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Perception of the Delboeuf Illusion by the Adult Domestic Cat (*Felis silvestris catus*) in Comparison With Other Mammals

Péter Szenczi, Zyanya I. Velázquez-López, Andrea Urrutia, Robyn Hudson, and Oxána Bánszegi
Universidad Nacional Autónoma de México

The comparative study of the perception of visual illusions between different species is increasingly recognized as a useful noninvasive tool to better understand visual perception and its underlying mechanisms and evolution. The aim of the present study was to test whether the domestic cat is susceptible to the Delboeuf illusion in a manner similar to other mammalian species studied to date. For comparative reasons, we followed the methods used to test other mammals in which the animals were tested in a 2-way choice task between same-size food stimuli presented on different-size plates. In 2 different control conditions, overall the 18 cats tested spontaneously chose more often the larger amount of food, although at the individual level, they showed interindividual differences. In the Delboeuf illusion condition, where 2 equal amounts of food were presented on different-size plates, all cats chose the food presented on the smaller plate more often than on the larger one, suggesting that they were susceptible to the illusion at the group level, although at the individual level none of them performed significantly above chance. As we found no correlation between the cats' overall performance in the control conditions and their performance in the illusion condition, we propose that the mechanisms underlying spontaneous size discrimination and illusion perception might be different. In the discussion, we compare the results of the present study with the results for other previously tested mammals and highlight some possible reasons for their similarities and differences.

Keywords: *Felis silvestris catus*, quantity discrimination, spontaneous two-way choice test, visual illusion, visual perception

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Many animal species obtain a significant amount of the information about their environment via their visual systems. However, the way this sensory information is captured and processed can vary notably across species. Within vertebrates, even within mammals, these differences originate from anatomical differences in the structure and position of the eyes (Heesy, 2008; Lamb, Collin, & Pugh, 2007; Veilleux & Kirk, 2014) and their underlying neural circuits (Eagleman, 2001; Mascalzoni & Regolin, 2011; Masland & Martin, 2007), both shaped by evolutionary processes. However, the visual assessment of a target object, for example, its color, shape, or size, can be distorted by the surrounding environment, leading to so-called visual illusions (Gregory, 1997).

Humans have long been known to perceive a wide range of optical illusions (Wade, 2017), and the comparative study of illusions between humans and nonhuman mammals is increasingly recognized as a noninvasive tool to better understand visual perception and its underlying mechanisms and evolution. Comparative studies have revealed both similarities and differences in susceptibility to geometrical visual illusions (pertaining to an object's size and shape) across species. It seems that, in general, most animals are susceptible to at least some geometrical optical illusions (e.g., 11 of 13 tested vertebrate species have been found to be susceptible to the Ponzo and Müller-Lyer illusions in the same manner as humans; Byosiere, Feng, Rutter, et al., 2017; Byosiere et al., 2018; review in Feng, Chouinard, Howell, & Bennett, 2017), albeit with some notable differences. In contrast, in the case of the Ebbinghaus illusion, which has been amply studied in a variety of species with different ecological and taxonomical backgrounds, no discernible pattern is apparent in susceptibility to the illusion or the direction in which it is perceived

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Péter Szenczi, Zyanya I. Velázquez-López, Andrea Urrutia, Robyn Hudson, and Oxána Bánszegi, Instituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México.

Péter Szenczi is now at Unidad Psicopatología y Desarrollo, Instituto Nacional de Psiquiatría Ramón de la Fuente Muñiz, Mexico City, Mexico.

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Correspondence concerning this article should be addressed to Oxána Bánszegi, Instituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México, AP 70228, Ciudad de México CP 04510, Mexico. E-mail: oxana.banszegi@gmail.com

(Byosiere, Feng, Woodhead, et al., 2017; review in Feng et al., 2017; Fuss & Schluessel, 2017). Whereas some species reportedly lack susceptibility to certain illusions, others have been found to be susceptible in the opposite direction to humans (see reviews in Feng et al., 2017; Kelley & Kelley, 2014).

One of the most common geometrical illusions is when the size of a target object is misperceived because of its immediate surround. If the size of the target stimulus is processed globally (taking into account its surround) rather than locally (taking into account only its own physical dimensions), then the actual size of the target may be misperceived (Navon, 1977). A classic example is the Delboeuf illusion (Delboeuf, 1865), which is formed by a single ring surrounding the target stimulus, causing the target stimulus to be perceived as larger or smaller depending on how closely the inducer ring borders it (Figure 1). In humans, typically out of two target objects of the same size, the one bordered more closely by an inducer ring is perceived as larger (Mruczek, Blair, Strother, & Caplovitz, 2017). One theoretical explanation for the perception of the Delboeuf illusion is the assimilation–contrast theory: If the target stimulus and its inducer ring are close together, they will merge and be perceived as one, whereas if the inducer circle is farther away from the target object (it does not circle it closely), this creates a distinction between the two, hence the target object appears to be smaller (Girgus, Coren, & Agdern, 1972; Goto et al., 2007; Oyama, 1960). The contour interaction theory is another, not necessarily competing theory, which proposes that the contours that are proximal to an object perceptually attract, whereas contours that are further away and exceed a certain distance perceptually repel, which in turn causes a change in apparent size (Jaeger, 1978). The Delboeuf illusion is even used commercially; for example, a food portion on a small plate appears larger than the same amount of food on a larger plate, thus influencing and exploiting human's misperception of a target object's size (Davis, Payne, & Bui, 2016; Murphy, Lusby, Bartges, & Kirk, 2012; Van Ittersum & Wansink, 2012; Wansink & Van Ittersum, 2013).

