

Do domestic dogs (*Canis lupus familiaris*) perceive the Delboeuf illusion?

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Abstract In the last decade, visual illusions have been repeatedly used as a tool to compare visual perception among species. Several studies have investigated whether non-human primates perceive visual illusions in a human-like fashion, but little attention has been paid to other mammals, and sensitivity to visual illusions has been never investigated in the dog. Here, we studied whether domestic dogs perceive the Delboeuf illusion. In human and non-human primates, this illusion creates a misperception of item size as a function of its surrounding context. To examine this effect in dogs, we adapted the spontaneous preference paradigm recently used with chimpanzees. Subjects were presented with two plates containing food. In control trials, two different amounts of food were presented in two identical plates. In this circumstance, dogs were expected to select the larger amount. In test trials, equal food portion sizes were presented in two plates differing in size: if dogs perceived the illusion as primates do, they were expected to select the amount of food presented in the smaller plate. Dogs significantly discriminated the two alternatives in control trials, whereas their performance did not differ from chance in test trials with the illusory pattern. The fact that dogs do not seem to be susceptible to the Delboeuf illusion suggests a potential discontinuity in the perceptual biases affecting size judgments between primates and dogs.

Keywords Visual illusions · Comparative perception · Canine · Quantity discrimination

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Introduction

How different species see the world is one of the most relevant questions in animal cognition studies. Neurobiological investigation has revealed interesting similarities across vertebrates in the way some components (e.g. photoreceptors, Lamb et al. 2007) of the visual system work, although it is undeniable that different sensory information is captured across species because of the evolutionary differences in the vertebrate eye (Lamb et al. 2007). Substantial similarities exist between neural circuits underlying vision in human and non-human primates and to a lesser extent across all mammals (Masland and Martin 2007). However, even an accurate description of the physiological processes underlying vision in a species cannot provide us with a reliable picture of global perception of shapes, sizes, motion and other perceptual features of objects.

In the last decades, visual illusions have been commonly used in comparative research as a tool to compare global perception of static and dynamic objects among vertebrates (for a recent review see Kelley and Kelley 2014). The assumption underlying these comparative studies is that, if two species show a similar/dissimilar sensitivity to illusory phenomena, they are likely to have similar/dissimilar perceptual mechanisms. Most studies have involved non-human primates: rhesus monkeys and baboons, for instance, perceive the Zöllner illusion (Agrillo et al. 2014a; Benhar and Samuel 1982); capuchin monkeys are sensitive to the Müller-Lyer illusion (Suganuma et al. 2007) and seem to perceive the Solitaire illusion (Parrish et al. 2016). Illusory perception of dynamic events has also been found in rhesus monkeys (rotating snakes illusion, Agrillo et al. 2015).

All of the studies mentioned involved extensive training. However, in the last few years researchers have adopted a different approach by observing spontaneous behaviour of

untrained subjects. For instance, Kelley and Endler (2012) observed the untrained behaviour of great bowerbirds and found that males in their natural environment maintain size-distance gradients of objects on their bower courts. This behaviour is supposed to create a perspective illusion for their potential mates viewing their displays from within the bower avenue by causing males to appear larger than their physical body size, increasing their mating success. This example illustrates the potential of this approach to reveal the possible impact that visual illusions have on fitness of a species. Therefore, the use of methodological approaches that involves the observation of the untrained behaviour of animals in the presence of biologically relevant stimuli is necessary to complement laboratory studies using training procedures. This would especially help us to assess whether animals' sensitivity to illusory phenomena reflects a natural perceptual bias of the visual system that affects subjects' behaviour in their environment.

The spontaneous preference paradigm has often been employed in human research and typically consists in observing which stimulus participants choose, out of two alternative options. This paradigm has been used to investigate one of the most popular size illusions, called the "Delboeuf illusion". This illusion occurs when we misperceive the size of a central item because of its surrounding context. For instance, when a test circle is encompassed by a larger circle, human participants often estimate the test circle as smaller compared to when the same circle is encircled by a smaller concentric circle (Fig. 1). This illusion often affects our choices in everyday life. There is indeed evidence that the perception of food size is spontaneously affected by the context in Delboeuf-like fashion, with human participants overestimating portion sizes and hence under-serving onto smaller dishes (e.g. Van Ittersum and Wansink 2007; Davis et al. 2016; Wansink et al. 2005).

