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Chimpanzees Can Point to Smaller Amounts of Food to Accumulate Larger Amounts But They Still Fail the Reverse-Reward Contingency Task

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Abstract

The reverse-reward contingency task presents two food sets to an animal, and they are required to choose the smaller of the two sets in order to receive the larger food set. Intriguingly, the majority of species tested on the reverse-reward task fail to learn this contingency in the absence of large trial counts, correction trials, and punishment techniques. The unique difficulty of this seemingly simple task likely reflects a failure of inhibitory control which is required to point towards a smaller and less desirable reward rather than a larger and more desirable reward. This failure by chimpanzees and other primates to pass the reverse-reward task is striking given the self-control they exhibit in a variety of other paradigms. For example, chimpanzees have consistently demonstrated a high capacity for delay of gratification in order to maximize accumulating food rewards in which foods are added item-by-item to a growing set until the subject consumes the rewards. To study the mechanisms underlying success in the accumulation task and failure in the reverse-reward task, we presented chimpanzees with several combinations of these two tasks to determine when chimpanzees might succeed in pointing to smaller food sets over larger food sets and how the nature of the task might determine the animals' success or failure. Across experiments, three chimpanzees repeatedly failed to pass the reverse-reward task, whereas they accumulated nearly all food items across all instances of the accumulation self-control task, even when they had to point to small amounts of food to accumulate larger amounts. These data indicate that constraints of these two related but still different tasks of behavioral inhibition are dependent upon the animals' perceptions of the choice set, their sense of control over the contents of choice sets, and the nature of the task constraints.

Keywords

Self-control; Reverse-reward contingency; Delay of gratification; Accumulation task; Chimpanzees

The reverse-reward contingency task is a problem presented to nonhuman animals in which a subject must choose the smaller of two food sets in order to receive the larger food set. Crucially, the task requires the quantity discrimination skills to differentiate set size and the behavioral inhibition to select a smaller food set in the presence of a larger food set

(Shifferman, 2009). Originally designed to test deception in chimpanzees (*Pan troglodytes*), the reverse-reward task first was presented in a social context, such that a partner animal received the food set chosen by the subject animal (Boysen & Berntson, 1995). Thus, it was in the subject's best interest to select the smaller set, thereby earning the larger food amount for itself. Despite the impressive cognitive capacities demonstrated by the chimpanzees first tested on the reverse-reward task (e.g., advanced numerical competency and symbol acquisition, Boysen, 1993; Boysen & Berntson, 1989), they failed to learn the contingencies of the task, repeatedly choosing the larger of the two food sets that was then delivered to the partner animal. Intriguingly, the substitution of Arabic numerals for actual food items resulted in optimal performance, with the symbol-trained chimpanzee Sheba immediately solving the task (but subsequently failing with the re-introduction of food stimuli).

This paradigm has been extended to a variety of primate species, including lemurs (*Eulemur fulvus*, *macaco*: Genty, Palmier, & Roeder, 2004; Genty & Roeder, 2007), squirrel monkeys (*Saimir sciureus*: Anderson, Shunji, & Fujita, 2000; Anderson, Awazu, & Fujita, 2004), mangabeys (*Cercocebus torquatus lunulatus*: Albiach-Serrano, Guillen-Salazar, & Call, 2007), capuchin monkeys (*Cebus apella*: Addessi & Rossi, 2010), macaques (*Macaca fuscata*: Silberberg & Fujita, 1996; *Macaca mulatta*: Murray, Kralik, & Wise, 2005), and all four species of great apes (*Gorilla*, *Pan paniscus*, *Pan troglodytes*, and *Pongo pygmaeus*: Boysen, Mukobi, & Berntson, 1999; Shumaker, Palkovich, Beck, Guagnano, & Morowitz, 2001; Uher & Call, 2008; Vlamings, Uher, & Call, 2006). When afforded a great deal of experience with the task contingencies, chimpanzees and other primate species have demonstrated some ability to successfully point to the smaller food set, with substantial individual differences within and between species (e.g., Albiach-Serrano et al., 2007; Murray et al., 2005; Vlamings et al., 2006). For example, rhesus macaques (*Macaca mulatta*) overcame their predisposition to select the larger food set and successfully learned to choose the smaller set following a large number of trials (an average of 1087 trials, or 54 testing days, to demonstrate above-chance performance; Murray et al., 2005). Modified reverse-reward procedures, in which qualitative differences between food sets are introduced, selection of the larger set is not rewarded, and/or correction procedures are instituted, provide further evidence of an associative basis for successful reverse-reward performance (e.g., Anderson et al., 2000; Anderson, Hattori, & Fujita, 2008; Silberberg & Fujita, 1996). Nevertheless, all animals that have succeeded in selecting the smaller of two food sets in a reverse-reward contingency procedure have taken several hundred trials, at a minimum, before demonstrating stable, above-chance performance.

Success with the reverse-reward task also follows from the introduction of arbitrary numeric symbols (e.g., different-colored tokens or Arabic numerals) that remove the quantitative nature of the choice options (Addessi & Rossi, 2010; Boysen & Berntson, 1995; Boysen, Mukobi, & Berntson, 1999; Kralik, Hauser, & Zimlicki, 2002). Crucially, symbol-mediated success only emerges when a symbolic token is presented (e.g., the Arabic numeral "6" or a single red token that represents six food items) versus tokens that represent a one-to-one ratio between token number and food amount (e.g., six individual tokens that represent six food items; Addessi & Rossi, 2010; Boysen, Berntson, Hannon, & Cacioppo, 1996; see Carlson, Davis, & Leach, 2005, for similar results with human children). These results indicate that the prepotent value of food stimuli and items directly associated with food

quantities naturally motivate animals to obtain the largest option presented. Further, the natural incentive properties of foods may be exceedingly difficult to inhibit in the reverse-reward task, leading to immediate and repeated gestures towards a larger, more valuable food set, and subsequent failures in the task (Addessi & Rossi, 2010; Boysen & Berntson, 1995; Boysen et al., 1996; Shifferman, 2009).

