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Perception of Food Amounts by Chimpanzees (*Pan troglodytes*): The Role of Magnitude, Contiguity, and Wholeness

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Abstract

We investigated choice behavior by chimpanzees in five experiments involving choices between different amounts of food. Chimpanzees did not maximize the amount of food they obtained when choosing between a single 20 g banana piece and another option containing a 20 g piece and a 5 g piece. This was true even though they successfully discriminated between 20 g and 25 g banana pieces in other trials. When items in the mixed option were stacked, however, the chimpanzees chose the larger amount. Later experiments indicated that changing the magnitude of the two amounts did not change performance if the difference in magnitude between the two options remained the same (e.g. 40 g plus 10 g vs. 40 g). However, chimpanzees did improve when the two-item option was increased in its magnitude relative to the single slice (e.g. 20 g plus 10 g vs. 20 g). These results indicated that chimpanzees under-valued the total amount of food in sets when items differed in size and did not appear to be whole. Another experiment confirmed that it was this notion of wholeness that evoked suboptimal responding because chimpanzees were successful in the same comparisons with a different type of food that appeared less fractionated when presented as two pieces. These results provide evidence of suboptimal responding in some natural choice situations that prevents chimpanzees from maximizing food intake.

Keywords

Chimpanzees; *Pan troglodytes*; Choice; Magnitude; Contiguity; Wholeness; Foraging; Decision-making

One of the least controversial claims about animal behavior and decision-making is the claim that animals prefer more food over less food. This behavior is non-controversial because it is assumed to offer as immediate a survival advantage as almost any other skill except perhaps for predator detection. Most natural environments provide strong and continual competition for available caloric resources, and clear survival and reproductive advantages exist for those

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animals that can obtain more food. This assumption is supported among laboratory species in which food is in abundance and provided evenly to all animals in the group. Even in these situations, a variety of animals choose larger amounts of foods when given choices between discrete sets of identical food items (e.g., Addessi, Crescimbeni, & Visalberghi, 2008; Anderson, Awazu, & Fujita, 2000; Anderson et al., 2005; Beran, 2001; Call, 2000; Hanus & Call, 2007; Rumbaugh, Savage-Rumbaugh, & Hegel, 1987; Uller, Jaeger, Guidry, & Martin, 2003) and continuous quantities such as liquids (e.g., Suda & Call, 2005; vanMarle, Aw, McCrink, & Santos, 2006; Wood, Hauser, Glynn, & Barner, 2008). Extensive research has shown that magnitude of food reward guides choice behavior in a variety of contexts even when other variables such as delay length to reward and unpredictability of reward also are manipulated (e.g., Green, Myerson, Holt, Slevin, & Estle, 2004; Landon, Davidson, & Elliffe, 2003; MacDonall, 2008; Steinhauer, 1984; Young, 1981).

This preference for the larger amount often appears within very few trials and thus, the assessment of this apparently spontaneous behavior has come to be called the *natural choice procedure* (Silberberg, Widholm, Bresler, Fujita, & Anderson, 1998). This is a useful technique for assessing the perceptual discrimination capacities of many species, and consistent findings have emerged that support continuity in this ability across species.

Typically, one finds that a given species can choose the larger total amount of food provided the difference between the two options is larger as opposed to being smaller (the distance effect), and performance for a given absolute difference is better when both options offer smaller amounts of food as opposed to larger amounts of food (the magnitude effect). This has been confirmed for both discrete quantities in which each set offers a different number of identical food pieces (e.g., Beran, 2004; Beran & Beran, 2004; Call, 2000; Hanus & Call, 2007) and for continuous quantities (e.g., Suda & Call, 2005; vanMarle et al., 2006). Given that such performance seems to depend on perceptual thresholds, and that performance is so similar across species and situations, it would appear that animals' natural choice behavior is *rational* in the economic sense of the term. By this we simply mean that an optimizing rule is followed in which more food is preferred to less food, given a perceivable difference in amount. This matches other reports of foraging behavior in which animals choose patches of food that will provide the most plentiful amount of food and remain at a food source until they have depleted the supply and it becomes worth the effort and risk to move to a new location (Di Fiore & Suarez, 2007; Garber, 1989; Janson & Byrne, 2007; Suarez, 2006).

Discovering when and why responses sometimes do not afford maximization of intake is important because such suboptimal responses may relate to perceptual errors or biases that interfere with maximization. These biases might offer insight into potential information processing mechanisms that play a special role in decision making even to the effect of producing suboptimal responding. This paper concerns such biases in responding to food sources in a natural choice situation.

