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Chimpanzees (*Pan troglodytes*) Can Wait, When They Choose To: A Study with the Hybrid Delay Task

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Abstract

Self-control has been studied in nonhuman animals using a variety of tasks. The inter-temporal choice (ITC) task presents choices between smaller-sooner (SS) and larger-later (LL) options. Using food amounts as rewards, this presents two problems: (i) choices of the LL option could either reflect self-control or instead result from animals' difficulty with pointing to smaller amounts of food; (ii) there is no way to verify whether the subjects would not revert their choice for the LL option, if given the opportunity to do so during the ensuing delay. To address these problems, we have recently introduced a new protocol, the hybrid delay task, which combines an initial ITC with a subsequent accumulation phase in which selection of the SS option leads to its immediate delivery, but choice of the LL option then leads to one-by-one presentation of those items that continues only as long as the subject does not eat any of the accumulated items (delay maintenance). The choice of the LL option therefore only reflects self-control when the number of items obtained from LL choices during the accumulation phase is higher than what could be received in the SS option. Previous research with capuchin monkeys demonstrated that their apparent self-control responses in the ITC task may have over-estimated their general self-control abilities, given their poor performance in the hybrid delay task. Here, chimpanzees instead demonstrated that their choices for the LL option in the ITC phase of the hybrid delay task were confirmed by their ability to sustain long delays during accumulation of LL rewards.

Keywords

Self-Control; Chimpanzees; Pan troglodytes; Intertemporal choice; Hybrid delay task; Delay of gratification

Introduction

Self-control occurs when an organism chooses (or waits to obtain) a more delayed, but better outcome rather than taking a more immediate, but less preferred outcome (Ainslie 1974; Logue, Forzano and Ackerman 1996; Rachlin and Green 1972). Situations in which self-control would be advantageous are numerous, as when an animal can forego eating

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immediately available food of low value to travel some distance to a better food patch, or when a subordinate can inhibit a (likely futile) attempt to mate in the presence of a more dominant animal and instead get a better mating opportunity later when the dominant animal has left the area. In our everyday lives, this is also frequently true, as one can wait a few minutes for a fresher cup of coffee rather than drink the old coffee available now, or one can wait decades for money saved for retirement to accrue rather than spending that money immediately at each pay period. In the laboratory, a variety of self-control tests have been given to humans, with some individuals showing successful self-control and others showing lack of self-control, or what is called impulsivity (Logue 1988). In fact, some of the most maladaptive human behaviors are the result of impulsive behaviors where self-control and other forms of behavioral inhibition are most needed (e.g., smoking, gambling, overeating, risky sexual behavior; Baumeister and Vohs 2004; Mischel 1974; Tangney, Baumeister and Boone 2004; White et al. 1994).

There are a number of ways to assess self-control across species. In one test, the subject can be given a food item, and then be allowed to trade that item (rather than eating it) for something better, and this test has been given to a number of species to varied degrees of success (e.g., Auersperg, Laumer, & Bugnyar, 2013; Dufour, Pele, Sterck, & Thierry, 2007; Dufour, Wascher, Braun, Miller, & Bugnyar, 2012; Pele, Dufour, Micheletta, & Thierry, 2010). Alternately, one can use a test in which a lower preference reward is offered immediately, and is available continuously, whereas a higher preference reward is offered after some time delay as long as the immediate item is not consumed. This test, sometimes called the “marshmallow test,” has been used with children and with other species (e.g., Beran, Savage-Rumbaugh, Pate, & Rumbaugh, 1999; Grosch & Neuringer, 1981; Mischel, 1974, 1981; Mischel, Shoda, & Rodriguez, 1989).

Often human participants are tested for self-control using the intertemporal choice task (ITC), in which discrete choices are made between two options, one of which leads to a less preferred/sooner or smaller/sooner (SS) outcome versus a more preferred/later or larger/later (LL) outcome (Logue 1988; Logue et al. 1996; Rachlin 1995; Rachlin and Green 1972). This task has shown many important features of human self-control and impulsivity (e.g., Green, Fry and Myerson 1994; Lawyer et al. 2010; Logue et al. 1996). This kind of task has also been used with some nonhuman animal species, and again has shown that other animals vary in their levels of self-control (e.g., Addessi, Paglieri and Focaroli 2011; Cheng et al. 2002; Chelonis et al. 1994; Green and Estle 2003; Logue and Pena-Correal 1985; Mazur 2007; Stevens, Hallinan and Hauser 2005; Stevens and Mühlhoff 2012; Tobin et al. 1996; Tobin, Chelonis and Logue 1993; van Haaren, van Hest and van de Poll 1988).

