Published in final edited form as:

Behav Processes. 2014 March ; 103: 184–191. doi:10.1016/j.beproc.2013.12.011.

Chimpanzees Sometimes See Fuller as Better: Judgments of Food Quantities Based on Container Size and Fullness

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Abstract

The context in which food is presented can alter quantity judgments leading to sub-optimal choice behavior. Humans often over-estimate food quantity on the basis of how food is presented. Food appears larger if plated on smaller dishes than larger dishes and liquid volumes appear larger in taller cups than shorter cups. Moreover, smaller but fuller containers are preferred in comparison to larger, but less full containers with a truly larger quantity. Here, we assessed whether similar phenomena occur in chimpanzees. Four chimpanzees chose between two amounts of food presented in different sized containers, a large (2 oz.) and small (1 oz.) cup. When different quantities were presented in the same-sized cups or when the small cup contained the larger quantity, chimpanzees were highly accurate in choosing the larger food amount. However, when different-sized cups contained the same amount of food or the smaller cup contained the smaller amount of food (but looked relatively fuller), the chimpanzees often showed a bias to select the smaller but fuller cup. These findings contribute to our understanding of how quantity estimation and portion judgment is impacted by the surrounding context in which it is presented.

Keywords

Quantity Judgment; Context Effects; Misperception; Chimpanzees; *Pan troglodytes*

1. Introduction

At your local bakery, you are given one of two options – a blueberry muffin overflowing its wrapper or a slightly larger muffin in an oversized wrapper. Expected Utility Theory predicts that one should choose the larger muffin as this alternative maximizes returns (Kahneman and Tversky, 1979; Kahneman et al., 1991). However, one might instead opt for the muffin that overflows its wrapper and thus appears to be bigger and better in comparison to the larger muffin. This is a clear example of how the context in which stimuli are presented directly affects choice behavior, sometimes leading to suboptimal outcomes in terms of maximization. Human decision-making research has shown that the framework of a decision often affects peoples' judgments, including classic framing effects and preference reversals as dictated by the availability of multiple options (e.g., Hsee, 1996, 1998;

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Kahneman and Tversky, 1979; Tversky and Kahneman, 1981). An interesting line of research extends these questions of human decision-making to other species to determine whether similar factors also affect the choice behavior of nonhuman species (e.g., framing effects: Lakshminarayanan et al., 2011; Marsh and Kacelnik, 2002) in ways that might lead to suboptimal choice behavior, and also whether such phenomena do or do not match what is seen in humans when different species are given similar tests (e.g., Silberberg et al., 1998, 2013; Smith and Silberberg, 2010). Here, we investigated whether context effects impact food quantity judgments among chimpanzees (*Pan troglodytes*) to determine if they too may show suboptimal decision making as a function of the choice setting.

Contextual variables have affected food-quantity judgment and consumption behavior in a variety of human decision-making studies. Humans often over-estimate amounts of food on the basis of how that food is presented. For example, food presented on small plates appears to be a larger amount than the same food presented on large plates, directly affecting how much people eat and how subjectively full they feel (e.g., Van Ittersum and Wansink, 2012; Wansink 2004, 2006). Glass size and shape also influence the visual perception of liquid volumes; taller cups are perceived as capable of holding more liquid than equal-capacity but shorter cups with larger diameters, influencing perception and pouring/consumption behavior in children (Piaget et al., 1960; Wansink and Van Ittersum, 2003) and adults (Chandon and Ordabayeva 2009; Raghubir and Krishna 1999; Wansink and Van Ittersum, 2005).

Another line of research has shown that humans value a smaller amount of food that appears to fill or even overflow its container more than a larger amount of food that does not fill its container. Hsee (1998) demonstrated a ‘less-is-better’ effect in which a less valuable option was considered to be worth more than an objectively more valuable option if it appeared to be more cohesive or fuller in comparison to its truly larger alternative. Human subjects were asked to report how much they were willing to pay for different amounts of ice cream. Despite the objective value of the ice cream (in terms of ounces), people used the ice cream’s volume in relation to the cup to determine its monetary value. These results suggested that people might prefer an objectively lower-value option to an objectively higher-value option on the basis of their relation to certain contextual variables such as container size. In the current study, we investigated the ‘less-is-better’ effect among chimpanzees (*Pan troglodytes*) to determine whether they might also show biases to choose less food over more food when the context in which that food was presented varied such that the smaller quantity appeared to fill its container more than the larger quantity filled its container.