Susceptibility to the Delboeuf illusion has been reported in several nonhuman mammals, but because these studies have been conducted only in few species and the methodological differences between them are considerable (e.g., trained or spontaneous testing, whether the target object was food or computer-generated two-dimensional stimuli; further details in the Discussion), not many comparative conclusions can yet be drawn. Generally it seems that nonhuman primates perceive the Delboeuf illusion in a manner akin to humans (chimpanzees *Pan troglodytes*, Parrish & Beran, 2014; rhesus monkeys *Macaca mulatta* and capuchin monkeys *Cebus apella*, Parrish, Brosnan, & Beran, 2015; but also see preliminary results on ring-tail lemurs *Lemur catta*, Santacà, Regaiolli, Miletto Petrazzini, Spiezio, & Agrillo, 2017). On the other hand, dogs (*Canis lupus familiaris*) do not appear to perceive the Delboeuf illusion, at least at the population level (Byosiere, Feng, Woodhead, et al., 2017; Miletto Petrazzini, Bisazza, & Agrillo, 2017, but note that in the first study, two dogs did appear to demonstrate susceptibility, although in the opposite direction to humans). Consequently, there is a need for more cross-species comparisons using similar methods to be able to assess which evolutionary pressures and/or environmental factors affect a species' susceptibility to such illusions (Feng et al., 2017), and also to better understand their possible relevance in natural contexts (review in Kelley & Kelley, 2014; see also Doerr & Endler, 2015; Griggio, Hoi, Lukasch, & Pilastro, 2016; Møller, 2017).

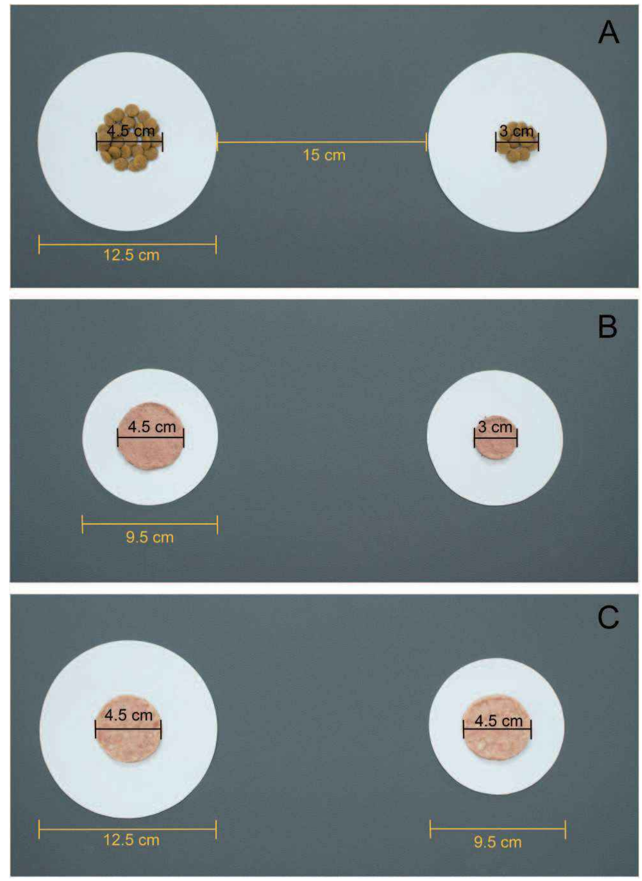

Figure 1. The three stimulus conditions that were presented in random order multiple times to each cat. (A) Large plate control in which different quantities of the same food, in this example dry cat food, were presented on large, same-size white plastic plates, with food-to-plate diameter ratios of 0.36 (large food) and 0.24 (small food). (B) Small plate control in which different quantities of the same food, in this example canned cat food, were presented on small, same-size white plastic plates, with food-to-plate diameter ratios of 0.47 (large food) and 0.32 (small food). (C) Delboeuf illusion condition in which the same quantity of food, in this example canned tuna, was presented on a large and on a small white plastic plate of the same sizes as in the control Conditions A and B, respectively, with food-to-plate diameter ratios of 0.36 (large plate) and 0.47 (small plate). Note that each cat was tested with the same kind of food in all trials in all three conditions according to its food preference (details in Method). See the online article for the color version of this figure.

For the following reasons, we consider that the domestic cat (*Felis silvestris catus*) is a good candidate species for the comparative study of susceptibility to geometrical illusions. Like the other species mentioned above, cats depend in large part on visual cues that are likely similar to those used by other mammalian species, including humans, to navigate in their environment (see for some comparison, Blake, 1979; Byosiere, Chouinard, Howell, & Bennett, 2017; Miller & Murphy, 1995). Like dogs, they belong to the order Carnivora, but in contrast, they have a semiarboreal lifestyle. They regularly move and hunt in three dimensions, similarly to most primates, where the precise assessment of depth and distance is vital. In addition, in previous studies, it has been shown that cats perceive subjective contours (Bravo, Blake, & Morrison, 1988; De Weerd, Vandenbussche, De Bruyn, & Orban, 1990) and a motion illusion (Bååth, Seno, & Kitaoka, 2014). They also discriminate between quantities (Pisa & Agrillo, 2009) and do so even without training. Out of two different quantities of food, they spontaneously and reliably choose the larger one if the size ratio between them is below 0.5 (Bánszegi, Urrutia, Szenczi, & Hudson, 2016). Finally, as in a growing number of countries, cats are now one of the most common companion animals (Bernstein, 2007; Driscoll, Macdonald, & O'Brien, 2009), there is increasing interest in their cognitive abilities (American Pet Products Association, 2015; Gunn-Moore, Moffat, Christie, & Head, 2007; Vitale Shreve & Udell, 2015).