One interesting finding from the natural choice procedure that suggests non-rational, non-optimal responding is the *selective value effect* (Silberberg et al., 1998). This occurs when organisms only assign value to the most preferred food type within a mixture. In one report (Silberberg et al., 1998), monkeys and a chimpanzee chose a single preferred food item over a mixture that contained that item plus another piece of less preferred food. Recently, Beran, Ratliff, and Evans (in press) attempted to replicate this effect, but did so only partially, finding that temporal aspects of trial presentation led to choices of the single item over the mixture. When trials were separated by longer intervals, chimpanzees showed greater preference for the mixture (and therefore the larger total amount of food) compared to when intervals were short, in which case the chimpanzees then were indifferent or even preferred the single item compared to the mixture. Despite accounting for these changing preferences, their existence

was an instance of non-rational responding from the perspective of maximization of food intake given that the chimpanzees gave up larger overall amounts of food to obtain smaller amounts instead.

Boysen, Berntson, and Mukobi (2001) reported another example of a bias in responding that worked against maximization of food intake. Chimpanzees in that study showed a bias to point to sets of food items that had the larger individually sized items, even when those items were not in the set containing the larger amount of food. Beran, Evans, and Harris (2008) also found that chimpanzees would choose a set of food items that contained the largest individual piece even if the total amount of food in that set was smaller than in the alternate choice. Thus, in both of those studies responses by chimpanzees were not optimal because of perceptual biases that worked against maximizing the total amount of food obtained.

Beran et al. (2008) speculated that chimpanzees might use the relative size of the largest food item as a dominant cue even when this conflicts with total amount of food so that the relative contributions of smaller food items to the overall amount in a set is inaccurately represented. They proposed that chimpanzees might have used something akin to a heuristic in which the best individual component within a choice situation guides decision-making. This best cue might be the largest piece of food. Although using this cue resulted in a suboptimal response pattern in choice tests, a bias for the largest piece of food usually would lead to optimal responses in more natural situations (Hutchinson & Gigerenzer, 2005).

Therefore, laboratory-based natural choice tests do not always yield results that support maximization of food intake. These kinds of results stand in stark contrast to other studies that show chimpanzees to be excellent at perceiving slight differences between food items (e.g., Menzel, 1960, 1961; Menzel & Davenport, 1962). Given the deviations just reported, we presented four chimpanzees with an additional test in which a perceptual bias might lead to suboptimal responding rather than maximization of intake. We devised this test to avoid both the selective value effect and the reported bias of chimpanzees toward sets of food that contain the individually largest item. In this test, chimpanzees compared two amounts of the same food type. Therefore, selective value on the basis of food type could not occur. Additionally, the test involved presenting nearly identical (to within less than 1 g) food items in both options to be compared. These identical food items were always the largest items presented on each trial, and so the bias to choose a food option based on the presence of the largest item did not apply. On each trial, therefore, the chimpanzees chose between one option comprised of a single food item and another option with an identically sized single food item plus an additional, smaller food item of the same type. Maximization theory predicts that this test would produce a bias to choose the larger amount of food (i.e., the option of two items). However, suboptimal responding might also manifest because of perceptual biases, such as a bias against roughly similar amounts of discrete food items when one set is fractionated and one is not. This would be non-rational, and it would illustrate another way in which natural responding can be misguided by perceptual factors other than total amount.

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 experiments. These chimpanzees had extensive testing histories in a variety of different tests including some that made use of the natural choice procedure (e.g., Beran, 2004; Beran & Beran, 2004; Beran et al., 2008; Rumbaugh et al., 1987).

Apparatus—The apparatus consisted of a wooden bench (48 cm high, 67 cm wide, and 36 cm deep) on which two clear plastic bowls were placed. This bench allowed the experimenter to bait the bowls out of view of the chimpanzee and then move the bowls onto opposite ends of the bench. The experimenter then 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 food options to the chimpanzee at the same time, and the chimpanzees could indicate their selection by pointing to and touching one of the bowls.

Design and Procedure—All tests were conducted at approximately the same time of day (between 10:30 and 12:00). Prior to testing, chimpanzees received only their normal small morning feeding that consisted of low preference vegetables. This ensured a similar motivational state across all experiments.