Chimpanzees have shown similar effects in which their food quantity judgments were directly influenced by presentation style. For example, Parrish and Beran (2013) presented chimpanzees with two different quantities of food on same or different sized plates. Chimpanzees were excellent at choosing the larger quantity of food when the foods were presented on identical plates (small plate versus small plate; large plate versus large plate). However, like humans (Van Ittersum and Wansink, 2012), chimpanzees sometimes preferred the smaller food quantity to the larger food quantity if the smaller quantity was presented on the smaller plate, thus appearing to be fuller or larger in that context than the truly larger food option. These results demonstrate that for chimpanzees, like for humans, context matters in food choice behavior, sometimes resulting in a preference reversal or suboptimal decision making in which subjects choose the smaller or less valuable option due to its contextual features.

Similarly, Beran et al. (2008) and Boysen et al. (2001) reported that chimpanzees used cues other than the total amount of food in choice sets to guide decision-making. Despite a high

accuracy in choosing the larger amount of food across most conditions, chimpanzees' choice-behavior was influenced by the location of the largest single piece of food, leading to suboptimal decision-making if that item was not in the set with the overall larger amount of food. These results reflect sub-optimal decision making in food quantity judgment tasks that are the result of the effects of individual food items on choice behavior, rather than the overall value of each quantity (also see Beran et al., 2009, and Silberberg et al., 1998, for other sub-optimal choice biases in monkeys and apes). We attempted to extend these previous findings with chimpanzees into food quantity judgments like those made by humans who show choice biases based on the context in which food is presented.

The study of chimpanzee quantity judgment has a long-standing history in comparative psychology. Early studies demonstrated that chimpanzees were highly accurate in selecting the larger of two sets of food quantities and were sensitive to very small differences in quantity (Menzel, 1960, 1961; Menzel and Davenport, 1962; Menzel and Draper, 1965). More recent studies have confirmed and contributed to these findings; chimpanzees are proficient in choosing the larger amount of food across a range of conditions (e.g., Beran 2001, 2004, 2012; Beran and Beran, 2004; Boysen and Berntson, 1995; Dooley and Gill, 1977; Hanus and Call, 2007; Rumbaugh et al., 1987). Furthermore, chimpanzees and other great apes also are proficient in conservation tasks (Piaget, 1965) in which they accurately judge quantities when they are spatially transformed into new arrangements (e.g., when liquids are poured into new container shapes and sizes, Muncer, 1983; Suda and Call, 2004, 2005; Woodruff et al., 1978). Thus, chimpanzees should easily navigate a task in which two food quantities are presented without any contextual effects that might bias how those quantities are perceived. But, what if the context in which the foods are presented is altered in such a way that it might produce perceptual illusions and choice biases like those seen with humans? Here, we manipulated the presentation of food quantities so that sometimes they were presented within identical contexts whereas other times the context was such that the chimpanzees might have misrepresented the true quantities.

In the current study, chimpanzees chose between two amounts of food presented in different sized containers, a large cup (2 oz. in capacity) and a small cup (1 oz. in capacity). In baseline conditions, chimpanzees chose between the same-sized cups with different quantities in each cup. In test conditions, they chose between different-sized cups with either the same quantities or different quantities within them. Critical test trials were presented in which equal quantities were presented in the small and large cup such that the small cup appeared fuller, despite having the same quantity as the large cup. Additionally, we presented trials in which the small cup contained a smaller quantity than the large cup, but the small cup appeared subjectively fuller because the food took up more of its capacity. These were quantity comparisons that would rarely lead to errors when cup size was the same on a given trial, and so any errors would reflect that context matters in how chimpanzees perceived food amounts.

In Experiment 1, we tested how fullness of a container affected quantity judgments for a continuous food type (Jell-O). We varied the difficulty of the task across testing phases as we introduced objectively more difficult quantity discriminations in terms of the relative differences between the presented quantities. In Experiment 2, we extended this investigation to the perception of discrete food items (mini-marshmallows) to determine how the perception of overflow of containers might also contribute to misperceptions of quantity.

In critical test trials in which an equal or smaller amount of food was presented in the smaller but fuller cup, we predicted biases in which the chimpanzees would choose the small cup over the large cup more than they would make the same error when cup sizes were the

same within a trial. Moreover, we predicted that the relative fullness of the small cup would impact choice behavior such that the fuller a small cup appeared, the more likely they would choose this cup in comparison to an equal or larger alternative presented in a large cup. Such misperceptions of quantity by chimpanzees would match the same misperceptions sometimes seen in humans and chimpanzees in similar tasks (e.g., Hsee, 1998; Parrish and Beran, 2013).

2. Experiment 1

2.1 Methods

2.1.1 Subjects—We tested four chimpanzees from Georgia State University's Language Research Center, including two males (Sherman, age 39; Mercury, age 26) and two females (Lana, age 42; Panzee, age 27). The chimpanzees were group housed but separated voluntarily into adjacent enclosures for testing. All chimpanzees worked for preferred foods, but received their normal diet of primate chow, fruits and vegetables and were never food or water deprived.