Recently, Parrish and Beran (2014) used the spontaneous preference paradigm to investigate the perception of the Delboeuf illusion in apes. The authors used the natural tendency of chimpanzees to choose the larger quantity when

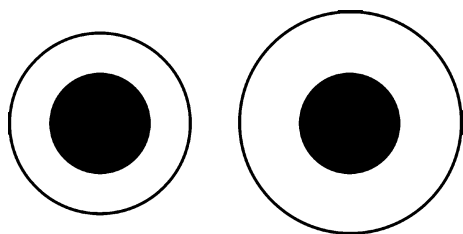


Fig. 1 Delboeuf illusion. This illusion occurs when two same-sized objects are perceived to be different depending upon the surrounding context. In this example, the *black circles* are physically identical, but human observers typically underestimate the size of the *black circle* encompassed by the larger ring and tend to overestimate the size of the *black circle* encompassed by the smaller ring

presented with two plates containing food. In control trials, different-sized food portions were presented to three chimpanzees on the same-sized plates, and chimpanzees were expected to select the larger amount of food. In test trials, chimpanzees could choose between two food portions that were both identical in size but were presented on different-sized plates, and a condition that generates a misperception of size in human observers. Results showed that all three subjects spontaneously selected the larger portion of food in control trials; in test trials, they selected the portion of food presented in the smaller plate, thus providing the first evidence of Delboeuf illusion in non-human animals.

Visual illusions have been investigated in a handful of mammals besides primates (e.g. cats, Bravo et al. 1988; mice, Kanizsa et al. 1993), but there is a complete lack of information for other species that are commonly employed in cognitive studies. One such species is the domestic dog. Dogs have been often subjected to studies on visual cognition (e.g. Range et al. 2008; Racca et al. 2010). For instance, there is evidence that dogs can make quantity discriminations between of visual stimuli (West and Young 2002). Dogs presented with two groups of food items differing in quantity are able to select the larger group both when all items are simultaneously presented (Miletto Petrazzini and Wynne 2016; Baker et al. 2012) and when items are sequentially presented (Ward and Smuts 2007; Range et al. 2014). Testing dogs' sensitivity to size illusions might help us to understand similarities and differences in perceptual biases affecting quantitative/size judgments in mammals that strongly rely on visual information, like humans and chimpanzees, and those who are less reliant on vision, like dogs.

In the present study, we investigated whether domestic dogs perceive the Delboeuf illusion. To compare the performance of chimpanzees with that of dogs, we used the spontaneous choice paradigm adopted by Parrish and Beran (2014). We observed dogs' spontaneous preference to reach for one of two plates containing food. In control trials, the two plates were identical in size and we presented a physically different portion of food to ensure that the dogs could discriminate between the food quantities in the present context. In the test phase, we presented the same portion of food in two plates differing in size. If the dogs perceived the Delboeuf illusion, they were expected to select the portion included in the smaller plate, as in the case of chimpanzees.

Methods

Subjects

Thirteen adult dogs of various breeds and ages participated in this study. As previous studies suggested potential

differences between pet dogs and shelter dogs in cognitive tasks (Fagnani et al. 2016; Udell et al. 2008), we decided to assess size judgments and their sensitivity to Delboeuf illusion dogs of both origins. Our sample consisted of pet dogs ($N = 6$) and shelter dogs ($N = 7$, Table 1). All pet dogs were living in human homes at the time of testing and were volunteered by their owners. Shelter dogs were currently living in an animal shelter in individual indoor/outdoor runs and were selected for their willingness to approach the experimenter. No written informed consent was required for this study. None of the subjects had previous experience with any experimental task.

Materials and procedure

All pet dogs were individually tested in a familiar room in the owner's house. Shelter dogs were individually tested in their own pens. Only one experimenter was involved in this study, and she was unfamiliar to the dogs.

The food used consisted of discrete items (biscuits). They were small enough to be easily clustered into a circle in the middle of the plates (approx. diameter of each biscuit: 1 cm). Prior to testing, the experimenter evaluated their palatability by offering the dogs a few pieces. White plastic plates of two different sizes were used to present the food: two large plates (24 cm in diameter) and two small plates (18 cm). We used cake moulds to bunch the biscuits together on the plates and to give the portions a round contour. Two different portion sizes were presented to the dogs: the larger portion was 8.6 cm in diameter and 1.5 cm in height (volume = 57.72 cm³), whereas the smaller portion was 7 cm in diameter and 1.5 cm in height (volume = 87.14 cm³). By weight of biscuits, the larger portion was 32 g and the smaller portion 18 g.

At the beginning of each trial, the experimenter arranged the portions in both plates out of the dog's view. After baiting, the experimenter approached the dog and simultaneously placed both plates on the ground 1 m apart, never looking at the dog in order to prevent any potential cueing. The dog was tied with a leash to the wall and stood at a distance of 1.5 m from the midline between the plates facing the experimenter. Subsequently, the experimenter placed herself behind the dog, waited until the dog had looked at both plates, and after 10 s released it to make its choice. Once the dog had chosen one plate by approaching and touching it, it was allowed to eat the contents of the plate while the non-chosen plate was quickly removed by the experimenter. Choices were totally unambiguous; the experimenter noted the dog's response after each trial and then started to set up a new trial with clean plates.

