

NIH Public Access

Author Manuscript

Learn Motiv. Author manuscript; available in PMC 2010 May 1.

Published in final edited form as:

Learn Motiv. 2009 May 1; 40(2): 186–196. doi:10.1016/j.lmot.2008.11.002.

Natural Choice in Chimpanzees (*Pan troglodytes*): Perceptual and Temporal Effects on Selective Value

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Abstract

In three experiments, four chimpanzees made choices between two visible food options to assess the validity of the selective value effect (the assignment of value to only the most preferred type of food presented in a comparison). In Experiment 1, we established that all chimpanzees preferred single banana pieces to single apple pieces before presenting the critical test. In this test two chimpanzees preferred a mix of one banana piece and one apple piece to a single banana piece when both banana piece were approximately the same size, but two chimpanzees were indifferent between the two options, exhibiting the selective value effect. In Experiment 2, when the banana pieces in both options were more closely equated in size the chimpanzees then were biased to choose the single banana piece over the mixed array even though this was the smaller total amount of food. However, in Experiment 3, when we introduced longer intervals between each trial, the chimpanzees preferred the mixed set and thus the larger total amount of food. The results demonstrate that only some chimpanzees exhibit the choice pattern indicative of the selective value effect, and they do so only when item size is not carefully controlled and trials are presented quickly in succession. Thus, the behavior pattern originally labeled the selective value effect may actually be explained by a combination of chimpanzees' sensitivity to small differences in preferred food amount and chimpanzees tendency to avoid less preferred foods that would delay the acquisition of further preferred food items.

Keywords

Chimpanzees; Pan troglodytes; Natural Choice; Selective Value Effect; Foraging; Decision-making

When given repeated choices between discrete sets of identical food items, animals almost always prefer the larger amount (Addessi, Crescimbene, & Visalberghi, 2008; Anderson, Awazu, & Fujita, 2000; Beran, 2001; Beran, Evans, & Harris, 2008; Call, 2000; Hanus & Call, 2007; Rumbaugh, Savage-Rumbaugh, & Hegel, 1987; Suda & Call, 2005; Uller, Jaeger,

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Guidry, & Martin, 2003; Ward & Smuts, 2007; Wood, Hauser, Glynn, & Barner, 2008). High performance in selecting the larger amount emerges within very few trials. This means no training is necessary, and this procedure has been called a *natural choice procedure* (Silberberg, Widholm, Bresler, Fuijita, & Anderson, 1998). It is a useful technique for assessing food preferences, for determining the perceptual sensitivity of species in discriminating between items on the basis of size, number, or amount, and for determining subjective values of various sets of food items differing in type and quantity.

One interesting finding from the natural choice procedure is the selective value effect (Silberberg et al., 1998). This effect occurs when organisms presumably assign value only to the most preferred food within a mixture. For example, Silberberg et al. (1998) reported that four monkeys and a chimpanzee, offered a choice between a mixture of a nonpreferred food item and a preferred food item versus only one preferred food item, showed indifference in their choices because they were interested in only the preferred item and assigned no value to the nonpreferred item. These findings led Silberberg et al. (1998) to suggest that the selective value effect may distinguish human behavior from that of other primates, as humans would not show the indifference that their primates showed when offered the same food in both sets and an additional, less preferred food in only one set. We offer two suggestions regarding this hypothesis. First, humans might also show a selective value effect in certain scenarios, and we offer an anecdotal situation in which just such a result might occur. Humans choosing between two lunch options, each of which contains a piece of chicken and only one of which also contains a pickle, may very well choose the piece of chicken alone if it is perceived to be larger (and if the person presumably does not find pickles more appealing than chicken). Of course, we speculate as did Silberberg et al. (1998) about the truthfulness of this outcome in actual choice situations faced by humans, but it seems a reasonable consideration, and it directed us toward this procedural change for controlling the amount of the preferred food item in both sets.