Three of the four chimpanzees, excluding Mercury, were language-trained via a lexigram system comprised of arbitrary symbols representing objects, food, people, places, and activities (Rumbaugh and Washburn, 2003). All chimpanzees had extensive experience in making quantity judgments in a variety of contexts and with a variety of stimuli, including quantities of food items (e.g., Beran 2001, 2004, 2012; Beran and Beran 2004; Rumbaugh et al. 1987).

2.1.2 Apparatus: Trials were presented via a rolling cart with a sliding tray (86 cm by 28 cm) and a set of retractable mini-blinds. The cart was placed flush to the cage mesh so that the sliding tray could be pushed towards the chimpanzee. The retractable mini-blind was used to reduce cuing; the blind was fully lowered during baiting of the tray and then was raised slightly during the chimpanzee's cup-selection so that the experimenter could see the chimpanzee's choice only once it had been made, and the chimpanzee could not see the experimenter during this selection period.

Two sizes of transparent cups were used throughout the study. The large cup measured 2 oz. and the small cup measured 1 oz. We used Jell-O as the food reward. Cups were pre-filled with the relevant amounts of Jell-O the night before testing and then refrigerated so that it would solidify. The filled cups were weighed to within a tenth of a gram to ensure consistency across presentations.

2.1.3 Design and Procedure: Subjects were given a two-choice discrimination task on each trial, choosing between one of two cups that were either the same size (both 1 oz. or both 2 oz.) or different sizes (see Figure 1). The experimenter baited the tray with the two cups, approximately 40 cm apart. For all baseline and testing sessions, we randomized the cup placement (right or left) and the side on which the larger quantity was placed across trials. In addition, we randomized trial type within and across sessions for all phases. Once the tray was baited out-of-sight from the subject, the experimenter slightly raised the blind, waited approximately 3 seconds, and pushed the tray towards the chimpanzee. The chimpanzee then selected one of the two cups by pointing to the preferred cup. These responses were unambiguous as the chimpanzees have a long history of making such responses in a clear manner. Following a choice, the experimenter immediately distributed the selected cup's contents to the chimpanzee by placing the Jell-O into a bowl that was pushed into the chimpanzee's enclosure. The inter-trial interval was approximately 15 seconds, and was largely determined by the actions of the chimpanzee in terms of how long it took for the food to be eaten.

2.1.3.1 Testing Phase 1: *Phase 1* presented the easiest discriminations between quantities. We used five different quantities of Jell-O using a 13 g increase between quantities - 13 g, 26 g, 39 g, 52 g, and 65 g.

The chimpanzees began with two baseline sessions. The first session involved trials with only the small cups, and the second session involved trials with only the large cups. The specific trials that were presented are shown in Table 1. For the small cup session, each comparison was presented four times for a total of 12 trials. For the large cup session, each comparison was presented two times each for a total of 10 trials. This phase was conducted to ensure that the chimpanzees could discriminate between all quantities when presented in equal cup sizes prior to the testing phase, and to ensure they would select the cup containing the larger quantity. Criterion was set to 90% accuracy for each session, and all chimpanzees met the criterion on their first session.

Next, we presented four test sessions to each chimpanzee, with 10 trials per session, and one session per day. Ten comparisons were randomly presented once within each session (see Table 1), and these were classified into three trial types. *Larger Amount in Small Cup* trials consisted of different-sized cups with the larger quantity always presented in the small cup and the smaller quantity presented in the large cup. This should have been an easily discriminable quantity difference; the larger quantity in the small cup was exaggerated in this trial type because it was not only the truly larger amount, but also it could have appeared even more so in the small cup as it came closer to filling the cup. Thus, we predicted that the chimpanzees would accurately select the larger quantity at very high levels in this condition. *Equal Amounts* trials consisted of the same quantity of Jell-O in different-sized cups. This trial type tested whether the chimpanzees would misperceive the quantity in the small cup as being larger than the same quantity in the large cup due to the more pronounced fullness of the small cup. We predicted that the chimpanzees would select the small cup over the large cup significantly more often than chance, despite the equal quantities. *Smaller Amount in Small Cup* trials consisted of different-sized cups with the larger quantity always presented in the large cup and the smaller quantity presented in the small cup. This trial type was included to test for true errors in quantity perception in which the chimpanzees might choose the objectively smaller quantity if it appeared to fill the small cup more fully than a larger quantity filled the large cup. Here, we predicted that the chimpanzees might sometimes sub-optimally choose the small cup with a smaller quantity over the large cup with a larger quantity.

