



# The rewarding effects of number and surface area of food in rats

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## Abstract

Visual cues have an important role in food preference for both rats and humans. Here, we aim to isolate the effects of numerosity, density, and surface area on food preference and running speed in rats, by using a forced-choice maze paradigm. In Experiment 1, rats preferred and ran faster for a group of multiple smaller pellets rather than a single large pellet, corroborating previous research (Capaldi, Miller, & Alptekin *Journal of Experimental Psychology: Animal Behavior Processes*, 15(1), 75–80, 1989). Further experiments tested the prevailing hypothesis that multiple food pieces are more reinforcing because they occupy a larger surface area. Experiment 2 controlled for numerosity by utilizing a continuous food: mashed potatoes flattened to cover a larger surface area or rounded into a ball. The rats preferred and ran faster for the flattened potatoes, suggesting surface area plays a role in quantity estimations. Finally, in Experiment 3, rats displayed no preference or difference in running speed between a group of scattered and clustered pellets when number of pellets were kept constant. Taken together, these results suggest that density has an important role in food perception—that is, the rewarding effect of higher numerosity or larger surface area is removed when the food does not fill out the entire space. Alternative explanations and implications for human diet are discussed.

**Keywords** Food · Acquisition · Number · Surface area · Density

## Introduction

Animals prefer a larger portion of food to a smaller one and are responsive to visual cues that signal quantity. In the natural environment cues that represent more food include a larger size, more pieces, a denser collection, and a larger surface area. Here, we aim to isolate the effects of numerosity, surface area, and density to determine which is the dominating visual cue used by rats when assessing food quantity.

## Assessment procedures

In primates, quantity perception is assessed using the natural choice procedure: Animals must choose between two arrays of food that vary in single or multiple quantitative characteristics (Boysen, Berntson, & Mukobi, 2001; Hauser, Carey, & Hauser, 2000; Shumaker, Palkovich, Beck, Guagnano, & Morowitz,

2001; Stevens, Wood, & Hauser, 2007). This technique reliably yields expected results when one of the choices is the optimal response. For example, when given two arrays of food that varied in size, chimpanzees chose the portion containing larger elements over one containing smaller elements. Similarly, when varying the number of items, primates chose a larger number of food items over fewer items (Boysen & Berntson, 1995; Boysen et al., 2001; Silberberg & Fujita, 1996; Silberberg, Widholm, Bresler, Fujita, & Anderson, 1998).

Relative quantity discriminations based on size and number of pieces have also been examined in animals lower in the phylogenetic tree—rats (Campbell, Batsche, & Batsche, 1972; Capaldi, Miller, & Alptekin, 1989; Traupmann, 1971), birds (Ain, Giret, Grand, Kreutzer, & Bovet, 2009; Bogale, Kamata, Mioko, & Sugita, 2011), amphibians (Krusche, Uller, & Dicke, 2010; Stancher, Rugani, Regolin, & Vallortigara, 2015), fish (Kilian, Yaman, von Fersen, & Güntürkün, 2003; Yaman, Kilian, von Fersen, & Güntürkün, 2012), insects (Carazo, Font, Forteza-Behrendt, & Desfilis, 2009), and other nonprimate mammals (Utrata, Virányi, & Range, 2012; Vonk & Beran, 2012). In birds and rats, the magnitude of food varying in size and number of items was assessed by measuring choice or running speed—running speed increases as reward magnitude increases. Chickens ran faster for multiple rice grains than for a single rice

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grain (Grindley, 1929), showing that the reward value of food can be operationalized with running speed.

## Numerosity

Food presented in multiple pieces is more rewarding than the same quantity presented in a single piece. Wolfe and Kaplon (1940) found that chickens ran fastest for a popcorn kernel cut into four pieces, followed by a single intact popcorn kernel, and slowest for a single piece comprising one fourth of a kernel. Subsequent studies varying number of pieces found similar results. Shettleworth (1985) showed that pigeons preferred 300 mg of pellets in 15 pieces versus a single 300-mg pellet. Furthermore, rats ran faster for a group of small pellets than for a single large pellet, even when the single pellet contained slightly more calories (Campbell et al., 1972; Traupmann, 1971). These results were replicated using a T-maze forced-choice paradigm. Capaldi et al. (1989) found that rats preferred a T-maze arm containing four 75-mg pellets over one containing a single 300-mg pellet.

In a controlled laboratory setting, overreliance on visual cues can misrepresent quantity of food and lead to suboptimal responding. In a series of studies, primates chose an array of food containing a larger item, even when rewarded with less food for that choice (Beran, Evans, & Harris, 2008; Boysen & Berntson, 1995; Boysen, Berntson, Hannan, & Cacioppo, 1996; Boysen et al., 2001). Clearly, the visual system is a strong determiner of food selection, even when choosing the single piece is actually the suboptimal response.

## Density

Numerosity alone cannot explain why multiple pieces of food is more rewarding than a single piece. When a collection of pieces is laid out as a stimulus, it also differs visually from a single piece on other factors that have been shown to affect perception—layout (Beran, 2006; Davis & Pérusse, 1988; Ginsburg, 1976, 1980; Xu & Spelke, 2000), density (Davis & Pérusse, 1988; DeWind, Adams, Platt, & Brannon, 2015; Hollingsworth, Simmons, Coates, & Cross, 1991; Stevens et al., 2007; vanMarle & Wynn, 2011; Xu & Spelke, 2000), surface area (Davis & Pérusse, 1988; Feigenson, Carey, & Spelke, 2002), and contour length (Clearfield & Mix, 1999, 2001; Xu & Spelke, 2000). When the number of items is kept consistent, numerosity estimates in monkeys and humans are biased when comparing them in a regular versus random pattern (Beran, 2006; Ginsburg, 1976, 1980), in one large cluster versus multiple small clusters (Frith & Frith, 1972), and in regular versus nested patterns (Beran & Parrish, 2013; Chesney & Gelman, 2012).

Density, sometimes referred to as interstimulus distance, is the degree of closeness of the items presented—denser arrays have less empty spaces between the individual items. In human

subjects, density is negatively correlated with numerosity—as density decreases, estimated numerosity increases (Allik & Tuulmets, 1991, 1993; Durgin, 1995). Xu and Spelke (2000) controlled for differences in density and found that human infants chose the array with the larger number of items. However, when number of items are identical, infants rely on density for making quantity estimations. Four cookies densely placed were chosen over the same number of cookies sparsely placed (Uller, Urquhart, Lewis, & Berntsen, 2013). In animals, however, a different set of findings emerged. Cotton-top tamarins in a two-choice discrimination task chose a denser array of food even when amount and number of food items in both portions were the same (Stevens et al., 2007). However, density in this study was varied by changing item size, which would be a confounding factor. Certain primate species, such as orangutans, rely on foraging for their exclusive fruit-only diets. Even orangutans prefer visiting locations that contained dense fruit patches (Macdonald & Agnes, 1999). Similar sensitivities to density cues have been shown in birds (Mitchell, Calton, Threlkeld, & Schachtman, 1996; Vahl, Lok, Van der Meer, Piersma, & Weissing, 2005).