Second, we believe that the selective value effect might be limited to certain circumstances, as the foraging behavior of nonhuman animals including primates typically follows certain seemingly logical patterns designed for maximizing intake. Animals choose patches of food that will provide the most plentiful amount of food, and they remain at a food source until they have depleted the supply and it becomes worth the effort and risk for the individual or group to move on to a new location (Di Fiore & Suarez, 2007; Garber, 1989; Janson & Byrne, 2007; Suarez, 2006). Nonhuman animals, and great apes in particular, can discriminate between quantities of food items that slightly vary in size or amount (e.g., Menzel, 1961; Menzel & Davenport, 1962). For example, chimpanzees can match humans in selecting food items on the basis of size (Menzel, 1960). The findings of Silberberg et al. (1998) seem at odds with these other rational foraging behaviors and perceptual abilities that have been observed and documented in various species of nonhuman primates, and yet the data from that report were consistent across a range of different experiments and primate species. The questions raised by the inconsistencies in these different natural choice experiments are important to address because they relate to issues concerning the foraging habits of nonhuman primates, their perceptual abilities, and even the question of whether animals are capable of mental time travel (see McKenzie, Cherman, Bird, Nagshbandi, & Roberts, 2004; Silberberg et al., 1998). Therefore, we collected additional data in an attempt to resolve whether the selective value effect held true in a replication of the procedure used by Silberberg et al. (1998) and in novel variations of that test. Silberberg et al. (1998) tested only a single chimpanzee. It is possible that different results would be obtained from a larger sample size of chimpanzees, and so we tested four chimpanzees.

Our initial consideration for what might account for the reported selective value effect relates to the ability of nonhuman primates to discriminate between slight differences in food size or

amount (Menzel, 1961; Menzel & Davenport, 1962). Although the size of the less preferred food (sweet potato pieces) was controlled in the Silberberg study with the chimpanzee, to our knowledge the size of the highly preferred food (single, unshelled peanuts) was not controlled. In their studies with Old World monkeys, most subjects were offered choices between portions of bananas and apples, which varied across experiments from 1/12 of a banana to 10 whole bananas and 1/24 of a whole apple to 8 apple halves. Other monkeys were offered choices containing portions of carrot, which varied across experiments from 1/24 to 1/12 pieces, versus portions of either apple or banana. Individual pieces of fruits and vegetables vary widely in their size, weight, and color, as well as their general appearance and appeal. This could be a critical factor in the resulting pattern of responses by animals in natural choice tests.

We first adapted the method used by Silberberg et al. (1998) by presenting chimpanzees with apple and banana mixtures in comparison to single food pieces of those two types. To do that, we simply cut whole fruits into specific numbers of pieces but without carefully equating the size of each piece. After this replication, we carefully equated the size of the preferred food item in the mixture set and the single item set so that the chimpanzees could not discern slight differences in those items and re-tested the chimpanzees. We did this because we thought the selective value effect might be the result of subjects finding differences in the two pieces of preferred food and using those to guide responding. If, in each comparison, one preferred fruit portion was always slightly larger than the preferred fruit portion in other choice option, the larger piece would by chance be presented in the mixed array and on its own an approximately equal number of times. Thus, if the participant were to reliably choose the slightly larger banana piece, then they would appear to be indifferent between the mixed array and the independent banana piece.

Experiment 1

Methods

Participants—Four chimpanzees, Lana (female, 37 years of age), Sherman (male, 35 years of age), Panzee (female, 22 years of age), and Mercury (male, 21 years of age) participated in the experiment. These chimpanzees had extensive testing histories in a variety of cognitive tasks including tests that made use of the natural choice procedure (e.g., Beran, 2004; Beran & Beran, 2004; Beran, Harris, & Washburn, 2005; Rumbaugh et al., 1987).

Apparatus—We presented the food choices in two clear plastic bowls placed at opposite ends of a wooden bench (48 cm high, 67 cm wide, and 36 cm deep). An experimenter pushed forward a shelf that was mounted on a drawer slide at the top of the bench so that it moved within reach of the chimpanzees. This movement presented both sets of food items to the chimpanzee at the same time.

