received up to 20 raisins at 4 s intervals. We conducted a 2-way repeated measures ANOVA with Session Number (1–10) and Trial Within Session (1st trial or 2nd trial) to analyze the results. The outcome of the analysis indicated that there was no main effect of trial number within session, $F(1, 8)$ = 0.39, p = 0.55, ηp^2 = 0.05, no main effect of session, $F(9, 72)$ = 1.67, p = 0.11, ηp^2 = 0.17, and no interaction, $F(9, 72)$ = 1.98, p = 0.054, ηp^2 = 0.20. Fig. 2b presents the number of items obtained (out of 40 possible) for each session and each monkey. There again was variability among the monkeys.

We compared performance in Phase 1 to Phase 2 as a function of the mean delay duration the monkeys tolerated. For each trial, the duration was calculated as (delay interval) * (number of items obtained – 1). Delay interval was either 2 s (Phase 1) or 4 s (Phase 2). We subtracted one from the number of items obtained because the first item was given at trial start and so there was no delay to that point. Numerically, all monkeys waited longer on average in Phase 1 than in Phase 2 (Fig. 3). However, this effect did not reach conventional levels of statistical significance, paired $t(8)$ = 2.26, p = 0.054.

4.2.3. Phase 3 and Phase 4

In Phase 3, monkeys received up to 50 raisins at 5 s intervals, and in Phase 4, monkeys received up to 50 raisins at 2 s intervals. Fig. 4a presents the mean number of items obtained in Phase 3 and Phase 4. As expected, the monkeys obtained significantly more items when the inter-item interval was two seconds versus five seconds, $t(5)$ = 2.79, p = 0.039. We also compared performance in Phase 3 to Phase 4 as a function of the mean delay duration the monkeys tolerated (Fig. 4b). For each trial, the duration was calculated as (delay interval) * (number of items obtained – 1). Delay interval was either 5 s (Phase 3) or 2 s (Phase 4). There was not a significant difference in delay duration between these phases $t(5)$ = 0.82, p = 0.45. Thus, although monkeys obtained numerically more items with the faster presentation pace, their delay maintenance times were highly similar across these two phases.

Finally, we compared the performance of the six capuchins (Gabe, Griffin, Liam, Logan, Lily, and Wren) that had performed the 50-item accumulation test in Evans et al. (2012) with their performance in Phase 4, to see if it had improved. The group was significantly better at the accumulation test in the present phase than in the previous experiment, $t(6)$ = 2.91, p = 0.033. Every monkey improved, showing increases that ranged from 92% improvement to 515% improvement in the present experiment relative to Evans et al. (2012; see Table 4).

4.3. Discussion

Three critical results emerged from this experiment. First, we confirmed that capuchin monkeys can perform well on an accumulation task, although there were individual differences. Second, the results indicated that delay maintenance was driven not by the number of items obtained but instead by the delay interval. This is an important outcome, as it matches other previous work using intertemporal choice tasks with monkeys (e.g., Evans et al., 2014) and also the accumulation task with orangutans (Parrish et al., 2014), and this highlights that improving self-control in this species will likely progress better when attention is paid to delay intervals rather than food amounts. Third, and perhaps most impressively, we documented that this group of monkeys now showed much stronger self-control in a task that they had not performed well at in earlier. Gains of more than 100%, and in some cases much more, were documented in multiple phases.

The results from these first three experiments show improved accumulation performance over past efforts that gave the same task to most of these monkeys, and no advantage for one task over the other (RT and AC) in terms of proficiency in showing self-control. From this, we cannot draw firm conclusions about the extent to which one task more reliably induces self-control or provides the scaffolding on which broad capacities to inhibit taking immediate rewards to gain better, later rewards emerge. However, all monkeys that were tested in Experiments 1–3 had come into those experiments with extensive past experiences with these tasks (e.g., Bramlett et al., 2012; Evans et al., 2012), and so it was possible that this experience may have improved self-control in general. To assess this possibility, we need an additional series of tests with naïve monkeys that have no experience with either of these tasks