## Surface area

Pelham, Sumarta, and Myaskovsky (1994) suggest that other quantitative characteristics that covary with number (surface area, amount, or weight) also affect numerosity estimates. A multiple-piece food in the natural environment may be judged based on area, size, and weight—numerous items may be perceived as heavier, as occupying a larger surface area, and as containing a greater quantity of food. These characteristics may influence quantity perceptions and ultimately the incentive value of a food reward in animals. Human infants chose one large cracker over two small crackers, reliably choosing the larger food reward using amount or volume rather than number as a cue (Feigenson, Carey, & Hauser, 2002). When surface area or volume was equated, infant food choice was not based on number. Furthermore, female mosquitofish placed in a novel environment showed no difference in time spent with larger or smaller shoals of fish when total surface area was controlled for, showing that decisions on numerosity can be based on total surface area occupied by larger arrays (Agrillo, Dadda, Serena, & Bisazza, 2008).

## Current research

Preference for multiple pieces over a single piece may be partly based on the larger surface area that they occupy. In this series of studies, we aim to separate the confounding influences of numerosity, surface area, and density on food choice in rats. In Experiment 1, the choices were a single pellet or a calorically equivalent group of smaller pellets, differing on all three variables. Consistent with previous research, rats preferred the group of pellets, but it is inconclusive whether they

did so due to numerosity or surface area. In Experiment 2, rats preferred flattened mashed potatoes that took up a greater surface area to a rounded ball of mashed potatoes. Finally, Experiment 3 tested whether a greater surface area would be preferred even when the food was less densely populated: the choices were two groups of pellets in a scattered or clustered configuration. Rats did not show a preference, indicating that they consider density and do not automatically prefer food that takes up a larger surface area. Collectively, these results suggest that rats prefer food that takes up a larger surface area, unless that surface area is punctuated by visible space between the pieces.

## Experiment 1

Animals can be divided into two types, based on their dietary selection strategies: generalists and specialists. Many carnivores, herbivores, and insectivores are specialists because they are genetically programmed to select from a very narrow, uniform range of foods. On the other hand, omnivores, like humans and rats, are generalists because they tend to forage for foods by exploring their environments to eat a wider and varied range of foods (Galef, 1996). Foraging for food is a complex task because it involves obtaining the maximal amount of food with the least energy and time expenditure, known as the optimal foraging theory (Stephens & Krebs, 1986). In the wild, rats must explore environments to find food while simultaneously protecting their food from conspecific rats and themselves from predators.

Several studies have shown that many pieces of food are more reinforcing to rats than single, large pieces. Perhaps this preference for a greater number of food pieces is adaptive because multiple pieces of food may amount to more food in the natural environment. However, as mentioned previously, number varies naturally with several other dimensions, such as item size, surface area, and density. Few studies have isolated these characteristics in rats.

The purpose of Experiment 1 was to replicate the findings of Capaldi et al. (1989), showing that multiple small pieces of food are more rewarding than a single piece. Experiment 1 measures both choice and running speed to examine the incentive value of food in a single experiment. In rats, preference is a measure of the relative incentive value of foods, whereas running speed is a measure of motivation for a reward. We hypothesized that both metrics would produce the same conclusions. However, measuring both choice and running speed in a single experiment allows us to compare our results with those obtained previously in rats (Amsel, Hug, & Surridge, 1968; Campbell et al., 1972; Capaldi et al., 1989; Traupmann, 1971) and with primates (Beran, 2006; Beran et al., 2008; Boysen & Berntson, 1995; Boysen et al., 1996; Boysen et al., 2001).

## Method

**Subjects** Subjects were 40 experimentally naïve male Sprague-Dawley rats purchased from Harlan Co. (Indianapolis, IN). One rat did not complete the training trials because of sickness and was removed from the experiment, leaving a final sample size of 39. Rats were 85 days old upon arrival and 92 days old upon the start of deprivation. Animals were single-housed and maintained on a 12-hour light/dark cycle. Upon arrival to the laboratory, rats were given ad libitum food and water. Consistent with studies that used visual cues to examine behavior (Phelps & Roberts, 1989; Wishaw, Dringenberg, & Comery, 1992; Wishaw & Tomie, 1989), animals in these experiments were also run in the light part of their cycle. Experimental procedures were approved by the Arizona State University Institutional Animal Care and Use Committee and adhered to Guidelines for the Care and Use of Laboratory Animals.

**Materials** Noyes Precision Pellets (10 mg and 300 mg), purchased from Test Diet (Richmond, Indiana), were used for this study.

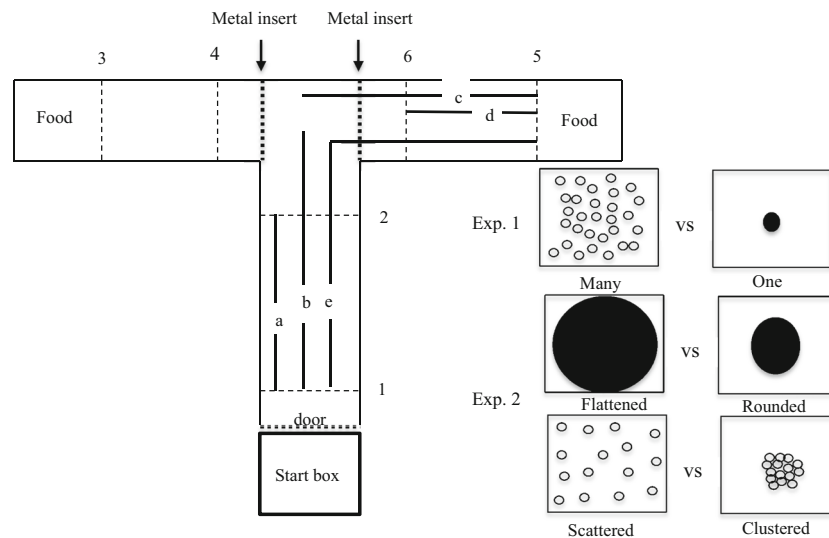
**Apparatus** A T-maze (purchased from Columbus Instruments) was used, as shown in Fig. 1.