On each trial, the chimpanzees were offered a choice between a larger amount of food, composed of one slice of peeled banana that weighed 20 g and a second peeled slice that weighed 5 g presented in one container, and a smaller amount of food, composed of just a single peeled slice of banana that weighed 20 g. In this and all experiments, weights were assessed using a scale accurate to 0.1 g. All pieces were sliced across the diameter of the banana and were within a .5 g range for the stated weights. A pilot test confirmed that none of the chimpanzees could reliably select the larger of two slices of banana when they differed by 1 g or less, and so the two large slices were practically identical in this task. The left-right positioning of the small and the large amounts was determined pseudo-randomly for each trial with the restriction that each amount was presented equally often on the left and right sides across all experimental trials.

On each trial, Experimenter 1 loaded the two food options into two clear plastic bowls out of view of the chimpanzee. All banana slices were placed in a vertical orientation, and when two slices were in a bowl they were separated by approximately 3 cm. The experimenter then brought both bowls into view of the chimpanzee and placed them on opposite ends of the test bench. He closed his eyes and immediately pushed the shelf forward. The chimpanzee made a selection by reaching through the cage mesh and touching one of the bowls. When the chimpanzee indicated its choice, Experimenter 2, who was seated out of view of the chimpanzee, announced the selection. Experimenter 1 then presented the chosen food item or items to the chimpanzee by emptying its contents all at once into the cage (and typically into the chimpanzee's hand, although occasionally a chimpanzee would catch the piece or pieces in its mouth). He then removed both bowls from the bench. Items in the unselected container were never reused as part of the same quantity on the subsequent trial. For example, if a chimpanzee chose the container with the 20 g piece instead of the 20 g and 5 g option, those two pieces were not used in the next trial as the 20 g plus 5 g option. This was true in this experiment and all subsequent experiments, and it ensured that chimpanzees could not make successive responses on the basis of avoiding specific banana pieces. After an inter-trial interval of approximately 5 s, the next trial was presented.

This method of choosing from discrete options is well established in these chimpanzees. This procedure was used for all subsequent choice tests. Each chimpanzee completed two separate sessions of 20 trials, each given on a different day.

Results

The data were subjected to individual two-tailed binomial sign tests in this and all subsequent experiments unless otherwise noted. The results are presented in Figure 1. Lana ($p = .64$) and Mercury ($p = .08$) showed no bias in selecting either the single 20 g slice or the pair containing a 20 g and 5 g slice. Sherman ($p = .001$) and Panzee ($p = .006$) both showed a bias in selecting the single banana slice over the pair of banana slices.

Discussion

None of the four chimpanzees made selections that led to maximizing the amount of banana obtained. Two of the four were indifferent in their selections, and the other two chimpanzees showed a bias to select the choice that contained less food overall. Therefore, Experiment 1 showed suboptimal responding from the perspective of maximizing intake.

Given these results, we next attempted to determine what perceptual features of the task led to this inability to maximize intake. First, we needed to confirm that the chimpanzees could discern a difference between these two amounts of food. If they could not, this would explain why the pair of banana slices was not always selected. However, because of the significant preference for *less* food by Panzee and Sherman in Experiment 1, we also needed to assess the role of spatial discontiguity in this natural choice situation. In other words, it was possible that these individuals preferred the smaller food option solely because it was represented by a single whole item. While Lana and Mercury may have been simply ignoring the smaller banana piece in the 2-item option and therefore choosing indifferently between the food options, Panzee and Sherman seemed to be deterred from choosing the 2-item option. To Panzee and Sherman, the fractionated two-item option may have appeared less attractive in comparison to the whole single item option. This possibility was examined in the next experiment.

Experiment 2

We conducted Experiment 2 in two phases to examine separately the influence of a perceptual threshold and spatial discontiguity on the chimpanzees' natural choice behavior. We gave the chimpanzees two types of trials in the first phase. The first type involved a comparison identical to the comparison tested in Experiment 1 (20 g plus 5 g vs. 20 g). The second type involved presenting the exact same amounts of food as in the first trial type, but in this case the larger amount was presented as a single 25 g slice of banana rather than a 20 g slice and a 5 g slice. If the chimpanzees selected the larger of the two pieces in the second trial type this would indicate that they could discern this level of difference in food amount. If they were indifferent between the choices in the first trial type, as they were in Experiment 1, this would indicate that spatial discontiguity somehow contributed to this bias in a way that prevented chimpanzees from accurately perceiving the true value of sets of food items that differed in size. Specifically, the two-slice option would lead to an underestimation of the total amount of food in that option.