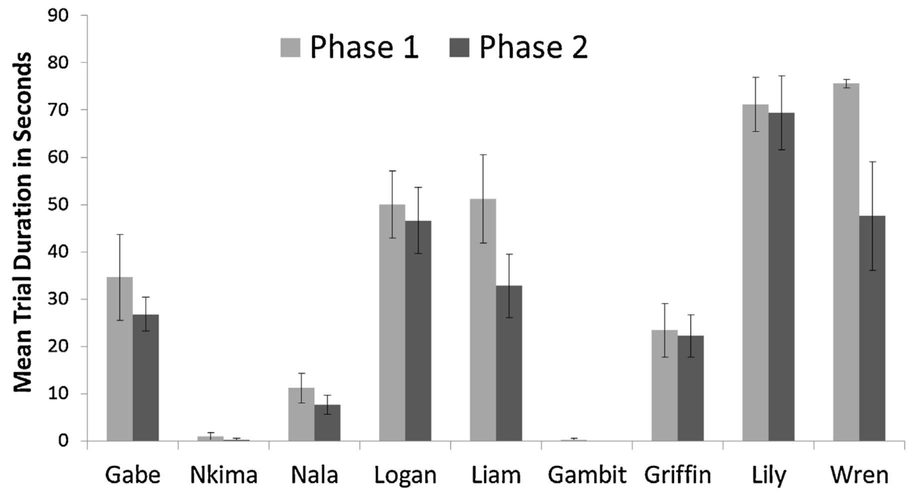

Fig. 3. Mean duration of delay maintenance during the AC task by each monkey in Phase 1 and Phase 2 of Experiment 3. In Phase 1, monkeys could receive up to 20 raisins at 2 s intervals. In Phase 2, monkeys could receive up to 20 raisins at 4 s intervals. Errors bars indicate 95% confidence intervals.

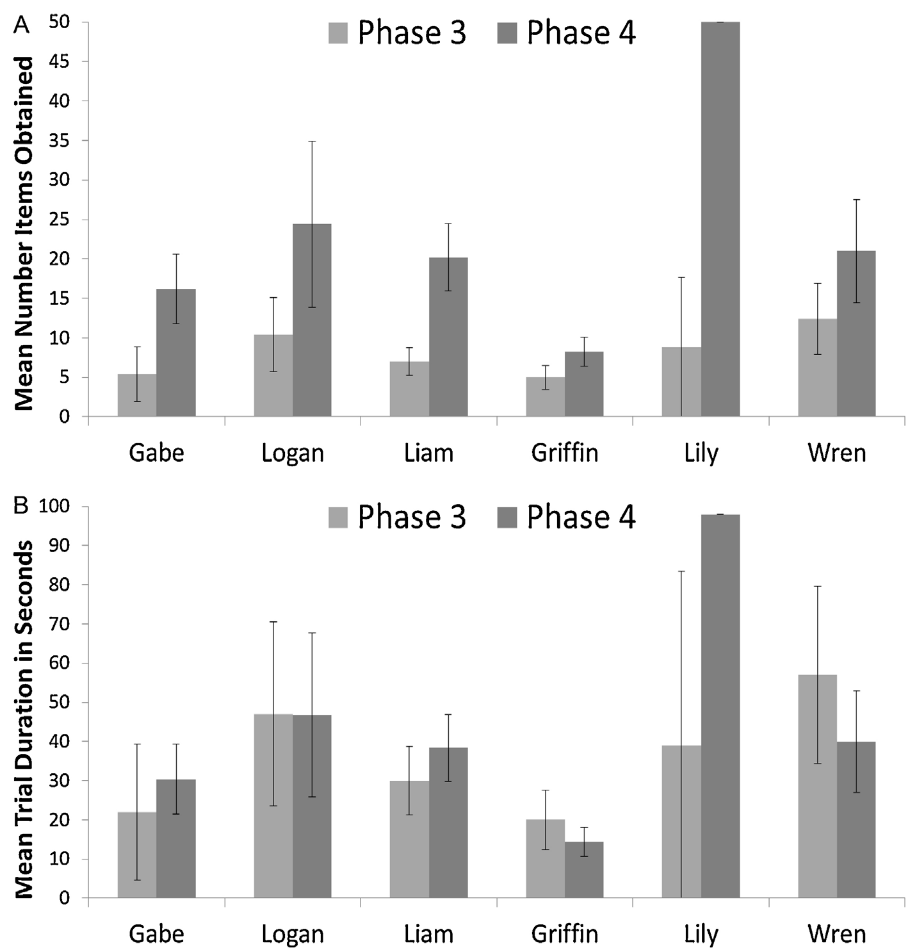

Fig. 4. A. Mean number of items obtained (out of 50) during the AC task for each monkey in Phase 3 and Phase 4 of Experiment 3. B. Mean delay maintenance duration for each monkey in Phase 3 and Phase 4. In Phase 3, monkeys could receive up to 50 raisins at 5 s intervals. In Phase 4, monkeys could receive up to 50 raisins at 2 s intervals. Errors bars indicate 95% confidence intervals.