The length of the start box was 16.5 cm, and the stem of the maze was 61-cm long from the start box (located at the base of the stem) to the choice area (at the intersection of the T). The length of each T-maze arm was 45.7 cm. The entire maze was covered with transparent, plastic lids. Metal inserts separated the stem of the maze from the start box (guillotine door) and the arms of the maze. The maze was set up with six invisible, infrared beams connected to a computer that recorded the time (in milliseconds) that the beams were interrupted when the rats crossed the area. Each arm of the maze contained two beams 25.5 cm apart, and the stem of the T-maze contained two beams 49.5 cm apart.

The food was placed at the end of each arm. In the Many arm of the maze, thirty 10-mg pellets were laid out randomly to mimic natural foraging situations, whereas the One arm contained a single 300-mg pellet. The arms were equicaloric at 1 kcal total. To prevent any effect of a side preference, for half of the rats, the Many arm was the left arm and the One arm was the right arm, and the other half saw the reverse. Animals upon entering the arm were confined there by lowering the metal insert. Once they had finished eating the food, or after 10 min had elapsed (whichever came first), they were removed from the arm.

## Procedure

**Adaptation** On arrival at the laboratory, animals were placed on adaptation for a week, and their ad lib weights were taken for 3 days. Ad lib water was present throughout the experiment in clear plastic bottles mounted on the right of the food hopper in the front of each cage. Following 1 week of adaptation, on Day 1,



**Fig. 1** T-maze showing numbered infrared beams (represented as dashed lines within the maze) and location of metal inserts used to block arms on forced trials. A beam break was recorded when a rat touched the infrared beam, and a beam make was recorded when a rat crossed the beam. Running speed calculations were based on beam breaks and makes. Diagram shows running speed calculations for a rat entering the right arm. <sup>a</sup> Runway (Beam Break 1 to Beam Break 2), <sup>b</sup> runway to choice

area (Beam Break 1 to Beam Make 2), choice area to food (Beam Make 2 to Beam Break 3 or Beam Break 5), chosen arm to food (Beam Break 4 to Beam Break 3 or Beam Break 6 to Beam Break 5), and runway to food (Beam Break 1 to Beam Break 3 or Beam Break 5). The illustrations on the right show the type of food used in each trial in all experiments. Placement of these foods were counterbalanced in each experiment

all food was removed from the cages. On Days 2–15, all rats were given a restricted food ration to maintain them at 85% of their free-feeding body weight. The following procedures were similar to Capaldi et al. (1989). On Day 16, each rat got both a 300-mg pellet and thirty 10-mg pellets in their home cage to familiarize them with the pellets and to ensure they tasted both samples. The pellets remained in the home cage for at least 10 min or until rats ate both samples. In the final stage of adaptation, rats were placed in the maze with the food in the Many and One arms. The rats could freely enter both arms of the maze to explore and habituate to the maze. The location of food in the arms (i.e., which arm had a single pellet and which had multiple pellets) was consistent in rats throughout training and testing.

**Training** Rats were brought into the experimental maze room in squads of two. During the focal rat's trial, the conspecific rat was placed in another box away from the maze area. Similar to Capaldi et al. (1989), rats within a squad were run in an alternate sequence (Rat 1 ran its first trial, followed by Rat 2, and then Rat 1 ran its second trial, followed by Rat 2, and so on). The maze was cleaned with a 70% ethanol solution after every trial to remove traces of residue or smells left behind by the previous rat (Izquierdo et al., 2012; Ostrander et al., 2011). During the acquisition or initial phase of training (1 to 3 days), the intertrial interval was 12 min, as rats took longer to make a choice. Following acquisition, this procedure produced an intertrial interval of 2 min.

The purpose of the training session was to familiarize the rats with what would be in each arm of the maze during testing

and with the idea that their choice would eliminate their ability to eat the other option. At the beginning of each trial, rats were placed in the start box, and the trial began by raising the guillotine door 3 s later for entry into the maze. On a free trial, both arms were open, and the rat could enter either arm. On a forced trial, rats were forced into the arm they did not previously enter by blocking the entered arm with a metal insert. Thus, the arm open on Forced Trial 1 was opposite of Free Trial 1, and that on Forced Trial 2 was opposite of Free Trial 2, and so on. This procedure (Capaldi et al., 1989) gives rats equal exposures to both food types before being tested, preventing unequal entries during training from being a confounding explanation for findings in testing.

We trained rats for 7 days. On Day 17, rats had one free and one forced trial. On Days 18–23 of training, rats received a total of four trials each, two free and two forced trials. Thus, rats had a total of 13 free trials in training. Each squad received its first trial before the next trial began (i.e., each squad member ran its first trial before the partner rat ran its second trial, and so on). The order of the free and forced trials was counterbalanced across days in an ABBA fashion. Half the rats received a free-free-forced-forced order of trials on A days and free-forced-free-forced order on B days, and the other half received the reverse. The arm choice on each free trial was recorded. Five minutes after the last trial of the day, rats received their food ration (laboratory chow) in their home cage. The amount of food given to rats was calculated based on growth rate of normal male Sprague-Dawley rats and the amount needed to maintain them at 85% of their weights.



**Testing** We tested rats for 3 days. The purpose of testing was to evaluate the arm preference and running speed of the rats as a function of Many and One foods. Over 3 days of testing, each rat ran four free trials per day. The procedure was identical to training, except for the lack of forced trials. Five minutes after the last trial of the day, rats were fed laboratory chow.

**Data analyses** Running time (in milliseconds) of each trial was recorded by the maze software by tracking beam breaks (a rat touching an infrared beam) and beam makes (a rat crossing an infrared beam). Speed was calculated using the location of the beams, timing of the beam breaks and makes, and distance. The researchers recorded arm choice.

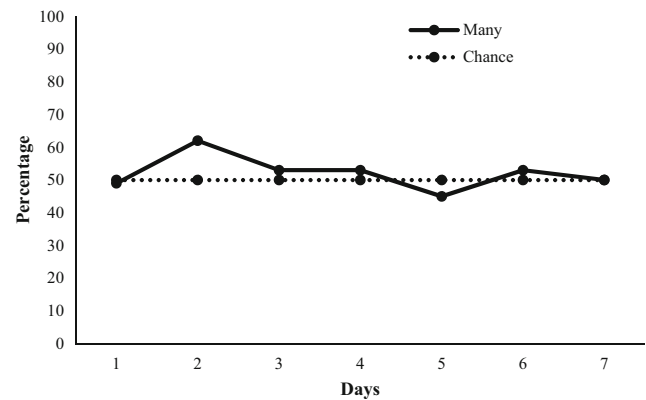
A one-sample *t* test was conducted to compare the number of times that the multiple pellet arm was chosen compared to that obtained by chance for each day in training and testing. In training, the Many arm could be selected up to two times (two free trials/day, except for Day 17, when there was one free trial), and both were compared to chance (.5 for Day 17 and 1.0 for Days 18–23). In testing, the Many arm could be selected up to four times and was compared against a chance level of 2.0. Effect size for significant results on arm choice was calculated using Cohen's *d*.