In the study of chimpanzees (Parrish and Beran 2014), each subject was tested repeatedly (eight daily sessions), as often done in spontaneous preference tests (e.g. Agrillo

et al. 2014b; Banzegi et al. 2016; Stancher et al. 2015), in order to have a reliable measure of the subject's preference. Like the chimpanzees, the dogs received eight daily sessions; each session consisted of six trials, for a total of 48 trials. Sessions were composed of four control trials ($N = 2$ "Control A", $N = 2$ "Control B" for each session) and two test trials (Fig. 2). In control A, the two different food portions were presented on the two large plates, whereas in control B the two portions were presented on the two small plates. Control trials were set up to assess whether the dogs selected the larger portion of food in the present context. In both control types, the ratio between the smaller and the larger volume of food was equal to 0.66. This ratio is commonly used in spontaneous quantity discrimination of non-primate species (Agrillo et al. 2012; Banzegi et al. 2016; Hunt et al. 2008; Uller et al. 2003). In particular, a recent study using a similar methodology showed that this ratio can be discriminated by dogs (Miletto Petrazzini and Wynne 2016). In test trials, equal food portions (both large, 32 g) were presented on different-sized plates (one large plate and one small plate). The order of presentation of the different types of trials was varied according to a pseudo-random sequence. However, each daily session always started with a control trial. The position (left/right) of both the large/small portion and the large/small plate was counterbalanced over the trials in order to inhibit side biases. Trials were conducted depending upon the dogs' motivation.

Statistical analyses were conducted using SPSS 22.0. For what concern group-level analyses, as data were normally distributed (Shapiro–Wilk test, $P > 0.05$), they were analysed using parametric statistics. As dependent variable we used the most common measure collected in quantitative studies on dogs (e.g. Miletto Petrazzini and Wynne 2016; Range et al. 2014), namely the proportion of choices for the larger quantity of food (in control trials) and the proportion of choices for the portion of food inserted in the smaller plate (in test trials). To assess whether the dogs were able to discriminate between the two quantities in control trials or whether the dogs selected one plate more than chance in test trials, we performed one-sample t tests (chance level was 0.50). Effect sizes for these analyses were calculated using Cohen's d (Lakens 2013). One-sample t tests were also used to assess the presence/absence of side biases, independent t tests were used to compare the performance of pet and shelter dogs, and paired t tests were used to compare the performance between the first two sessions and the last two sessions to assess whether performance changed across sessions. Pearson's correlations were calculated to establish whether dogs' choices varied as a function of age, and a linear mixed-effects model was used to compare the performance among conditions (Control A/Control B/Test trials). In the individual

Table 1 Information of the subjects participating in the study and individual performance for control (frequency of choices for the larger quantity) and test trials (frequency of choices for the portion of food included in the smaller plate)