Therefore, the aim of this study was to test whether the domestic cat is susceptible to the Delboeuf illusion, either in a manner similar to the primate species studied to date possibly due to the similarities in lifestyle (e.g., semiarboreal, moving in three dimensions to a greater degree than other carnivores), or rather similar to the taxonomically more closely related domestic dog. To make the cats' performance comparable with previously tested species, we followed the methods used to test dogs (Miletto Petrazzini et al., 2017) and primates (Parrish & Beran, 2014; Santacà et al., 2017), but adjusted slightly to make the test situation more species-appropriate for the cat.

Method

Animals, Housing, and Sample Sizes

As in a previous study (Bánszegi et al., 2016), cat owners interested in participating in the study were recruited via an Internet advertisement sent to students of the Faculty of Sciences, Universidad Nacional Autónoma de México. The advertisement included a brief description of the study and listed the following inclusion criteria: (a) the cat should be at least 1 year old; (b) it should be friendly toward strangers, not fleeing from or behaving aggressively toward them; (c) agreement to deprive the cat of food for 4 hr before each test session; and (d) agreement to have experimenters visit and test the cat on at least eight separate occasions. Most owners evaluated their cats appropriately, although we had to reject four cats before testing because they were not calm enough with strangers present to be easily handled during the experiments.

We began the tests with a total of 25 mixed-breed cats but had to exclude four that exhibited a strong lateral bias (defined as the cat always going to the same side during the tests on 3 consecutive test days regardless of the stimuli presented), and three more cats that were not motivated to perform the tests on 3 consecutive test days. The remaining 18 cats finally included in the study were 10 males (four intact and six neutered) and eight females (three intact and five neutered), average age of 2.9 years ± 0.4 SEM. Ten were exclusively indoor cats, and the rest were indoor/outdoor cats (Table 1). None had received any training with the test procedures before the experiments.

Food Stimuli

As cats show marked individual differences in food preference (Bradshaw, Goodwin, Legrand-Defrétin, & Nott, 1996; Bradshaw, Healey, Thorne, Macdonald, & Arden-Clark, 2000; own observations), the experimenter identified a food preferred by each cat to effectively motivate it to attend to the stimuli and to perform the tasks. To this end, before the start of testing, the experimenter briefly offered each cat an array of three different foods: the cat's usual canned food, canned tuna, and dry cat food. The first food eaten by the cat was the stimulus used in all trials with that individual. Two cats were tested with canned cat food, 14 were tested with canned tuna, and two were tested with dry food. A previous study on the Delboeuf illusion in chimpanzees (*Pan troglodytes*) found that performance was independent of food type, be it "discrete" or "continuous" (cereal pieces or lunch meat, respectively; Parrish & Beran, 2014).

Experimental Setup

Each cat participated in three different spontaneous two-way food choice tasks. For comparative purposes, we closely followed the methods previously used to test dogs (Miletto Petrazzini et al., 2017) and primates (Parrish & Beran, 2014; Santacà et al., 2017), although adjusting them slightly for cats. These adjustments included (a) resizing the food and plates: we reduced the size of both because cats are smaller mammals (see details below); (b) the cats were able to go to and eat immediately from the chosen food like the dogs, but unlike the primates, which had to point to the preferred food quantity after which the experimenter gave them whatever was on the selected plate (see details below); (c) all cats were tested in their home environment with a preferred food to keep them motivated (see Food Stimuli above); (d) we tested the cats only in one standard illusion trial and they received only six trials a day to maintain their motivation and avoid satiation (see details below); (e) finally, the starting point for the cats was not at floor level but instead they were placed at a certain height to give them a better visual overview of the two stimuli (see Test Procedure below).

The cats were tested individually in their home environment. The food stimuli were presented on white plastic plates of two different sizes: large plates 12.5 cm in diameter and small plates 9.5 cm in diameter. In the center of each plate, the food was formed into a circle using molds of two different sizes: a larger portion 4.5 cm in diameter and 0.2 cm in height (volume = 3.18 cm^3) and a smaller portion 3 cm in diameter and 0.2 cm in height (volume = 1.41 cm^3). The plates were presented on the floor on a washable matte gray plastic sheet (47 cm × 68 cm), 15 cm apart (distance between the edges of the plates). We used a chair as the starting point to provide the cat with a nondistorted overview of the nearly flat stimuli (chair height: 48–50 cm, placed 25 cm from the edge of the plastic sheet). All tests were video recorded (GoPro 4 Session, GoPro Inc., California) for later analysis.