Each rat's running speed (cm/s) for the Many and One arms was calculated only for the last 2 days of training and all days of testing. Since running speeds were dependent on arm choice in testing, running speed data on the unchosen arms were missing. Thus, to prevent missing data from affecting the analysis, we averaged across the last 2 days of training and combined it with testing. We combined testing with the last 2 days of training because rats were consistent in their choices by then, defined as making repeat entries in the same arm on a minimum of 2 days in free trials during training. Running speed was computed by dividing the time (seconds) taken from distance traveled (cm) in the runway, from the runway to the choice area, choice area to the food, chosen arm to food, and runway to food. Average running speed scores for the Many and One arms over trials in the last 2 days of training and all days in testing were then used as a dependent variable in a between–within repeated-measures ANOVA, with choice (many vs. one) as the within-subject factor and counterbalancing (left arm/many vs. right arm/many) as the between-subject factor. This was done separately for each area of the T-maze. Partial eta-squared ( $\eta_p^2$ ) was reported for effect sizes for the significant results in running speed.

## Results

### Food choice

**Training** Choice of the Many arm did not exceed chance on any day of training, all *t*s < 1, as shown in Fig. 2.



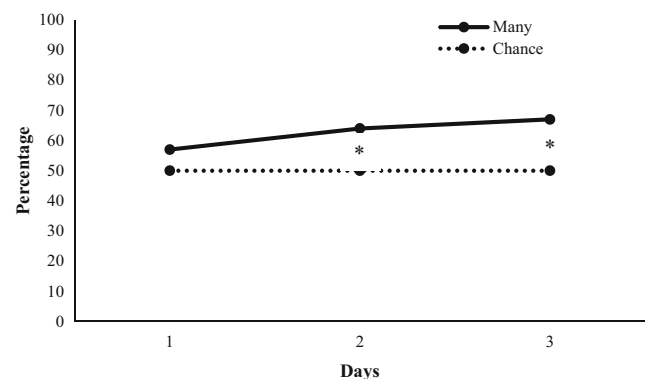
**Fig. 2** The percentage of time that the Many arm was chosen by 39 rats on each day of training is represented by the solid line. If performance was operating by chance, then the Many arm would be selected 50% of the time, as represented by the broken line

**Testing** Choice of the Many arm exceeded chance on Day 2,  $t(38) = 2.1$ ,  $p < .05$ ,  $d = .34$ , and Day 3,  $t(38) = 2.56$ ,  $p < .05$ ,  $d = .41$ , as shown in Fig. 3.

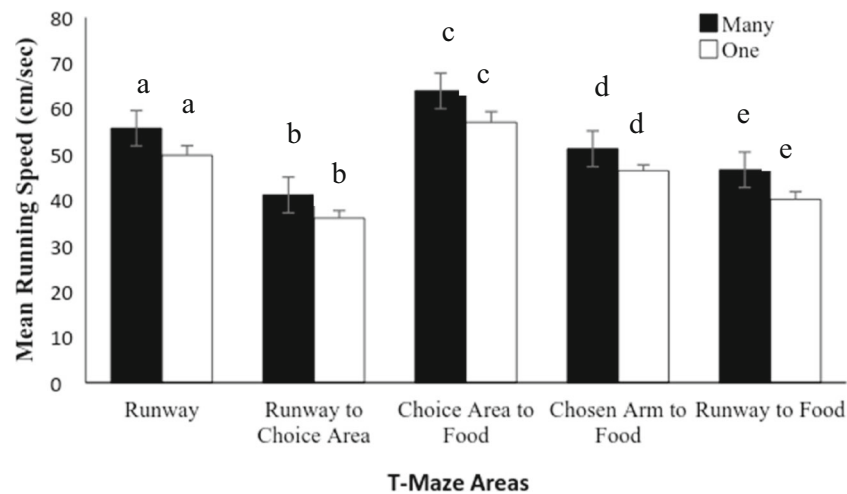
**Running speed** Running speed for the Many and One arms (last 2 days of training combined with testing) is shown in Fig. 4. Rats ran significantly faster for the Many arm than for the One arm in all areas of the T-maze: runway,  $F(1, 37) = 8.52$ ,  $p < .01$ ,  $\eta_p^2 = .19$ ; runway to choice area,  $F(1, 37) = 8.39$ ,  $p < .01$ ,  $\eta_p^2 = .19$ ; choice area to food,  $F(1, 37) = 4.56$ ,  $p < .05$ ,  $\eta_p^2 = .11$ ; chosen arm to food,  $F(1, 37) = 10.22$ ,  $p < .01$ ,  $\eta_p^2 = .22$ ; and runway to food,  $F(1, 37) = 8.13$ ,  $p < .01$ ,  $\eta_p^2 = .18$ .

## Discussion

Experiment 1 showed that rats preferred multiple pellets of food to a single equicaloric pellet. Preference was consistent when operationalized as both arm choice (Capaldi et al., 1989) and running speed (Amsel et al., 1968; Campbell et al., 1972; Traupmann, 1971).



**Fig. 3** The percentage of time that the Many arm was chosen by 39 rats on each day of testing is represented by the solid line. If performance was operating by chance, then the Many arm would be selected 50% of the time, as represented by the broken line. Asterisks represent a significant difference in choice of the Many arm from chance



**Fig. 4** Running speed for the Many and One arms in all areas of the T-maze. Vertical lines represent standard errors of the mean. Means with a common letter differ at  $p < .05$

Rats did not prefer the multiple over the single pellet of food in training. However, in testing, rats significantly preferred the multiple pieces of food over the single piece. This is not surprising, given that preference for four 75-mg pellets of food over the single 300-mg pellet was not significant until the 24th trial in Capaldi et al. (1989), which is equivalent to the sixth day of training in our experiment. Thus, in our study and in Capaldi et al. (1989), preference for the multiple over the single pellet condition was not spontaneous but developed over time. These results are inconsistent with primate studies where choice of one array over another is obvious and easily expressed on the first trial. Differences in the presentation of stimuli may explain these inconsistencies. Most primate studies utilize a two-choice discrimination task where both food options are available and visible simultaneously (Boysen et al., 2001; Hauser et al., 2000; Shumaker et al., 2001; Stevens et al., 2007). In ours and other studies (Capaldi et al., 1989), rats must first explore the maze arms and remember the available food portions before making a choice.

In Experiment 1, the food choices differed in numerosity, surface area, and density, making it difficult to draw conclusions about the cause of the preference. Experiments 2 and 3 isolated these factors.