We conducted a more direct test of the spatial discontiguity hypothesis in the second phase of Experiment 2. We presented the same two types of trials as in Phase 1, except that, in the trials in which one option contained two slices of banana, we stacked those slices rather than placing them next to each other. This reduced the spatial discontiguity of the two-item option while still preserving the fact that those options contained two slices of banana instead of just one. If performance in selecting the option with two banana slices increased in the second phase compared to the first, this would provide additional evidence that fractioning and spatial separation of food items of differing sizes leads to perceptual biases that operate against maximization of intake in chimpanzees.

Methods

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

Design and Procedure—All procedural details were the same as in Experiment 1. Experiment 2 consisted of two phases. On one half of the trials presented in each session of Phase 1, one option contained a single slice that weighed 20 g, and the other option contained a 20 g slice and a 5 g slice. The other half of the trials involved comparisons between one 25 g slice of banana and one 20 g slice of banana. These trial types were intermixed within sessions.

Each chimpanzee completed two sessions of 20 trials each (10 trials of each type in each session). The small amount and the large amount were equally often presented on the left and right sides of the apparatus.

In Phase 2, the exact same types of trials were presented except that in the condition with the 20 g slice and the 5 g slice, the smaller slice was placed directly on top of the larger slice. It was placed slightly off to the side, however, so that the chimpanzees could see clearly that the set consisted of two stacked slices rather than just one large slice. Each chimpanzee completed one session of 20 trials with one half of the trials involving comparisons of a 25 g slice to a 20 g slice, and one half involving comparisons of a 20 g slice plus a 5 g slice to a 20 g slice. As in Phase 1, these trial types were intermixed within the session. The side of presentation of the small amount and the large amount was randomly determined for each trial.

Results

There were clear differences in performance across the phases and conditions (Figure 2). In both phases, the chimpanzees almost always selected the larger item in the 25 g versus 20 g condition (all $p < .05$ except for Lana in Phase 1). In Phase 1 trials involving a spatial separation between a large and small banana slice (20 g plus 5 g vs. 20 g condition), none of the chimpanzees differed from chance in selecting the larger total amount (all $p > .05$). Two chimpanzees performed identically in both of their sessions on the 20 g plus 5 g versus 20 g comparison and the other two differed by only one trial across their two sessions (in all cases, all chimpanzees performed at chance level with the 20 g plus 5 g vs. 20 g comparison).

However, in the Phase 2 condition in which the small slice was stacked on the large slice, 3 of 4 chimpanzees were above chance in selecting the larger amount in the first and only session (all $p < .05$ except for Mercury). A comparison of these two tests involving identical comparisons of food amounts showed that, in Phase 1, the chimpanzees selected the larger amount on only 38 of 80 trials (47.5%) as a group, whereas, in the Phase 2 stacked condition, they selected the larger amount on 35 of 40 trials (87.5%). This difference was statistically significant, paired $t(3) = 3.49$, $p = .04$.

Discussion

This experiment showed that spatial discontiguity in the presentation of two different-sized slices of banana led to suboptimal responding in terms of maximization. The four chimpanzees were indifferent between the two choices when the two-slice option was not contiguous, whereas they showed a significant bias to select a 25 g slice over a 20 g slice within the same test sessions. This was striking given that the difference in total food amount between the two choices was the same in both conditions. This difference between selection patterns was eliminated in Phase 2 when the smaller banana slice was stacked on the larger one, bringing performance in line with that shown when two whole pieces were compared.

These results indicate that chimpanzees have difficulty in choosing the larger total amount of food when one option is a single food item and the other is a set consisting of different-sized, spatially distinct pieces. This result contrasts with their ability to perform well and maximize intake when the two pieces are stacked, a manipulation that restores contiguity to the set. Note that this difficulty in Phase 1 cannot be the result of the chimpanzees choosing on the basis of the largest individual piece, as has been reported in previous studies (Beran, Evans, & Harris, 2008; Boysen et al., 2001), because each option contained a copy of the largest available food item. Instead, one of two things appeared to be happening. The chimpanzees have ignored the contribution of the small banana slice, as animals apparently ignored the value of a less preferred food type in Silberberg et al.'s (1998) selective value effect. In other words, they may have assigned that slice no value in their evaluation of the choices presented to them, and

therefore they responded at chance levels. Alternatively, they may have assigned value to both slices in the set, but the fractioning of the set and the resulting spatial discontinuity may have led the chimpanzees to underestimate the total amount of food in that set. This underestimation could lead to them perceiving the two options as basically equal in food amount, and this would result in chance levels of selection between the two choices. Experiment 3 was designed to distinguish between these two possibilities.