All cats were tested in three stimulus conditions: (a) large plate control: two different food portions were presented on two large plates (Figure 1A); (b) small plate control: two different food portions were presented on two small plates (Figure 1B); and (c) illusion: two equal, large food portions were presented on different-size plates (one large plate and one small plate; Figure 1C). The two types of control conditions were set up to test

Table 1
Number of Times Each Cat Chose the Larger Portion of Food in Each of the Two Control Conditions, in the Two Control Conditions Overall (Pooled), and the Smaller Plate in the Delboeuf Illusion Condition (Seemingly Larger Portion According to the Illusion)

Cat name	Sex	Age (years)	Sexual status	Living condition	Large control	Small control	Overall control	Delboeuf illusion
Balam	M	7	Neutered	Indoor	9/16 $p = .80$	12/16 $p = .08$	21/32 $p = .11$	9/16 $p = .80$
Chufi	F	3	Neutered	Indoor	8/16 $p = 1$	11/16 $p = .21$	19/32 $p = .38$	10/16 $p = .45$
Crazy	F	3	Neutered	Indoor	10/16 $p = .45$	9/16 $p = .80$	19/32 $p = .38$	9/16 $p = .80$
Darcy	M	3	Intact	Outdoor	11/16 $p = .21$	**14/16** $\mathbf{p = .004}$	**25/32** $\mathbf{p < .01}$	9/16 $p = .80$
Erik	M	2.5	Intact	Outdoor	10/16 $p = .45$	**13/16** $\mathbf{p = .02}$	**23/32** $\mathbf{p < .05}$	10/16 $p = .45$
Gigi	F	2	Neutered	Indoor	12/16 $p = .08$	**14/16** $\mathbf{p = .004}$	**26/32** $\mathbf{p < .001}$	10/16 $p = .45$
Grafit	F	4	Neutered	Outdoor	**13/16** $\mathbf{p = .02}$	**13/16** $\mathbf{p = .02}$	**26/32** $\mathbf{p < .001}$	10/16 $p = .45$
Hendri	M	1.5	Neutered	Outdoor	**13/16** $\mathbf{p = .02}$	11/16 $p = .21$	**24/32** $\mathbf{p < .01}$	10/16 $p = .45$
Ivy	F	1	Intact	Outdoor	10/16 $p = .45$	12/16 $p = .08$	**22/32** $\mathbf{p = .05}$	12/16 $p = .08$
Lilith	F	1	Intact	Outdoor	12/16 $p = .08$	12/16 $p = .08$	**24/32** $\mathbf{p < .01}$	9/16 $p = .80$
Lolo	M	6	Neutered	Indoor	6/16 $p = .45$	8/16 $p = 1$	14/32 $p = .6$	11/16 $p = .21$
Misifustófeles	M	3	Neutered	Indoor	11/16 $p = .21$	10/16 $p = .45$	21/32 $p = .11$	11/16 $p = .21$
Pancho	M	6	Neutered	Indoor	11/16 $p = .21$	8/16 $p = 1$	19/32 $p = .38$	10/16 $p = .45$
Pinky	F	3	Neutered	Indoor	8/16 $p = 1$	8/16 $p = 1$	16/32 $p = 1$	10/16 $p = .45$
Quetzalcóatl	M	2	Intact	Indoor	10/16 $p = .45$	10/16 $p = .45$	20/32 $p = .29$	10/16 $p = .45$
Shiro	M	2	Intact	Outdoor	12/16 $p = .08$	11/16 $p = .21$	**23/32** $\mathbf{p < .05}$	9/16 $p = .80$
Solange	M	1.5	Neutered	Outdoor	10/16 $p = .45$	12/16 $p = .08$	**22/32** $\mathbf{p < .05}$	9/16 $p = .80$
Zumba	F	2	Intact	Outdoor	8/16 $p = 1$	10/16 $p = .45$	18/32 $p = .59$	11/16 $p = .21$

Note. p values refer to the results of testing each cat's choices against chance as reported by binomial tests. Conditions when choices were significantly different from chance ($p < .05$) are in bold.

whether the cats would choose the larger portion of food in the two contexts (plate size). Based on previous studies mentioned in the introduction, we expected that in the control trials the cats would spontaneously choose the plate with the larger quantity of food. If cats perceive the Delboeuf illusion under these experimental conditions, then we expected that during the illusion trials they would predominantly choose the food stimulus presented on the smaller plate as this stimulus should appear to be larger. In both control conditions, the ratio of the surface area between the smaller and the larger food portions was equal to 0.44, which was found to be sufficiently distinct for cats to perceive in a previous study of spontaneous quantity discrimination, as below ratios of 0.5, the cats chose the larger of two amounts of food significantly above chance (Bánszegi et al., 2016).

Test Procedure

Time of day of the tests depended on the owners' availability and was between 09:00 am and 07:00 pm. The cats were deprived of food for 4–6 hr previously to motivate them to perform the task. Out of view from the owner and cat, the experimenter placed the appropriate stimuli (see Figure 1) on the plastic sheet, turned on the camera, and walked to the farthest point at a right angle to the stimulus array. Staying aligned with the middle of the plastic sheet, the experimenter turned away from the experimental setup and remained motionless. The experimenter then asked the owner to come in carrying the cat. The owner placed the cat on the chair facing the stimuli and gently held it there from behind for 5 s to give it the chance to view both plates before releasing it to make its choice. We defined "choice" as the cat going to one of the plates and manipulating the food (licking, eating, or pawing). As soon as the cat chose a plate, the experimenter removed the other plate and allowed the cat to eat briefly from the chosen stimulus. We only allowed brief eating to prevent the cats becoming satiated and losing motivation to participate in further trials. To avoid cueing the cats, neither the owner nor the experimenter looked at the cat, instead focusing their attention straight ahead at the opposite wall until the cat made its choice (see video of typical trials in the online supplementary material). Owners handling the cats were not aware of the hypothesis of the study and, therefore, what choices would be "correct" in any of the conditions (see more details about the possibility of inadvertent cueing in Discussion).