## Experiment 2

Because the multiple pellets offered in Experiment 1 took up more surface area than the single pellet, either surface area or numerosity could explain the preference. The two factors are related, as numerosity estimates are affected by surface area—stimuli occupying a large area tend to be overestimated in quantity as compared to the same stimuli occupying a smaller area (Bevan, Maier, & Helson, 1963; Hollingsworth et al., 1991; Krueger, 1972). As mentioned previously, discriminations based

on number are attenuated when surface area is controlled for (Agrillo et al., 2008; Feigenson, Carey, & Hauser, 2002; Xu, 2003), suggesting that attendance to surface area may be critical in quantity estimations. Since we gave rats a choice between 30 and one pellet in Experiment 1, the rats may have perceived the 30 pellets to be a larger quantity because they took up a larger surface area than a single pellet. To isolate surface area from numerosity, we necessarily needed to use a continuous food that is spread out instead of being broken into distinct pieces.

Previous research utilizing a continuous food have yielded mixed results. Several studies have shown that human infants and monkeys (brown lemurs) cannot discriminate between different quantities of a continuous object (e.g., pile of sand; Huntley-Fenner, Carey, & Solimando, 2002), or they can only do so when there is a large difference (Hespos, Dora, Rips, & Christie, 2012; vanMarle & Wynn, 2011). However, human infants and monkeys have more success discriminating quantity when the continuous stimuli is food based or a liquid (Gao, Levine, & Huttenlocher, 2000; vanmarle, Aw, McCrink, & Santos, 2006; Wood, Hauser, Glynn, & Barner, 2008). So far, no study has investigated the rewarding effect of a continuous food in rats. One study in rats examined the rewarding effects of number using a continuous, liquid food (sucrose solution) and found no corresponding changes in behavior (Flaherty, Riley, & Spear, 1973). However, number in their study was manipulated by presenting a sucrose solution in a discrete number of same-size cups. Here, we varied the surface area of a single, solid, continuous object (i.e., mashed potatoes) by flattening or rounding the food into a ball. If surface area is a critical component of food reward, rats will prefer the portion that is flattened.

## Method

**Subjects** Twenty-four experimentally-naive male Sprague-Dawley rats purchased from Harlan Co., (Indianapolis, IN)

were used. A power analysis showed that for a small effect size of .20, power of .80, and a .05 alpha level to detect statistical significance, 24 rats are sufficient. Rats were 85 days old upon arrival and 92 days old upon the start of deprivation. Two rats were excluded from analyses because they showed consistent variations in food choices during all free trials in training. Data from the remaining 22 rats were included for analyses.

**Procedure** Apparatus, procedure, and data collection were identical to Experiment 1. Rats were trained for 22 days and tested for 7 days. The number of days of training was increased in order to establish each rat as having a consistent side preference; the number of days of testing was increased to investigate the lasting degree of the preference.

**Materials** We used instant potato flakes (purchased from Bashas, AZ) to make mashed potatoes. Three hundred and sixty-two grams of potato flakes were mixed with 1,542 mL of water. On each trial, rats were given 9 g (6.3 kcal) of potatoes, which contained 19% potato flakes (wt/vol). The potatoes were served in petri dishes that measured 90 mm.

In the Flattened arm, the potatoes were spread out to cover the entire petri dish, measuring 90 mm in circumference and approximately 1 mm in height and covering an area of approximately 644.9 mm<sup>2</sup>. In the Rounded arm, the potato portion was rounded into a ball and placed in the center of the petri dish. The rounded ball had a circumference of approximately 72.2 mm, a height of approximately 18 mm, and covered an area of 415 mm<sup>2</sup>.

Similar to Experiment 1, rats were habituated to the portions in their home cages for 30 min in the 2 days before training. Once both types of foods were sampled, the food was removed from the cage. Rats were given lab chow (adjusted for potato intake) 30 min after the last trial of the day in training and testing. We used a longer delay (30 min) between the trials and presentation of the lab chow here than in Experiment 1 because the amount of calories in the portion given was higher.

**Data analyses** Data analysis was similar to Experiment 1. However, because there was no missing data from the unchosen arm, running speeds in testing were analyzed separately from training.

## Results

### Food choice

**Training** Choice of the Flattened portion exceeded chance on Day 6,  $t(21) = 2.16, p < .05, d = .46$ ; Day 7,  $t(21) = 2.35, p < .05, d = .50$ ; Day 8,  $t(21) = 2.35, p < .05, d = .50$ ; Day 16,  $t(21)$

$= 2.89, p < .05, d = .62$ ; Day 19,  $t(21) = 2.41, p < .05, d = .51$ ; and Day 21  $t(21) = 2.16, p < .05, d = .46$ , as shown in Fig. 5.

**Testing** Choice of the Flattened arm exceeded chance on Day 3,  $t(21) = 2.32, p < .05, d = .50$  and Day 4,  $t(21) = 2.11, p < .05, d = .45$ , as shown in Fig. 6.

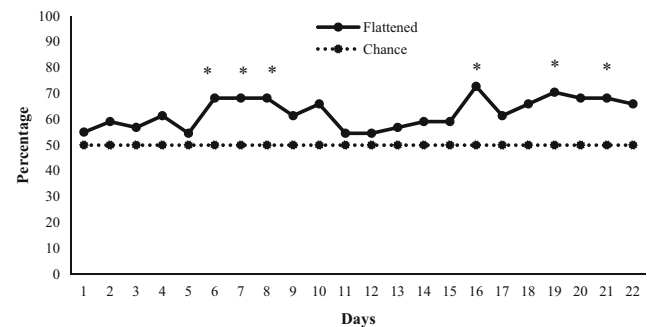
**Running speed** Running speed for the Flattened and Rounded arms in the last 3 days of training and all days in testing are shown in Fig. 7. Rats ran significantly faster for the Flattened than Rounded arm from the choice area to the food,  $F(1, 20) = 8.5, p < .01, \eta_p^2 = .30$ ; chosen arm to food,  $F(1, 20) = 9, p < .01, \eta_p^2 = .31$ ; and from the runway to the food,  $F(1, 20) = 6.99, p < .05, \eta_p^2 = .26$ .

