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When Less is More: Like Humans, Chimpanzees (*Pan troglodytes*) Misperceive Food Amounts Based on Plate Size

Audrey E. Parrish^{1,2} and Michael J. Beran¹

¹Language Research Center, Georgia State University, Atlanta, GA, USA

²Psychology Department, Georgia State University, Atlanta, GA, USA

Abstract

We investigated whether chimpanzees (*Pan troglodytes*) misperceived food portion sizes depending upon the context in which they were presented, something that often affects how much humans serve themselves and subsequently consume. Chimpanzees judged same-sized and smaller food portions to be larger in amount when presented on a small plate compared to an equal or larger food portion presented on a large plate, and did so despite clearly being able to tell the difference in portions when plate size was identical. These results are consistent with data from the human literature in which people misperceive food portion sizes as a function of plate size. This misperception is attributed to the Delboeuf illusion which occurs when the size of a central item is misperceived on the basis of its surrounding context. These results demonstrate a cross-species shared visual misperception of portion size that affects choice behavior, here in a nonhuman species for which there is little experience with tests that involve choosing between food amounts on dinnerware. The biases resulting in this form of misperception of food portions appear to have a deep-rooted evolutionary history which we share with, at minimum, our closest living nonhuman relative, the chimpanzee.

Keywords

Visual Illusions; Delboeuf illusion; Misperception; Chimpanzees; *Pan troglodytes*; Quantity Discrimination

Many modern humans often over-serve and over-consume foods which directly influences dietary intake and can lead to deleterious health effects including obesity, diabetes, and heart disease (Allison et al. 1999; Must et al. 1999; Wolf and Colditz 1998). Although the super-sized portions that have quickly become the norm in some modern cultures are undoubtedly a culpable factor in this epidemic (Cutler et al. 2003; Hill and Peters 1998; Rolls 2003; Young and Nestle 2002, 2003), we are beginning to understand that there are also deep-seated perceptual influences at play.

Some of the things that clearly and consistently influence how we perceive food portion sizes include the context in which foods are presented, including the size, color, and shape of dinnerware (e.g., Wansink 2004, 2006). Across a wide variety of naturalistic tests with people, it has been shown that dinnerware and serving behavior interact so that people tend to underestimate the amount of food and subsequently over-serve onto larger dishes and, conversely, overestimate portion sizes and under-serve onto smaller dishes (e.g., Murphy et al. 2012; Van Ittersum and Wansink 2007, 2011; Wansink and Cheney 2005; Wansink et al.

*Corresponding author: Audrey E. Parrish, Language Research Center, Georgia State University, University Plaza, Atlanta, GA, 30302, USA; audrey.parrish1@gmail.com.

2005, 2006). Sometimes, perceptual biases can work in favor of reduced caloric intake. For example, a “less-is-better” bias has been documented in which smaller quantities of food are actually perceived to be larger when they are presented in a fuller manner (e.g., a smaller but overflowing ice cream cone is considered more valuable than a truly larger, but not overflowing one; Hsee 1998). Thus, equivalent portions are judged to be quantitatively different depending upon the context in which they are presented, and sometimes even smaller quantities of food are preferred to a truly larger option if presented on smaller dishware.

It can be very difficult to overcome these strong illusory influences on judgment and decision-making regarding portion size estimates and subsequent consumption behavior. Although increased attention to the judgments can sometimes attenuate these effects (Van Ittersum and Wansink 2011), attempts to eliminate these biases via education and experience have largely failed (Wansink and Cheney 2005; Wansink et al. 2006). Difficulty in overcoming such biases may stem from humans’ consumption norms surrounding portion estimation and intake behavior that are largely shaped by societal influences and personal habits (Chandon and Wansink 2006; Wansink and Van Ittersum 2007) including some that are evident even at very young ages (Fisher et al. 2003; McConahy et al. 2004). These consumption norms are further compounded by our seeming unawareness of these influences (Wansink and Sobal 2007) and by our inability to accurately measure and monitor how much we have consumed (Chandon and Wansink 2007; Wansink et al. 2005).

Consumption behavior is shaped not only by societal and environmental influences, but also by our own perceptual and representational biases that interact with such variables. Some of the biases that lead to misperceptions of food portion sizes in different contexts have been attributed to the Delboeuf illusion (see Van Ittersum and Wansink 2011). As originally described by Delboeuf (1865), this illusion occurs when the size of a central item is misperceived on the basis of its surrounding context. When a larger concentric circle encompasses a test circle, the test circle is generally perceived to be smaller than when it is encircled by a relatively smaller concentric circle (see Figure 1A). In the case of food on plates, portions on small plates appear to be more food than the same portions served on large plates, and this can affect how much people serve themselves and subsequently consume (Van Ittersum and Wansink 2011).