Similar to previous studies with dogs and primates, the cats received a total of 48 trials across a minimum of 8 days. Each daily session consisted in a maximum of six trials; two trials for each of the three conditions. If cats lost motivation (if they stopped making choices) during a session, we stopped testing for that day and continued testing on additional days until each cat had completed the full experimental program. In all cases, we left at least one day between sessions. To control for possible side preferences (see Animals, Housing, and Sample Sizes), we counterbalanced the left–right presentation of the small/large plates and small/large portions of food for all cats across trials. We also reversed the location of the stimuli in the test room in each session and randomly assigned the order of presentation for each condition across sessions and subjects.

Ethics Note

Animals in this study were all household pets tested in their own homes in the presence of their owners and with the owners' informed consent. The experimental protocol complied with the guidelines for the care and use of animals in research of the American Psychological Association and with the National Guide for the Production, Care and Use of Laboratory Animals, Mexico (Norma Oficial Mexicana NOM-062–200-1999).

Data Treatment and Statistical Analysis

Statistical analyses were performed using R Version 3.4.1 (R Core Team, 2017). To assess interrater reliability, 200 videos of 864 trials (18 cats × 48 trials, approximately 23% of all trials) were coded independently by two of the authors. There was no difference in the raters' judgments of the side chosen by the cats (Krippendorff's $\alpha = 1$, Krippendorff (2011)). Because the number of cats tested with each of the three kinds of food was different, and the number of individuals with two out of the three options was low, we compared their performance using a two-sample Fisher–Pitman permutation test (Boik, 1987) with 9,999 Monte Carlo resamplings.

For the analyses of individuals' performance, binomial tests were conducted on the proportion of choices for the larger quantity of food (control trials) and for the proportion of choices for the portion of food presented on the smaller plate (illusion trials). Population-level values were analyzed using parametric statistics, as they were normally distributed (Shapiro–Wilk test, $p > .05$; Shapiro & Wilk, 1965). To assess whether the cats could discriminate between the two quantities in the two control conditions and select one plate more often than expected by chance in the illusion condition, we performed one-sample Student's t tests (two-tailed with chance level = .50) on the proportion of choices for the larger quantity of food in control trials and the proportion of choices for the food presented on the smaller plate in the illusion trials. Cohen's d values (Cohen, 1988) were calculated to estimate effect sizes. Comparisons of performance according to the animals' sex, whether they were neutered or intact, and whether they were exclusively indoor or indoor/outdoor pets were done using Welch's t test for unequal sample sizes (Welch, 1947). To assess correlations between individual cats' performance in the two control conditions, between their performance in the control and illusion conditions, and to check whether their performance changed with age and across trials, we calculated Spearman's rank-order correlations (Spearman, 1904). A generalized linear mixed-effects model (GLMM) with binomial distribution (Nelder & Wedderburn, 1972) was used to compare performance among conditions (large control/small control/illusion).

Results

A first question was whether the cats' performance during testing could have been influenced by the type of food presented. We found no difference in performance based on the type of food used (Fisher–Pitman permutation tests: canned food vs. tuna: $p = .65$, 95% confidence interval [CI] [.64, .66]; canned food vs. dry food: $p = .12$, 95% CI [.11, .13]; tuna vs. dry food: $p = .34$, 95% CI [.33, .35]).

Control Trials

Cats chose the larger quantity of food more often in both control conditions. In the large-plate condition (e.g., Figure 1A), 14 of the 18 cats (78%) chose the larger amount more often, three cats chose the larger and smaller amounts equally often, and one cat chose the smaller amount more often (see Table 1). The cats' overall performance ($M = .64$, 95% CI [.58, .70]) was significantly above chance, one-sample Student's t test: $t(17) = 4.97$, $p < .001$ (Cohen's $d = 1.17$; Figure 2), even though at the individual level, only two of them reached significance (see Table 1). In the small-plate condition (e.g., Figure 1B), 15 of the 18 cats (83%) chose the larger amount of food more often, and the rest chose the larger and smaller amounts equally often. In this condition, overall performance was also significantly above chance ($M = .69$, 95% CI [.63, .75]), $t(17) = 6.60$, $p < .0001$ (Cohen's $d = 1.55$; Figure 2), although at the individual level, only four of the cats reached significance (see Table 1). The low number of cats choosing the larger amount of food significantly above chance during the control trials might be explained by the low number of repetitions they were given for each of the two control conditions: with 16 repetitions each, a high number of "correct" choices (at least 13/16) would be needed for the results to be significant (see Table 1).