Early research using the ITC task relied on arbitrary stimuli as the response stimuli that locked an animal (or human) into either the SS or LL outcome. Thus, participants had to learn the contingencies of selecting these stimuli, and often the result was that the SS outcome was more preferred in nonhuman species, although sometimes increased LL choices would occur if animals were given, for example, the option to pre-commit to only being offered the LL choice at a later time (see Rachlin and Green 1972). More recently, a trend has emerged in the comparative literature to replace arbitrary stimuli with actual food amounts, so that animals choose either a larger amount of food that is more delayed in its delivery or a smaller amount of the same food that is given more immediately (e.g. Rosati et al. 2007). The aim of this task is to find the point of indifference, in which the animal chooses each option equally often, and the longer the delay is for the LL choice, the more “self-controlled” the subject is reported to be. This form of the ITC task has demonstrated that some species show relatively high levels of self-control, even in relation to humans given the exact same test (e.g., Rosati et al. 2007). However, this type of experiment has a potential design flaw that makes interpretation of these data difficult because there is no way to distinguish whether an animal's selection of the LL option is a choice to delay reward (i.e., to show self-control) or an attempt to point at more food versus less food. The latter explanation is highly likely, at least early in these kinds of experiments, because animals spontaneously choose more food over less food, and this is true across all genera tested to date, from insects and amphibians to birds and mammals, including many primate species (e.g., Abramson et al. 2011; Beran 2001, 2004; Evans et al. 2009; Hanus and Call 2007; Perdue et al. 2012; Uller et al. 2003). So, if a subject consistently points to the larger food amount or makes any response that is directed to a larger amount of food, one cannot know what motivation underlies this behavior. What we do know is that it is very difficult for animals to inhibit pointing to larger food amounts versus smaller ones, even when doing so is the only way to actually receive the larger amount of food (e.g., Boysen and Berntson 1995; for overview of this test given to many species, see Shifferman 2009). Thus, ITC tasks that use food amounts as part of the response stimuli are ambiguous as to what they might show about actual self-control of participants (see Addessi et al. in press; Genty, Karpel and Silberberg 2012).

In addition, in most ITC tasks, choosing the LL option does not require any inhibition during delay, since subjects cannot alter their choice: the LL option, once selected, is kept outside their reach, and will be delivered only once the delay is expired, whereas the SS option is no longer available. This procedure separates delay choice from delay maintenance, so there is no way to know, without further testing on different tasks, whether LL choices are sustainable for the animals that made them – that is, we do not know whether those animals would be able to actually sustain the chosen delay, if given the opportunity to reconsider their choice. Thus, the ITC task provides an indication of the subjects' *choice to attempt* to wait, but not on their *ability* to do so, whereas successful self-control typically requires both.

These problems were illustrated with a study using capuchin monkeys and a new kind of self-control test called the hybrid delay task (Paglieri et al. 2013). The hybrid delay task begins by offering subjects two response options, an SS and an LL option consisting of visible food items, as in a standard ITC task. However, after selection of one of those sets, a secondary phase of the trial begins. If the SS is selected, the reward is given immediately, and therefore there is no delay. However, if the LL is selected, then an accumulation process begins, whereby each item in the LL set is transferred, one at a time, to within reach of the subject until they take the items. This accumulation process has been used as a self-control test in its own right in a number of studies with children (e.g., Toner and Smith 1977) and was then modified into a version used with chimpanzees (Beran 2002; Beran and Evans 2006; Evans and Beran 2007) and other nonhuman animals (Addessi et al. in press; Anderson, Kuroshima and Fujita 2010; Evans et al. 2012; Pelé et al. 2011; Stevens et al. 2011; Vick, Bovet and Anderson 2010). Thus far, some species perform very well in accumulating food items by inhibiting taking the food array as it accumulates until a large number of items are available (e.g., Beran 2002; Beran and Evans 2006), and some species may even strategically act to improve their performance (e.g., Evans and Beran 2007), although not all species are proficient with this test (e.g., Vick et al. 2010). The critical feature of the accumulation task is that there is no ambiguity about what it purports to measure, as the duration of waiting to take the accumulating reward is a clear measure of self-control through the delay of gratification of the subject. This is why it was added to the hybrid delay task, as a means to discern, within the same trial, whether choice of the LL option is indicative of self-control (as would be evident if subjects then waited to accumulate what they just indicated they were willing to wait to get) or instead indicative of a prepotent response to more food in the choice phase and/or of an inability to sustain prolonged inhibition of prepotent responses in the face of tempting stimuli. One of the essential features of the task is that it also allows for objectively scoring this kind of response as an error, a designation that cannot be made in any of the tasks that are used to assess self-control. It also requires only minimal training for animals to learn the contingencies of their choice behavior and to learn about the consequences of taking items as they accumulate.