2.1.3.2 Testing Phase 2: *Phase 2* presented a more difficult discrimination between quantities. We used five different quantities with an 8 g increase between quantities. The quantities included 25 g, 33 g, 41 g, 49 g, and 57 g of Jell-O. *Phase 2* was otherwise identical to *Phase 1* in design, and we repeated all comparisons in the baseline and test sessions with the new quantities (see Table 1) using identical procedures.

2.1.3.3 Testing Phase 3: *Phase 3* used the same quantities from *Phase 2*. Thus, we did not include baseline sessions before moving to the test sessions. However, during testing we now included *Equal Size Cups* trials that were functionally similar to baseline trials along with the other three previous trial types within the same session. This was done so that we could investigate whether the chimpanzees would make more errors in the *Smaller Amount in Small Cup* comparisons than in the *Equal Size Cups* comparisons, a comparison that was not possible in *Phase 2* because all of the trials with equal size cups occurred before any of the other trial types. We were particularly interested in Lana and Mercury's performance in these comparisons as they demonstrated a significant preference for the small cup over the large cup in the *Equal Amounts* condition from *Phase 2*. We predicted that the chimpanzees would make more errors in mixed-cup comparisons than in the same-sized cup comparisons,

choosing the small cup more often in the *Smaller Amount in Small Cup* condition, as it appeared to be fuller than the large cup.

In this phase, each chimpanzee completed four sessions of 16 trials per session, and each session was completed on a separate day. Nine different comparisons were presented in random order within each session (see Table 1). Each session included one trial of each *Larger Amount in Small Cup* comparison and two trials of each of the comparisons in the *Equal Amounts*, *Smaller Amount in Small Cup*, and *Equal Size Cups* conditions.

2.2 Results

In *Phase 1* and *Phase 2*, all chimpanzees were 100% accurate on both the small (12/12) and large (10/10) baseline trials in the first session, picking the larger quantity on all trials.

The results for each chimpanzee in each test phase are shown in Table 2. In *Phase 1*, all chimpanzees were 100% accurate in the *Larger Amount in Small Cup* condition (Binomial test: all chimpanzees, $p < .001$). In the *Equal Amounts* condition, all chimpanzees were indifferent between the cup sizes (Binomial tests: Sherman $p = .77$; Panzee $p = 1.0$; Mercury $p = .39$; Lana $p = 1.0$; see Figure 2). In the *Smaller Amount in Small Cup* condition, all chimpanzees showed a significant preference for the large cup with the large quantity (Binomial tests: all chimpanzees, $p < .001$). Thus, the chimpanzees' quantity judgments in *Phase 1* were not affected by the experimental manipulations of cup size.

In *Phase 2*, all chimpanzees again were highly accurate in choosing the larger quantity in the *Larger Amount in Small Cup* condition (Binomial test: Sherman $p < .01$, Panzee $p < .01$, Mercury $p < .001$, Lana $p < .001$). For the *Equal Amounts* condition, two chimpanzees showed a significant preference for the small cup over the large cup (Binomial tests: Mercury $p < .01$, Lana $p = .039$) whereas two chimpanzees were indifferent between the cup sizes (Sherman $p = 1.0$, Panzee $p = .77$; see Figure 2). For the *Smaller Amount in Small Cup* condition, three out of the four chimpanzees had a significant preference for the larger cup with the larger quantity (Binomial tests: Sherman $p < .001$, Panzee $p < .001$, Lana $p = .021$) whereas one chimpanzee did not (Mercury $p = .08$). Thus, there was some indication that the manipulation of cup size had an effect for some chimpanzees.

In *Phase 3*, all chimpanzees were 100% accurate in the *Larger Amount in Small Cup* condition (Binomial test: all chimpanzees, $p < .01$). Again, in the *Equal Amounts* condition, Mercury and Lana showed a significant preference for the small cup over the large cup (Binomial tests: Mercury $p < .01$, Lana $p < .001$) whereas Sherman and Panzee did not (Sherman $p = .15$, Panzee $p = 1.0$; Figure 2). In the *Equal Size Cups* condition, all chimpanzees had a significant preference for the larger quantity (Binomial tests: Sherman $p < .001$, Panzee $p < .01$, Mercury $p < .001$, Lana $p < .001$). For the *Smaller Amount in Small Cup* condition, Mercury and Lana were indifferent between the cup sizes (Binomial tests: Mercury $p = .08$, Lana $p = .45$), and Sherman and Panzee had a significant preference for the larger quantity in the large cup (Sherman $p < .001$, Panzee $p < .001$).

In *Phase 3*, we compared performance in the *Equal Size Cups* condition and the *Smaller Amount in Small Cup* condition to determine whether the chimpanzees made more errors in the latter condition when the small cup looked fuller than the large cup. This was true for Lana and Mercury (Fisher's Exact test: Mercury $p < .001$, Lana $p = .017$), but not for Sherman and Panzee (Sherman $p = .49$, Panzee $p = .24$). This indicates that Mercury and Lana were more likely to erroneously choose the smaller quantity when it was presented in a fuller context (small but full cup) than the larger quantity (large but less-full cup) compared to when the context did not differ for the two quantities because the cups were the same size.