In addition, we found a significant positive correlation between individual cats' performance in the two control conditions (Spearman $r_s = .46$, $p < .05$) and no difference in overall performance in the two conditions, paired t test: $t(17) = 1.74$, $p = .10$. Therefore, we combined the data from all the trials of the two control conditions, resulting in nine of the 18 cats choosing the larger amount of food significantly above chance according to the binominal test (see Table 1). We found no difference in performance between sexes, Welch's t test: $t(13.51) = 0.03$, $n_{\text{female}} = 8$, $n_{\text{male}} = 10$, $p = .97$, or between intact and neutered cats, Welch's t test: $t(15.99) = 1.03$, $n_{\text{intact}} = 7$, $n_{\text{neutered}} = 11$, $p = .32$. However, we did find a difference according to the cats' living conditions. Overall, indoor/outdoor cats chose the larger food portion more often than exclusively indoor cats (72% vs. 61%, respectively), Welch's t test: $t(14.12) = 2.62$, $n_{\text{indoor}} = 9$, $n_{\text{outdoor}} = 9$, $p < .05$. There was no correlation between age and overall performance (Spearman $r_s = -.37$, $p = .13$), which is consistent with previous findings for cats (Bánszegi et al., 2016) and dogs (Miletto

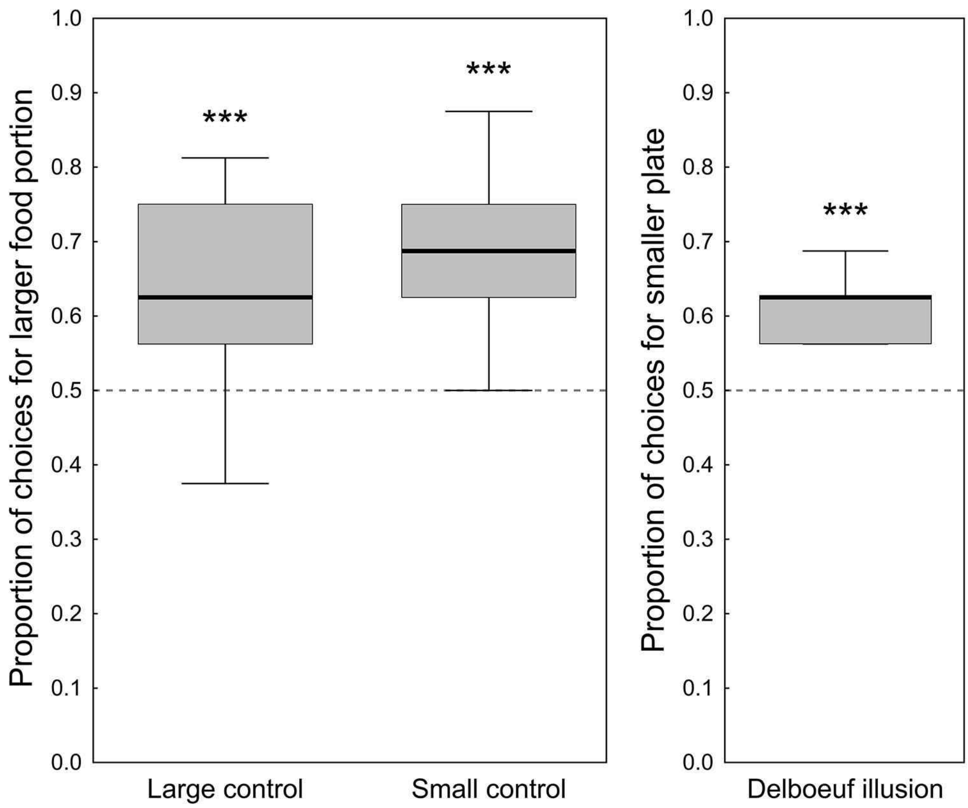

Figure 2. Performance of the cats ($N = 18$) when tested in the two control conditions (left panel, see Figure 1A, B) and in the Delboeuf illusion condition (right panel, see Figure 1C). Solid horizontal lines give medians, boxes indicate 25th and 75th percentiles, and vertical lines show the minimum and maximum values. In all three conditions, performance was significantly above chance (horizontal dotted line, *** $p < .001$), as reported by one-sample t tests (see text for statistics).

Petrazzini et al., 2017; Ward & Smuts, 2007) on similar tasks. There was also no correlation between the overall percentage of cats that chose the larger stimulus in either of the control conditions and the order of the trials ($r_s = -.21$, $p = .43$), suggesting that there were no significant learning effects in the control trials during the study.

Illusion Trials

In the Delboeuf illusion trials (e.g., Figure 1C), all 18 cats chose the food presented on the smaller plate more often than on the larger one ($M = .62$, 95% CI [.59, .65]), Student's t test: $t(17) = 9.45$, $p < .001$ (Cohen's $d = 2.23$; Figure 2, Table 1), which suggests that they were susceptible to the Delboeuf illusion, although at the individual level none of them performed significantly above chance according to the binomial tests. We found no difference between sexes, Welch's t test: $t(13.4) = 0.76$, $n_{\text{female}} = 8$, $n_{\text{male}} = 10$, $p = .46$, or between cats that were reproductively intact or neutered, $t(8.85) = 0.19$, $n_{\text{intact}} = 7$, $n_{\text{neutered}} = 11$, $p = .85$, nor between exclusively indoor or indoor/outdoor pets, $t(14) = 0.26$, $n_{\text{indoor}} = 9$, $n_{\text{outdoor}} = 9$, $p = .80$. We found no correlation between age and performance (Spearman $r_s = .001$, $p = .99$), between overall performance in the control trials and performance in the illusion trials ($r_s = -.32$, $p = .20$), nor between the cats' performance in the illusion trials and the order of the tests ($r_s = .32$, $p = .22$), suggesting that there were no learning effects across the illusion trials.