Design and Procedure—All tests were carried out at approximately the same time of day (between 10:30 and 12:00). Chimpanzees received only their normal small morning feeding before testing that consisted of one or two low preference vegetables. This ensured a similar motivational state across all experiments.

Phase 1: Preference Testing: Initially, we confirmed that all chimpanzees preferred banana pieces to apple pieces. Chimpanzees were tested individually, over 20 trials in a single session, on their preference for apples or bananas. The side of food presentation (left or right) was varied randomly across trials throughout this and other all phases. Experimenter 1 was seated at the choice table in front of the chimpanzee. He selected two food items (1/8 piece of a whole apple and 1/6 piece of a whole banana, with the peels intact) from a bowl in front of him and placed those items into two clear plastic containers on the presentation table. He then closed his eyes, lowered his head, and pushed the tray forward. When the chimpanzee indicated his or her

choice, by pointing at one container, Experimenter 2 would announce the selection, and Experimenter 1 would hand the chosen food item to the animal. Experimenter 2 was seated out of view of the animal and therefore could not cue the animal. This method of choosing from discrete sets is well established in these chimpanzees. This procedure was used for all subsequent choice tests.

Phase 2: Mixture vs. Unitary Food Choice: During Phase 2, the testing procedure was similar to that of Phase 1 except that the animals were offered a choice between a larger amount of food, composed of one piece of apple and one piece of banana, in one container, and a smaller amount of food, composed of either a single piece of apple or a single piece of banana, in the other container. The unitary food type and side of presentation were randomly determined for each trial, and there were 10 trials in each session where the unitary food was apple and 10 trials where it was banana. One other difference in the Phase 2 procedure was that, on each trial, one experimenter prepared the two bowls of food in a separate location and then handed them to the experimenter sitting across from the chimpanzee for presentation. Each chimpanzee completed two separate sessions of 20 trials, each given on a different day.

Results

The data were subjected to a two-tailed binomial sign test in this and all subsequent experiments. In Phase 1, each chimpanzee selected the banana piece 100% of the time. This confirmed high preference for banana over apple. In Phase 2, the chimpanzees preferred the larger amount of food (the mixture) to the smaller amount of food (unitary) 82% of the time (p < 0.001). More specifically, the animals chose the mixture over the apple 98% of the time (p < 0.001), and they chose the mixture over the banana 66% of the time (p = 0.005). There was variability in the performance of individual animals (Figure 1) with regard to trials in which a banana piece was paired with the mixture. Lana and Panzee preferred the mixture over the banana piece (p = 0.002, p = 0.041, respectively) whereas Mercury and Sherman were indifferent (p = 0.824, p = 0.503, respectively). When selecting the mixture, all animals always consumed the banana piece before the apple piece.

Discussion

Lana and Panzee did not show the selective value effect reported by Silberberg et al. (1998). However, Mercury and Sherman did show indifference between the two options. This indicates that there may be some validity to the idea of selective value in natural choice situations, but not all chimpanzees performed in this way, instead maximizing intake and making more rational responses. Our goal, however, was to determine whether indifference in choice in this task really reflects selective value (and the attendant non-value that is assigned to the nonpreferred item) or whether something else might account for the pattern of responding. One possible explanation for Mercury and Sherman choosing the smaller amount of food may lie in their ability to discriminate slight size differences in portions of the preferred food item. For example, when these chimpanzees were offered a choice between a mixture of apple and banana versus a unitary banana and they chose the unitary banana, this may have been because the unitary banana piece was slightly larger than the piece offered in the mix. Of course, this would also mean that some chimpanzees are more sensitive to such size differences in banana pieces, or at least are more motivated to capitalize on such differences, than other chimpanzees. To investigate this possibility, we needed to determine the limit of the animals' ability to discriminate between differences in portion size for banana pieces.

Experiment 2

This experiment was conducted to establish a limit on the chimpanzees' perceptual ability for differentiating between slightly different amounts of banana, and then to replicate the choice

procedure from Experiment 1 using nearly identical banana pieces. If preference for the mixture changed (particularly for Sherman and Mercury) after the difference in amount had been controlled, this would require a reinterpretation of the selective value effect.