Capuchin monkeys (*Cebus apella*) from two laboratories were given the hybrid delay task (Paglieri et al. 2013). Previous to that experiment, there was conflicting evidence about the self-control abilities of this species, with performance on a food-stimulus version of the ITC task showing relatively high levels of self-control (Addessi et al. 2011), but performance on an accumulation task showing relatively poor performance and relatively high levels of impulsivity (Evans et al. 2012). In the hybrid delay task, monkeys frequently chose the delayed reward but then failed to wait for it, due to poor delay maintenance. With experience, performance improved, but the overall results indicated that the high error rates observed (in which LL was selected, but then fewer items than in the SS option were accumulated before being taken) were indicative of the need for cautious interpretation of data coming from this form of the ITC task, at least with capuchin monkeys.

The purpose of the present study was to expand the use of the hybrid delay task to another nonhuman primate species, and specifically to select a species for which more proficient performance might be expected. We chose to test chimpanzees (*Pan troglodytes*) given their past successes with both ITC tasks (Rosati et al. 2007) and accumulation tasks (Beran 2002; Beran and Evans 2006). We predicted that chimpanzees, unlike capuchin monkeys, would accumulate enough items after selecting the LL option to justify those selections, and such data would confirm that some species can make choices between SS and LL food options decisionally, rather than through prepotent, and potentially impulsive, responses that can be misdiagnosed in the food-item ITC task as being self-control responses. If chimpanzees were successful, this also would provide further evidence of their self-control abilities relative to capuchin monkeys. Critically, as with the hybrid delay test given to capuchin monkeys (Paglieri et al. 2013), we tested chimpanzees in two laboratories to ensure that the results would generalize across testing locations and provide a more robust assessment of the inhibitory abilities of this species.

Methods

Participants

Four chimpanzees housed at the Language Research Center of Georgia State University participated in this study: females: Lana – 41 years, Panzee – 26 years; males: Sherman – 38 years, Mercury – 25 years. These chimpanzees had participated in multiple quantity judgment and self-control studies prior to the present experiment (e.g. Beran 2001, 2002, 2004; Beran, Evans and Hoyle 2011; Beran and Evans 2006; Evans and Beran 2007). Fifteen additional chimpanzees housed at the Yerkes National Primate Research Center (YNPRC) of Emory University also participated in this study: females: Julie – 18 years, Cissie – 36 years, Brandy – 27 years, Foxy – 44 years, Brodie – 28 years, Callie – 21 years, Edwina – 21 years, Melissa – 31 years, Sylvia – 19 years, Katrina – 25 years, Frannie – 20 years, and Faye – 20 years; males: Artemus – 21 years, Socrates – 25 years, and David – 35 years. All chimpanzees were housed in social groups between 2 and 16 individuals but they were temporarily separated from their groups during test sessions. All of the YNPRC chimpanzees have been previously involved in studies of communication and a variety of cognitive studies (Leavens & Hopkins 1998; Leavens, Hopkins and Thomas 2004; Leavens et al. 2004; Russell et al. 2011), but none had received any previous testing on the hybrid task. Chimpanzees participated for preferred food treats. Otherwise, they were maintained on their normal diet of fruit, vegetables, and primate chow. No food or water deprivation was used.