Dog	Age	Sex	Group	Breed	Control A	Control B	Test trials
1	2	M	Pet dog	Jack Russell Terrier	11/16 $\chi^2(1) = 2.250, P = 0.134$	14/16 $\chi^2(1) = 9.000, P = 0.003^*$	10/16 $\chi^2(1) = 1.000, P = 0.317$
2	8	M	Pet dog	West England White Terrier	11/16 $\chi^2(1) = 2.250, P = 0.134$	12/16 $\chi^2(1) = 4.000, P = 0.046^*$	9/16 $\chi^2(1) = 0.250, P = 0.617$
3	5	F	Pet dog	Pinscher	7/16 $\chi^2(1) = 0.250, P = 0.617$	10/16 $\chi^2(1) = 1.000, P = 0.317$	7/16 $\chi^2(1) = 0.250, P = 0.617$
4	6	M	Pet dog	English Setter	10/16 $\chi^2(1) = 1.000, P = 0.317$	13/16 $\chi^2(1) = 6.250, P = 0.012^*$	8/16 $\chi^2(1) = 0.000, P = 1.000$
5	2	F	Pet dog	Mixed	10/16 $\chi^2(1) = 1.000, P = 0.317$	10/16 $\chi^2(1) = 1.000, P = 0.317$	11/16 $\chi^2(1) = 2.250, P = 0.134$
6	6	F	Pet dog	English Bulldog	10/16 $\chi^2(1) = 1.000, P = 0.317$	9/16 $\chi^2(1) = 0.250, P = 0.617$	9/16 $\chi^2(1) = 0.250, P = 0.617$
7	4	M	Shelter dog	Leonberger	9/16 $\chi^2(1) = 0.250, P = 0.617$	10/16 $\chi^2(1) = 1.000, P = 0.317$	10/16 $\chi^2(1) = 1.000, P = 0.317$
8	3	M	Shelter dog	Mixed	9/16 $\chi^2(1) = 0.250, P = 0.617$	15/16 $\chi^2(1) = 12.250, P < 0.001^*$	7/16 $\chi^2(1) = 0.250, P = 0.617$
9	2	M	Shelter dog	Mixed	8/16 $\chi^2(1) = 0.000, P = 1.000$	9/16 $\chi^2(1) = 0.250, P = 0.617$	7/16 $\chi^2(1) = 0.250, P = 0.617$
10	1	M	Shelter dog	Mixed	11/16 $\chi^2(1) = 2.250, P = 0.134$	10/16 $\chi^2(1) = 1.000, P = 0.317$	8/16 $\chi^2(1) = 0.000, P = 1.000$
11	3	M	Shelter dog	Mixed	8/16 $\chi^2(1) = 0.000, P = 1.000$	10/16 $\chi^2(1) = 1.000, P = 0.317$	10/16 $\chi^2(1) = 1.000, P = 0.317$
12	3	M	Shelter dog	Mixed	12/16 $\chi^2(1) = 4.000, P = 0.046^*$	8/16 $\chi^2(1) = 0.000, P = 1.000$	7/16 $\chi^2(1) = 0.250, P = 0.617$
13	6	M	Shelter dog	Mixed	9/16 $\chi^2(1) = 0.250, P = 0.617$	12/16 $\chi^2(1) = 4.000, P = 0.046^*$	10/16 $\chi^2(1) = 1.000, P = 0.317$

* Significant departure from chance at Chi-square test ($p < 0.05$)

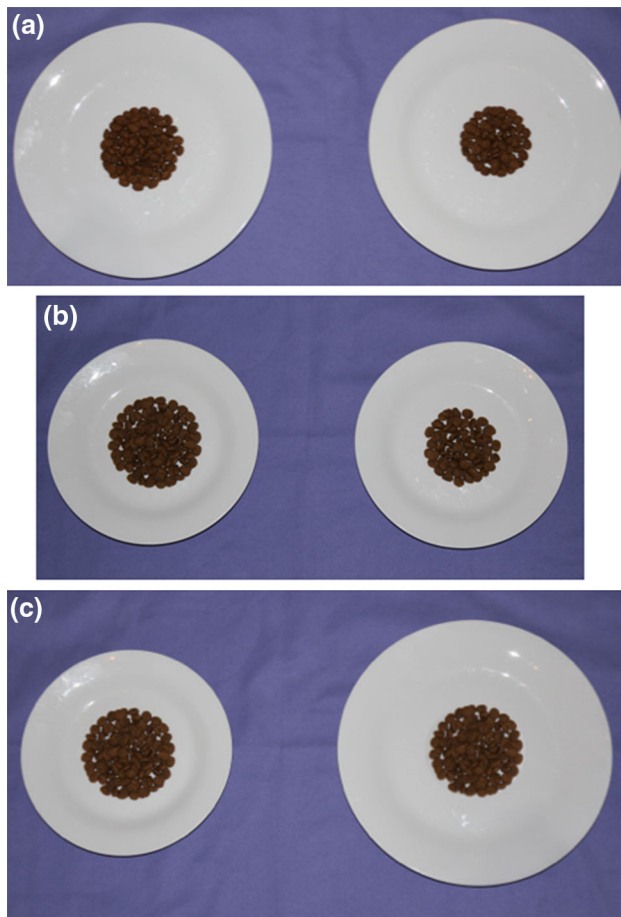


Fig. 2 Example of stimuli. Two plates containing different or equal-sized food were presented. **a** Control trial A with different food portions in two identical large plates; **b** control trial B with different food portions in two identical small plates; **c** test trials with equal-sized food portions in two plates differing in size

analyses, Chi-squared tests were performed on the frequency of choices for the larger quantity of food (control trials) or for the portion of food included in the smaller plate (test trials). In the absence of previous studies on size illusions in dogs, we could not make any a priori prediction; hence, all statistical tests were two-tailed; α was set at 0.05.