## Discussion

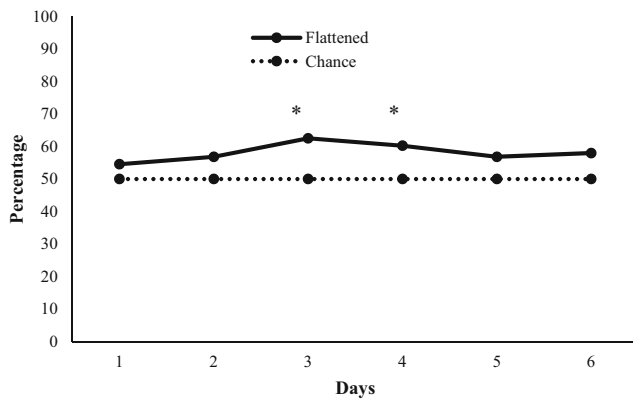
Rats preferred and ran faster for a portion of mashed potatoes flattened than for potatoes rounded together into a ball, suggesting that surface area occupied by food is an important determinant of reward in rats.

Running speed was significantly different in some areas of the T-maze and not others. While rats ran significantly faster for the flattened than for the rounded portions from the choice area and the chosen arm to the food, speed was not different in the runway area. Visibility of food from the choice area and the chosen arm than the runway may explain differences in these findings—seeing the food may have sensitized running behavior exaggerating differences in running speed between the flattened and rounded portions.

The flattened portion may have appeared larger to the rats because of the Delbouef illusion. In this illusion, an inner circle looks bigger when surrounded by a smaller, contrasting circle and smaller when surrounded by a larger, contrasting circle (Nicolas, 1995). This difference in perceived distance between the edge of the inner circle and edge of the outer circle affects the perceived size of the inner circle. In our



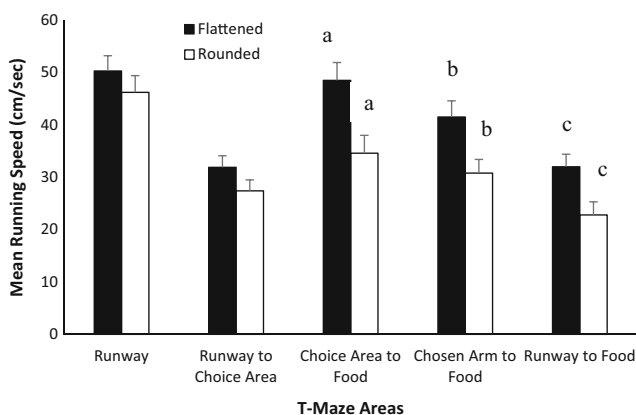
**Fig. 5** Percentage of time the Flattened arm was chosen by 22 rats on each day of training is represented by the solid line. If the results were obtained by chance, then the Flattened arm would have been selected 50% of the time, as represented by the broken line. Asterisks represent choice significantly different from chance



**Fig. 6** Percentage of times that the Flattened arm was chosen by 22 rats on each day of testing is represented by the solid line. If the results were obtained by chance, then the Flattened arm would have been selected 50% of the time, as represented by the broken line. Asterisks represent choice of the Flattened arm that was significantly different from chance.

study, since both food portions were placed in a petri dish, the lack of space between the edge of the flattened portion and outer rim of the dish may have exaggerated the perceived quantity of the flattened as compared to the rounded portion, and hence affected choice and running speed in rats.

The perceptual distortion of food in relation to the size of the plate has been shown to apply to food serving behaviors and consumption in both humans and nonhuman primates. Van Ittersum and Wansink (2012) found that people underestimate a food portion covering a smaller surface area and therefore serve and eat more to compensate for the lower amount being served than those given the same portion but covering a larger area. In a recent study with chimpanzees, Parrish and Beran (2014) found that the amount of food was misperceived based on the size of the plate on which food was served. An identical or smaller portion of food served on a smaller plate was judged to be a larger quantity of food than an identical or larger portion served on larger plates. The authors



**Fig. 7** Mean running speed (cm/sec) for the Flattened and Rounded potato arms in all areas of the T-maze. Means with a common letter differ. Vertical lines represent standard errors of the mean

suggested that quantity discriminations in chimpanzees may be heavily influenced by the context in which food is presented, i.e., the food-to-plate ratio. In our study, we kept the size of the petri dishes identical and manipulated the surface area occupied by food by flattening or rounding the portion of food and found a greater preference for the flattened than the rounded portion. This perceptual bias in favor of a portion of food occupying a larger area may suggest an evolutionary explanation. Perhaps flattened food portions may equate to a larger portion of food in the natural environment or may be a more natural way of coming upon food in the wild for rats as opposed to food already piled or rounded up. Although this is a possible explanation for these findings, future work must design studies that allow rats to compare each array of food simultaneously.

### Experiment 3

If rats relied mainly on surface area, then they would choose the same amount of food spread out over a large area, even if that spread was less dense than the alternative. To test this notion, we kept amount, size, and number of pellets constant and varied the surface area occupied by the food. A nonsignificant result or a preference for the clustered pellets would indicate the role of density in the rewarding effect of food.

### Method

**Subjects** Twenty-four experimentally naïve male Sprague-Dawley rats purchased from Harlan Co. (Indianapolis, IN) were used for this study. A power analysis showed that for a small effect size of .20, power of .80, and a .05 alpha level to detect statistical significance, 24 rats are sufficient.

**Procedure** The apparatus, procedures, and data analyses were identical to Experiment 1, except here the pellets were not placed in a petri dish. The pellets in each arm were fifteen 10-mg pellets (totaling 150 mg, 0.5 kcal). Pellets in the Scattered arm were placed in a random pattern, with no pellets touching each other. The spatial layout changed from trial to trial to imitate the natural food environment, but the overall surface area covered by the pellets did not vary. In the Clustered arm, the same number of pellets were placed in the middle of the arm, with all pellets touching. Rats were trained for 21 days and tested for 3 days.

### Results

#### Training

**Food choice** Choice of the Scattered arm exceeded chance on Day 5,  $t(23) = 3.72$ ,  $p < .01$ ,  $d = .10$ , and was significantly



lower than chance on Day 18,  $t(23) = -2.15, p < .05, d = .07$ , as shown in Fig. 8.

**Testing**

**Choice** Choice of the Scattered arm did not exceed chance on any day of testing, all  $t_s < 1$ , as shown in Fig. 9.

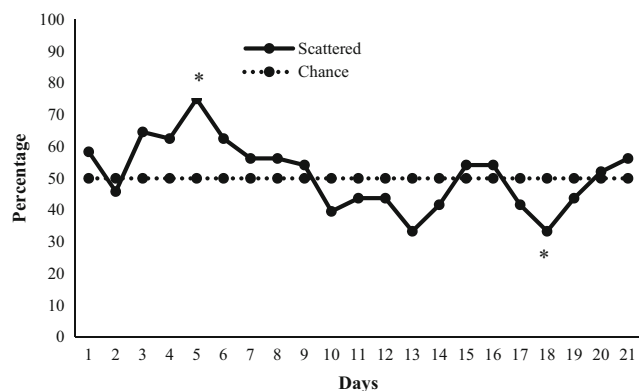
**Running speed** Running speed towards the Scattered and Clustered arms collapsed across the last 2 days of training and all days in testing are shown in Fig. 10.