Finally, we analyzed whether the cats' performance differed between the control and illusion trials using a GLMM with binomial distribution that included the type of test and the individuals' living conditions (indoor or indoor/outdoor), as this was found to have an effect in the control trials. We found no difference in overall performance for the type of trials, whereas living conditions had a significant effect on the number of "successful" trials (choice of the larger portion of food in the control trials or the seemingly larger portion of food in the illusion trials was greater by indoor/outdoor cats), but the interaction of these two factors was not significant (GLMM trial: $\chi^2 = 0.24$, $p = .62$, conditions: $\chi^2 = 4.87$, $p < .05$, Trial × Condition: $\chi^2 = 0.05$, $p = .83$; Table 1 summarizes individual performance of subjects).

Discussion

The results of the two control conditions (different quantities of food with a ratio of 0.44 in their surface area, presented on large or on small plates; Figure 1A, B) confirm that with no previous training, domestic cats distinguish between different quantities of food presented in a standardized experimental paradigm and that they choose the larger amount above chance, at least at the group level. This result is consistent with our previous findings in the domestic cat (Bánszegi et al., 2016). Despite this finding, at the individual level only two cats chose the larger amount of food significantly above chance in the large-plate condition and only four of them in the small-plate condition. However, when we combined the data from the two control conditions (as overall performance did not differ between the two), 50% of the cats chose the larger amount of food significantly above chance at the individual level. Consistent with results from a previous study of quantity discrimination in cats (Bánszegi et al., 2016) and with reports for other carnivores (Baker, Shivik, & Jordan, 2011; Miletto Petrazzini et al., 2017; Ward & Smuts, 2007), we also did not find a correlation between the overall performance of the cats in either of the control conditions and the order of the trials, suggesting that there were no significant learning effects during the study.

Adjusting the paradigm slightly to create (for human viewers, Figure 1C) the Delboeuf illusion, we obtained the first suggestive evidence that cats, like humans (McClain et al., 2014; Van Ittersum & Wansink, 2012) and some nonhuman primates (Parrish & Beran, 2014; Parrish et al., 2015), are also susceptible to this illusion. When presented simultaneously with two equal quantities of a preferred food on a large and on a small plate, the cats, as a group, chose the food on the small plate significantly above chance, presumably because it appeared to be a larger quantity compared with the food on the large plate, even though no individual cat performed significantly above chance. This result can be explained by the fact that all cats chose the small plate more often (~62%), and the standard deviation for the cats as a group was quite small, which resulted in a relatively large effect size. Furthermore, this was true even though the position of the two food stimuli (left/right) and their arrangement in the room were randomized across trials. Consistent with previous findings on the judgment of food quantity by coyotes (Baker et al., 2011), dogs (Ward & Smuts, 2007), cats (Bánszegi et al., 2016), and rats (Wadhera, Wilkie, & Capaldi-Phillips, 2017), the animals of the present study must have made their choice based on visual cues alone; as the food portions in the illusion condition were of the same size, olfaction could not have played a part.

There has been relatively little comparative work on perception of the Delboeuf illusion across mammalian species, and so we aimed to make our methods comparable with at least some of the previous work in primates (Parrish & Beran, 2014; Santacà et al., 2017) and in the domestic dog (Miletto Petrazzini et al., 2017). Our results indicate that cats, like several nonhuman primates, perceive the Delboeuf illusion (Parrish & Beran, 2014; Parrish et al., 2015). However, they differ from reports on domestic dogs in which only some individuals perceived the illusion (at the group level they do not) but in the opposite direction to humans, other primates, and the cats of the present study (Byosiere, Feng, Woodhead, et al., 2017; Miletto Petrazzini et al., 2017). One possible explanation for the difference between the results for dogs and cats could be differences in experimental methodology. In contrast with the above-mentioned canine studies, to reduce stress and increase concentration to perform the task, in the present study the cats were all tested in their home environment with an individually preferred food and, in addition, they were tested from an elevated starting position, not at floor level, so as to give them a clearer overview of the two stimuli.

But perhaps more importantly, it is not clear whether the effective ratio of the difference in size between a target stimulus (e.g., food) and surround (e.g., plate size) on which the Delboeuf illusion depends differs across species, as most have only been tested on few options (critique in Parrish et al., 2015). In the present study, following, for comparative purpose, Miletto Petrazzini et al. (2017), during the illusion trials the cats discriminated between food-to-plate diameter ratios of 0.5 (on the small plate) and 0.36 (on the large plate), preferring to choose the stimulus with a ratio of 0.5, where the rim of the plate bordered the food more closely. However, these ratios do not correspond to those found to be the most effective in producing the Delboeuf illusion in humans (reviewed in Nicolas, 1995). Thus, it is possible that by modifying these ratios, either by reducing the smaller of the two ratios (e.g., by making the large plate larger) or increasing the larger ratio (making the smaller plate smaller), the visual assimilation and/or contrast effects (Goto et al., 2007) would become stronger, and a corresponding shift would be observed in the results. For example, Parrish et al. (2015) found in a series of experiments that rhesus and capuchin monkeys were more susceptible to the illusion when tested with a smaller outer ring/target object ratio on the large plate and a larger outer ring/target object ratio on the small plate. Although in the present study, the cats appear to have perceived the Delboeuf illusion even with the ratios mentioned earlier, for future studies it remains a methodological concern to determine the most appropriate ratios. Thus, it may be that in some species such as dogs and lemurs reported not to perceive the Delboeuf illusion (Miletto Petrazzini et al., 2017; Santacà et al., 2017), by modifying the ratios of the test stimuli, the animals become susceptible to it.