Experiment 3

In this experiment, we manipulated the difference in magnitude between the two options, as well as the overall magnitude of those options, to determine what perceptual factors led to the indifference between the 20 g plus 5 g option and the single 20 g piece in earlier experiments. In the first phase, the chimpanzees again chose between a 25 g and 20 g slice in one condition, but in the other condition we increased the size of the small slice from 5 g to 10 g to increase the difference in magnitude between the two options. In the second phase, we increased the size of both the small and large slices, in comparison to those used in the original test, to increase the overall magnitude of the food options. If performance improved in choosing the pair of slices in Phase 1 but then dropped again in Phase 2, this would indicate that the small piece is not ignored and is assigned some value during the comparison process. However, it would also indicate that the small slice is not always accommodated appropriately as to its overall contribution to the total amount of food in that option (i.e., the chimpanzees underestimate the total amount of food in that option).

Participants and Apparatus

These were the same as in Experiment 1 and Experiment 2.

Design and Procedure

All procedural details were the same as in the previous experiments. In Phase 1, there were two trial types. On one half of the trials, one option contained a single slice that weighed 20 g, and the other option contained a 20 g slice and a 10 g slice. The other half of the trials involved comparisons between one 25 g slice of banana and one 20 g slice of banana. These trial types were intermixed within sessions. Each chimpanzee completed one session of 20 trials (10 of each type). The side of presentation of the small amount and the large amount was randomly determined for each trial.

In Phase 2, there also were two trial types. On one half of the trials, one option contained a single slice that weighed 40 g, and the other option contained a 40 g slice and a 10 g slice. The other half of the trials involved comparisons between one 50 g slice of banana and one 40 g slice of banana. Each chimpanzee completed one session of 20 trials (10 of each type). The side of presentation of the small amount and the large amount was randomly determined for each trial.

Results and Discussion

Performance was high in all conditions except for one (Figure 3). When comparing a set containing a 40 g slice plus a 10 g slice to an option with only a 40 g slice, the chimpanzees performed at chance levels. In all other conditions, they preferred the larger amount of food (all $p < .05$). This indicated that the absolute size of the smaller slice of banana did not influence whether chimpanzees showed indifference or selected the larger total amount of food. Instead, the relevant aspect of the test was the magnitude difference between the smaller total amount (the single food item) and the larger total amount (presented as two slices of banana). When this magnitude difference was larger than it had been in previous experiments, the chimpanzees then made responses that maximized their intake.

This leaves one remaining question: why do chimpanzees not perceive a difference in the total amount of food in comparisons such as 20 g plus 5 g versus 20 g or 40 g plus 10 g versus 40 g? In cases in which they compared the exact same two amounts of food presented as individual slices (20 g versus 25 g and 40 g versus 50 g), they performed at very high levels. Therefore, they can differentiate between those overall amounts of food, at least when those amounts are presented as only two food items. In addition, much previous research has shown that discrete sets of identical food items can be discriminated on the basis of their amount when one set contains 25% more food than the other (e.g., Beran, 2001, 2004; Rumbaugh et al., 1987). This indicates that such differences in amount, even when food items are not contiguous but are of a common size and quality, are discernible and promote maximization of intake through successful choice of the larger amount.

We offer a hypothesis for what may occur during this type of decision-making. Perhaps the chimpanzees were responding according to more than one rule or strategy during these experiments. We have assumed that obtaining more food instead of less food was the rule that guided decision-making. However, not all situations would promote such responding. For example, choosing the larger of two pieces of fruit would not be adaptive if the larger piece were rotten, or not yet ripe. In that case, some quality other than amount might provide a negative cue regarding selection of that item. In our tests, perhaps the chimpanzees applied a similar rule to the choice of the 2-slice sets, particularly when the overall amounts of food in both choices were relatively similar. In that case, the fact that one option was fractionated, or perhaps perceived as being broken, might bias the chimpanzees from choosing that option at the same high levels that they chose the larger of just two food slices. This hypothesis would also account for those less common instances (such as with Sherman and Panzee in Experiment 1) where the chimpanzees showed a significant preference for the option with less overall food. For these tests, this strategy is non-optimal given that all of the banana slices came from the same fruits and therefore did not differ in any qualitative way. However, such biases may be deeply ingrained in perception and choice situations.¹

An alternative explanation is that the chimpanzees may simply be hesitant to choose the pair of food items because they are afraid that they may only receive the smaller of the two slices. Therefore, indifference or even a bias to choose the single item prevents the possibility of being given only the small slice. This seems highly unlikely given the extensive training of these chimpanzees in natural choice tests. However, we presented the chimpanzees with one more test to assess both of these hypotheses.