Materials

We used a test bench with a sliding tray to present the initial choice between two sets of food items (honey flavored cereal pieces for the LRC chimpanzees and grape slices for the Yerkes chimpanzees). Subjects were familiar with the test bench, as it was used in several previous studies. For the LRC chimpanzees, food sets were presented in small clear bowls (approximately 15 cm in diameter) on opposite ends of the tray. An additional bowl sat on the floor next to the bench, positioned so that both the chimpanzee and the experimenter could access its contents at any time. For the YNPRC chimpanzees, food sets were presented on small plates (approximately 10 × 10 cm square). A clear plastic tube with a stopper at the midpoint was placed half way through the mesh of the caging. This allowed the grapes to accumulate in the tube without falling through while chimpanzees were able to pull in the tube at any time to eat the grapes. The differences in materials used between the two groups were the result of the previous experiences these groups had with an accumulation task, and we wanted to take advantage of that experience to allow for easier understanding of the task on the part of the individual chimpanzees in both groups.

Procedures

Every trial consisted of two parts – the choice part and the accumulation part. In the choice part, the experimenter placed 4 food items in one bowl/plate on the tray and twelve food items in the opposite bowl/plate (left/right position was randomized across trials). The experimenter then slid the tray forward, allowing the chimpanzee to make a choice by pointing to one of the two food sets. The experimenter removed whichever set the chimpanzee did not choose and placed it behind the bench and out of view. If the chimpanzee chose the set of four items (SS), then in the accumulation part of the trial, the experimenter transferred the four items, all at once, into the bowl on the floor (LRC) or tube in the mesh (YNPRC). However, if the chimpanzee chose the set of 12 items (LL), then in the accumulation part the experimenter transferred the twelve items, one at a time, into the bowl on the floor or tube in the mesh. If at any point during the transfer of items, the chimpanzee began eating the items, then the experimenter stopped transferring items and the trial was over. Each trial in a session was of a fixed duration, meaning that the same amount of time passed between the start of every trial and the start of the subsequent trial. This duration depended on the experimental phase (see below for more details).

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We conducted three test phases in which we varied the duration of time required to accumulate the larger set of food items. In Phase 1, the experimenter transferred food items from the larger set at a rate of one item every 3 seconds (as in Paglieri et al. 2013). Thus, the total amount of time required to accumulate all twelve items was 36 seconds. In this phase, the total trial duration (the time that passed between the beginning of one trial and the beginning of the next) was 120 seconds, and we conducted eight trials per session. The first two trials of the session were forced trials in which only one of the two bowls/plates of food items was presented (one trial involving four items, and one trial involving twelve items, randomly ordered). These were presented to make sure the subjects understood the outcomes of the two choices. The remaining six trials were test trials like those described above. The only difference between the procedure for forced trials and the procedure for test trials was that in forced trials for the LRC chimpanzees, the food items were transferred to a bowl just out of reach of the chimpanzee and the experimenter slid the bowl to the chimpanzee after all items were in the bowl. For the YNPRC chimpanzees, the tube was placed on the test bench while the grapes were transferred. Upon completion, the tube was passed through the mesh. Chimpanzees completed five 8-trial sessions in this phase before beginning Phase 2, resulting in a total of 30 test trials and 10 forced trials.

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Phase 2 was similar to Phase 1 except that the experimenter took 10 seconds to transfer each item in the larger set to the bowl within reach of the chimpanzee. Because the total time required to obtain all twelve items in this phase was longer (120 seconds), we increased the total trial duration to 180 seconds. Also, due to time restraints for testing the LRC chimpanzees and the previous experience these chimpanzees had with the forced trials, we reduced the number of trials to four per session, all of which were test trials. LRC chimpanzees completed five 4-trial sessions in this phase before beginning Phase 3, resulting in a total of 20 test trials. YNPRC chimpanzees were not limited by the same time restraints and therefore completed the same amount of test sessions and trials as in Phase 1.

In Phase 3, the experimenter took 20 seconds to transfer each item when the larger set had been selected, and so the total amount of time required to accumulate all twelve items in this phase was 240 seconds. To accommodate this longer duration, we again adjusted the total duration of trials to 300 seconds. For the LRC chimpanzees the number of trials per session remained at four, but we reinstated the forced trials to be sure that the chimpanzees still knew what happened when they selected each option. Two forced trials were conducted at the beginning of the session, exactly as in Phase 1, and were followed by two test trials. LRC chimpanzees completed ten 4-trial sessions in this phase resulting in a total of 20 test trials and 20 forced trials. As with Phase 1 and 2, YNPRC chimpanzees were not limited by time constraints and therefore completed the same number of test sessions and trials.