Although such misperceptions in food portion estimation are likely common among humans, little is known about whether they extend to nonhuman animals as well. However, there is an extensive comparative literature on visual illusions among nonhuman species, including but not limited to the Ebbinghaus-Titchener illusion (*Columbidae*: Nakamura et al. 2008; *Papio papio*: Parron and Fagot 2007; *Gallus gallus*: Salva et al. 2013), the Ponzo illusion (*Equus*: Timney and Keil 1996; *Macaca mulatta*: Bayne and Davis 1993; Fujita 1996; *Pan troglodytes*: Fujita 1997), the Zollner illusion (*Papio papio*: Benhar and Samuel 1982; *Gallus gallus*: Watanabe et al. 2013), and the corridor illusion (*Papio papio*: Barbet and Fagot 2007). This literature suggests a continuity of illusory perception across some nonhuman species and humans. Here, we extended this line of research to determine whether chimpanzees (*Pan troglodytes*) also fall prey to the Delboeuf illusion at one of the most inopportune times - when they are trying to choose between differing amounts of highly preferred food types. Critical to this study, and atypical of most comparative visual illusion experiments, we used edible stimuli to mimic the food portion estimation studies in humans. We also used food items to ensure that the chimpanzees were highly motivated to choose between the presented options. The use of high preference food items as stimulus sets to be discriminated is an excellent way of ensuring this degree of motivation. Should chimpanzees show biases to choose smaller amounts of preferred food over larger amounts, this would be compelling evidence of how a perceptual bias leads to suboptimal decision

making in a highly natural and significant context (food choice), especially given chimpanzees' established proficiencies in discerning among food quantities in many previous studies (see below).

Chimpanzee choice behavior, as in other animals (Stephen and Krebs 1987), is related largely to the maximization of energy intake (Sayers and Menzel 2012). Additionally, chimpanzees perform very well in quantity discrimination tasks when judging visual or auditory food stimuli, presented sequentially or simultaneously (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). Chimpanzees also can discriminate very small differences between quantities of food items (e.g., Menzel 1961; Menzel and Davenport 1962), sometimes even matching or exceeding the performance of human adults in these judgments (e.g., Menzel 1960). And, chimpanzees and other great apes accommodate the effect (or non-effect) of spatially transformed quantities that are moved to new arrangements or poured into different sized containers, thereby showing evidence of quantity conservation (e.g., Call and Rochat 1996; Muncer 1983; Suda and Call 2004, 2005; Woodruff et al. 1978). But, they also may experience illusory percepts that constrain accurate representation of quantities and therefore disrupt optimal choice behavior that maximizes intake. Cross-species evidence of the Delboeuf illusion in a food portion estimation study would provide complementary support that humans' proclivity for making food-related choices that lead to overconsumption occurs partially due to perceptual biases that are evolutionarily entrenched (Van Ittersum and Wansink 2007, 2011) and may be difficult to change through environmental manipulations alone.

In this experiment, chimpanzees chose between food portions that were either identical in size or different, and those portions were presented either on same-sized or different-sized plates. Critically, we were interested in whether the chimpanzees misperceived same-sized or even smaller food portions to be larger when they were presented on smaller plates. These test trials were examined in comparison to control trials where different-sized food portions were presented on the same-sized plates (large plate versus large plate and small plate versus small plate) to ensure that the chimpanzees could discriminate between the food quantities when presented in an identical context.

We predicted that the chimpanzees would be proficient in control trials given their success in multiple quantity judgment experiments (e.g., Beran and Beran, 2004). In addition, we predicted that they would perceive the Delboeuf illusion in a manner similar to that of humans in which equal or smaller-sized foods presented on small plates would be preferred over food on large plates. This result would provide new evidence about the nature of chimpanzee choice behavior and also about the continuity across primates for illusory biases that impact choice and decision-making.

Methods

Subjects

We tested three chimpanzees (*Pan troglodytes*) from the Language Research Center at Georgia State University, including two males (Sherman: age 39, Mercury: age 25) and one female (Lana: age 42). Apes 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.

Two of the three chimpanzees (excluding Mercury) had extensive exposure to language-training using a symbol-based lexigram system in which individual lexigrams represented various objects, people, places, and activities (Rumbaugh and Washburn 2003). All three

chimpanzees had demonstrated proficiency in numerous tests of quantity judgments (e.g., Beran 2001, 2004, 2012; Beran and Beran 2004; Rumbaugh et al. 1987).