¹Throughout this study, a debate emerged among the authors and other colleagues about this avoidance of food items that appeared fractionated or broken. In general, most of us agreed that it would not be uncommon for humans to choose a smaller food item over a larger one that presented some loss of “wholeness” in its appearance. For example, we concluded that people might choose a smaller cookie over a larger one on a buffet table if the larger one had a piece that was broken off (but still available to be eaten along with its larger section). We agreed that this would be most likely if the relative difference in size between the choices was smaller rather than if it was larger. However, we disagreed as to why this bias might occur. Some argued that this was the result of learning that broken foods were more likely to have already been touched, but we also agreed that this bias might still occur even for foods that were wrapped. Therefore, finding a similar bias in chimpanzees that certainly have no prohibition against eating things touched by humans is particularly interesting from the perspective of understanding whether such human biases really are learned, or whether they are more reflective of inherent perceptual biases that match nicely what we later learn about the relation between brokenness and handling. At present, this is speculative because there are limited data available on exactly what humans might do in these kinds of situations with whole and broken foods of differing amounts. However, we do know that many factors affect food choice in humans besides maximization of intake (for example, see Shepard & Raats, 2006). To give just one example, Geier, Rozin, and Doros (2006) reported that when food items were freely available in natural situations (such as in candy dishes on a table in an office building), people’s consumption of those items varied on the basis of item size and the size of the scoop available for collecting candies. In the most similar circumstance to the data we have, people also were found to eat more pretzels when they were presented as whole units as compared to partial pieces (cut in half) which might also relate to the idea of brokenness or wholeness.

Experiment 4

In this experiment, we again presented chimpanzees with two food choices in which the larger amount of food was 25% greater than the smaller amount. However, we introduced a new food type: graham crackers. These crackers are machine manufactured to precise dimensions. As such, we can present pieces that maintain a greater resemblance of wholeness than with peeled, sliced bananas. We presented each chimpanzee with trials in which they compared one option with a half-sheet of graham cracker and an eighth-sheet of cracker (produced by cutting a half-sheet into four equal pieces) to a second option comprised of only a half-sheet. The dimensions of these pieces were less likely to produce an impression that the little piece had broken off of the big piece, as these pieces did not share a single dimension other than thickness. Therefore, if the chimpanzees were responding due to a perceptual bias about the brokenness or discontinuous nature of the banana slices in earlier experiments, this bias should be reduced in the current experiment because the individual cracker pieces maintained a much clearer impression of wholeness than did individual banana slices. Therefore, the chimpanzees should succeed in choosing the larger amounts of food across all trials. However, if the chimpanzees made suboptimal responses because of fear of receiving only the smallest individual piece, performance should remain at or below chance levels in choosing the larger total amount in this experiment for the same reason.

Participants and Apparatus

These were the same as in the previous experiments.

Design and Procedure

Each chimpanzee completed a single session of 20 trials. On each trial, the chimpanzee was presented with one option containing one half-sheet (6.5×5.5 cm section) and one eighth-sheet (3.25×2.75 cm section) of graham cracker. The other option contained only a half-sheet of cracker. All procedural details were otherwise the same as in the previous experiments.

Results and Discussion

Overall, the chimpanzees selected the larger amount of food on 63 of 80 trials (78.75%). Performance of three of the four chimpanzees was perfect or near perfect in choosing the larger option (Sherman – 100%, Lana – 95%, Mercury – 90%; all $p < .01$ as assessed with a two-tailed binomial test). This supported the contention that the presentation of food items that were less likely to appear fractionated or broken would alleviate the previous failure to maximize intake. Panzee, however, selected the larger option on only 6 of 20 trials, and this did not differ from chance levels of responding ($p = .11$). Therefore, she continued to have difficulty in maximizing intake, suggesting that some other aspect of the trial presentation may be at work (such as the fear of only receiving the smaller item) or that graham crackers still were not a sufficiently holistic in their appearance to mitigate her bias against broken or fractionated sets.

Experiment 5

Despite the changes in selection pattern that occurred in all previous experiments, it is possible that the chimpanzees' more adaptive responses, in terms of maximizing intake in Experiment 3 and Experiment 4, were the result of experience in making these choices rather than shifts away from perceptual biases against fractionated sets of items. In other words, it was possible that the chimpanzees learned to reduce their maladaptive choices with more experience in these tasks. We hypothesized that the chimpanzees would still show difficulty in the critical 20 g plus 5 g versus 20 g banana slice comparison even after these other manipulations and this additional experience. To assess this, we again presented these types of trials, and we gave the

chimpanzees many more trials than in previous experiments to determine whether performance changed with experience.