Analyses

We conducted two analyses to assess the chimpanzees' performance in the two-part hybrid delay test trials. First, for each chimpanzee, we conducted a binomial test (two-tailed, $\alpha = .05$) to assess whether the proportion of choices of the set of 12 items differed significantly from chance (i.e., .50). Also, for each chimpanzee, we conducted a one-sample *t*-test (two-tailed, $\alpha = .05$) to assess whether the number of accumulated items (following selection of the set of 12 items) differed significantly from four (the amount contained in the smaller, immediately available set).

Results

Table 1 summarizes the performance of the LRC chimpanzees in the choice and accumulation parts of the hybrid delay test. LRC chimpanzees chose the set of 12 items in nearly all trials of all three phases (all $p < 0.001$). When these chimpanzees chose the set of 12 items, they then accumulated significantly more items than four in all three phases (all $t > 2.2$, $p < 0.05$). Only rarely did these chimpanzees accumulate four items or fewer after choosing the set with 12 items (1% of Phase 1 trials, 1% of Phase 2 trials, and 10% of Phase 3 trials). This was an outcome that could be objectively scored as an error because it involved the chimpanzees receiving an amount of food from the LL set that was equal to or less than what could have been received with no delay at all by selecting the SS set.

Table 2 summarizes the performance of the YNPRC chimpanzees. None of these chimpanzees showed a significant preference for the SS option. Some of the YNPRC chimpanzees chose the set of 12 items in a proportion of trials exceeding .50 (all $p < 0.05$). Five of these chimpanzees did so in Phase 1, three chimpanzees did so in Phase 2, and three chimpanzees did so in Phase 3. When these chimpanzees did choose the larger set, many of them accumulated greater than four food items (all $t > 2.29$, $p < 0.01$). In Phase 1, all 15 YNPRC chimpanzees exhibited this pattern. Eleven chimpanzees also did so in Phase 2, and eight chimpanzees did so in Phase 3. Only one individual (Foxy) chose the set of 12 items significantly more often than 50%, but then did not accumulate significantly more than four items across trials (she did this in Phase 1 and Phase 3). YNPRC chimpanzees chose the set of 12 items and then accumulated four items or less in 7% of the trials in Phase 1 trials, 17% of the trials in Phase 2, and 32% of trials in Phase 3.

We observed that six of the Yerkes chimpanzees exhibited substantial biases for one side of the test apparatus during the choice part of trials (Table 2a). Therefore, we conducted a post-hoc examination of all of the chimpanzees' quantity judgment capacities to assess whether they could discriminate between the quantities presented in the hybrid task. In this test, 12 items and 4 items were presented on every trial, and the selected set was immediately given to the chimpanzees. The accumulation tube was not present, and so the optimal response was to always choose the 12 items. Three of the six chimpanzees with the extreme side biases, plus two chimpanzees that did not exhibit a side bias in the hybrid task, did not choose 12 items over 4 items in a statistically significant portion of trials in either of two test sessions that were administered (two-tailed binomial test, $p > 0.05$; Table 2). We therefore did not consider the data of these five individuals when discussing the results of the study because we could not be confident that these chimpanzees would reliably choose more food over less food even without the need for delay of gratification.