Materials and Procedure

We introduced a two-option choice task by presenting a testing tray on which we placed two plates, each containing a separate portion of food. To avoid possible cuing, a retractable blind was attached to the testing bench and was lowered during plate presentation so that the experimenter could see the chimpanzee's choice only after it had been made. After baiting the tray out of sight of the chimpanzee (i.e., with the blind fully lowered), the experimenter raised the blind slightly so that the subject could clearly see the plates and then waited three seconds before sliding the tray toward the chimpanzee. The chimpanzee then could point to one plate, following which the experimenter immediately gave whatever was on the selected plate to the chimpanzee for consumption and removed the unselected plate and its contents from the tray.

Testing involved two types of foods, a discrete type (cereal pieces) and a continuous type (round pieces of lunch meat). We used both discrete and continuous food types as human studies have used a range of foods and we were interested in the generality of this illusion to different food types. Only one food type was ever used in a given trial, thus we did not directly pit continuous and discrete foods against each other.

We used two different sizes of identical white dinner plates. The larger of the two plates measured 26.67 cm in diameter and the smaller plate measured 19.05 cm in diameter. We used two different portion sizes for both the discrete and continuous food types. For the discrete food type (cereal), round cookie cutters were used to mold the cereal pieces into a round presentation form. For the large cereal amount, the cutter had an area of 99.8 sq cm and for the smaller cereal amount the area of the cutter was 86.2 sq cm. By weight of cereal, the larger cereal portion was 10 g and the smaller cereal portion 8 g.

For the continuous food type (lunch meat slices), cookie cutters were again used to cut the lunch meat into a round presentation form. The large lunch meat portion was cut to an area of 86.2 sq cm and the small lunch meat portion was cut to an area of 71.3 sq cm for Sherman and Lana, and 62.1 sq cm for Mercury. This was necessary because pilot tests in which both food amounts were presented on identical plates indicated that Mercury needed the difference between pieces of lunch meat to be larger than did Lana or Sherman in order to discriminate between the two when both were presented on the same sized plate. By weight of lunch meat, the larger portion was 30 g, the smaller portion for Sherman and Lana was 25 g, and the smaller portion for Mercury was 21.3 g. Figure 1 provides examples of the food and plate combinations for some test trials.

We presented four trial types, including Small Plate Control trials, Large Plate Control trials, Standard Illusion trials, and Non-Standard Illusion trials. All trial types were presented for both types of food, continuous and discrete. Control trials involved presenting the two different food portions on the same sized plates (both small or both large) to determine whether the chimpanzees could discriminate between the two portion sizes when presented in an identical context. Standard Illusion trials used a mixed-plate design in which equal food portions were presented (Figure 1B). These trials matched the standard Delboeuf illusion in which different sized concentric circles (i.e., plates) encompassed the same-sized inner circle (i.e., food portions) so that the food should appear larger when placed on the smaller plate (Figure 1A). The Non-Standard Illusion trials used a mixed-plate, mixed-portion design in which a smaller portion of food was placed on a smaller plate in comparison to a larger food portion on the larger plate (Figure 1C; as outlined in Van

Ittersum & Wansink, 2011). In this case, the illusion occurs when the different-sized foods appear to be equal in size. Table 1 outlines all of the trial types.

Each session consisted of eight trials, with four trials of each food type (continuous and discrete) per session. For each food type, we presented one of each trial type so that in each session, chimpanzees received a Small Plate Control, Large Plate Control, Standard Illusion, and Non-Standard Illusion trial for both food types. All four continuous (lunch meat) trials were run first, followed by the four discrete (cereal) trials. Within each four-trial block, trial type was randomized as was plate position (i.e., right versus left placement on tray). A total of eight sessions were conducted, with one session conducted per day.

Results

The first question was whether performance differed depending on the type of food that was presented. To assess this, we examined the proportion of choices made by each chimpanzee in each condition as a function of food type. For eight of nine of these analyses, those proportions were not statistically different (Fisher's exact test, all chimpanzees: $P > 0.22$). For one chimpanzee (Mercury) in only one condition (Non-Standard Illusion), the choice proportions were statistically different between food types (Fisher's exact test: $P = .001$). Thus, choice behavior was highly consistent across the two food types, and we therefore collapsed across food type for the remaining analyses.