Results

Control trials

Dogs significantly selected the larger array in both control A (one-sample t test on the proportion of choices for the larger quantity of food, mean \pm std. dev. 0.601 ± 0.090 , $t(12) = 4.029$, $P = 0.002$; Cohen's $d = 1.117$) and control B (0.683 ± 0.131 , $t(12) = 5.019$, $P < 0.001$, Cohen's $d = 1.392$, Fig. 3a). As no significant difference was found

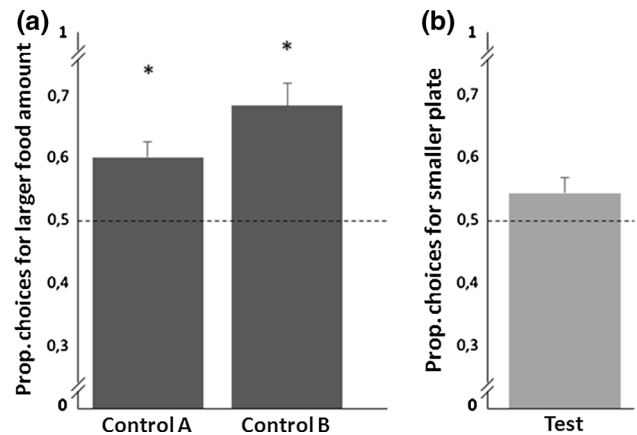


Fig. 3 Results of training and test phase. Dogs proved able to select the larger food amount in both control trials (a). On the contrary, they did not select any array more than chance in the test trials with the illusory pattern (b). Bars represent the standard errors. Asterisks denote a significant departure from chance level

between Control A and B (see “linear mixed-effects model” below), data were pooled together. The performance of pet dogs did not differ significantly from that of shelter dogs (pet dogs, 0.661 ± 0.093 ; shelter dogs, 0.625 ± 0.072 , independent t test $t(11) = 0.793$, $P = 0.444$). We found no correlation between dogs' accuracy and their age (Pearson $r = 0.100$, $P = 0.746$). No side bias was found (proportion of choices for left side: 0.523 ± 0.119 , $t(12) = 0.802$, $P = 0.438$). When we compared the choices of dogs in control trials included in the first two sessions and control trials included in the last two sessions, we found no difference, suggesting that no learning effect occurred (average first 2 sessions: 0.654 ± 0.116 , last 2 sessions: 0.692 ± 0.150 ; paired t test, $t(12) = -1.075$, $P = 0.303$). Table 1 summarizes individual performance of subjects.

Test trials

Dogs did not select either array more often than chance (proportion of choices for the portion of food presented in the smaller plate, 0.543 ± 0.090 , $t(12) = 1.737$, $P = 0.108$, Cohen's $d = 0.481$, Fig. 3b). We found no significant difference in dogs' choices between pet dogs and shelter dogs (pet dogs, 0.563 ± 0.088 ; shelter dogs, 0.527 ± 0.094 , $t(11) = 0.700$, $P = 0.499$). Dogs' performance was not significantly correlated with their age ($r = 0.047$, $P = 0.879$). No side bias was found (proportion of choices for left side: 0.514 ± 0.189 , $t(12) = 0.274$, $P = 0.788$). When we compared the choices of dogs in test trials included in the first two sessions and the choices of dogs in test trials included in the last two sessions, no difference was found (average first two sessions: 0.577 ± 0.188 , last two sessions: 0.596 ± 0.240 ; paired

t test, $t(12) = -0.234$, $P = 0.819$). Table 1 summarizes individual performance of subjects.

Comparison of control and test trials

Finally, we analysed whether dogs' performance differed between control and test trials using a linear mixed-effects model with planned contrasts and Bonferroni's correction for multiple comparisons. We found a main effect of the type of trial ($F(2, 24) = 6.125$, $P = 0.007$, partial eta-squared $\eta^2_p = 0.338$). Post hoc analyses showed a significant difference between the two controls and the test ($P = 0.009$) but no significant difference between Control A and Control B ($P = 0.082$).

Conclusions

The present study represents one of the first attempts to investigate whether domestic dogs perceive visual illusions. To achieve this goal, we adapted the procedure used by Parrish and Beran (2014) on chimpanzees to test the existence of the Delboeuf illusion in dogs.

Individual analyses of control trials showed that five subjects significantly selected the larger quantity of food in the presence of small plates (control B), while only one exhibited a significant choice in the presence of two large plates (control A). However, the two types of controls did not differ at group level. On the whole, group analyses showed that dogs were able to select the larger quantity of food with no significant difference between shelter and pet dogs. This aligns with previous literature on chimpanzees (Parrish and Beran 2014), cats (Banszegi et al. 2016) and guppies (Lucon-Xiccato et al. 2015) showing that several species tend to maximize food intake when two plates containing different amounts of food are simultaneously presented. The performance reported in control trials also aligns with a previous study that showed that dogs can discriminate between two quantities of discrete items (2 vs. 3 pieces of food) with the same ratio used in our control trials (Miletto Petrazzini and Wynne 2016). There is a debate in the literature as to whether human and non-human animals have the same (Agrillo et al. 2011; Brannon et al. 2006) or different (Lucon-Xiccato et al. 2015; Piffer et al. 2013; Agrillo et al. 2013) sensitivity to changes in number (discrete quantity, e.g. 2 vs. 3 items) or area (continuous quantity, e.g. ratio between areas). Even though the present study was not specifically devoted to investigating this issue, the comparison of our data with those reported in the study by Miletto Petrazzini and Wynne (2016) suggests a similar quantitative ability in dogs when fragmented quantities are presented in two separate arrays and when quantities are grouped together in each array.