Comparative Analysis of Capuchins and Chimpanzees

Since, in Phase 1, the basic parameters of the task (in terms of experimental protocol, reward size, accumulation rate, and number of trials per session) were identical to those used with capuchin monkeys in Study 1 of Paglieri et al. (2013), this allowed for some inter-species comparison in performance on the hybrid delay task. We performed a Kruskal-Wallis one-way ANOVA on the percentages of LL choices and mean items accumulated by each animal in Phase 1 (for chimpanzees) and in Study 1 (for capuchins; data from Paglieri et al. 2013), with the four different groups as the between-subjects variable (LRC chimpanzees, YNPRC chimpanzees [excluding individuals that did not pass the post hoc quantity judgment test], LRC capuchins, Rome capuchins). Regarding LL choices, LRC chimpanzees opted for the LL option much more often than all other groups, $\chi^2 = 20.543$, df = 3, $p < .001$ ($\%LL^{LRC\text{-}Pan} = 99.3$, $\%LL^{YERK\text{-}Pan} = 65.9$, $\%LL^{LRC\text{-}Cebus} = 66.9$, $\%LL^{ROME\text{-}Cebus} = 53.2$; Mann Whitney U test, $p < .01$ for all pairwise comparisons between LRC chimpanzees and other groups), whereas YNPRC chimpanzees differed, in terms of delay choice, from Rome capuchins, but not LRC capuchins. However, both groups of chimpanzees clearly outperformed capuchins in the accumulation phase of the task, $\chi^2 = 24.499$, $p < .0001$ ($Acc^{LRC\text{-}Pan} = 11.97$, $Acc^{YERK\text{-}Pan} = 10.45$, $Acc^{LRC\text{-}Cebus} = 4.71$, $Acc^{ROME\text{-}Cebus} = 2.75$; Mann Whitney U test, $p < .05$ for all pairwise comparisons between chimpanzees and capuchins). Additionally, LRC chimpanzees outperformed YNPRC chimpanzees, and LRC capuchins outperformed Rome capuchins, all $p < .05$. Moreover, our results show that chimpanzees maintained high accumulation performance even with inter-item intervals (10 s and 20 s) that, according to current evidence, are well beyond the tolerance exhibited by all capuchins tested to date (Addessi et al. in press; Anderson et al. 2010; Evans et al. 2012).

Discussion

Overall, chimpanzees performed differently than capuchin monkeys in the hybrid delay task. Capuchin monkeys chose the delayed reward, but then often failed to maintain that choice long enough to obtain a number of rewards greater than what was available in the immediate option (Paglieri et al. 2013). Chimpanzees (particularly those from the LRC) chose the delayed reward, and then maintained that choice. This represents a species difference in self-control, and one that matches that seen in some previous reports (e.g., the accumulation task; Beran 2002; Beran and Evans, 2006; Evans et al. 2012). However, this species difference, like those seen in other cognitive domains, may not be a sharp difference but instead a difference that interacts with other relevant variables such as rearing, experience, and individual differences in cognitive ability.

The performance of LRC chimpanzees was clear and consistent. They chose the LL option, and then waited for the accumulation to complete before they began eating the food items. This result confirms that LRC chimpanzees were not pointing to the larger amount of food solely because they wanted that food immediately. These chimpanzees, however, are unusual in their rearing histories relative to most captive apes, having been language-trained (e.g., Rumbaugh 1977; Rumbaugh & Washburn 2003; Savage-Rumbaugh 1986). However, it is also the case that chimpanzee Mercury is *not* a language-trained chimpanzee with the same rearing experiences as his conspecifics at the LRC but he nonetheless performed very well on these tasks.

Some YNPRC chimpanzees also showed this adaptive pattern of responding, but there were clearly more individual differences among this group of apes. Some of these chimpanzees did not show a preference, even without any delay, for more food items over less food items. This was odd, given that most great apes that have been tested will point to more food rather than less food (e.g., Beran, 2001; Hanus and Call, 2007; Russell et al. 2011), but the side biases that these chimpanzees exhibited likely accounted for this oddity. Excluding those individuals, it was still the case that some YNPRC chimpanzees showed no preference between the SS and LL outcomes, although in all cases where there was a preference, it was a preference for the LL option. Crucially, though, all of these chimpanzees, when they chose the LL option, then waited for at least 4 items on average to accumulate before taking the rewards. This is objectively a successful outcome in terms of maximizing the food that could be obtained between the SS and LL options. Thus, even some of these less test-experienced chimpanzees showed a behavioral pattern that indicated choice of the LL was decisional rather than impulsive.

The overall results of both groups of chimpanzees confirm that at least one nonhuman species can successfully navigate the demands of the hybrid delay task by choosing the LL option with prepotent food items constituting the items in the choice options, and then waiting to get enough of those food items during the accumulation process to justify that choice of the LL option. This is delay choice followed by delay maintenance, and our contention is that pattern must occur to confirm that LL choices that are made when prepotent stimuli constitute the choice sets are truly reflective of self-control. Thus, we conclude that chimpanzees do exhibit a multi-faceted form of self-control that is both decisional in terms of the ITC choices that are made and controlled in terms of the delay maintenance that occurs after choice of the LL option has been made. Their performance clearly contrasts with that of capuchin monkeys, which were not as successful in the maintenance part of the hybrid delay task, as they often chose the LL option but then failed to validate that choice by obtaining more food than they could have received by instead choosing the SS option (Paglieri et al. 2013).