The failure by chimpanzees and other primates to spontaneously pass the reverse-reward contingency using food items is striking given the impressive feats of behavioral inhibition they exhibit in a variety of other paradigms. For example, chimpanzees have consistently demonstrated a high capacity for delay of gratification in order to maximize accumulating food rewards. In the accumulation task, food items continually accumulate within reach of the subject so long as none are eaten (Beran, 2002). Once the subject consumes any of the food items the accumulation of rewards ends and the trial ends. Therefore, subjects experience an increasingly difficult demand to delay their gratification because the longer that the animal waits, the bigger or better the accumulating reward option becomes. Chimpanzees have excelled in the accumulation task across extended delay periods (up to 11 minutes), when food items were not visible to the animals, in the absence of an experimenter (Beran & Evans, 2006), and even in the face of sustained effort (Beran & Evans, 2009) or when coordination with a social partner was required to facilitate reward delivery (Parrish, Perdue, Evans, & Beran, 2013). Chimpanzees also demonstrate impressive levels of self-control in other paradigms, including food-exchange tasks that require subjects to trade a food item in their possession for a potentially higher-valued reward (e.g., Beran, Rossettie, & Parrish, 2016; Dufour, Pelé, Sterk, & Thierry, 2007).

Because of the apparent disconnect between the behavioral inhibition expressed by chimpanzees across paradigms, we examined the potential mechanisms underlying success in one self-control task (the accumulation task) and failure in a different, but related, inhibition task (the reverse-reward contingency task). Chimpanzees first completed standard versions of the accumulation and reverse-reward tasks to establish baseline performance (Experiment 1). These chimpanzees had participated in a variety of accumulation tasks (Beran, 2002; Beran & Evans, 2006; Evans & Beran, 2007); however, the current design differed from previous testing in that the chimpanzees now had to repeatedly point to single food items to facilitate continued accumulation of those items. The chimpanzees were presented with a single marshmallow that was transferred to an accumulation bowl by the experimenter whenever the chimpanzee pointed to that single item. In this modified design, the chimpanzees had to inhibit pointing to the accumulation bowl, which often contained a much larger quantity of marshmallows compared to the single marshmallow, and instead point to the single marshmallow repeatedly. This new version of the accumulation task therefore required the exact “point to small food” response that animals consistently failed to make in food-based versions of the reverse-reward task.

Following the accumulation and reverse-reward tasks, we then presented a series of variations of the accumulation task, including a phase with non-visible supply sets (Experiment 2) and high-valued and low-valued food items (Experiment 3) to determine the factors underlying self-control successes in these versions of the accumulation task. We then introduced experiments that merged the accumulation task with the reverse-reward task in

attempts to increase success in the reverse-reward paradigm and to isolate the mechanisms underlying the different performance patterns documented for these two inhibition tasks (Experiments 4–7; see Table 1 for an outline of all experimental procedures).

Experiment 1

Methods

Participants—Three adult chimpanzees participated in the study, including Sherman (42 year-old male), Mercury (29 year-old male), and Lana (45 year-old female). The chimpanzees were socially housed in multiple indoor-outdoor enclosures, with access to climbing structures, towers, swings, and other forms of enrichment. The chimpanzees voluntarily separated from one another for the current test sessions, but remained in constant visual and auditory access to one another during testing. These chimpanzees had participated in a wide range of cognitive-behavioral testing, including tests of self-control that require delay of gratification (e.g., Beran, 2002; Beran & Evans, 2006; Beran et al., 2016; Beran, Savage-Rumbaugh, Pate, & Rumbaugh, 1999; Evans & Beran, 2007; Parrish et al., 2013).

The chimpanzees were housed and tested at the Language Research Center (LRC) of Georgia State University (GSU) in Atlanta, Georgia. They were never food or water deprived for testing purposes and had 24-hour access to water, including during test sessions. They received a daily diet of fruits, vegetables, and primate chow regardless of participation in testing, and caloric intake was kept consistent by taking into account the amount of food earned from testing when determining the diet. 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.

Apparatus—Trials were presented on an 80 cm wide by 28 cm deep tray mounted to a 45 cm high bench outside of the chimpanzees' enclosure. The sliding tray could be pushed in towards the chimpanzees to allow the chimpanzees to point to one of several options, or the tray could be retracted toward the experimenter and out of reach of the chimpanzees.

Design and Procedure

Phase 1 - Accumulation Task: At the outset of each accumulation trial, the experimenter placed an empty accumulation bowl on either end of the bench (randomized left-right placement across trials) along with a single mini-marshmallow on the opposite side of the bench. The experimenter then pushed the tray towards the chimpanzees' enclosure, through which the chimpanzees could point to the bowl or to the single marshmallow. These pointing responses are highly familiar to the chimpanzees, and they are made discretely and clearly. However, to confirm that this was true, we video recorded some test sessions of this study so that post hoc coding by two independent observers (AP and BJ) could be compared to the real-time scores of the chimpanzees' pointing by the experimenter working directly with the chimpanzees (MB). One session for each chimpanzee was coded for inter-rater reliability in Experiment 1. There was 100% agreement between all three individuals for all pointing responses with regard to which choice option was indicated.

Pointing to the marshmallow led to its transfer to the accumulation bowl by the experimenter. Pointing to the accumulation bowl at any point in the trial ended the trial, and the experimenter gave all of the accumulated contents of the bowl to the chimpanzees for immediate consumption. Until the accumulation bowl was touched, there were repeated presentations of a single marshmallow versus the bowl option. The experimenter replaced the single marshmallow option using a supply bowl held in his hand and the remaining marshmallows in the supply bowl were visible to the chimpanzees throughout the trial. When there were no more remaining marshmallows in the supply bowl, the chimpanzees were presented with only the accumulation bowl. However, even on this iteration, the experimenter reached into the empty supply bowl, moved his hand to the opposite end of the bench from the accumulation bowl, and mimicked placing an item there. Success in this phase involved pointing repeatedly to a single marshmallow rather than the increasingly larger set of marshmallows in the bowl, until all single marshmallows had been transferred to the bowl.

Each chimpanzee completed three sessions, each conducted on a separate day. Within each session, each chimpanzee completed two trials. Each of those trials involved up to 10 marshmallows presented per trial, depending on how the chimpanzee responded. The marshmallows were presented every three seconds. The inter-trial interval was four minutes, after which the experimenter would refill the supply bowl to 10 marshmallows for the second trial.