Methods

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

Design and Procedure

Phase 1: Sensitivity Testing: Prior to the formal experiment, we first established the extent to which these chimpanzees could discern differences in the amount of two banana pieces. We initially attempted this by randomly cutting bananas into 5 to 7 pieces per fruit and removing the banana peels. We then weighed all banana pieces on a commercially available scale sensitive to 1 g differences before presenting them to the animals. Each chimpanzee completed two sessions (twenty trials per session) in which they were offered a choice between banana pieces that ranged in weight from 14 to 28g and that differed by as much as 5 g. Pieces were chosen randomly on each trial so that each chimpanzee would receive a range of differences in the size of the two pieces that they compared. This pilot study indicated that three of the four chimpanzees (Sherman, Lana, and Mercury) were significantly better than chance in choosing banana pieces that were only larger by 2 g compared to the other piece. We then used a more sensitive scale so that we could determine the minimal difference that the chimpanzees could discriminate, and we used this value to determine the maximum difference between comparison items in the formal test.

Phase 2: Mixture vs. Unitary Food Choice: The test itself was similar to that used in Phase 2 of Experiment 1, except that now we used unpeeled banana pieces weighing 19g +/- the value determined in Phase 1. The only other difference was that these pieces were pre-cut and were in a supply bowl in front of the experimenter working with the chimpanzees (but hidden from view of the chimpanzee). Each chimpanzee completed two sessions of 15 trials in which each trial included a banana piece and a mixture with a banana piece and an apple piece (1/8 of an apple).

Results

The results of Phase 1 are presented in Figure 2. We found that chimpanzees were indifferent between two banana pieces only when they differed in size by less than 2 g. So, in Phase 2, all banana pieces were allowed to differ in weight by no more than 1 g. Unexpectedly, in Phase 2 the animals were biased against the mixture and chose the mixture over the unitary banana piece on only 17% of the trials (p < 0.001). Sherman chose the mixture on 10% of trials (p < 0.001), Panzee chose the mixture on 17% of trials (p < 0.001), Mercury chose the mixture on 30% of trials (p = 0.043), and Lana chose the mixture on 10% of trials (p < 0.001). When selecting the mixture, the chimpanzees ate the banana before the apple on 19 of 20 trials.

Discussion

Three of the four chimpanzees were highly sensitive to slight differences in food amount (as measured by weight), and they were able to correctly discriminate weight differences in peeled banana pieces that exceeded 2 g. This outcome indicates that, for some individuals, perhaps the selective value effect is less about the role of the non-preferred food and more the result of these primates discerning slight differences in the preferred food items and responding on that basis. For Mercury and Sherman, this would account for their choice patterns (indifference) in Experiment 1. Lana also showed good performance in discriminating between slight differences in the size of banana slices. This, of course, does not mean that Lana also should have shown indifference in Experiment 1, because even if she discerned small differences in

the banana slices, the accompanying apple slice in one set may have added sufficient value to that set to produce her bias in choosing the mixed set.

Controlling the portion size of the more preferred food had a major impact on the pattern of responding in these chimpanzees, but the results were seemingly more at odds with maximization theory than even those reported by Silberberg et al. (1998). Preference for the mixture over the unitary banana dropped from 66% in Experiment 1 to 17% in Experiment 2, and all four chimpanzees preferred the single food piece over the mixture, even though the banana pieces were nearly identical in the two sets.