We examined more closely some of the choices that the chimpanzees made in the *Equal Amounts* and *Smaller Amount in Small Cups* condition in *Phase 2* and *Phase 3*. For the *Equal Amounts* condition, Lana and Mercury selected the small cup over the large cup on 63 of 72 trials. We predicted that such rare choices of the large cup would more often occur when the small cup did not appear to be filled to capacity than when it did appear to be filled, and this was true. For 8 of those 9 trials in which they selected the large cup, the small cup was not filled to capacity.

For the *Small Amounts in Small Cup* condition, we again predicted that the chimpanzees would erroneously select the small cup more often when it appeared filled to capacity than when it did not. For *Phase 2* and *Phase 3*, there were 28 trials in which the chimpanzees selected the small cup with the smaller quantity. In 20 out of 28 of these trials, the small cup was filled to capacity. These results combined suggest that the relative fullness of the containers led to differential outcomes; specifically, the fullest containers typically led to the strongest misperception that the small cup held more food than the large cup even when this was not true.

2.3 Discussion

When cup size was the same within a trial, the chimpanzees were nearly perfect in choosing the larger quantity across all phases of Experiment 1. These results match previous experiments in which these chimpanzees were highly sensitive to small differences in quantity (e.g., Beran, 2001, 2004, 2012). Furthermore, as predicted, when the small cup contained a larger quantity than the large cup so that it potentially appeared objectively but also subjectively fuller, the chimpanzees were highly accurate in choosing the larger quantity across all phases.

The chimpanzees were not affected in the first phase with the 13 g differences between quantities as they consistently chose the larger quantity across all conditions. This unit of difference was probably sufficiently large that no illusion occurred that was strong enough to offset the perceived difference in true quantity. However, when we presented the more difficult discriminations (8 g differences) in *Phase 2* and *Phase 3*, two of the four chimpanzees (Mercury and Lana) significantly preferred the small cup to the large cup, suggesting that perhaps they saw this cup as being fuller. In *Phase 3*, these chimpanzees also made significantly more errors in the mixed-cup versus same-cup comparisons. This likely occurred because the small cup looked fuller in comparison to the large cup, even though the large cup contained the truly larger quantity of Jell-O. Furthermore, their choices in both of these conditions were consistent with our prediction that the relative fullness of a container impacted quantity judgment such that proportionately fuller small cups led to more misperceptions. Thus, there was evidence of a perceptual illusion when the smaller cup held less food but appeared to be more filled, although not all chimpanzees showed this effect in all situations.

3. Experiment 2

In Experiment 2, we wanted to further explore whether the fullness of a small cup led to the overestimation of quantity in comparison to a less-full large cup. Here, we assessed whether fullness and, more specifically, overflow of containers affected quantity judgments by chimpanzees. We used mini marshmallows as the food item. The use of discrete items such as these allowed us to create on some trials the effect of overflow that was not possible with Jell-O.

3.1 Methods

3.1.1 Subjects and Apparatus—The same chimpanzees were tested, using the same apparatus (including presentation of the task and the cup sizes) as in Experiment 1. The quantities used in this experiment were measured in terms of the number of mini marshmallows (hereafter Ms). The quantities included 5 Ms, 8 Ms, 12 Ms, and 15 Ms. 15 Ms very clearly overflowed the small cup whereas they approached but did not quite fill the large cup (Figure 3).

3.1.2. Design and Procedure—We first presented a small and large baseline session (see Table 1 for all comparisons). In the small baseline session, each comparison was presented four times, for a total of 12 trials. In the large baseline session, each comparison was presented two times each for a total of 10 trials. Criterion was set to 90% accuracy for each session.

We then presented five test sessions to each chimpanzee, with 18 trials per session, and one session per day. Nine comparisons matching the conditions used in Experiment 1 were randomly presented within each session (see Table 1). We included two trials of each comparison in each of the four conditions, again counterbalancing side of presentation across trials, and otherwise using the same trial presentation procedures and data recording methods that were used in Experiment 1.

3.2 Results

The results are shown in Table 2. All chimpanzees reached criterion in both baseline conditions within the first session. As predicted, all chimpanzees were 100% accurate in the *Larger Amount in Small Cup* condition (Binomial test: all chimpanzees, $p < .01$). In the *Equal Amounts* condition, Mercury, Lana, and Panzee had a significant preference for the small cup over the large cup (Binomial tests: Mercury $p < .001$, Lana $p < .001$, Panzee $p < .001$) whereas Sherman did not ($p = .43$; see Figure 2). In the *Equal Size Cups* condition, all chimpanzees were 100% accurate in choosing the larger quantity (Binomial tests: all chimpanzees, $p < .001$). For the *Smaller Amount in Small Cup* condition, all chimpanzees had a significant preference for the larger quantity in the large cup (Binomial tests: Sherman $p < .001$, Panzee $p < .001$, Mercury $p = .026$, Lana $p < .001$).