Phase 2 - Reverse-Reward Task: At the outset of each reverse-reward trial, the chimpanzees were presented with two food sets via the sliding tray. The chimpanzees made a selection by pointing directly to one of the sets. As with the accumulation task, we coded one session of this task for the same reliability check. There again was 100% agreement between all three individuals for all pointing responses with regard to which choice option was indicated.

For each trial, the chosen set was removed immediately, and the chimpanzees were then given the food set that they *had not* selected. Thus, in order to receive the greater number of items, the chimpanzees had to point to the smaller number of items. The larger food set was randomized for left-right placement on the tray across trials.

Each chimpanzee completed one session with 16 trials in that session. Four trials each of four different quantity comparisons of marshmallows were presented in random order. These comparisons were one versus four marshmallows, one versus five marshmallows, two versus five marshmallows, and three versus eight marshmallows.

Phase 3 – Repeat of the Accumulation Task: We then returned the chimpanzees to the accumulation task for a single session with two trials. In each trial, up to 10 food items could be presented depending on the responses of the chimpanzee. In this return to the accumulation task, the accumulation bowl again contained a larger number of items on 8 out of 10 accumulation iterations relative to the single marshmallow (first iteration - bowl contained zero items, second iteration – bowl contained one item, etc.).

Results

In Phase 1, the chimpanzees successfully transferred and accumulated all food items on 17 of 18 trials. The only exception was Mercury's second trial in the first session, in which he pointed to the bowl instead of the single marshmallow on the second iteration.

In Phase 2, the chimpanzees pointed at the larger food quantity (and, thus, received the smaller quantity through the reversed-reward procedure) on 47 of 48 trials. The one exception was a trial in which Sherman pointed to the smaller quantity (trial 12 of 16 total trials).

In Phase 3, when returned to the accumulation task, the chimpanzees accumulated all marshmallows (by repeatedly pointing to only a single marshmallow instead of the larger accumulated set) on all six trials combined across animals.

Discussion

The juxtaposition of these two methods in terms of behavioral responses from the chimpanzees was striking. In this new version of the accumulation task, the chimpanzees excelled at repeatedly pointing to a smaller amount (a single item) instead of a larger amount (a growing accumulation of up to 10 items of that same food type). The transfer of items to the bowl apparently was intuitive for them (likely due to past experience with the accumulation task in other formats), and the responses needed to gain the most food were made with ease. However, the same response – pointing to smaller food sets over larger – could not be sustained to any degree when the reverse-reward task was presented. There was no indication of improvement. In fact, there were only indications of frustration from the chimpanzees when they repeatedly pointed at larger sets but then received smaller quantities.

Thus, points to small amounts of food over large amounts can be generated, and fairly easily, from chimpanzees, but the task demands matter. When points do not remove food items, but instead transfer them to a growing accumulation, chimpanzees can make such responses. This is a novel demonstration, and this is also the first time that the accumulation task has been presented to nonhuman animals in a manner that required them to actively assist with the accumulation of items through their pointing responses. Typically, accumulation events occur in a way that does not require the animals to point to the smaller amounts of food in order to increase the larger amounts. This experiment therefore indicated that pointing to smaller amounts of food to eventually obtain larger amounts can be accomplished.

But, as has been repeatedly demonstrated (e.g., Boysen & Berntson, 1995; Boysen et al., 1999), chimpanzees cannot point to what they will lose when that requires pointing to smaller amounts. Subsequent experiments further assessed this apparent limitation in chimpanzee choice behavior in the reverse-reward task. First, however, we assessed whether chimpanzees could succeed with a more difficult version of the accumulation task. The motivation for Experiment 2 was to ascertain whether visibility of the items remaining for possible accumulation may have provided a visual reminder or was otherwise facilitative in allowing the chimpanzees to point at the single item. Those remaining items, at least early in trials, were from a larger visible set than either the single item or the accumulation, and yet they were out of reach. We wanted to ensure that the visibility of those items did not play

any role in the success of the chimpanzees in Experiment 1, and so we removed that visibility.

Experiment 2

Methods

Participants and Apparatus—These were the same as in Experiment 1.

Design and Procedure—Chimpanzees were presented with the accumulation task as described in Experiment 1 with one major difference in the testing procedure. In Experiment 1, the experimenter held the supply bowl in his hand so that the chimpanzees could view and potentially monitor the remaining food items and the end of the trial. This may have facilitated the chimpanzees' ability to continually point to the single marshmallow even in the presence of the accumulated set that contained a greater number of food items. To specifically test whether the visibility of the supply bowl impacted performance in the accumulation task we moved the supply bowl underneath the testing bench, so that it was out of view of the chimpanzees.

Each chimpanzee completed two sessions, each conducted on a separate day. Within each session, each chimpanzee completed two trials. Each of those trials involved up to 10 marshmallows presented per trial, depending on how the chimpanzee responded. Marshmallows were presented every three seconds. The inter-trial interval was two minutes, after which the experimenter would refill the supply bowl out of view of the chimpanzees to 10 marshmallows for the second trial.

Results

In 9 of 12 trials, the chimpanzees pointed to the single marshmallow on all 10 iterations, and then pointed to the bowl when no marshmallows were left to accumulate. In two trials, a chimpanzee ended a trial early by pointing to the bowl before all marshmallows had been accumulated. This occurred on Sherman's first trial of his second session when he received only six marshmallows, and on Mercury's second trial of his second session when he received only five marshmallows. On his very first trial, Mercury also made the unique "error" of pointing to the empty spot on the tray on the 11th iteration (when no more marshmallows were left), but when given the empty versus bowl choice on the 12th iteration, then selected the bowl.