(RT or AC), to determine whether one task or the other leads to the stronger emergence of self-control and whether general experience with one task (RT) can improve performance in another (AC). Experiment 4 addressed this issue.

The goal of Experiment 4 was to take naïve monkeys and specifically contrast performance in each of these two experimental procedures when they were presented for the first time to each monkey. More specifically, we were interested in whether experience with the RT task might improve performance on the AC task. Thus, monkeys first completed an AC phase, and then they were given extensive experience with the RT task before being reassessed on their performance in the AC task. Our prediction was

Table 5
Performance of each monkey in Experiment 4.

	AC Pretest	RT Phase 1	RT Phase 2	RT Phase 3	RT Phase 4		AC Post-test
	Mean # Raisins Obtained	Sessions to Criterion	Sessions to Criterion	Sessions to Criterion	Sessions to Criterion	Larger/Later Pieces Obtained	Mean # Raisins Obtained
Bias	1.6	1	1	1	5*	5/15	2.4
Gonzo	3.2	1	3	4	5*	0/15	2.6
Gretel	4.2	1	1	3	2	5/6	2.8
Bailey	6.8	1	3	3	5*	3/15	2.4
Benny	1.0	1	3	2	5*	1/15	1.0
Mason	1.6	1	3	6	5*	0/15	3.6

Note: The * indicates that a monkey did not reach criterion in that phase.

that such experience would improve AC performance in these monkeys, given that the results of Experiments 1–3 seemed to suggest that our more experienced monkeys who have performed the RT task now perform better on AC tasks than we reported previously.

5. Experiment 4

5.1. Method

5.1.1. Participants

Six new monkeys were included in this experiment (ages 9–17 years; 4 females, 2 males). These new monkeys had far less previous experience in cognitive and behavioral tests compared to the monkeys in the first three experiments. They had participated in only a few cognitive studies in our laboratory that involved different quantity judgments (Beran and Parrish, in press; Parrish et al., 2016, 2015a). One monkey (Mason) was trained on a touchscreen computer and had participated in several facial-recognition studies that involved discriminating conspecific faces (Pokorny and de Waal, 2009a,b; Pokorny et al., 2011). This was the first effort to assess their self-control using the RT and they had only very limited experience with the AC tasks used in Experiments 1–3. Husbandry and housing procedures with these monkeys were identical to those described in Experiment 1.

5.1.2. Apparatus

The apparatus for the RT and AC tasks previously described was used in this experiment.

5.1.3. Design and procedure

Monkeys alternated between the AC task and the RT task through a series of phases designed to assess performance in each task and in comparison to each other.

In the Pre-AC phase, three monkeys (Bias, Gonzo, and Gretel) completed five sessions of the AC task whereas the other three monkeys (Bailey, Benny, and Mason) completed 10 sessions of the AC task. These differing numbers of sessions were used to assess whether more experience with the AC task would generate faster acquisition of the RT task criteria. In these AC sessions, the first trial was a forced observation trial with five raisins accumulated before the pan could be opened. Then, monkeys received one test trial with up to 20 raisins delivered at a rate of two seconds per raisin, matching the "easiest" phase given in Experiment 3. The supply bowl of raisins remained visible throughout the trial, and the total trial duration was 60 s.

Next, the monkeys moved to the RT task, and we used the methods from Bramlett et al. (2012). In Phase 1 of the RT task, the monkeys received five forced observation trials with each food item (banana and carrot), presented in random order. In the five forced carrot trials, a 3 g piece of carrot was placed on the first (nearer) food bar. In the five forced banana trials, a 3 g banana slice was placed on the first food bar. In both of these forced observation trial types, nothing was placed on the second (farther) food bar. The arms were at 90° angles from each other, and the rotation speed led to a full rotation every 20 s. The baited food bar came within reach after 5 s. The criterion for moving to Phase 2 was collecting 10 items from the tray within the session.