Next, we compared performance in the *Equal Size Cups* condition and the *Smaller Amount in Small Cup* condition as we did in Phase 3 of Experiment 1. All chimpanzees performed equally well in both conditions (Fisher's Exact test: Sherman $p = .49$, Panzee $p = .99$, Mercury $p = .23$, Lana $p = .99$).

We again examined the effect of relative container fullness on choice behavior with the prediction that the fuller (i.e., more overflowing) the small cup, the stronger the bias to select that small cup. In the *Equal Amounts* condition, 20 out of 24 of the trials in which Mercury, Lana, and Panzee selected the large cup were in non-overflow trials where the small cup was not filled to capacity or overflowing. In the *Small Amounts in Small Cup* condition, 6 out of 7 trials in which the chimpanzees chose the small cup (and thus made an error) were in the overflow trials. These results suggest that the relative fullness of containers impacted biases in quantity judgment such that overflowing and full cups over-contributed to the misperception that the small container held more food than the large container with equal or smaller amounts of food.

3.3 Discussion

As in Experiment 1, chimpanzees were accurate in selecting the larger quantities across a range of conditions, including baseline trials and trials in which the small cup contained the

truly larger quantity. However, three of the four chimpanzees made errors that were consistent with the prediction that equal quantities presented in smaller but fuller cups might lead to a bias in choice behavior. In this experiment, none of the chimpanzees made more errors in the mixed-cup comparisons versus the same-cup comparisons. However, as in Experiment 1, the relative fullness of the small cup impacted quantity perception such that overflowed and full cups led to more errors in judgment than cups that did not appear to be at or above their capacity.

4. General Discussion

Chimpanzees were very successful in choosing the larger food quantity among alternatives when its presentation accurately reflected its true quantity because no context cues were presented that might create visual illusions. These results are consistent with previous food quantity judgment tasks with chimpanzees, in which they were highly accurate in choosing the larger of two food sets across a range of conditions (e.g., Beran, 2001, 2004, 2012; Boysen and Berntson, 1995; Boysen et al., 1999; Hanus and Call, 2007; Menzel, 1961; Rumbaugh et al., 1987). Here, when cups were equal in size, the chimpanzees were nearly perfect in discriminating the larger quantity across all testing phases. Furthermore, when the small cup contained the larger amount of food, the chimpanzees again were highly accurate in choosing the larger quantity. In this condition, they received both objective and subjective cues that the small cup contained the larger amount of food, as it was both the truly larger amount but also appeared even more so in the small cup as it came closer to filling the cup.

When different-sized cups contained the same amount of food, the chimpanzees should have been indifferent between containers. However, three of the four chimpanzees instead showed some preference for the small cup in one or both experiments, whereas no chimpanzee showed the opposite bias in any circumstance. Moreover, some chimpanzees even chose a smaller amount of food in the small cup over a truly larger amount of food in the large cup when the small cup appeared fuller. It is important to note that the relative fullness of the small cup impacted judgments such that fuller small cups (i.e., those that were completely full or overflowing) led to more choice biases than less-full small cups. Thus, despite high proficiency in relative quantity judgments (e.g., Beran, 2001, 2004), and evidence of conservation of quantity (e.g., Muncer, 1983; Woodruff et al., 1978), some chimpanzees experienced a 'less-is-better' effect in which smaller or equal quantities were preferred to larger quantities in contexts in which they appeared more full or overflowing.

These results are consistent with a recent study in which these same chimpanzees preferred smaller food quantities when they were presented in a context in which they appeared to fill a dish in comparison to a truly larger alternative (Parrish and Beran, 2013). In that study, chimpanzees were highly accurate in discriminating food quantities when presented in an identical context (i.e., same sized plates). However, when a smaller food quantity was plated on a small dish and thus appeared fuller than a larger food quantity on a large plate, chimpanzees were biased towards the smaller food amount. Similarly, in both Beran et al. (2008) and Boysen et al. (2001), chimpanzees sometimes showed a bias to choose the food set containing the individually largest single food item rather than the overall larger set. In those studies, the features (i.e., size) of the individual elements in a set took precedence over the total amount of food in the set. This led to sub-optimal decision-making in which the chimpanzees did not maximize food intake.