As dogs successfully select the larger portion of food in control trials, we expected a choice for the portion of food inserted in the smaller plate in the test phase if dogs perceived the Delboeuf illusion. However, when we presented the illusory patterns, no dog selected one plate more than chance, a conclusion also supported by group analysis. This result seems to suggest that dogs do not perceive the Delboeuf illusion. Previous studies have shown remarkable differences in perceptual abilities between dogs and primates. For instance, dogs are known to have dichromatic colour vision (Neitz et al. 1989), while Old World primates and some New World primates have trichromatic colour vision (Dominy and Lucas 2001). Dogs showed a somewhat different visuospatial attention bias compared to human and non-human primates when viewing heterospecific faces (Guo et al. 2009). Humans and chimpanzees also display a rather robust global-to-local precedence (e.g. Kimchi 1992; Navon 1977; Fujita and Matsuzawa 1990; Hopkins 1997; Hopkins and Washburn 2002), whereas evidence of this effect for dogs remains less clear, with dogs showing an overall global advantage but also exhibiting a larger variability in global–local precedence than that reported in primates (Pitteri et al. 2014). Even though we can only speculate on this issue, it is possible that the larger variability observed in global-to-local precedence of dogs may explain the difference here reported between dogs and primates tested in similar conditions (Parrish and Beran 2014). Indeed, the illusory phenomenon requires the overall perception of the array (food portion and the circumference of the plate); hence, a species that exhibits a reduced global advantage may focus more on local information (e.g. food portions only), thus avoiding the contrast/assimilation effect produced by the surrounding plates. Another explanation for the different performance reported between dogs and primates may involve the potential different ability in size discrimination. As far as we are aware, no study has directly assessed whether the capacity to estimate objects' size is similar/dissimilar in dogs and primates, and we cannot exclude the possibility that dogs might be more specialized in size estimation; if so, our subjects would have been more accurate in revealing the lack of difference between the two portions of food in the illusory pattern.

Alternative interpretations of our data are possible. One may argue that the procedure was not sensitive enough to investigate the illusory size effect. For instance, the sample size or number of trials could have been too limited. We acknowledge that the number of trials might be limited for individual-level analyses. However, it is important to remember that we replicated the procedure adopted by Parrish and Beran (2014). Hence, we presented 16 trials per condition, as in the chimpanzee study. As for the sample size, we tested a more than four times number of subjects

(13 vs. 3); hence, we believe that neither sample size nor number of trials per condition could primarily explain the differences here found between chimpanzees and dogs. Furthermore, in the control trials the dogs significantly discriminated the larger quantity of food, showing that our methodology was appropriate to investigate spontaneous size discrimination in this species.

Also, although we attempted to reduce methodological variability between the two studies, we cannot exclude that some contextual variables were different. For instance, viewing angle of chimpanzees and dogs could be different. Unfortunately, the visual angle of chimpanzees was not specified (Parrish and Beran 2014), a fact that prevents the possibility to draw specific conclusions about. However, even assuming that the viewing angle of dogs differed from that of apes, it is unlikely that this variable could have strongly affected the perception of the illusion, as size illusions remains under a variety of viewing distances and are known to be generated by a wide range of visual patterns having different shapes (Rose and Bressan 2002) and dimensions (2D vs. 3D stimuli, Kwok and Braddick 2003).

Finally, one may argue that the dogs were driven by non-visual information. The subjects might have performed accurately in control trials by using olfactory information; subsequently, they could have chosen randomly in the test trials because both alternatives actually provided the same amount of olfactory cues. With respect to this issue, it is important to note that dogs' ability to discriminate between two quantities of food items by using olfactory cues is surprisingly poor, with several studies having shown that dogs tested with a procedure similar to the one used here cannot discriminate even a 0.2 or 0.17 ratio when only olfactory cues are available (Baker et al. 2012; Horowitz et al. 2013; Miletto Petrazzini and Wynne 2016; Ward and Smuts 2007). In control trials, we used a more difficult ratio; hence, there is no support for the hypothesis that olfactory information could have played an important role in our study.