In Phase 2, each session began with two forced observation trials. One forced observation trial presented 3 g of carrot on the first bar and nothing on second bar. On the other forced observation trial, a 9 g banana slice was placed on the second bar and nothing was placed on the first bar. On all trials, the first item came within reach after a 5 s delay and the second item came within reach after a 10 s delay. The total trial duration for these forced observation trials was 60 s. After the forced observation trials, the monkeys were presented with three trials in which a 3 g carrot slice came within reach first and a 9 g banana slice came within reach second and three trials in which the 9 g banana slice came within reach first and the 3 g carrot slice came within reach second. These trials were presented in randomized order. The arms on the apparatus again were at a 90° angle from each other. The total trial duration was 90 s. The criterion to move to Phase 3 was obtaining the banana slice in 11 of the last 12 trials across two sessions.

In Phase 3, the only change to sessions involved moving the second arm so that it was now 180°, rather than 90°, from the first arm. On these trials, the first food item arrived after a 5 s delay and the second arm arrived after a 15 s delay (instead of 10 s). All other details of this phase were the same as in Phase 2.

In Phase 4, we presented two banana slices on each trial. There were no forced observation trials. One banana slice was 3 g and the other was 12 g. There were six trials per session, half with the smaller piece of banana moving within reach first and half with the larger banana piece moving within reach first. The times for food arriving within reach again were 5 s and 15 s. The criterion for this phase was 11 of 12 trials obtaining the largest banana piece, at which point the monkey returned to the AC task in its next session. If a monkey did not pass this criterion after 5 sessions, the monkey still moved back to the AC task in the next session.

In the Post-AC Phase, the procedure was the same as in the Pre-AC Phase. A five-raisin forced observation trial was given first in each session, and then a single 20-raisin test trial with 2 s delivery rate was given.

5.2. Results

Table 5 outlines the results. There was not an improvement over time for any monkey in the Pre-AC phase, no matter whether five sessions or 10 sessions were presented, as all correlations of session number and number of raisins obtained for individual monkeys failed to reach statistical significance (all $p > 0.10$).

All monkeys met criterion for Phase 1, Phase 2, and Phase 3 of the RT task, and most did so quickly. Thus, all monkeys learned to let a low preference food item go past in order to obtain a high preference food item; although when only a low preference item was available, all monkeys took that item when it approached. However, Phase 4 with differing food quantities was difficult for these monkeys. None met the criterion for this phase, and the vast majority of trials ended when the monkeys selected the smaller first item rather than waiting for the larger second item. Thus, unlike in past research (Bramlett et al., 2012), these monkeys could not wait for a quantitatively larger reward. Finally, there was no evidence of improving in the AC task after RT training. There was no difference in the mean number of raisins obtained in the Pre-AC phase and the Post-AC phase for these six monkeys, $t(5) = 0.67$, $p = 0.53$.

5.3. Discussion

Contrary to our hypothesis, RT task training did not improve AC task performance in this group of fairly naïve and less-experienced capuchin monkeys. The AC task was quite difficult for them, suggesting limited capacities for accumulating food rewards through self-control behavior. In a final effort to instill self-control behavior, we presented these monkeys with the escalating accumulation procedure used in the earlier experiments with the other, more experienced monkeys in an attempt to improve self-control performance through further experience with the RT task.

6. Experiment 5

6.1. Method

6.1.1. Participants

The same six monkeys participated from Experiment 4.

6.1.2. Apparatus

The apparatus for the RT and AC tasks previously described was used in this experiment.

6.1.3. Design and procedure

Monkeys completed five sessions of the escalating AC task and then five sessions of the escalating RT task. These two tasks were highly similar to those presented in Experiment 1 to the other monkeys and involved presenting food pellets at different intervals.

In the escalating AC task, there was one forced observation trial at the start of each session, and then two test trials. The total trial duration was 120 s, pellet sets were accumulated every 5 s, and the number of accumulated items for each iteration were the same as those presented in Experiment 1 (see Table 1). We recorded the set that was selected by the monkey on each trial.

In the escalating RT task, there was one forced observation trial and then two test trials in each session. The total trial duration also was 120 s, and the tray made a full rotation every 10 s, thus bringing each food set within reach every 5 s. The two cups on the apparatus were located 180° from each other. Pellets were added to these cups according to the schedule for the RT task outlined in Table 1.