The second question concerned whether performance differed in the two Control trial types. All chimpanzees significantly preferred the larger portion of food over the smaller portion in Control trials; Binomial test, all chimpanzees: $P < 0.001$. There was not a significant difference between control trials presented on small plates and those presented on large plates for any of the chimpanzees, as they were equally good at selecting the larger amount of food. Sherman chose the larger amount of food on 14 of 16 trials with the small plates and 14 of 16 trials with the large plates (Fisher's exact test: $P = 1.00$). Mercury chose the larger amount of food on 16 of 16 trials with the small plates and 14 of 16 trials with the large plates (Fisher's exact test: $P = 0.48$). Lana chose the larger amount of food on 15 of 16 trials with the small plates and 13 of 16 trials with the large plates (Fisher's exact test: $P = 0.60$).

The third question was whether the chimpanzees would show any bias toward a particular plate size in Standard Illusion trials when identical food portions were presented on large and small plates. Preferring the small plate would be an indication of the Delboeuf illusion, and this did occur. All chimpanzees significantly preferred the small plate over the large plate when both plates contained the same portion of food in the Standard Illusion trials (Figure 2A); Binomial test, Sherman: $P = 0.004$, Mercury: $P < 0.001$, Lana: $P < 0.001$.

As shown in Figure 2B, two of the three chimpanzees chose the smaller food portion over the larger food portion in the Non-Standard Illusion trials significantly more often than they selected the smaller food portion over the larger food portion in the Control trials, Fisher's Exact Test, Sherman: $P = 0.01$, Mercury: $P = 0.01$, and one chimpanzee approached but did not exceed conventional levels of statistical significance, Lana: $P = 0.06$. This indicated a clear bias to choose the small food portions over large food portions in mixed-plate conditions (Non-Standard Illusion trials) relative to making that mistake in the same-sized plate control conditions where the chimpanzees were highly accurate in choosing the larger portions over the smaller portions. In addition, for the control trials depicted in Figure 2B, selection of the larger amount of food always exceeded chance levels (Binomial test: $P < 0.01$) whereas performance did not differ from chance on the Non-Standard Illusion trials

(Binomial test: $P > 0.10$). This also reflected the Delboeuf illusion because in both cases the exact same amounts of food were presented for comparison, and only the context differed.

Discussion

In the current study, when plate sizes were identical, chimpanzees accurately chose the larger food portion consistently. In contrast, they appeared to perceive same-sized and smaller food portions that were presented on smaller plates to be larger in amount than an equal or larger food portion presented on a larger plate. This is an interesting result, because it means that they overestimated and subsequently preferred or were biased towards an equal or even smaller-sized food portion over a larger food quantity when placed on a small dish, and did so despite clearly being able to distinguish quantity when plate size was identical. The implication is clear: for chimpanzees, as for humans, context matters. It has a direct impact on the visual perception of food portion size and preference in a nonhuman species for which there is little experience with choosing between amounts of food on dinnerware. The biases resulting in this form of misperception of food portions appear to have a deep-rooted evolutionary history which we share with, at minimum, our closest living nonhuman relative, the chimpanzee.

Chimpanzees have demonstrated sensitivity to very minor differences in quantities of food items, sometimes matching or even outperforming human adults in similar tasks (e.g., Menzel 1960, 1961; Menzel and Davenport 1962). Moreover, the chimpanzees tested in the current study are highly proficient on a wide range of quantity judgment tasks (Beran 2001, 2004, 2012; Beran and Beran 2004; Beran et al. 2013; Rumbaugh et al. 1987). Beyond their quantitative capacities, chimpanzee choice behavior is likely motivated by maximization of energy intake (Sayers and Menzel 2012). The combination of quantitative skills and a focus on energy maximization places a premium on judgment behavior that leads to the selection of the largest food portion available. Sub-optimal choice behavior in the current study by chimpanzees suggests that the visual illusion created by a misleading surrounding context is salient enough to disrupt this system, and even does so repeatedly across time and food type.

These results are in line with other investigations of visual illusions among nonhuman animals using non-edible stimuli (e.g., Fujita 1996, 1997; Nakamura et al. 2008; Parron and Fagot 2007; Salva et al. 2013; Timney and Keil 1996; Watanabe et al. 2013), and in that sense the results provide another indication of the general similarities in perceptual processing across species. However, it is striking here that the illusion manifests during food quantity discriminations, which are arguably the best possible stimuli to use because they naturally motivate the animal to respond and attempt to find the largest food item, and also require little or no training with regard to what the animal should be attempting to do (maximize food intake). It will be interesting to see if this illusion occurs in some of the species tested in other visual illusion tasks, or if it occurs when non-food stimuli are presented.