That the chimpanzees tested in this experiment were largely successful can be taken as complementary evidence of self-control abilities in past work with chimpanzees using intertemporal choices tasks (e.g., Rosati et al. 2007), despite the methodological issues that arise from using that form of the ITC task. However, the present positive results do not necessarily confirm previous claims using the ITC test about the degree to which chimpanzees or other animals show self-control relative to other species, including humans, because those relative comparisons can as easily reflect impulsive responses on the basis of the prepotent stimuli as they reflect self-control responses. Therefore, we encourage future research efforts that include the use of food stimuli as part of the choice options in an ITC task to add the accumulation component and thereby adopt the hybrid delay task. Otherwise, claims that responses to the LL option in the ITC task reflect self control or "patience" are prone to overestimation of those capacities due to the inherent drive of animals to point to or try to obtain larger amounts of food over smaller amounts. Of course, alternative tests exist that are not subject to that criticism, such as tests in which animals trade one food item for a larger or better item (e.g., Pelé et al. 2010, 2011), or tests where animals either transport one edible item to another location to use it as a tool to obtain a second, better item (e.g., Evans and Westergaard 2006) or have to travel through space and pass by less preferred rewards to get to more preferred rewards (e.g., Stevens et al. 2005). These creative tests also provide insights into the nature of self-control in animals, and help provide a fuller comparative account of this form of behavioral inhibition. The hybrid delay task joins those other tasks, as well as the ITC task, as part of a developing, comprehensive suite of tasks for uncovering the evolutionary foundations of our own self-control.

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Table 1

LRC chimpanzees

a. Choice part

	Inter-item interval for accumulation					
	3s (Phase 1)		**10s (Phase 2)**		**20s (Phase 3)**	
	% choice of 12 items	**binomial test (n = 30)**	**% choice of 12 items**	**binomial test (n = 20)**	**% choice of 12 items**	**binomial test (n = 20)**
Lana	100.00	$p < .001$	100.00	$p < .001$	100.00	$p < .001$
Mercury	100.00	$p < .001$	100.00	$p < .001$	95.00	$p < .001$
Panzee	100.00	$p < .001$	100.00	$p < .001$	90.00	$p < .001$
Sherman	96.67	$p < .001$	95.00	$p < .001$	100.00	$p < .001$

b. Accumulation part

	Inter-item interval for accumulation					
	3s (Phase 1)		**10s (Phase 2)**		**20s (Phase 3)**	
	mean items	**one-sample t test**	**mean items**	**one-sample t test**	**mean items**	**one-sample t test**
Lana	12.00	N/A	11.65	$t(19) = 42.1^{***}$	10.05	$t(19) = 19.95^{***}$
Mercury	12.00	N/A	10.75	$t(19) = 10.28^{***}$	11.58	$t(18) = 36.64^{***}$
Panzee	12.00	N/A	11.95	$t(19) = 159.0^{***}$	11.33	$t(17) = 32.07^{***}$
Sherman	11.86	$t(28) = 120.65^{***}$	10.58	$t(18) = 12.92^{***}$	5.70	$t(19) = 2.21^{*}$

Note:

*** $p < .001$;

* $p < .05$; N/A = not applicable (a t-test could not be conducted due to zero variance)