On trials in which the chimpanzees chose the mixture, they nearly always ate the banana piece first and then usually took a longer time to eat the apple piece. This delay was rather substantial, and it slowed the overall pacing of the task considerably. It was also the case that, because chimpanzees were not selecting and eating apple pieces in most trials, the pacing of trials was much faster compared to Experiment 1. In Experiment 1, the food sets were prepared on each trial in another location about 3 meters away from the test area and then brought in to the experimenter for presentation. In Experiment 2, however, all food items were already in reach of the experimenter, and he could prepare each trial more quickly. Further, the intervening testing with bananas only to determine the quantity discrimination sensitivity may somehow have sensitized the monkeys to rate of banana delivery and consumption. We had not anticipated that these methodological changes would have any impact in selection patterns, but the results of Experiment 2 indicated to us a possible explanation for why chimpanzees would prefer less food over more food if the larger food amount contained the non-preferred item. Rather than assign no value to the apple pieces, those items may have accrued negative value because, in addition to being of low motivational value (preference), they also required more time to consume, and thus slowed the overall pace of the task. We required the chimpanzees to finish eating whatever food they had before we set up the next trial, and this may have contributed to the bias against the mixed set. Therefore, we next examined the effect of slowing the pace of trials on chimpanzees' relative preference for the mixed array of food items.

Experiment 3

In the previous experiments, each chimpanzee worked to completion (with brief inter-trial intervals) and then another was tested. To slow the pace of the task, in Experiment 3 all four animals were tested in rotation on one trial at a time, with each chimpanzee waiting at least 3 minutes between trials. We hypothesized that this delay would increase motivation to obtain more food because it would be much longer before another trial could be performed, and thus longer before more food could be obtained. Also, unlike in previous experiments in which the inter-trial interval was determined by the speed at which the chimpanzees consumed their food choice, in Experiment 3 this delay was constant and independent of the most recent selection. If we found a change in responding (with significantly more selections of the mixed set with the slower task pace) we would then return to the faster trial pace to see whether selection patterns then reverted to those found in Experiment 2. This would confirm that the temporal pacing of trial presentation contributed to differential selection patterns and differential use of maximization responding in the natural choice situation presented in this study.

Methods

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

Design and Procedure

<u>Phase 1: Slow Trial Presentation Pace:</u> In each trial, a chimpanzee was offered a choice between a single unpeeled piece of banana, weighing between 18.5 and 19 g, and a mixture of

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an 18.5 to 19 g unpeeled piece of banana and 1/8 unpeeled piece of apple. Unlike in the previous experiments, each chimpanzee completed one trial in turn until all four had made a selection. The time between the start of one trial and the start of the next trial for the same chimpanzee was 3 min, and this was much longer than required to eat the selected food. The experimenter prepared the food options in a nearby location and then moved to each chimpanzee's cage in turn and offered both options while closing his eyes. A second experimenter who was out of sight of the chimpanzees announced their selections. All other procedural details were identical to those of the previous experiments. Each chimpanzee completed two sessions of 20 trials each.

Phase 2: Fast Trial Presentation Pace: Trials were identical to those of Phase 1 in this experiment except that each chimpanzee completed all of its trials at the faster pace of the test phase of Experiment 2. Each chimpanzee completed one session of 20 trials.

Results

Lana, Mercury, and Panzee selected the mixed set significantly more often than expected by chance in Phase 1 (p = 0.017, p < 0.001, p < 0.001, respectively). Sherman was indifferent between the two options (p = 0.154). Because the chimpanzees rarely alternated trials with one another in previous tests using the natural choice procedure, we considered that they might require multiple trials in each session to realize that further food rewards would be more delayed. Figure 3 presents performance for each chimpanzee on the first 10 trials of each of the two sessions (for a total of 20 trials) and the last 10 trials of each of the two sessions (for a total of 20 trials) and the last 10 trials of each of the two session; Sherman p = 1.00, Lana p = 0.502) to a statistically significant preference for the mixed set in the last 20 trials (10 from each session; Sherman p = 0.041, Lana p = 0.012). Panzee and Mercury showed statistically significant preferences for the mixed set in the first and last trials of the two sessions (Panzee first 20 trials of both sessions combined - p < 0.001; Mercury first 20 trials of both sessions combined - p = 0.041).