Discussion

Item visibility was not a necessary aspect to the chimpanzees' accumulation performance in Experiment 1. Even when the chimpanzees could not see that marshmallows remained in the supply bowl, they still repeatedly pointed to single items over larger sets of items, when such responses led to the transfer of those single items to the accumulation. This result indicates that the supply bowl plays little or no role in choice behavior beyond informing the chimpanzees as to how many items might yet still be forthcoming. Next, we assessed the role of food value in the accumulation task to determine whether chimpanzees flexibly engaged this task, accumulating foods when such accumulations led to the best possible

rewards. Specifically, we wanted to see whether the chimpanzees would choose to place a low preference food item into the accumulation, and concurrently avoid taking that accumulation, when such a response would lead to later additional chances to add more of the preferred item. Success in this task might provide some evidence of future-oriented responding, given that the chimpanzees would have to point to and accumulate something that they did not want in order to facilitate accumulation of a desired food reward at future choice points in the trial.

Experiment 3

Methods

Participants and Apparatus—These were the same as in previous experiments.

Design and Procedure—Chimpanzees again were presented with the accumulation phase as used in Experiment 1, including a visible supply bowl. However, we introduced two additional food types, cucumber and celery. These are low-valued foods relative to the marshmallows (as evidenced by tests showing that chimpanzees always chose a marshmallow over either of these other foods when given free choices between them). This was done to investigate whether chimpanzees monitored the quality of the food items in the accumulation set and selectively accumulated the items on the basis of their value and preference.

Each chimpanzee completed three sessions, each conducted on a separate day. Within each session, each chimpanzee completed three trials. Now, the supply bowl held 10 marshmallows and three low-valued food items (either cucumber slices or celery slices, randomly chosen each day). The low-valued items were presented at choice positions 7, 12, and 13 (and the single marshmallows were presented at positions 1 to 6 and 8 to 11). Choices were presented every three seconds. The inter-trial interval was two minutes, after which the experimenter would refill the supply bowl for the next trial.

The optimal response pattern in this experiment was to allow all marshmallows to accumulate before taking the accumulation bowl. This meant that the chimpanzees would have to point to a celery or cucumber slice midway through the trial (and not point at the bowl of six accumulated marshmallows) to continue the trial and accumulate the remaining marshmallows. The inclusion of low preference items as the final two food items was to confirm that chimpanzees would *not* point to such items when there were no longer high-valued items left to accumulate (i.e., that the chimpanzees had not learned to only point to the bowl when nothing else was offered).

Results

The results are presented in Figure 1. The x-axis shows the successive items that were presented as the potentially accumulated item, presented with the bowl of already-accumulated items. All three chimpanzees always chose to accumulate a single marshmallow into the bowl rather than take the bowl on those iterations (shown as M1 to M6 and M7 to M10 in Figure 1).

When the first vegetable was presented in ordinal position 7 within the trial, Lana accumulated that item on 88.9% of trials and Mercury did so on 77.8% of trials. Sherman, however, only did so on 33.3% of the trials. Thus, Lana and Mercury showed the response that indicated self-control and inhibition by not pointing to the six marshmallows in the bowl and instead pointing to a single, low preference vegetable item. This was true even though the chimpanzees rarely ate those items when the accumulated set was given to them.

In the last two iterations, when no more marshmallows were available to accumulate in the supply bowl, Lana and Mercury accumulated those vegetables on only 12.5% and 14.3% of the trials, respectively. Thus, in the majority of cases, Lana and Mercury stopped accumulating single items as soon as it was no longer beneficial to do so, in terms of being able to gain more of the preferred marshmallows. Sherman, however, accumulated those items on 66.7% of trials, although there were only three such trials for Sherman where he waited this long in the trial without having already selected the bowl.

Discussion

Lana and Mercury performed exactly as one would expect if pointing to less preferred items to gain future, more preferred items was the goal. They chose to accumulate a low preference vegetable piece in the middle of the trial, even though the other option was six immediately available marshmallows. This allowed them to accumulate four more marshmallows on those trials, which they always did. However, they did not simply put any food into the accumulation bowl, because when there were no more of the marshmallows left to add to the bowl, they typically avoided pointing to the single vegetable pieces and instead took their accumulation.

Sherman, however, was not as proficient. Sherman appeared to stop accumulating once the first vegetable piece was offered (he did this on two thirds of his trials). On those few trials where he accumulated beyond the initial vegetable piece, he seemingly adopted the strategy of putting all food items into the accumulation bowl, even though he often did not eat the vegetables. Thus, not all chimpanzees were equally successful when the best option in the present was not the option to be chosen to obtain the greatest number of preferred foods. Despite this variability, the chimpanzees were largely successful on the various phases of the accumulation task in Experiments 1 to 3, and so we re-introduced the reverse-reward task in the next three experiments with the goal of adopting the accumulation task setup in a way that might have increased reverse-reward performance.

The idea behind these experiments was to include some of the aspects of the accumulation task in an RR task. The accumulation task specifically involves longer temporal delays to reward than does the RR task, but it also involves the consistent visibility and transfer of single food items that become a part of an eventual larger reward. In this way, single items come to be part of the accumulation, and in Experiment 1 it seemed as if this approach engendered clear and easy points to those single items. We therefore considered that using an accumulation component might evoke small-set pointing even in a comparison judgment such as that which occurs in the two-choice RR task. In addition, the temporal differences in the RR and AC tasks can be eliminated with a hybrid version of these two tasks. One can instantiate the delays inherent in the AC task in versions of the RR task that also involve

similar trial durations before food is obtained. Thus, in Experiment 4, we manipulated the RR task so that responses would not lead to immediate reward of either the larger or smaller set. If the delay interval inherent in making accumulation responses in the first three experiments contributed to better performance by the chimpanzees, including that delay within an RR task might also generate more points toward the smaller set so that the larger set could be accumulated.

Experiment 4

Methods

Participants and Apparatus—These were the same as in previous experiments.

Design and Procedure—Chimpanzees were presented with a hybrid version of the accumulation and reverse-reward tasks in which they chose between two food sets (one marshmallow versus three marshmallows). As in the reverse-reward task outlined in Experiment 1, the selected set was removed from the tray and from view. The chimpanzees received the alternative set, so that the chimpanzees had to point to the single marshmallow to obtain the three marshmallows. However, unlike in the reverse-reward task of Experiment 1, the non-selected set was transferred to an accumulation bowl positioned directly to the left of the testing bench and out of reach of the chimpanzees. This bowl was given to the chimpanzees at the end of the trial. Thus, the new manipulation in this experiment was to delay delivery of any foods that were eventually delivered after *not* being pointed to by the chimpanzees. Because the chimpanzees had demonstrated excellent performance across all prior accumulation tests in this study, the current experiment allowed us to investigate the impact of accumulating rewards on choice behavior in the reverse-reward paradigm.