Participants and Apparatus

Sherman, Lana, and Mercury participated in this experiment. Panzee was not included for reasons not related to this study.

Design and Procedure

We presented the chimpanzees with two phases, both of which included the original 20 g plus 5 g versus 20 g comparison and the 25 g versus 20 g control trials. In one phase, we also included one previously tested magnitude manipulation to confirm the effect of magnitude difference on choice in this paradigm as seen in Experiment 3. These manipulations maximized the chance that the chimpanzees might finally succeed on the 20 g plus 5 g versus 20 g comparison because of the additional experience and because we offered more trials than in the previous experiments.

In Phase 1, each chimpanzee completed four sessions (one per day) of 18 trials. There were three trial types, each presented six times within the session in random order, with the larger amount of food presented equally often on the left and the right side of the apparatus. The first comparison was between a 20 g banana slice plus a 5 g banana slice versus a single 20 g slice. The second comparison was between a 20 g slice and a 25 g slice. The third comparison was between a 20 g slice plus a 10 g slice versus a 20 g slice.

In Phase 2, each chimpanzee completed four sessions (one per day) of 20 trials. There were only two trial types in this phase, each presented 10 times within the session in random order, with the larger amount of food presented equally often on the left and the right side of the apparatus. The first comparison was between a 20 g slice plus a 5 g slice versus a single 20 g slice. The second comparison was between a 20 g slice and a 25 g slice. Therefore, by the end of this experiment, the chimpanzees had received another 64 trials of the critical 20 g plus 5 g versus 20 g comparison. If this additional experience was helpful in overcoming the hypothesized perceptual bias shown in the first experiments, performance now should exceed chance levels for these chimpanzees.

Results and Discussion

The results for trial comparisons in both phases are presented in Figure 4. With only one exception, the chimpanzees never exceeded chance levels of performance on the 20 g plus 5 g versus 20 g comparison in either phase (all $p > .05$). The exception was that Lana was better than chance on that comparison for Phase 1 (but not for Phase 2). All chimpanzees were better than chance in choosing 20 g plus 10 g slices versus 20 g slices in Phase 1 and in choosing 25 g slices over 20 g slices in Phase 1 and Phase 2 (all $p < .01$).

These results indicated that simply having more chances to choose between food sets did not increase performance on the critical 20 g plus 5 g versus 20 g comparison (in five of six cases, the chimpanzees were at chance level for this comparison). However, they could easily discern that same absolute difference in food amounts when comparing 25 g slices to 20 g slices. They also easily chose the larger amount of food when it was fractionated but was also of a greater magnitude than the single food piece (as in the 20g plus 10 g versus 20 g comparison), as was seen originally in Experiment 3.

General Discussion

When presented with two food amounts, chimpanzees sometimes failed to select the larger amount of food. In Experiment 1, this occurred when the larger option consisted of two pieces of banana, one large and one small. The large piece was indistinguishable from the single piece in the other option, and the chimpanzees responded at chance levels and even showed preference for the smaller amount of food. This failure contrasts with other well-established findings that support the idea that animals attempt to respond rationally in the sense of maximizing the food available from choice situations (e.g., Beran, 2001, 2004; Call, 2000).

We examined what factors might play a role in this suboptimal performance. One large factor was spatial discontiguity. When the larger amount of food contained two spatially separated items, the chimpanzees performed at chance levels. However, when those items were stacked, performance was high. Therefore, contiguity plays a critical role in accurate and efficient choice. However, certain qualifications to that statement are necessary. First, when food items are all of a homogenous type and size, chimpanzees perform much differently, and much more efficiently. When viewing visible (e.g., Rumbaugh et al., 1987) or sequentially presented sets (e.g., Beran, 2001, 2004) of the same food item, this discontiguity is not a problem. Chimpanzees perform very well in choosing the larger amount of food. Rumbaugh et al. (1987) even reported that chimpanzees could sum amounts across different locations that were paired as part of the same choice option. Some of the chimpanzees tested in this experiment are the same individuals that succeeded in these other kinds of tests. Therefore, the negative effect of discontiguity seems to be restricted to the presentation of different size food items within a set. Beran et al. (2008) reported a related effect whereby chimpanzees failed to maximize food intake by too often choosing sets with the individually largest piece of food. This suggests that individual food items somehow failed to be perceived accurately during the comparison process. In the present study, this misperception seemed to involve assigning too little value to the small item.