In Phase 2, with the fast trial presentation pace, three of the four chimpanzees returned to a statistically significant preference for the single banana piece over the mixed set (Figure 3). Lana, Mercury, and Sherman selected the mixed set on 5 of 20 trials each (p = 0.041). Panzee, however, selected the mixed set on 15 of 20 trials (p = 0.041). When selecting the mixture, in both phases, all animals always consumed the banana piece before the apple piece.

Discussion

Changing the pace of trial presentation had a major effect on the natural choice behavior of these chimpanzees. When the pace of the task was slowed, and the chimpanzees had to wait much longer between choice opportunities, they selected the mixed set more often and 3 of 4 chimpanzees preferred that set overall. When the pace was again faster, preference against that set returned for 3 of 4 chimpanzees. This indicates that these chimpanzees may have chosen the single banana piece in the fast-paced phase because the apple piece was assigned negative value, presumably because it slowed the pace until the next consumption of banana could occur. ¹ Although this is a form of selective value assignment, it is not of the form suggested by

¹An alternative explanation for Lana, Mercury and Sherman choosing the mixed set more often in Phase 1 than in Phase 2 of Experiment 3 is the sensory-specific satiety effect, or the tendency to prefer a new type of food after consumption of large amounts of some other food (i.e., seeking different food types across time). These chimpanzees might have satiated to eating bananas in Phase 1 but not in Phase 2 because of the 3 min delay. To assess this possibility, we conducted a post hoc preference test with Lana, Mercury, and Sherman, having them choose between a single banana piece and a single apple piece on 20 consecutive trials with a 3 min inter-trial interval. The chimpanzees selected the banana piece on 59 of 60 trials (Mercury selected the apple piece on his 8th trial). Thus, it appears that these chimpanzees' Experiment 3 selection patterns are not the result of a sensory-specific satiety effect.

Silberberg et al. (1998) in which less preferred items are given no value and make no contribution to natural choice behavior. Rather, the selective value that is assigned to the less preferred item may be negative because of the effect on the temporal parameters of the task itself and the pace at which the animals can consume the preferred food items.

General Discussion

Across three experiments, four chimpanzees showed changing preferences for different arrays of food items. The main findings are summarized in Table 1 for clear comparison across experiments. Our initial goal was to assess the selective value effect proposed by Silberberg et al. (1998) to account for why various primates they tested were indifferent between a single food item and another food source that contained that same type of item plus another piece of a less preferred food. The selective value effect was proposed to occur because the less preferred food. Such an effect would have important implications for nonhuman primate foraging behavior and for understanding choice behavior, and it would highlight a difference between human and nonhuman behavior. However, this effect seems greatly at odds with other reports that indicate primates do maximize intake in ways that are seemingly rational (e.g., Jensen, Call, & Tomasello, 2007) and highly sensitive to overall amount of food in the choice arrays (e.g., Beran, 2001;Menzel, 1961).

Our initial efforts at replicating this effect were only partially successful. Two of four chimpanzees showed preference for the mixture over the single food item. However, two other chimpanzees showed indifference, indicating the need to investigate further what might account for such indifference beyond the failure to assign value to the less preferred food item. Our next experiment controlled the weight of the preferred food items in both choice sets to ensure that slight differences in amount were not guiding responses. This was an important step because the chimpanzees proved highly attuned to slight differences in amounts of the same food, choosing the heavier piece in most cases in which there was a difference of more than 1 g and performing very well when the difference was 2 or more grams. When comparing banana pieces to identically weighted banana pieces plus apple pieces, the chimpanzees then showed a new and unanticipated bias against the mixture. This outcome did not occur in the Silberberg et al. (1998) report, and it certainly indicated an even stronger failure of maximization in these chimpanzees, and one that needed to be explained.

We considered that trial pacing may have been responsible for these results, and the results of Experiment 3 confirmed that suspicion for 3 of 4 chimpanzees. When these chimpanzees' selections of the mixture slowed the rate at which they could obtain the next banana piece, they avoided choosing that mixture. When the pace of the task was not the result of their choices, they then maximized intake by choosing the overall larger amount of food.