Each chimpanzee completed one session first in which two trials were presented. Each chimpanzee then completed two more sessions, each on a separate day, in which three trials were presented. On each trial in all of these sessions, eight choices occurred in which chimpanzees chose one or three marshmallows, randomized for left-right placement on the testing tray. The inter-trial interval was two minutes. After the last trial was completed, the accumulation bowl was given to the chimpanzees so they could eat all marshmallows in it. Thus, the chimpanzees could earn a total of 24 marshmallows per trial if they pointed toward the 1-marshmallow option in each food choice. However, pointing to the larger set at every choice would lead to only eight marshmallows being accumulated.

Results

The success seen in Experiments 1–3 completely disappeared in Experiment 4. All three chimpanzees overwhelming pointed to three marshmallows over one marshmallow. Sherman did so on 100% of his 60 choices, Mercury did so on 86.7% of his 60 choices, and Lana did so on 85% of her 60 choices. There was no indication of improvement in this task over time. Sherman chose the 3-marshmallow set in 100% of the trials in the first half of the experiment and 100% of the trials in the second half. Mercury chose the 3-marshmallow set in 90% of the trials in the first half of the experiment and 83.3% of the trials in the second half. Lana actually performed more poorly across the experiment, choosing the 3-

marshmallow set in 76.7% of the trials in the first half of the experiment and 93.3% of the trials in the second half.

Discussion

Experiment 4 offered a stark contrast to Experiment 3. All chimpanzees showed no capacity to point to the smaller amount of food so as to accumulate the larger amount, and experience did not improve performance either. Simply put, the chimpanzees could not point to less food to accumulate more food under the reverse-reward contingencies. However, we continued with this method of accumulating the rewards obtained by RR responses in Experiment 5, but now we included the accumulation itself as a choice option for each response point. The idea here was to ensure that, as in the accumulation task in Experiment 1 to Experiment 3, the chimpanzees could take the accumulated items at any response point during a trial. This would more closely mimic the accumulation task given in those earlier experiments.

Experiment 5

Methods

Participants and Apparatus—These were the same as in previous experiments.

Design and Procedure—Experiment 5 was similar to Experiment 4 in that the chimpanzees were presented with a reverse-reward task in which they chose between a single marshmallow and a set of three marshmallows. As before, the selected set was removed from the tray and the non-selected set was moved to the accumulation bowl. However, the accumulation bowl now was positioned on the tray as a third option in the choice set (rather than out of reach as in Experiment 4). During each choice point, the chimpanzees could select the single marshmallow, the set of three marshmallows, or the accumulation bowl. Selection of the bowl ended the trial and the experimenter gave its full contents to the chimpanzees for immediate consumption. Selection of the single marshmallow or the set of three marshmallows continued the trial with the non-selected amount added to the bowl of accumulated items. Up to eight choices were offered on a trial, provided the accumulation bowl was not chosen during that time.

Each chimpanzee completed two sessions, each conducted on a separate day. Within each session, each chimpanzee completed three trials. The first trial in each session was an accumulation trial identical to that outlined in Experiment 1. The remaining two trials in each session presented eight choices per trial. Each choice offered the single marshmallow, the set of three marshmallows, and the accumulation bowl. The accumulation bowl always was on the chimpanzees' left, with randomized placement of the single marshmallow and set of three marshmallows in the other two positions. The inter-trial interval was two minutes.

As a reliability check, we coded two sessions of this task that were scored by AP and BJ to confirm that each pointing response made by the chimpanzees matched what was recorded by MB in real time during trials. There again was 100% agreement between all three individuals for all pointing responses with regard to which choice was made by the chimpanzees.

Results

On the first trial, which replicated the single marshmallow accumulation task of Experiment 1, the chimpanzees were highly successful. Lana and Mercury accumulated 100% of the single items, repeatedly pointing to those items over the larger set of food items in the bowl. Sherman did so on 87.5% of his choices.

However, performance dropped precipitously in the reverse-reward trials, where the chimpanzees had to point to single marshmallows to accumulate three marshmallows. Sherman and Mercury only pointed to the single marshmallow on two occasions in the entire experiment, and Lana did so on only one occasion. Crucially, Lana and Mercury never pointed to the accumulation bowl (0 of 32 iterations) until the end of the trial when that was the optimal response since nothing else could be accumulated. Sherman only rarely did so (1 of 30 iterations). This was striking because the bowl often held more than 3 marshmallows, meaning that the chimpanzees inhibited points to the largest food set, but could not select the single marshmallow over the three marshmallow option.

Discussion

Experiment 5 offered another failure to inhibit points to larger food amounts over smaller ones, but now with the striking result that the accumulation bowl was rarely selected. This was true even though it often held the most food. Clearly, the chimpanzees treated that choice option differently from the three-marshmallow and one-marshmallow options, which appeared again to be contrasted with each other, and with the outcome that the chimpanzees almost always pointed to the larger amount even though this hurt their chances to obtain the most food. In this case, the use of an accumulation method to put the non-selected set into the accumulation bowl might have proved helpful, if such a presentation generated a new understanding of the RR task for the chimpanzees. However, this did not appear to be true.

In Experiment 6, we attempted to more strongly highlight the cost of pointing at the larger number of items in the RR task by starting each trial with a large accumulation of items that the chimpanzees could receive at the trial's end. Now, we subtracted items equal to the set pointed to at each choice point (one or three food items), until trial end, at which point any remaining items were given to the chimpanzee. This design change should illustrate that points to sets now directly impacted, in a negative way, how much food was taken from the chimpanzees, and might spur greater numbers of points to the single item if the chimpanzees could learn to preserve as many items in the initial set as possible.

Experiment 6

Methods

Participants and Apparatus—These were the same as in previous experiments.