A compelling explanation for why some species are susceptible to the Delboeuf illusion but others are not is not yet available, although the differences in test design and methods could potentially contribute. For example, studies differ in whether spontaneous choice tests or (sometimes extensive) training were used. Whereas spontaneous choice tasks can show how the animals behave in more naturalistic situations, studies using trained animals are useful for exploring the absolute perceptual or cognitive abilities of a species (Agrillo & Bisazza, 2014). Another methodological inconsistency is whether the subjects were tested with food-related or nonecologically relevant stimuli (e.g., computer-generated two-dimensional stimuli) and whether they were rewarded in the case of a particular choice, as both of these factors can influence the animals' motivation. In the present study, we tested the cats in a spontaneous choice task, with the aim of exploring their natural perceptual tendencies. In addition, we tested them with preferred food stimuli to make the test naturally relevant and to maintain a high level of motivation.

However, one possible methodological problem in the present study, namely, inadvertent cuing by the person holding the cat, could have been an issue because the cats were held by a person (owner) in contrast to previous primate (where the animals were completely separated) or dog (where the animals were on a leash) studies. We cannot exclude the possibility that the handlers may have cued the cats, but as mentioned in Method, we think this is unlikely, as the handlers were blind to the experimental questions and rational of the test design. Furthermore, if the handlers had cued the cats in any way, they should have done so in all three conditions, yet we did not find any correlation between the performance of the cats at the individual level in the control and the illusion trials. In addition, we followed the same methods used in previous experiments (Bánszegi et al., 2016) where we found that the cats chose the larger quantity of food from two quantities only if the size difference between them was of a certain ratio (0.5 or above), even though it was clear for the handlers restraining the cats which were the larger quantities even below that ratio. This last finding suggested that the cats were using their own judgment and without cueing from the handlers. And finally, in most cases the cats did not need any encouragement to make their choice and the handlers' main role was in fact simply to restrain them. Certainly, further systematic investigation is required to explain divergent findings across studies, including the recruitment of other species with different evolutionary backgrounds and diverse sensory and perceptual characteristics.

A notable finding of the present study was the lack of correlation between individual performance in the control conditions and performance in the illusion condition; that is, individuals who were more accurate in choosing the larger item in the control trials did not necessarily show a correspondingly higher susceptibility to the Delboeuf illusion, even though at the group level the cats were susceptible. As the sample size (and the tested ratios, both in the control and illusion conditions) was quite low, we are limited in the ability to make this connection using the present data and must be cautious regarding the interpretation of this lack of correlation. Nevertheless, it might suggest a difference in the processing of visual information involved in size judgment in the presence or absence of a misleading surround. A possibility is that whereas size discrimination, uncomplicated by a distorting surround, depends mainly on peripheral, bottom-up mechanisms, the perception of illusions is the product of more central, top-down processes, possibly dependent on continuing early maturational processes and/or experience gained during development. However, a recent experiment with guppies on perception of the Solitaire illusion showed that fishes that performed at higher levels in control trials discriminating quantities at the 0.78 ratio were more likely to perceive the illusion in the test trials (Miletto Petrazzini, Parrish, Beran, & Agrillo, 2018).

Nevertheless, consistent with such a possible perceptual disjunction in our study, children under 7 years of age are able to judge the size of a target object with great accuracy, but it is not until later in development that they become susceptible to the influence of misleading contexts creating visual illusions (Doherty, Campbell, Tsuji, & Phillips, 2010; Káldy & Kovács, 2003; Parrish, Agrillo, Perdue, & Beran, 2016). As illusion-mediating neural circuits probably involve higher cortical areas (Livingstone & Hubel, 1988), the connectivity that supports contextual sensitivity might not be fully developed at a younger age (Káldy & Kovács, 2003). This is consistent with the research of Poirel et al. (2011), that loss of gray matter in the right parietal and visual areas of children around 6 years of age may reflect anatomical maturation. Thus, lack of correlation between judgment of a target's actual size and susceptibility to related illusions suggests that the perception of visual illusions and discrimination of actual size are processed by the nervous system differently. It is also possible that different illusions might invoke different underlying neural mechanisms, as suggested by studies that tested the susceptibility to different illusions in the same individuals (Byosiere, Feng, Woodhead, et al., 2017; Song, Schwarzkopf, & Rees, 2011). In humans, for example, interindividual variability in the strength of the perception of two illusions was not significantly correlated across participants (Schwarzkopf, Song, & Rees, 2011). Future research in which cats are tested with different types of visual illusions may help reveal differences in the processing of visual information even compared, for example, with other Carnivora. In addition, taking the cat as an experimentally accessible example, this also raises the question as to when during development kittens discriminate between, for example, different quantities of food, at what age they become susceptible to the Delboeuf illusion, and if there is a disjunction in developmental timing between the two? This is currently under investigation.

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