From the standpoint of maximizing overall intake, bias against the mixture appears to be nonrational. However, if one assumes that temporal parameters play a role in decision-making, and that delays to preferred foods are aversive, the chimpanzees' performances are viewed in a different light. When delays were inevitable, most chimpanzees maximized their food intake through their selections of the mixture. When delays to the next opportunity to obtain banana were under the control of these chimpanzees, they made responses that minimized those delays².

We conclude that chimpanzees may in fact show a selective value effect, but we interpret the cause of that effect differently than Silberberg et al. (1998). When chimpanzees can discriminate which of two preferred food items is larger, some may ignore the less preferred item in order to maximize intake of the preferred food item. When selection of the mixture

results in longer intervals before the preferred food can be obtained again, the mixture is not chosen presumably because the less preferred item actually contributes negatively to the overall valuation of that array. This idea can be evaluated further by systematically varying the degree of preference between the two foods. We predict that foods that are closer in value will produce more choices of the mixture compared to those of greater difference in value (recall that our chimpanzees preferred banana to apple in 100% of the trials in which those foods were compared). Less preferred foods that are easy to process might lessen the bias against mixtures over single preferred food items. We also think that empirical data from similar, repeated-trials experiments with humans would be informative regarding the issue of whether humans truly behave differently (and rationally) in this situation. We remain agnostic as to exactly how humans would perform in such a test, but we would not be surprised to find more similarities than differences in their performance and that of nonhuman primates.

Acknowledgments

This research project was supported by grant HD-38051 from the National Institute of Child Health and Human Development.

References

- Addessi E, Crescimbene L, Visalberghi E. Food and quantity token discrimination in capuchin monkeys (*Cebus apella*). Animal Cognition 2008;11:275–282. [PubMed: 17901990]
- Anderson JR, Awazu S, Fujita K. Can squirrel monkeys (*Saimiri sciureus*) learn self-control: A study using food array selection tests and reverse-reward contingency. Journal of Experimental Psychology: Animal Behavior Processes 2000;26:87–97. [PubMed: 10650546]
- Beran MJ. Summation and numerousness judgments of sequentially presented sets of items by chimpanzees (*Pan troglodytes*). Journal of Comparative Psychology 2001;115:181–191. [PubMed: 11459165]
- Beran MJ. Chimpanzees (*Pan troglodytes*) respond to nonvisible sets after one-by-one addition and removal of items. Journal of Comparative Psychology 2004;118:25–36. [PubMed: 15008670]
- Beran MJ, Beran MM. Chimpanzees remember the results of one-by-one addition of food items to sets over extended time periods. Psychological Science 2004;15:94–99. [PubMed: 14738515]
- Beran MJ, Beran MM, Harris EH, Washburn DA. Ordinal judgments and summation of nonvisible sets of food items by two chimpanzees (*Pan troglodytes*) and a rhesus macaque (*Macaca mulatta*). Journal of Experimental Psychology: Animal Behavior Processes 2005;31:351–362. [PubMed: 16045389]
- Beran MJ, Evans TA, Harris EH. Perception of food amount by chimpanzees based on the number, size, contour length, and visibility of items. Animal Behaviour 2008;75:1793–1802. [PubMed: 19412322]
- Call J. Estimating and operating on discrete quantities in orangutans (*Pongo pygmaeus*). Journal of Comparative Psychology 2000;114:136–147. [PubMed: 10890585]
- Di Fiore A, Suarez SA. Route-based travel and shared routes in sympatric spider and woolly monkeys: Cognitive and evolutionary implications. Animal Cognition 2007;10:317–329. [PubMed: 17387530]
- Garber PA. Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. American Journal of Primatology 1989;19:203–216.
- Hanus D, Call J. Discrete quantity judgments in the great apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla, Pongo pygmaeus*): The effect of presenting whole sets versus item-by-item. Journal of Experimental Psychology: Animal Behavior Processes 2007;121:241–249.