Design and Procedure—Chimpanzees again were faced with a choice of three marshmallows versus one marshmallow as part of the reverse-reward task. However, the selected set now reflected a *reduction* in the total number of marshmallows that would be available at the end of the trial. In Experiment 6, the chimpanzees began each trial with a

pre-set number of marshmallows that would be delivered to the animal at the end of the trial. Pointing to the smaller food set within each choice (one marshmallow over three marshmallows) was the optimal strategy in the current experiment, as the selected set represented a reduction in the total number of items that could be obtained by the chimpanzees at the end of the trial. This experiment allowed us to investigate an alternate version of the accumulation paradigm, one in which pointing to the smaller food set led to the best possible outcome of obtaining a predetermined larger amount of food. Again, the optimal strategy for eventually obtaining an overall larger amount of food required the chimpanzees to point to a smaller amount of food in the immediate choice set.

Each chimpanzee completed three sessions, each conducted on a separate day. Within each session, each chimpanzee completed three trials. Each trial presented eight successive choices, in which chimpanzees were offered a set with a single marshmallow and a set with three marshmallows, with placement on the tray randomized each trial. Following each choice, the unselected option was removed from the testing tray and the selected set was left on the testing tray. Subsequently, the experimenter removed an identical number of marshmallows from the chimpanzee's supply bowl and placed these marshmallows next to the selected set. The selected set and the marshmallows removed from the supply bowl were then removed from the testing tray.

At trial onset, the bowl began with 32 marshmallows. Thus, selecting the larger set of marshmallows (three) across the eight choices would result in a total loss of 24 marshmallows on any given trial, whereas selecting the smaller set (one marshmallow) across the eight choices would result in a total loss of only eight marshmallows. The accumulation bowl always was positioned within view of the chimpanzees (but out of reach), directly to the left of the testing bench. The inter-trial interval was two minutes.

Results

As in previous experiments, the chimpanzees greatly struggled to make the response that maximized the food they received. Sherman pointed to the three-marshmallow set on 98.6% (71 of 72) iterations across all trials. Lana did so on 90.3% (65 of 72) iterations, and Mercury did so on 79.2% (57 of 72) iterations. Neither Lana nor Mercury showed any improvement, either. Lana pointed to the three-marshmallow set on 19 of the first 24 iterations and on 24 of the last 24 iterations. Mercury pointed to the three-marshmallow set on 18 of the first 24 iterations and on 20 of the last 24 iterations.

Discussion

The attempt to generate points to smaller amounts of food items by using the selected set as an indicator of what would be lost did not facilitate any improvement. The chimpanzees continued to point to the larger number of marshmallows on the vast majority of their choices. Success in this task would have indicated that framing the RR task in terms of loss of reward was a key design feature for allowing chimpanzees to master the task, but this did not occur.

In a final experiment, we returned to the AC task one more time, now to present a new variation in which we offered a new temptation that mimicked part of the 1-item versus 3-

item choices offered in the RR task. Trials were similar to those of the AC task in Experiment 1, except that at two choice points, we offered a third option in addition to the single item that could be transferred and the accumulation set. This third option was a fully visible set of three food items. If the chimpanzees chose that set, they received all three items but then the trial ended, and they forfeited all items in the accumulated set. This allowed us to again present choices between one and three items, but within a context of accumulation rather than reverse-reward. If chimpanzees successfully accumulated all of the single items, avoided the temptation of the 3-item sets that terminated trials, and selected the accumulated set only when no more items could be added to it, this would be a compelling example of pointing to less over more within the same choice option (one versus three items) that was previously presented in the RR task, even when pointing to the set with more items led to receiving those items immediately.

Experiment 7

Methods

Participants and Apparatus—These were the same as in previous experiments.

Design and Procedure—Chimpanzees completed the accumulation task as outlined in Experiment 1, with one change. Now, chimpanzees periodically were offered within a trial a third option of a cup of three marshmallows. Pointing to the single marshmallow placed on the bench led to its transfer to the accumulation bowl (as in Experiment 1). Pointing to the accumulation bowl ended the trial and the chimpanzees were given the bowl's contents, but no other food could be obtained on that trial. Pointing to the cup option (when present) ended the trial and the chimpanzees were given the three marshmallows in that cup.

The cup option was presented twice in each trial. On its first presentation it was contrasted with the single marshmallow and the accumulation bowl with only two marshmallows in it. This meant that, to keep the accumulation going, the chimpanzees had to point to the smallest food set over two larger sets. On its second presentation, the cup of three marshmallows was presented against the single marshmallow and the accumulation bowl with six marshmallows. In that case, taking the cup with three marshmallows was a poor choice because the accumulation bowl had twice as many items and also was immediately available. The best choice, from the perspective of obtaining the most food, was to point to the single marshmallow again to keep the accumulation going until all eight possible marshmallows in the supply bowl had been transferred to the accumulation bowl.

This experiment was designed to shed light on how the chimpanzees structured the accumulation task. Thus far, the chimpanzees had been very successful in accumulating rewards even if it meant pointing to a single marshmallow repeatedly over a growing set of accumulating rewards. However, they repeatedly failed to solve the reverse-reward task that required the same behavior (pointing to a smaller food set). If the chimpanzees understood that the accumulation phase led to the eventual obtainment of a larger set of food, even if this included having to repeatedly point to a smaller set of food (the single marshmallow), we predicted that they would not choose the cup option even if it contained a greater number of marshmallows than the accumulation bowl.

Each chimpanzee completed five sessions, each conducted on a separate day. Within each session, each chimpanzee completed three trials, with eight marshmallows presented per trial for the accumulation phase. The single marshmallow (for accumulation), the accumulation bowl, and the cup option were randomized for location on the tray. Choices were presented every three seconds. The inter-trial interval was two minutes, after which the experimenter would reset the supply bowl for the next trial.

Results

Mercury performed perfectly in this experiment. He pointed to the single marshmallow every time in every trial, accumulating all single marshmallows and then taking the accumulation bowl when no more marshmallows were available. Lana did the same thing on 13 of 15 trials. On the remaining two trials, she selected the cup of three marshmallows when it was presented with the single marshmallow and an accumulation of 6 marshmallows in the bowl (this occurred on her very first trial), and she selected the cup with three marshmallows over the single marshmallow and an accumulation of two marshmallows in the bowl (this occurred on the first trial in her fourth session).