In conclusion, we saw no evidence that dogs spontaneously misperceive the size of food items as a function of context the way that human and non-human primates do. Although alternative explanations cannot be excluded, our data suggest that dogs are not sensitive to the Delboeuf illusion. In line with our conclusion, a very recent work (Byosiere et al. 2016) using an operant conditioning procedure showed that dogs, initially trained to make fine discrimination between a larger and smaller black circle, performed randomly at group level in the presence of the Delboeuf pattern (two identical-sized circles encompassed by a larger and a smaller ring). The authors hypothesized that dogs are less sensitive to size contrast effects than primates, a further hypothesis that needs to be tested in the future. Regardless of the exact reason underlying dog-

primate differences in visual perception, the fact that two studies that used a very different approach (untrained behaviour with biologically relevant stimuli vs. trained behaviour with two-dimensional figures on the screen) found the same result is intriguing and suggestive of the existence of an evolutionary discontinuity between dogs and primates in the perceptual biases affecting the precision of size judgments in the Delboeuf illusion.

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References

- Agrillo C, Piffer L, Bisazza A (2011) Number versus continuous quantity in numerosity judgments by fish. *Cognition* 119:281–287
- Agrillo C, Miletto Petrazzini ME, Tagliapietra C, Bisazza A (2012) Inter-specific differences in numerical abilities among teleost fish. *Front Psychol* 3:483
- Agrillo C, Piffer L, Adriano A (2013) Individual differences in non-symbolic numerical estimation predict mathematical abilities but contradict ATOM. *Behav Brain Funct* 9:26
- Agrillo C, Parrish AE, Beran MJ (2014a) Do rhesus monkeys (*Macaca mulatta*) perceive the Zöllner illusion? *Psychon Bull Rev* 21(4):986–994
- Agrillo C, Parrish AE, Beran MJ (2014b) Do primates see the solitary illusion differently? A comparative assessment of humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*). *J Comp Psychol* 128(4):402–413
- Agrillo C, Gori S, Beran MJ (2015) Do rhesus monkeys (*Macaca mulatta*) perceive illusory motion? *Anim Cogn* 18:895–910
- Baker JM, Morath J, Rodzon KS, Jordan KE (2012) A shared system of representation governing quantity discrimination in canids. *Front Psych* 3:387
- Bánszegi O, Urrutia A, Szenczi P, Hudson R (2016) More or less: spontaneous quantity discrimination in the domestic cat. *Anim Cogn* 19(5):879–888
- Benhar E, Samuel D (1982) Visual illusions in the baboon (*Papio anubis*). *Anim Learn Behav* 10:115–118
- Brannon EM, Lutz D, Cordes S (2006) The development of area discrimination and its implications for number representation in infancy. *Dev Sci* 9:F59–F64
- Bravo JM, Blake R, Morrison S (1988) Cats see subjective contours. *Vis Res* 28:861–865
- Byosiere SE, Feng LC, Woodhead JK, Rutter NJ, Chouinard PA, Howell TJ, Bennett PC (2016) Visual perception in domestic dogs: susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions. *Anim Cogn*. doi:10.1007/s10071-016-1067-1
- Davis B, Payne CR, Bui M (2016) Making small food units seem regular: how larger table size reduces calories to be consumed. *J Ass Consum Res* 1(1):115–124
- Dominy NJ, Lucas PW (2001) Ecological importance of trichromatic vision to primates. *Nature* 410:363–366