There were no significant differences in running speed between the scattered and clustered pellets in any area, all  $F_s < 2$ .

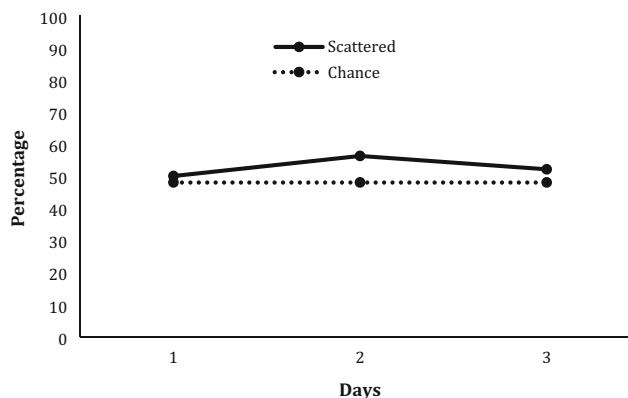
**Discussion**

Rats showed a small, initial preference for scattered pellets and then a small preference for clustered pellets, but these differences disappeared with increased training. No difference in running speed was found in any area of the T-maze. Unlike Experiment 1 and other studies (Capaldi et al., 1989), where preference for multiple food items continues to increase with extended training, there was significant variability in choices when the same number of pellets were scattered and clustered. The lack of a significant and consistent preference indicates that the rats did not find either choice more incentivizing than the other.

Experiment 2 showed that rats preferred a food with a greater surface area. The fact that we did not find a preference for the scattered pellets here therefore indicates that rats take food density into account when assessing surface area—the lower density of the scattered pellets counteracted the benefit of a larger surface area. It would be evolutionarily advantageous for foragers such as rats to prefer denser food arrangements. In foraging situations, a food that is clustered together



**Fig. 8** Percentage of times the Scattered arm was chosen by 24 rats on each day of training is represented by the solid line. If the results were obtained by chance, then the Scattered arm would have been selected 50% of the time, as represented by the broken line. Asterisks represent choice significantly different from chance

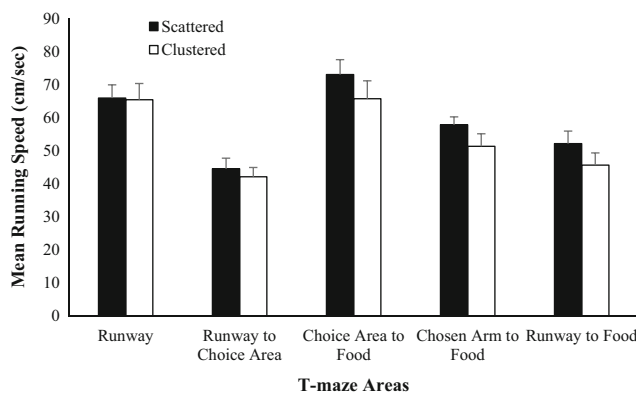


**Fig. 9** Percentage of time the Scattered arm was chosen by 24 rats on each day of testing is represented by the solid line. If performance was operating by chance, then the Scattered arm would be selected 50% of the time, as represented by the broken line

would lead to less energy and time expenditure than a food that is spread apart (Uller et al., 2013). Highlighting the difference between species, rhesus macaques, mosquitofish, and chickens fail to attend to density in quantity discriminations (Agrillo, Dadda, & Bisazza, 2007; Parrish, James, & Beran, 2017; Rugani, Regolin, & Vallortigara, 2008), while capuchin monkeys prefer dense to sparse arrays of food (Parrish et al., 2017).

**General discussion**

Experiment 1 showed that rats preferred and ran faster for multiple pieces of food than for a single piece. Possible explanations were then examined in the next studies. In Experiment 2, using the continuous stimuli of mashed potatoes, we found that food covering a larger area is more rewarding than one occupying a smaller area. However, Experiment 3 showed an important limitation to the surface area finding: Greater surface area is not an incentive for rats when the density of the



**Fig. 10** Running speed for the Scattered and Clustered arms in all areas of the T-maze. There were no significant differences in running speed between the Scattered and Clustered arms in any area of the maze. Vertical lines represent standard errors of the mean

food was correspondingly lowered. Thus, we propose that rats consider both surface area and density when assessing food quantity.

## Interpretations

One interpretation for Experiment 1's findings is that perhaps animals, like humans, are susceptible to conservation effects. According to the conservation theory posed by Piaget (1952), children fail to understand that an object's physical properties remain the same even if its arrangement or appearance is changed. Bruner (1966) found that children perceive the same amount of liquid to be more when served in six beakers than in two. Consistent with this theory, rats may have failed to understand that when the same amount of food is served in a single piece or served in multiple pieces, the quantity of food does not change. This error in quantity discrimination makes evolutionary sense because multiple-piece foods may typically contain more food in the natural environment (Honig & Stewart, 1989). This may be an evolutionary genetic bias since, in nature, multiple small pieces tend to be more. However, since both size and number of pieces varied, we may speculate that there is some acceptable, yet untested, limit to this perceptual error in discrimination.

Another perceptual feature that distinguished the multiple-pellet from the single-pellet portion was the surface area occupied by the two portions: multiple-unit foods cover a larger surface area than a single-unit food. This dispersion of food over a larger area may be perceived as a greater quantity of food similar to findings observed in children (Gelman & Baillargeon, 1983). We tested this notion in Experiment 2 and found that, indeed, rats preferred and also ran faster for a portion of food occupying a larger area than the same portion occupying a smaller area. However, this effect was eliminated when the density of the larger area was lowered in Experiment 3.

Since number varies with size, it is possible that rats preferred the smaller pieces over the larger piece (i.e., performance may have been based on the size of pellets rather than number). An early study by Yoshioka (1930) showed that rats ate more of the larger than smaller sunflower seeds when presented mixed together, but this preference quickly attenuated with extended training. In a subsequent experiment (Yoshioka, 1930), hungry, but not satiated, rats ate more of the larger than the smaller seeds, even though the quantity of food was identical. Yoshioka's (1930) findings suggest some implicit bias in responding for a larger size in rats. Our findings, consistent with other studies (Amsel et al., 1968; Campbell et al., 1972; Capaldi et al., 1989; Traupmann, 1971), showed that rats preferred the smaller pellets over the single, large pellet, suggesting that the number of pellets may be more rewarding to rats than the size.