In Experiment 3, we confirmed that this effect was not restricted to a particular size range, but we also confirmed that relative magnitude plays a role in accurate food perception and judgment. When increasing the size of the smaller food item provided an overall larger magnitude change for the two-item food option in relation to the single-item food option, the chimpanzees then selected the larger total amount. However, it was not simply increasing the absolute size of the small food item that made the difference, because when that same-sized item was presented in a comparison in which all food pieces were increased proportionally in magnitude, the chimpanzees remained at chance levels of responding. Therefore, the role of magnitude in accurate choice responding is based on the relative magnitude between the comparison choices, not the absolute magnitude of a single food item. In essence, the discontiguity between food items of differing sizes in a set requires an increase in the relative magnitude of that set to the other food option in order to match the level of performance that is exhibited when only two individual items are compared.

We propose that part of the difficulty for the chimpanzees in the first three experiments and Experiment 5 pertained to some aversion to the pairs of food items because those items may have appeared fractionated, or even broken, to the chimpanzees. Wholeness of stimuli (particularly food stimuli) as a cue for biasing responding is not well understood in these kinds of assessments. In this study, we found that the problem of suboptimal responding could be overcome simply by changing to a food type that offered less perceptual evidence of this wholeness/fractioning. With a new food type, three of four chimpanzees immediately succeeded in choosing the larger amount of food. Importantly, this experiment discounted the possibility that the chimpanzees avoided the small piece of food out of fear that it might be the only piece they received. However, graham cracker pieces are typically a more preferred food

than bananas for these chimpanzees, so performance might also have improved as a result of a change in the hedonic value of the reward, although bananas also are a highly preferred food type for the chimpanzees. Further research will be needed to better outline the likelihood that choice behavior may be guided in part by some aversion to fractionated, non-homogenous sets of certain food types, and to relate such biases to learning factors as well as more innate perceptual biases.

What did not improve performance was experience. When we returned the chimpanzees to the critical trial comparisons with banana slices (in Experiment 5), they returned to chance levels in almost all cases, despite their recent experience (and success) in choosing the larger amount of food when it was graham cracker pieces. This is not to say that the chimpanzees could not eventually learn to do well with a comparison like the 20 g plus 5 g versus 20 g comparison. We believe that they could, particularly if we instituted a contingency whereby they only received food for picking the larger amount. In that case, performance might improve, as has been demonstrated in other choice tasks in which non-maximizing response biases are found in some cases but not others on the basis of the reward contingency that is used (e.g., Anderson et al., 2000; Boysen, Berntson, Hannan, & Cacioppo, 1996; Boysen et al., 2001; Genty, Palmier, & Roeder, 2004; Kralik, 2005). However, our interest is in more spontaneous, untrained choice procedures in which perceptual processes can manifest in natural responses.

Certainly, choice behavior is not solely dictated by attempts to maximize food obtained. This study adds to others (e.g., Beran et al., 2008; Boysen et al., 2001) in showing that, although maximization of intake is critical to survival, not all perceptual faculties are attuned to serving that purpose in a straightforward manner. Perceptual biases may exist that work against maximization in some cases because they are adaptive for other reasons. One possibility is that there is a bias to approach largest items and avoid smallest ones when comparing food sources. This bias would be detrimental when summation of food items within a source was required, but for many animals such summation is not of primary concern in group foraging situations where only one food item at a time might be available to be eaten. Therefore, a fuller understanding of the features and processes of decision-making in foraging situations requires varied situations in which perceptual and cognitive factors can be controlled and manipulated to determine their relative contributions to such decision-making.

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Figure 1.

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

Figure 2.

Performance of the chimpanzees for each trial type in each phase of Experiment 2. Phase 1 trials that involved 20 g plus 5 g options had those two items located next to each other. Phase 2 trials that involved 20 g plus 5 g options had the smaller item stacked on top of the larger item. The 20 g versus 25 g trials were identical in both phases. Asterisks indicate performance that differed from chance responding as assessed with a two-tailed binomial test (all $p < 0.05$).

Figure 3.

Performance of the chimpanzees for each trial type in each phase of Experiment 3. Asterisks indicate performance that differed from chance responding as assessed with a two-tailed binomial test (all $p < 0.05$).

Figure 4.

Performance of the chimpanzees for each trial type in each phase of Experiment 5. Asterisks indicate performance that differed from chance responding as assessed with a two-tailed binomial test (all $p < 0.05$).