Table 2

Yerkes chimpanzees

a. Choice part

	Inter-item interval for accumulation					
	3s (Phase 1)		**10s (Phase 2)**		**20s (Phase 3)**	
	% choice of 12 items	**binomial test (n = 30)**	**% choice of 12 items**	**binomial test (n = 30)**	**% choice of 12 items**	**binomial test (n = 30)**
Artemus	73	$p = .016$	80	$p = .001$	63	$p = .200$
Brandy	*60*	$p = .362$	*63*	$p = .200$	*57*	$p = .585$
Brodie[S]	67	$p = .099$	53	$p = .856$	53	$p = .856$
Callie	*57*	$p = .585$	*67*	$p = .099$	*57*	$p = .585$
Cissie	93	$p < .001$	77	$p = .005$	93	$p < .001$
David[S]	*53*	$p = .856$	*53*	$p = .856$	*63*	$p = .200$
Edwina[S]	60	$p = .362$	60	$p = .362$	53	$p = .856$
Faye[S]	60	$p = .362$	57	$p = .585$	50	$p = 1.000$
Foxy	70	$p = .043$	47	$p = .856$	77	$p = .005$
Frannie	53	$p = .856$	60	$p = .362$	57	$p = .585$
Julie	60	$p = .362$	73	$p = .016$	70	$p = .043$
Katrina[S]	*73*	$p = .016$	*53*	$p = .856$	*63*	$p = .200$
Melissa	63	$p = .200$	67	$p = .099$	47	$p = .856$
Socrates[S]	*73*	$p = .016$	*67*	$p = .099$	*50*	$p = 1.000$
Sylvia	60	$p = .362$	63	$p = .200$	57	$p = .585$

b. Accumulation part

	Inter-item interval for accumulation					
	3s (Phase 1)		**10s (Phase 2)**		**20s (Phase 3)**	
	mean items	**one-sample t test**	**mean items**	**one-sample t test**	**mean items**	**one-sample t test**
Artemus	11.55	$t(21) = 16.60^{***}$	10.57	$t(23) = 17.41^{***}$	5.42	$t(18) = 1.74^{ns}$
Brandy	*11.72*	$t(17) = 27.80^{***}$	*9.05*	$t(18) = 17.28^{***}$	*2.88*	$t(16) = -2.38^{od}$

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b. Accumulation part

	Inter-item interval for accumulation					
	3s (Phase 1)		10s (Phase 2)		20s (Phase 3)	
	mean items	**one-sample t test**	**mean items**	**one-sample t test**	**mean items**	**one-sample t test**
Brodie	11.10	$t(19) = 11.46^{***}$	11.56	$t(15) = 37.17^{***}$	5.81	$t(15) = 1.43^{ns}$
Callie	*12.00*	*N/A*	*12.00*	*N/A*	*10.06*	$t(16) = 5.78^{***}$
Cissie	11.46	$t(27) = 23.70^{***}$	8.78	$t(22) = 5.48^{***}$	6.00	$t(27) = 2.90^{**}$
David	*11.50*	$t(15) = 15.0^{***}$	*9.51*	$t(15) = 16.01^{***}$	*8.63*	$t(18) = 5.29^{***}$
Edwina	11.11	$t(17) = 11.66^{***}$	9.83	$t(17) = 5.87^{***}$	6.94	$t(15) = 2.30^{*}$
Faye	11.72	$t(17) = 27.80^{***}$	12.00	N/A	11.40	$t(14) = 18.50^{***}$
Foxy	5.24	$t(20) = 1.14^{ns}$	2.14	$t(13) = -7.32^{od}$	2.35	$t(22) = -4.91^{od}$
Frannie	9.07	$t(14) = 4.26^{**}$	2.50	$t(17) = -2.28^{od}$	1.00	N/A
Julie	12.00	N/A	11.95	$t(21) = 175.0^{***}$	11.10	$t(20) = 11.73^{***}$
Katrina	*11.95*	$t(21) = 175.0^{***}$	*11.88*	$t(15) = 92.22^{***}$	*11.95*	$t(18) = 151^{***}$
Melissa	12.00	N/A	10.05	$t(19) = 8.67^{***}$	7.60	$t(14) = 3.96^{**}$
Socrates	*11.00*	$t(21) = 10.14^{***}$	*6.95*	$t(19) = 3.69^{**}$	*2.80*	$t(14) = -2.17^{od}$
Sylvia	9.28	$t(17) = 8.44^{***}$	2.89	$t(18) = -5.50^{od}$	1.94	$t(16) = -6.80^{od}$

Note:

^{s}exhibited a side bias in > 70% of trials;

$^{***}p < .001$;

$^{**}p < .01$;

$^{*}p < .05$;

^{ns}not significant;

^{od}significant in the opposite direction; N/A = not applicable (a t-test could not be conducted due to zero variance); italicized = failed to choose 12 items over 4 items in a post-hoc quantity judgment test