It is surprising that while both primates and rats prefer food occupying a larger area, the effects of size and number is not consistent between the species. In our studies and in others (Amsel et al., 1968; Campbell et al., 1972; Capaldi et al., 1989; Traupmann, 1971), rats found multiple, small pellets to be more rewarding than fewer, larger pellets. Primates, on the other hand, display a persistent bias in responding for larger food items even if they contained a smaller number of items (Beran et al., 2008). This discrepancy in findings based on size may stem from differences in evolved feeding habits, dietary behaviors, and foraging strategies of primates and rats. Rats and primates evolved foraging behaviors that were most adaptive for their species to survive. While primates use complex cognitive strategies (size, number, shape, length, mass, etc.) to optimally forage for the maximal amount of food (Zuberbuhler & Janmaat, 2010), optimal foraging behavior in rats involves handling food effectively to not only maximize energy intake but also promote survival and prevent food loss to conspecifics (Phelps & Roberts, 1989). Relative distance to safety, size, amount of food, and energy expenditure must all be considered by rats when foods of varying item sizes are encountered. Encountering a large piece of food in the natural environment requires that rats must calculate the potential energy loss of carrying the food with the potential benefits of consuming the food at the source. Larger pellets take more time and effort to eat than smaller ones (Phelps & Roberts, 1989; Wishaw, 1990; Wishaw et al., 1992; Wishaw & Tomie, 1989; Yoshioka, 1930). Longer eating times increase the time spent outside and can potentially increase the risk of predation. This means that selecting a larger piece of food may not always be the best decision for rats, and they may prefer eating smaller pellets immediately and carrying a single large pellet for later consumption. Consistent with this theory, rat hoarding behaviors in the laboratory increase as the size of the item increases. Rats will carry larger pieces of food away from the source to the center of the maze and eat smaller-sized foods immediately (Flannelly & Lore, 1977; McNamara & Wishaw, 1990; Phelps & Roberts, 1989; Wishaw, 1990; Wishaw & Tomie, 1989). Hence, in comparison to primates, rats may choose to eat smaller, multiple pellets, as this may lower the risk of predation, food loss to conspecifics, and energy loss.

Unlike primate studies where preference is typically expressed on the first trial, preference for the many over fewer pellets and flattened over rounded portions were expressed later in the study. These results were expected because primates are typically given two-choice discrimination tasks where they must make choices between arrays that are immediately and simultaneously visible. However, in our studies, we explored the acquisition of preference for one food array over another, as both food items are not visible until rats

explore the maze and enter and eat food in both arms. Future studies in laboratory rats can examine preference for food in a two-choice discrimination task where both options are visible.

### Limitations and future directions

Logistically, future studies would benefit from greater variation of presentation schedules (successive vs. simultaneous), maze types (four arm vs. eight arm), and food types (e.g., sweet vs. nonsweet foods).

While Experiment 2 measured the effects of surface area, an additional cue that may have influenced the reward value of the food was height. The rounded portion was necessarily taller than the flattened portion in order to contain the same amount of potato. In the natural environment, height of the food portion may equate to piled-up food, which might be a quantity cue. However, rats preferred the flattened over the rounded portions, suggesting that perhaps the total horizontal area occupied by food is a more salient cue in determining larger quantity of food than the height occupied by food items. To test this hypothesis, two groups of potato could be equal in grams and height but not frontal surface area (i.e., the area visible) or in the shape of a rectangle viewed from the shorter or longer side.

In Experiment 2, the preference for the food with the larger area began to wane over the 7 days of testing. The rats may have habituated to their choice over time. In the number experiments (Capaldi et al., 1989; Traupmann, 1971), we typically see that choice for the many over the single pellet becomes stronger over trials. The fact that this did not happen for a continuous food spread over a greater surface area suggests that, while surface area is an important component of preference, it is not as salient as numerosity.

Food stimuli and nonfood stimuli should be compared directly, to determine whether there is a unique visual system associated with processing quantity of food. Nonfood stimuli occupying a large area do tend to be overestimated in quantity as compared to the same stimuli occupying a smaller area (Bevan et al., 1963; Hollingsworth et al., 1991; Krueger, 1972). However, sensitivity to surface area over number varies. For example, in a violation of expectation paradigm, cotton-top tamarins looked longer at one large object than the expected two small objects in a 1 + 1 object task, showing that monkeys were sensitive to changes in number and were not encoding surface area occupied by the items (Uller, Hauser, & Carey, 2001). It is currently unclear whether this exception is due to another aspect of the experimental procedure.

Finally, to further test the interaction between surface area and density, future studies should isolate the two from each other. In order to keep surface area and calories consistent in two groups while varying density, the pieces in the dense group would need to be individually less caloric. Alternatively, we could examine the tipping point

of what appears to be a “surface-area-density trade-off.” Experiments could be designed to determine at what point a larger surface area of food will sway the preference away from denser food. Expanding on this topic, studies could also be implemented where the actual caloric value of the choice that *looked* like more food was lower than the choice that looked like less food. When compared with previous research in primates (Beran et al., 2008; Boysen & Berntson, 1995; Boysen et al., 1996; Boysen et al., 2001), these results could help illuminate the interaction between the visual and gastrointestinal feedback systems.

### Implications for diet

Studies on attendance to surface area in humans have had mixed results. Some research (Feigenson, Carey, & Spelke, 2002) suggests that human infants were responsive to changes in surface area, not number, while the opposite has been found for large number ratios (Brannon, Abbott, & Lutz, 2004) or when one array is at least 2 times larger in area than the other (Brannon, Lutz, & Cordes, 2006; Cordes & Brannon, 2008). In a recent review of the literature, Cordes and Brannon (2008) suggested that although human infants use both number and continuous variables to determine quantity, they preferentially attend to number and to continuous variables only when number is held constant between arrays.

For humans, concerns about overeating often lead to creative techniques to make less food appear like more, thus satisfying the brain while consuming fewer calories. The same amount of food served on a smaller plate looks larger (because there is no empty space) than when served on a larger plate (Van Ittersum & Wansink, 2012), leading researchers to suggest that reducing plate size can decrease food intake. However, dietary interventions that examine the effects of reductions in plate size on food intake have shown mixed results (Robinson et al., 2014). The studies presented here offer an alternative recommendation: spreading food out to cover the surface area of a plate. This technique would optimize both surface area and density, presumably appearing to be a larger amount of food. However, while earlier studies have found that results from rat experiments are often generalizable to humans (Galef, 1996), this hypothesis should be directly investigated with human subjects. Additionally, a spreading technique would only be available for continuous foods.

### Conclusion

Rats may share a perceptual bias with humans and chimpanzees in preferring portions of foods that perceptually look like a larger quantity of food. Here, we found that rats rely on both surface area and density to make that quantity assessment,

possibly due to the evolution of foraging behaviors that is most adaptive for that species.

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