Beran et al. (2008) attributed their results to a heuristics-based system in which animals relied on a shortcut during decision-making that typically led to a reliable strategy of choosing the biggest item as an indicator of the larger set. This strategy is described within

the “Take the Best” algorithm in which individuals use the best available cue to choose among alternatives rather than taking all available information into account to maximize intake (Gigerenzer and Goldstein, 1996; Todd and Gigerenzer, 2007). In food quantity judgment tasks, that cue might be an elemental feature (e.g., largest individual item in a set) or a contextual feature (e.g., the fullness of a container). In the current study with the *Equal Size Cups* and *Larger Amount in Small Cup* conditions, container fullness accurately indicated relative quantity. However, when the fullness of a container misrepresented true quantity in the *Smaller Amount in Small Cup* and *Equal Amounts* conditions, the chimpanzees may have continued to rely on this “fullness” cue despite the conflicting nature of this information that sometimes led to sub-optimal decision-making by a failure to maximize food intake.

These results also are in line with research in which humans misperceived quantities based on the fullness of containers. The consumption and conservation literatures demonstrate that dish size influences perception of food quantity (e.g., Chandon and Ordabayeva, 2009; Piaget et al., 1960; Raghubir and Krishna 1999; Van Ittersum and Wansink, 2012; Wansink and Van Ittersum, 2003, 2005). Most related to the present experiments, Hsee (1998) demonstrated a ‘less-is-better’ effect in which humans misperceived smaller quantities of full or overflowing ice cream as more valuable than a larger, but not full quantity of ice cream. Interestingly, this result only held under separate evaluation when the alternatives were presented sequentially. Under joint evaluation with simultaneous presentation, a preference reversal occurred in which subjects accurately chose the truly larger alternative when it was presented in conjunction with the overflowing, but smaller alternative. In contrast to this, the current results and the related results from Parrish and Beran (2013) demonstrated the ‘less-is-better’ effect under joint evaluation among chimpanzees in which they were able to directly compare their alternatives to one another. Under these evaluations, some chimpanzees consistently preferred a smaller or equal quantity option to a truly larger or equal alternative. Future studies might vary the presentation of stimuli to chimpanzees such that they are first given information regarding the true nature of each stimulus before it is presented in a context that may alter its perception. For example, the chimpanzees might overcome their bias towards small but fuller containers if they are first shown the stimuli outside of the cups, for example by placing the two sets of marshmallows directly on the tray and then transferring them to the cups in sight of the chimpanzee.

Despite our expectation that the overflow trials in Experiment 2 would lead to errors, none of the chimpanzees made more errors in the mixed-cup comparisons versus the same-cup comparisons in Experiment 2, whereas this did occur in Experiment 1. Experience may have been a factor in this performance difference. Another hypothesis is that the perception of continuous quantities such as Jell-O is less precise than the perception of discrete sets such as marshmallows, leading to this difference in performance. Similar effects have been reported in the developmental literature in which infants have more sensitive discrimination capacities for discrete/numerical sets than continuous sets (e.g., Cordes and Brannon, 2008, 2009). In those studies, infants discriminated smaller differences in discrete variables than in continuous variables. Properties of discrete stimuli may be more salient than continuous stimuli, resulting in less errors and misperceptions in quantity judgment. Future research that directly tests the differences between continuous versus discrete stimuli perception by chimpanzees is needed to clarify this aspect of chimpanzee perception (see also Agrillo et al., 2011; Ain et al. 2009; Mahajan et al. 2009; Parrish and Beran, 2013; vanMarle et al., 2006).

The present results indicate that quantity judgments among chimpanzees are highly accurate and robust across a wide variety of experimental manipulations. But, some chimpanzees’ choice-behavior was negatively impacted by the surrounding context in which quantities

were presented, suggesting analogous perceptual illusions to those experienced by humans. Research that further tests the quantitative and perceptual capacities of chimpanzees, and other species, will address the extent to which perception systems are “confused” by contextual variables, thereby providing insights into the limitations of these systems.

Acknowledgments

This research was supported by funding from the National Institutes of Health (Grant HD-060563) and by a 2CI Primate Social Cognition, Evolution and Behavior Fellowship from Georgia State University to AEP. We thank the Language Research Center staff for their care of the chimpanzees.

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Highlights

- Context effects alter food-quantity judgments, leading to biases in decision-making.
- Smaller but fuller cups appear to hold larger quantities than less full cups.
- Chimpanzees chose the larger food amount when cup size did not vary.
- Some chimpanzees chose a fuller small cup over a larger or equal quantity that was in a less full cup.
- This occurred most when the smaller quantity filled or overflowed its container.

Figure 1.

Example test stimuli for Experiment 1 – *Phase 2* and *Phase 3*. **A.** Stimuli for the *Equal Amounts* condition – Small-41 g. versus Large-41 g. of Jell-O. **B.** Stimuli for the *Smaller Amount in Small Cup* condition – Small-41 g. versus Large-49 g. of Jell-O.