 $^{^2}$ Silberberg et al. (1998) also reported that primates would choose two food items over one food item of the same type even though they were indifferent between mixtures and single food items of the preferred food type. They argued that the selective value effect could not be attributed to the order of food consumption or the delay between choice and consumption because choice of two items over one item when all were the same food type also instantiated a delay to consumption of the second item. However, according to our view, this result can be accommodated. Choice of two bananas over one banana does not delay future consumption of banana pieces because that is the only food that is consumed. Therefore, choosing two bananas over one banana leads even more quickly to consuming more banana as soon as the first is consumed because the animal already possesses a second banana.

- Janson CH, Byrne R. What wild primates know about resources: Opening up the black box. Animal Cognition 2007;10:357–367. [PubMed: 17393193]
- Jensen K, Call J, Tomasello M. Chimpanzees are rational maximizers in an Ultimatum Game. Science 2007;318:107–109. [PubMed: 17916736]
- McKenzie T, Cherman T, Bird LR, Naqshbandi M, Roberts WA. Can squirrel monkeys (*Saimiri sciureus*) plan for the future? Studies of temporal myopia in food choice. Learning and Behavior 2004;32:377–390. [PubMed: 15825880]
- Menzel EW. Selection of food by size in the chimpanzee, and comparison with human judgments. Science 1960;131:1527–1528. [PubMed: 17802497]
- Menzel EW. Perception of food size in the chimpanzee. Journal of Comparative and Physiological Psychology 1961;54:588–591.
- Menzel EW, Davenport RK. The effects of stimulus presentation variables upon chimpanzee's selection of food by size. Journal of Comparative and Physiological Psychology 1962;55:235–239.
- Rumbaugh DM, Savage-Rumbaugh ES, Hegel MT. Summation in the chimpanzee (*Pan troglodytes*). Journal of Experimental Psychology: Animal Behavior Processes 1987;13:107–115. [PubMed: 3572305]
- Silberberg A, Widholm JJ, Fujita K, Anderson J. Natural choice in nonhuman primates. Journal of Experimental Psychology: Animal Behavior Processes 1998;24:215–228. [PubMed: 9556910]
- Suarez SA. Diet and travel costs for spider monkeys in a nonseasonal, hyperdiverse environment. International Journal of Primatology 2006;27:411–436.
- Suda C, Call J. Piagetian conservation of discrete quantities in bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), and orangutans (*Pongo pygaeus*). Animal Cognition 2005;8:220–235. [PubMed: 15692813]
- Uller C, Jaeger R, Guidry G, Martin C. Salamanders (*Plethodon cinereus*) go for more: Rudiments of number in an amphibian. Animal Cognition 2003;6:105–112. [PubMed: 12709845]
- Ward C, Smuts BB. Quantity-based judgments in the domestic dog (*Canis lupus familiaris*). Animal Cognition 2007;10:71–80. [PubMed: 16941158]
- Wood JN, Hauser MD, Glynn DD, Barner D. Free-ranging rhesus monkeys spontaneously individuate and enumerate small numbers of non-solid portions. Cognition 2008;106:207–221. [PubMed: 17379202]



Figure 1.

Performance of each chimpanzee in the natural choisce test of Experiment 1. Asterisks indicate performance that differed from chance responding as assessed with a two-tailed binomial test (all p < 0.05).



Figure 2.





Figure 3.

Performance in Phase 1 and Phase 2 of Experiment 3. Phase 1 involved rotation of trials among all four chimpanzees with at least 3 minutes between each trial. Phase 2 involved repeated trial presentations with the same chimpanzees (inter-trial interval approximately 20 seconds). Phase 1 data are separated into the first 10 and last 10 trials of both combined sessions (20 trials in each of those two situations). Asterisks indicate performance that differed from chance responding as assessed with a two-tailed binomial test (all p < 0.05).

Table 1

Summary of preference of each chimpanzee across all tests

	Lana	Panzee	Mercury	Sherman
Experiment 1	Mixture	Mixture	None	None
Experiment 2	Single	Single	Single	Single
Experiment 3 (slow pace)	Mixture	Mixture	Mixture	None
Experiment 3 (fast pace)	Single	Mixture	Single	Single