Sherman performed more poorly. He pointed to the single marshmallow every time for only 3 of 15 trials. His preferred pattern was to select the cup of three marshmallows over the single marshmallow and accumulation of two marshmallows. He did this on 9 of the remaining 12 trials. On two trials, he selected the accumulation of three marshmallows over the single marshmallow, and on one trial, he selected the bowl with one marshmallow instead of the single marshmallow presented as the other option.

Discussion

Lana and Mercury performed nearly flawlessly. They easily accommodated choices in which a three-marshmallow set was offered as a true temptation against a single marshmallow and the bowl with only two marshmallows. If only quantity in the present choice mattered, they should have struggled here. Sherman did struggle at this point in trials, at least in terms of the goal of maximizing the number of marshmallows ultimately obtained, but Lana and Mercury moved forward with accumulating single items by pointing to the single marshmallow instead of the two alternative choice options. As in Experiment 3, we saw clear evidence that two of the three chimpanzees could choose small food sets over large ones, even when such choices did not lead to immediate reward (and, if anything, blocked the more immediate reward that other choices would have provided). In addition, this choice for the smaller food set was easily made by the chimpanzees even though, quantitatively, it was the same choice they had struggled to make during previous experiments in the RR task.

General Discussion

Through this series of experiments, a consistent and striking dissociation of inhibitory responses was evident. Three chimpanzees, highly experienced in a variety of cognitive tests, “passed” one series of experimental tasks with high proficiency (the accumulation task), and “failed” another series with convincing inadequacy (the reverse-reward task). These series of tasks both required inhibitory restraint in not pointing to the objectively most

valuable set of things in a choice array, but the two test series apparently invoked subjectively different task understanding, motivational states and decisional biases in these chimpanzees.

Past research had indicated that chimpanzees and other species typically failed to learn to point to less valuable rewards to gain more valuable ones in the reverse-reward task (at least without extensive experience or arbitrary token substitutions; see Shifferman, 2009). The three chimpanzees in this study showed the same failure. They could not point to a single food item (or a smaller set of food items) over larger sets of the same food items. This was true when the selected set was immediately taken away, when it was used to subtract from the chimpanzees' supply of food rewards delivered later, and when it acted to determine how many items would be added to an accumulating reward array. Simply put, these chimpanzees never learned to point toward less in order to get more when such choices were discrete and were about chimpanzees needing to point to what they *should not have wanted to receive* in the reverse-reward task context. By this, we mean that the failed tests all shared the feature that the best outcome required indicating what the chimpanzees *did not want* in the immediate or near future.

In stark contrast, the chimpanzees readily and almost immediately pointed to the objectively least valuable option during iterated choice events when the key feature of the task was about pointing to what they *wanted to retain for the future*. When the choice was between a single food item that could be kept as part of a growing accumulation versus taking the accumulated items already available, the chimpanzees easily accommodated a rule of choosing the single item to keep it as part of their growing but untouched larger array of items. Functionally, this meant that the chimpanzees could repeatedly point to less in order to ultimately get more in the accumulation task.

In addition, this new version of the accumulation method provided other evidence of flexible choices even when such choices required pointing toward items that were not in themselves valuable to the chimpanzees or even desired. Two of the three chimpanzees immediately recognized that sometimes they had to point to a non-preferred food item, rather than a large accumulation of preferred items, in order to keep available the chance to gain even more preferred items at a *later* time. This is a strong example of inhibitory self-control, where chimpanzees pointed to what they did not want, to add it to what they were accumulating, to ensure that they could make additional future accumulations of items that they did want. Such behavior was flexible in that such pointing responses to low preference food items almost exclusively occurred when those points served the goal of allowing more preferred items to be encountered and accumulated later, perhaps evidence of future-oriented choice behavior (see Roberts, 2002; Robert & Feeney, 2009; Suddendorf & Corballis, 2007; Zentall, 2006). The chimpanzees were flexible in this responding. When low preference items appeared and there was no chance for additional future accumulations of high preference items, the chimpanzees took what they had collected and avoided those low preference items.

The key "success" in this paper, and what is the broad result across all experiments, is that we have shown that the reverse-reward task is not difficult for nonhuman species simply

because animals have to point to less food from a choice array to eventually get more food. Rather, these results suggest that failures in the reverse-reward task are more fully in the “psychological realm” than in perceptual-motor responding. In other words, these data indicate that some tasks are seemingly more intuitive as to why pointing to smaller amounts leads to more food in the longer term, and chimpanzees succeed on those tasks (and perhaps other species would as well). These results indicate that failure on the reverse-reward contingency is about expectations for what might occur given different choices that lead to success in some cases, but failure in others. These results may suggest that failures in reverse-reward tasks could be instructional failures (i.e., difficulty in grasping the contingencies of choices), rather than inhibitory failures, at least in terms of the idea that it is just difficult to point at one item when other choices have more than one item (something these chimpanzees easily did in accumulation versions of the task).

The chimpanzees appeared to appreciate and accommodate the need to point to things that, at the moment of choice, were not the most valuable items, if such pointing led to increases in a future reward. However, when the reverse-reward paradigm was used to remove items instead, the chimpanzees struggled to accommodate this contingency. A key issue may be the goal of pointing to items. In the accumulation task, even with low preference food items that have to be added to get the chance to add more high preference items, the chimpanzees are still pointing to what they want to keep, in terms of adding those items to an accumulating set of rewards. The reverse-reward task, however, is about pointing to what one does not want to keep, and this is probably a much more difficult concept to instill in nonhuman animals (and even in humans), given that there is little ecological significance to indicating non-desired items by pointing at those items.