At the end of the RT task, all monkeys then were given five final sessions (one trial per day) of the item-by-item accumulation task with up to 20 raisins being delivered at a 2 s delivery rate, with accumulation continuing until the monkeys consumed any of the raisins.

6.2. Results

Table 6 presents the results of the experiment for each monkey. We conducted a 3-way repeated measures ANOVA with task (RT or AC), Session Number (1–5) and Trial Within Session (1st trial or 2nd trial) to analyze the results. The outcome of the analysis indicated that there was no main effect of task, $F(1, 5) = 0.10$, $p = 0.77$, $\eta p^2 = 0.02$, no main effect of trial number within session, $F(1, 5) = 0.14$, $p = 0.73$, $\eta p^2 = 0.03$, and no main effect of session, $F(4, 20) = 0.54$, $p = 0.71$, $\eta p^2 = 0.10$. There were no two-way interactions, all $F < 1.13$, $p > 0.07$. There was not a three-way interaction, $F(4, 20) = 1.85$, $p = 0.16$, $\eta p^2 = 0.27$.

Table 6
The mean number of additions to the set (maximum = 6.0) that was consumed by each monkey in each task, for each trial within sessions of Experiment 5.

	Rotating Tray Task		Accumulation Task	
	Trial 1	Trial 2	Trial 1	Trial 2
Bailey	4.4	3.4	5.5	4.2
Benny	1.6	1.2	1.6	1.4
Bias	3.4	4.4	3.6	4.0
Gonzo	2.0	2.2	1.2	1.6
Gretel	3.6	3.0	4.0	4.4
Mason	1.6	2.0	1.6	1.8

The monkeys did not show any improvement in the mean number of raisins accumulated on the accumulation task compared to the Post-AC phase of Experiment 4, $t(5) = 0.72$, $p = 0.50$. The additional experience with the escalating RT and AC tasks did not improve these monkeys' item-by-item accumulation abilities.

6.3. Discussion

The majority of the monkeys showed better success in this experiment than in Experiment 4, waiting for multiple escalating accumulations to occur in both the AC task and the RT task. This suggests that using increasingly larger additions to sets facilitates improvement in self-control, a finding also reported in Experiment 1. However, some monkeys (Benny and Mason) still performed poorly with both versions of the accumulation task. The present study showed no difference in performance between the two task types, despite our original predictions. Even after more successfully navigating the AC and RT tasks in this experiment, these naïve monkeys showed none of the improvements in item-by-item accumulation as we documented for the more experienced monkeys in the earlier experiments.

7. General discussion

Past research suggested that apes are capable of self-control when presented with tasks that require sustained delay maintenance in the face of appealing and immediately-available rewards (e.g., Beran, 2002; Beran and Evans, 2006; Parrish et al., 2014; Stevens et al., 2011), but such self-control has been less consistent with monkeys, in particular capuchin monkeys (Addessi et al., 2013; Evans et al., 2012; Paglieri et al., 2013). However, recent research (Bramlett et al., 2012) had presented a self-control task (the RT task) with a maintenance component that is presumably more intuitive in that subjects can visually track moving rewards throughout a trial and once a less-preferred food reward passes by the subject, that food reward is out of reach and thus less prepotent. Using this approach, it appeared that capuchin monkeys have better self-control than previously believed – when given the right type of test.

Our initial goal was to directly compare self-control tasks to show that some designs produce better levels of success than others in a species typically considered to be more impulsive than other primates (e.g., Addessi et al., 2011; Pelé et al., 2011). We expected that the RT (rotating tray) task again would lead to better performance than the repetition of the AC (accumulation) task that these monkeys already had been presented (Evans et al., 2012). However, we found that this was not true, and that in fact these monkeys had greatly improved in their capacity for tolerating delay in the AC task. Whether the number of items escalated with each addition (Experiment 1) or remained constant (Experiment 2), the monkeys did not show much difference in performance on the RT task compared to the AC task. There were consistencies in individual patterns of performance, though, with some monkeys generally performing better and others consistently responding impulsively. These individual differences might be particularly relevant for identifying potential interventions or behavioral correlates of impulsive behavior, and they highlight the importance of considering personality factors in behavior (for more discussion of this with regard to personality and selection bias in cognitive research with capuchin monkeys, see Morton et al., 2013a,b). Finally, we found that overall there were significant increases in performance on the current task compared to a previous assessment, perhaps indicating that continued exposure to these kinds of tasks plays a role in altering and improving self-control in nonhuman primates.