- Fagnani J, Barrera G, Carballo F, Bentosela M (2016) Is previous experience important for inhibitory control? A comparison between shelter and pet dogs in A-not-B and cylinder tasks. *Anim Cogn* 19:1165–1172
- Fujita K, Matsuzawa T (1990) Delayed figure reconstruction by a chimpanzee (*Pan troglodytes*) and humans (*Homo sapiens*). *J Comp Psychol* 104:345–351
- Guo K, Meints K, Hall C, Hall S, Mills D (2009) Left gaze bias in humans, rhesus monkeys and domestic dogs. *Anim Cogn* 12:409–418
- Hopkins WD (1997) Hemispheric specialization for local and global processing of hierarchical visual stimuli in chimpanzees (*Pan troglodytes*). *Neuropsychologia* 35:343–348
- Hopkins WD, Washburn DA (2002) Matching visual stimuli on the basis of global and local features by chimpanzees (*Pan troglodytes*) and rhesus monkeys (*Macaca mulatta*). *Anim Cogn* 5:27–31
- Horowitz A, Hecht J, Dedrick A (2013) Smelling more or less: investigating the olfactory experience of the domestic dog. *Learn Motiv* 44(4):207–217
- Hunt S, Low J, Burns K (2008) Adaptive numerical competency in a food-hoarding songbird. *Proc R Soc Lond B* 275:2373–2379
- Kanizsa G, Renzi P, Conte S, Compostela C, Guerani L (1993) Amodal completion in mouse vision. *Perception* 22:713–721
- Kelley LA, Endler JA (2012) Illusions promote mating success in great bowerbirds. *Science* 335:335–338
- Kelley LA, Kelley JL (2014) Animal visual illusion and confusion: the importance of a perceptual perspective. *Behav Ecol* 25:450–463
- Kimchi R (1992) Primacy of wholistic processing and global/local paradigm: a critical review. *Psychol Bull* 112:24–38
- Kwok RM, Braddick OJ (2003) When does the Titchener Circles illusion exert an effect on grasping? Two- and three-dimensional targets. *Neuropsychologia* 41:932–940
- Lakens D (2013) Calculating and reporting effect sizes to facilitate cumulative science: a practical primer for t-tests and ANOVAs. *Front Psychol* 4:863
- Lamb TD, Collin SP, Pugh EN Jr (2007) Evolution of the vertebrate eye: opsins, photoreceptors, retina and eye cup. *Nat Rev Neurosci* 8:960–976
- Lucon-Xiccato T, Miletto Petrazzini ME, Agrillo C, Bisazza A (2015) Guppies discriminate between two quantities of food items but prioritize item size over total amount. *Anim Behav* 107:183–191
- Masland RH, Martin PR (2007) The unsolved mystery of vision. *Curr Biol* 17:R577–R582
- Miletto Petrazzini ME, Wynne CD (2016) What counts for dogs (*Canis lupus familiaris*) in a quantity discrimination task? *Behav Proc* 122:90–97
- Navon D (1977) Forest before trees: the precedence of global features in visual perception. *Cogn Psych* 9:353–383
- Neitz J, Geist T, Jacobs G (1989) Color vision in the dog. *Visual Neurosci* 3:119–125
- Parrish AE, Beran MJ (2014) When less is more: like humans, chimpanzees (*Pan troglodytes*) misperceive food amounts based on plate size. *Anim Cogn* 17:427–434
- Parrish AE, Agrillo C, Perdue B, Beran MJ (2016) The elusive illusion: do children (*Homo sapiens*) and capuchin monkeys (*Cebus apella*) see the solitaire illusion? *J Child Exp Psychol* 142:83–95
- Piffer L, Miletto Petrazzini ME, Agrillo C (2013) Large number discrimination in newborn fish. *PLoS ONE* 8(4):e62466
- Pitteri E, Mongillo P, Carnier P, Marinelli L (2014) Hierarchical stimulus processing by dogs. *Anim Cogn* 17:869–877
- Racca A, Amadei E, Ligout S, Guo K, Meints K, Mills D (2010) Discrimination of human and dog faces and inversion responses in domestic dogs (*Canis familiaris*). *Anim Cogn* 13:525–533
- Range F, Aust U, Steurer M, Huber L (2008) Visual categorization of natural stimuli by domestic dogs. *Anim Cogn* 11(2):339–347
- Range F, Jenikejew J, Schröder I, Virányi Z (2014) Difference in quantity discrimination in dogs and wolves. *Front Psychol* 5:1299
- Rose D, Bressan P (2002) Going round in circles: shape effects in the Ebbinghaus illusion. *Spat Vis* 15:191–203
- Stancher G, Rugani R, Regolin L, Vallortigara G (2015) Numerical discrimination by frogs (*Bombina orientalis*). *Anim Cogn* 18:219–229
- Suganuma E, Pessoa VF, Monge-Fuentes V, Castro BM, Tavares MCH (2007) Perception of the Müller-Lyer illusion in capuchin monkeys (*Cebus apella*). *Behav Brain Res* 182:67–72
- Udell MAR, Dorey NR, Wynne CDL (2008) Wolves outperform dogs in following human social cues. *Anim Behav* 76:1767–1773
- Uller C, Jaeger R, Guidry G, Martin C (2003) Salamanders (*Plethodon cinereus*) go for more: rudiments of number in an amphibian. *Anim Cogn* 6(2):105–112
- Van Ittersum K, Wansink B (2007) Do children really prefer large portions? Visual illusions bias their estimates and intake. *J Am Diet Assoc* 107:1107–1110
- Wansink B, Painter JE, North J (2005) Bottomless bowls: why visual cues of portion size may influence intake. *Obes Res* 13:93–100
- Ward C, Smuts BB (2007) Quantity-based judgments in the domestic dog (*Canis lupus familiaris*). *Anim Cogn* 10:71–80
- West RE, Young RJ (2002) Do domestic dogs show any evidence of being able to count? *Anim Cogn* 5:183–186