The biases that cause us to misperceive portion sizes depending upon the context in which they are presented may be explained by the Delboeuf illusion (Delboeuf 1865). The Delboeuf illusion is attributed to the distance between a target (e.g., food) and an inducing annulus (e.g., plate) where larger distances lead to a contrast effect in which the inner circle-size is underestimated and smaller distances lead to an assimilation effect in which the inner circle is overestimated (e.g., Coren and Girgus 1978; Girgus and Coren 1982; Jaeger and Lorden 1980; Roberts et al. 2005). Van Ittersum and Wansink (2011) used the Delboeuf illusion to explain how equal food portion sizes appeared to be larger when placed on small dinnerware (assimilation) and smaller when placed on large dinnerware (contrast), leading to the over-serving (or under-serving) from larger (or smaller) dishes. The present results

coupled with those from the human literature suggest that the Delboeuf illusion can lead to a ‘less-is-more’ effect in food portion estimation studies in which smaller stimuli are preferred to larger alternatives. Similar sub-optimal responses have been seen among the chimpanzees tested in this experiment with regard to stimulus set size, at least if optimality is defined in terms of total caloric intake. For example, these chimpanzees sometimes selected a smaller food quantity over a larger quantity when the smaller set contained the largest individual food item (Beran et al. 2008). Boysen, Berntson, and Mukobi (2001) also reported that different chimpanzees showed a bias to point to collections of food items when they contained the larger individually sized items, even when those collections contained an overall smaller amount of food relative to an alternate choice. Thus, misperceptions and other biases can lead chimpanzees to choose between food sources in ways that reduce overall intake, highlighting an interesting conflict between the drive to maximize and how the chimpanzees respond to context cues that are non-quantitative in nature but impact how quantities are represented.

Understanding the salient features of stimulus sets (e.g., food-to-plate ratio or conflicting elemental features) that lead to perceived differences in quantity across multiple species is important in isolating and then attenuating such biases. Although these effects appear to be largely insulated from experience and training (Wansink and Cheney 2005; Wansink et al. 2006), increased attention can lead to a reduction in portion-size misperception as evidenced by a decrease in the illusion by increasing the time spent examining the stimuli (Van Ittersum and Wansink 2011) and the null results found for this effect in a study that used isolated, distraction-free subjects (Rolls et al. 2007). However, the present results are quite robust in demonstrating the Delboeuf illusion across time as these chimpanzees received multiple testing sessions over the course of several weeks, an aspect of comparative research that does not typically occur in human research because of the use of between-subjects designs that only test an individual one time. Here, the chimpanzees continued to fall prey to this illusion throughout the duration of the entire study, and across food types. Further research that manipulates presentation speed and exposure along with interference will be necessary to understand their impact on nonhuman animals in this task. In addition, research that investigates the impact of a more sparsely distributed discrete food type on the illusion is also of interest as the current design utilized a discrete food type (cereal pieces) that was organized quite similarly to the continuous food type (lunch meat). At present, what we can conclude is that chimpanzees’ judgment of food quantities can be heavily influenced by non-quantitative aspects of the context in which choices are presented. This comparative finding that matches results with human participants highlights the need to broaden our focus from the cultural aspects of consumption behavior to include the cross-species’ visual illusions created by the interaction of contextual variables and stimulus presentation.

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Figure 1.

A. The Delboeuf illusion occurs when two same-sized central circles are perceived to be different depending upon the context in which they are presented. The two equal-sized black circles are perceived differently so that when a larger concentric circle encompasses the test circle (left), the test circle is thought to be smaller than when encircled by a relatively smaller concentric circle (right). B. Test stimuli for the Standard Illusion trials are shown where equal-sized continuous food portions are presented on a large and small plate so that the food on the large plate (left) appears to be smaller than the food on the small plate (right). C. Test stimuli for the Non-Standard Illusion trials are shown where a larger discrete

food portion on a large plate (10 g of cereal - left) appears to be equal to the smaller portion on the small plate (8 g of cereal - right).

Figure 2.

A. The percentage of small plate choices in the Standard Illusion trials. All chimpanzees had a significant preference (from chance, depicted by the dashed line) for the small plate over the large plate when both plates contained an equal portion of food. B. The percentage of large food portion choices in control trials (gray bars) versus Non-Standard Illusion trials (black bars). All chimpanzees selected the larger food portion less often in the Illusion trials when presented on different-sized plates than in control trials when presented on same-sized plates, even though both conditions presented the same relative difference in food portions.

Table 1

Trial type descriptions, including food portion and plate combinations.

Trial Type	Comparison
Small Plate Control	Small Food on Small Plate vs. Large Food on Small Plate
Large Plate Control	Small Food on Large Plate Vs. Large Food on Large Plate
Standard Illusion Test	Large Food on Small Plate Vs. Large Food on Large Plate
Non-Standard Illusion Test	Small Food on Small Plate Vs. Large Food on Large Plate