Because all of these monkeys were adults in both test periods with the accumulation task, it is unlikely that the improvements that were seen in the AC task were due to developmental maturation. However, it is perhaps the case that their improvement was the result of cognitive development derived from experimental experience. All monkeys in Experiments 1–3 were task-savvy from plenty of experience in a wide variety of cognitive and behavioral tests (e.g., Agrillo et al., 2014; Beran, 2008; Beran et al., 2008, 2012; Beran and Parrish, 2012; Beran and Smith, 2011; Evans et al., 2009, 2012, 2014; Parrish et al., 2015a,b). Simply being involved in cognitive-behavioral testing of any sort may have improved the monkeys' ability to sustain self-control.

Experiment 4 and Experiment 5, with new, task-naïve adult capuchin monkeys, directly manipulated and assessed the hypothesis that specific training and experience in certain kinds of self-control tasks may transfer to other tasks. This effort recognized that task design is a critical factor in trying to demonstrate self-control, given that humans (e.g., Duckworth and Kern, 2011; Reynolds and Schiffbauer, 2005; Schwarz et al., 1983; Toner et al., 1977), rats (e.g., Reynolds et al., 2002) and monkeys (Addessi et al., 2013; Blanchard and Hayden, 2015) sometimes fail to show a strong relation between performance on different kinds of self-control tasks, such as intertemporal choice tasks and delay of gratification tasks. There is strong interest in the idea that, at least in some contexts, improvements in self-control in one area may lead to improved self-control more broadly (e.g., Baumeister et al., 2006; Muraven, 2010; Muraven et al., 1999).

Despite these predictions, however, we saw little evidence that one task was better than the other when naïve monkeys were given the RT and AC versions of delay of gratification tasks. Further, we found no evidence to support that training on one self-control task led to increases in self-control on a different, unrelated self-control task. In Experiment 4, performance was low, and monkeys rarely showed the levels of delay maintenance reported for apes, or even for the more experienced monkeys tested in Experiments 1–3. We saw little evidence that learning to perform the RT task improved performance on the AC task. This null result sheds light on the data from Experiments 1–3, and on our past work with capuchin monkeys (e.g., Addessi et al., 2013; Bramlett et al., 2012; Evans et al., 2012; Paglieri et al., 2013) by highlighting that there may not be a simple facilitative relation between one task and another, even when tasks all appear to engage similar delay maintenance processes in monkeys. The data from Experiment 4 and 5 tell us that task choice may afford evidence of success in individual tasks without transfer of capabilities across tasks. However, two caveats are needed: first, it may be that the experience given to the naïve monkeys was not extensive enough, and that with more experience on one or both tasks, performance may then have increased substantially, and perhaps equivalently in both tasks. Second, perhaps these tasks do not share cognitive underpinnings, in which case the improvements seen in Experiments 1–3 by our more generally test-savvy monkeys compared to their own past experiences are the result of some other factors, one of which may simply be broad testing experiences in a variety of domains. One highly speculative idea is that perhaps greater experience with joystick testing procedures (see Evans et al., 2008) carries over to certain forms of manual testing. We are intrigued by this idea because the use of computerized apparatus, with the spatial discontiguities of response loci (hands on joysticks) versus stimulus loci (computer screen at a distance) and reward loci (pellet dispensers), instills some interesting spatial and temporal aspects that may afford more "intelligent" responding to manual tests such as those outlined in the present study.

These results also highlight that the present pattern of inconsistency in performance and a lack of relation between tasks might not be a uniquely human aspect of self-control training. However, these results also indicate that capuchin monkeys can be a useful model in better understanding the nature of self-control in a species for which many more uniquely human aspects can be controlled (e.g., social norms, cultural expectations, parental behavior, formal education, and moral codes regarding patience and waiting for something else). For example, one important outcome of this study that matches previous work with great apes (e.g., Parrish et al., 2014) is that temporal aspects of self-control tasks play a strong role in delay maintenance. The capuchin monkeys showed that what appears to most strongly dictate delay maintenance levels is the overall temporal delay rather than the number of potential items that could be obtained or the inter-item delivery rate. Such consistencies in these aspects of intertemporal choice and delay of gratification highlight that a broad comparative approach for assessing self-control allows for a more thorough evaluation of the biological and evolutionarily-shared aspects of this type of behavioral inhibition across species.

Acknowledgments

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