In some ways, this difficulty with understanding the reverse-reward contingencies might also contrast with other instances in which chimpanzees (and other animals) have shown the ability to move away from what they want, both in naturalistic settings and more contrived experimental tests. For example, travel paths by primates in the wild sometimes require moving away from a goal in order to reach it because of boundaries or necessary route features (e.g., Garber, 1989; Garber & Hannon, 1993). Such requirements also can be instantiated in computerized maze tasks, which chimpanzees can perform with excellent skill, even when cursors sometimes must be moved away from goals in order to eventually reach those goals at a future point in the maze (e.g., Beran, Parrish, Futch, Evans, & Perdue, 2015; Frigaszy, Johnson-Pynn, Hirsh, & Brakke, 2003; Frigaszy et al., 2009; Menzel & Menzel, 2007; Völter & Call, 2014).

The accumulation tasks used in the present study are similar to those spatial problems in which the ultimate goal (collecting the most preferred food possible) often requires immediate responses that do not reflect the most preferred option in that specific choice state but might reflect the best long-term option. The reverse-reward task has no complimentary structure because it is a task in which something is to be obtained now, but not through the ecologically naturalistic response of reaching toward what one wants among the present choices. From this perspective, it is the future-oriented aspect of the accumulation task that instills optimal choices through pointing to least-preferred items in the present array. Such future-oriented decisions may allow activation of a “cool” system of responding that has

been invoked to explain self-control responses over impulsive, “hot” responses that are more automatic and focused on the present (see Metcalfe & Mischel, 1999). In this framework, the reverse-reward task therefore does not as readily engage self-control processes as does the accumulation task; although, perhaps the improvements seen with training on the reverse-reward task (e.g., Anderson et al., 2000, 2004; Albiach-Serrano et al., 2007; Murray et al., 2005; Vlamings et al., 2006) are the result of a shift to a more controlled choice process from a more automatic one.

This hypothesis is diminished somewhat, however, by the failures of the chimpanzees in the reverse-reward variations in which we withheld food delivery until the end of the trial and therefore eliminated the chance to receive any food right after points to food items. For example, when we asked the chimpanzees to point to food arrays to indicate how many items would be subtracted from a set delivered later, we objectively created a delayed reward situation. However, simply delaying reward delivery in the reverse-reward task was not enough to invoke controlled responses that involve pointing to something other than the objectively best thing offered (in terms of hedonic value of choice options in the present). Perhaps there may also be an aspect of possession inherent in the accumulation task contingencies. By this, we do not mean anything other than that when animals accumulate items they do so with the sense of control over when they will consume those items. From this perspective, keeping what one points towards is important in these choice tests. This idea of possessing items for later consumption aligns with evidence for the endowment effect among nonhuman primates (*Cebus apella*: Lakshminaryanan, Chen, & Santos, 2008; *Gorilla gorilla*: Drayton, Brosnan, Carrigan, & Stoinski, 2013; *Pongo*: Flemming, Jones, Mayo, Stoinski, & Brosnan, 2012), including chimpanzees (*Pan troglodytes* Brosnan, Jones, Lambeth, Mareno, Richardson, & Schapiro, 2007). This potential relation remains to be studied in more detail.

The present data highlight that choice behavior, inhibition, impulsivity, and self-control are intricately but not always clearly entwined. The accumulation task and the reverse-reward task offer insights into these processes, and also provide tools for examining successes, failures, and potential routes through which animals construe task demands and generate behavioral response patterns in an attempt to maximize reward. The present results show that chimpanzees sometimes can point to smaller or less-preferred food items, but other times cannot. Thus, the motor responses themselves, of pointing to food items, reflect different psychological processes in different contexts, an idea that illustrates the complexity of chimpanzee behavior and the constraints on how chimpanzees understand choice options in these different contexts. These results make clear that the story is not as simple as whether chimpanzees can or cannot point to less preferred things to get more preferred things, but rather that how chimpanzees frame their own responses seems to dictate how efficiently they can make those responses.

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Figure 1.

Performance of each chimpanzee for each choice point during trials in Experiment 3. The x-axis shows what was offered as the single item versus the accumulation bowl on each iteration of up to 13 choices. M stands for marshmallow and V stands for vegetable, and the bars show the percentage of choices to put that item into the accumulation bowl rather than take the contents of the accumulation bowl at that point in the trial.

Table 1

Progression of experiments in this study.

Experiment	Focus of Experiment	Description	Outcome
Experiment 1	Accumulation versus Reverse-Reward	In the accumulation task, chimpanzees pointed to a single food item to facilitate its delivery to an accumulating set. In the reverse-reward task, chimpanzees selected between two food sets, from which they received the unselected set.	Chimpanzees were highly successful in transferring single items to the accumulating set. However, they did not point to smaller sets to receive larger ones in the reverse-reward task.
Experiment 2	Non-Visible Accumulation	Chimpanzees accumulated food items as before, but the supply bowl was non-visible.	Chimpanzees continued to be successful in pointing to the single item to add it to the accumulation.
Experiment 3	Mixed-Value Accumulation	Chimpanzees participated in the accumulation task, which included low- and high-valued food items.	Chimpanzees added low value items to the accumulation set when more high preference items could be obtained later, but took the accumulation when only low preference items remained.
Experiment 4	Accumulating Reverse-Reward	Chimpanzees selected between two food sets. The unselected set was moved to an out-of-reach accumulation bowl.	Chimpanzees overwhelmingly pointed to the larger set of items, thereby only gaining the smaller set.
Experiment 5	Three-Choice Reverse-Reward	Chimpanzees selected between three options: smaller food set, larger food set, and accumulation bowl. The unselected food set was moved to a within-reach accumulation bowl.	Chimpanzees avoided taking the accumulation until the appropriate time, but they overwhelmingly pointed to the set of 3 items over 1 item, thereby only accumulating the single item.
Experiment 6	Reverse-Reward Subtraction	Chimpanzees selected between two food sets, the selected set reflected a <i>reduction</i> in the number of items removed from a supply bowl.	Chimpanzees overwhelmingly pointed to the larger set of items, thereby reducing their accumulation by the large number of items instead of the small number.
Experiment 7	Accumulation Bail Out	Chimpanzees pointed to a single food item to facilitate its accumulation. A third “bail out” option that was greater or lesser in value than the accumulation bowl was periodically presented.	Two of three chimpanzees avoided the “bail out” option and chose to accumulate single items until all food could be obtained. One chimpanzee often chose the “bail out” option, thereby reducing overall reward.