Figure 2.

Percentage of small cup choices in the *Equal Amounts* condition across Experiment 1 and Experiment 2. The dark horizontal line indicates chance level, and asterisks indicate a significant preference for the small cup, $p < .05$.

Figure 3.

Example test stimuli for Experiment 2. **A.** Stimuli for the *Equal Cups* condition – Small-8 versus Small-12 marshmallows. **B.** Stimuli for the *Larger Amount in Small Cup* condition – Small-8 versus Large-5 marshmallows. **C.** Stimuli for the *Equal Amounts* condition – Small-15 versus Large-15 marshmallows. **D.** Stimuli for the *Smaller Amount in Small Cup* condition – Small-12 versus Large-15 marshmallows.

Table 1

Trial comparisons presented in each experimental phase

		Experiment 1			Experiment 2
		Phase 1	Phase 2	Phase 3	
Baseline	<i>Small Cups</i>	S13 v S26 S13 v S39 S26 v S39	S25 v S33 S25 v S41 S33 v S41	--	S5 v S8 S5 v S12 S8 v S12
	<i>Large Cups</i>	L13 v L26 L13 v L39 L26 v L39 L26 v L52 L39 v L65	L25 v L33 L25 v L41 L33 v L41 L33 v L49 L41 v L57	--	L5 v L8 L5 v L12 L8 v L12 L8 v L15 L12 v L15
Testing	<i>Equal Size Cups</i>	--	--	L33 v L41 L41 v L49	S8 v S12 L5 v L8
	<i>Larger Amount in Small Cup</i>	L13 v S26 L13 v S39 L26 v S39	L25 v S33 L25 v S41 L33 v S41	L25 v S33 L33 v S41	L5 v S8
	<i>Equal Amounts</i>	L13 v S13 L26 v S26 L39 v S39	L25 v S25 L33 v S33 L41 v S41	L25 v S25 L33 v S33 L41 v S41	L5 v S5 L8 v S8 L12 v S12 L15 v S15
	<i>Smaller Amount in Small Cup</i>	L26 v S13 L39 v S26 L52 v S39 L65 v S39	L33 v S25 L41 v S33 L49 v S41 L57 v S41	L41 v S33 L49 v S41	L8 v S5 L15 v S12

Note. For each comparison, “L” indicates the large cup (2 oz) and “S” indicates the small cup (1 oz). In Experiment 1, Jell-O was presented in grams, and in Experiment 2 marshmallows were presented as individual numbers of items. Across trials, presentation side on the apparatus was randomized for the comparisons shown here.

Table 2

Choice behavior in each condition of each experiment.

		Equal Size Cups	Larger Amount in Small Cup	Equal Amounts	Smaller Amount in Small Cup
Experiment 1 Phase 1	Sherman	--	12/12 [*]	5/12	0/16 [^]
	Panzee	--	12/12 [*]	6/12	0/16 [^]
	Mercury	--	12/12 [*]	8/12	1/16 [^]
	Lana	--	12/12 [*]	6/12	0/16 [^]
Experiment 1 Phase 2	Sherman	--	11/12 [*]	6/12	1/16 [^]
	Panzee	--	11/12 [*]	5/12	1/16 [^]
	Mercury	--	12/12 [*]	11/12 ⁺	4/16
	Lana	--	12/12 [*]	10/12 ⁺	3/16 [^]
Experiment 1 Phase 3	Sherman	16/16 [~]	8/8 [*]	8/24	1/16 [^]
	Panzee	14/16 [~]	8/8 [*]	12/24	0/16 [^]
	Mercury	16/16 [~]	8/8 [*]	20/24 ⁺	12/16
	Lana	16/16 [~]	8/8 [*]	22/24 ⁺	6/16
Experiment 2	Sherman	20/20 [~]	10/10 [*]	23/40	2/20 [^]
	Panzee	20/20 [~]	10/10 [*]	32/40 ⁺	1/20 [^]
	Mercury	20/20 [~]	10/10 [*]	32/40 ⁺	3/20 [^]
	Lana	20/20 [~]	10/10 [*]	32/40 ⁺	1/20 [^]

Note. For the *Equal Size Cups* condition, the data shown indicate the number of trials in which the larger quantity of food was selected. For the other three columns, the data indicate the number of trials in which the small cup was selected over the large cup.

[~] indicates significant preference for larger quantity over smaller quantity in same-sized cups

^{*} indicates significant preference for small cup with large quantity over large cup with small quantity

⁺ indicates significant preference for small cup over large cup with equal quantities

[^] indicates significant preference for large cup with large quantity over the small (but fuller) cup with small quantity