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Visual perception in domestic dogs: Susceptibility to the Ebbinghaus-Titchener and Delboeuf illusions

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Abstract (150-250 words): Susceptibility to geometrical visual illusions has been tested in a number of non-human animal species, providing important information about how these species perceive their environment. Considering their active role in human lives, visual illusion susceptibility was tested in domestic dogs (*Canis familiaris*). Using a two-choice simultaneous discrimination paradigm, eight dogs were trained to indicate which of two presented circles appeared largest. These circles were then embedded in three different illusory displays; a classical display of the Ebbinghaus-Titchener illusion; an illusory contour version of the Ebbinghaus-Titchener illusion; and the classical display of the Delboeuf illusion. Significant results were observed in both the classical and illusory contour versions of the Ebbinghaus-Titchener illusion, but not the Delboeuf illusion. However, this susceptibility was reversed from what is typically seen in humans and most mammals. Dogs consistently indicated that the target circle typically appearing larger in humans appeared smaller to them, and that the target circle typically appearing smaller in humans, appeared larger to them. We speculate that these results are best explained by assimilation theory rather than other visual cognitive theories explaining susceptibility to this illusion in humans. In this context, we argue that our findings appear to reflect higher-order conceptual processing in dogs that cannot be explained by accounts restricted to low-level mechanisms of early visual processing.

Introduction

Visual perception occurs when information sensed by the retina is interpreted by the brain, allowing individuals to perceive the external world and act upon it accordingly (Haber and Hershenson 1973). Occasionally, the brain misrepresents physical reality, adapting it according to preconceptions rather than accurately processing retinal information (Gregory 2015). These preconceptions can be induced by geometrical illusions and reflect mechanisms that are generally helpful for perception, but that trick the brain into visually correcting an image when such a correction is not necessary.

Susceptibility to geometrical illusions is cognitively unavoidable, implying that individuals are incapable of stopping perception of the illusion even when they are aware of it (Pylyshyn 1999). Considering that perception of illusory phenomena occurs automatically in humans, enduring even when we are aware of its properties, it is possible that illusory susceptibility may occur in non-human animals (hereafter animals) (Feng et al. 2016). In humans, many illusions are rule-based, occurring only under certain conditions (Eagleman 2001; Gregory 1980; Von Helmholtz 1867). Thus, understanding whether animal species use such rules to interpret illusory figures, and the extent to which animals are susceptible to geometrical illusions, may shed light onto various evolutionary and environmental influences of visual perception.

One common geometrical illusion, the Ebbinghaus-Titchener illusion, consists of two identical target circles that are enclosed by a number of smaller or larger circles termed ‘inducers’ (Figure 1). In humans, and most other species tested thus far, the apparent size of the target circle typically increases when the inducers are small and decreases when the inducers are large (Pressey et al. 1977; Zigler 1960; Zigler and Phillips 1960). The prevailing theory to explain susceptibility to the Ebbinghaus-Titchener illusion is size contrast theory. According to this theory, high-level cognitive processes compare relative sizes between perceived objects and create a perceptual accentuation of apparent size differences (Coren and Miller 1974; de Fockert et al. 2007; Gold 2014; Massaro and Anderson 1971). Thus, a target appears smaller than it physically is in the context of large inducers and, conversely, larger than it physically is in the context of small inducers.

[Figure 1]

The Delboeuf illusion, an illusion thought to be related to the Ebbinghaus-Titchener in terms of its underlying mechanisms (e.g. Girgus et al. 1972; Sherman and Chouinard 2016), consists of a single inducer in the form of a ring surrounding the target circle (Girgus et al. 1972). The target circle appears larger to humans than it actually is when the inducer ring borders it closely, and smaller than it actually is when the inducer ring borders it less closely (Figure 1). In humans, a combination of assimilation and size contrast theories are typically used to explain susceptibility to the Delboeuf illusion (King 1988). The ring closest to the target circle is hypothesized to assimilate, making the overall stimulus appear larger, whereas the ring furthest away from the circle is said to contrast, making the overall stimulus appear smaller.

To date, research on susceptibility to the Ebbinghaus-Titchener and Delboeuf illusions has been conducted across a variety of animals, yielding intriguing results that indicate clear differences at both the species and individual level (see Feng et al. 2016;

Kelley and Kelley 2014 for detailed reviews of illusion susceptibility in animals). To our knowledge, six studies have assessed susceptibility to the Ebbinghaus-Titchener illusion in animals (Murayama et al. 2012; Nakamura et al. 2008; Nakamura et al. 2014; Parron and Fagot 2007; Salva et al. 2013; Sovrano et al. 2014). Guinea baboons (*Papio papio*), phylogenetically the closest species to humans tested to date, were found not to be susceptible to the Ebbinghaus-Titchener illusion (Parron and Fagot 2007). Conversely, a single bottlenose dolphin (*Tursiops truncatus*) was susceptible, experiencing the illusion the same way as humans do (Murayama et al. 2012).

Bantam chickens (*Gallus gallus*) have demonstrated susceptibility to the Ebbinghaus-Titchener illusion in two different directions (Nakamura et al. 2014; Salva et al. 2013). In one study (Salva et al. 2013) they experienced the illusion similarly to humans and the single dolphin tested. In another, however, they appeared to experience a reversed effect, indicating that the circle typically perceived by humans to be larger was smaller than its counterpart and vice versa (Nakamura et al. 2014). This intriguing anomaly is not unique to Bantam chickens, as homing pigeons (*Columba livia*) have also demonstrated this reversed perception of the Ebbinghaus-Titchener illusion (Nakamura et al. 2008). Explanations for these unexpected findings remain speculative, indicating that further research is required in a wider range of species.

The Delboeuf illusion has also been tested in animals, but to a lesser extent than the Ebbinghaus-Titchener illusion. To our knowledge, only three studies have attempted to address non-human susceptibility to this illusion (Parrish and Beran 2014; Parrish et al. 2015; Agrillo et al. in press). Parrish and Beran (2014) found that chimpanzees (*Pan troglodytes*) were susceptible to the Delboeuf illusion in the same direction as humans.

More recently, Rhesus (*Macaca mulatta)* and Capuchin (*Cebus apella)* monkeys were also found to be susceptible in the same direction as humans and chimpanzees, but with significant variability across individuals, highlighting task-based concerns (Parrish et al. 2015). In a size discrimination task used to test susceptibility, only two monkeys, out of the nineteen tested, perceived the illusion in the same direction as humans, while six perceived the illusion in a reversed manner, and eleven performed at chance (Parrish et al. 2015). In a subsequent absolute classification test, conducted to assess whether the monkeys could classify stimuli using large and small discrimination rules, 14 out of 17 monkeys were susceptible to the illusion in the same direction as humans. Thus, while the authors concluded that monkeys demonstrate susceptibility to the illusion in the same direction as humans, it is important to note the high individual variation in susceptibility and the performance differences across the tests conducted. Finally, Agrillo et al., (in press) observed that, when dogs were given the choice between equal food portion sizes, presented on two plates differing in size in a spontaneous preference paradigm, they did not seem to be susceptible to the Delboeuf illusion. This suggests that perceptual biases affecting size judgments may differ between primates and dogs, although, given the disparate results obtained in monkeys when different methodologies were employed, further research is required before any firm conclusions can be drawn.

In the last 20 years, many studies have investigated the cognitive abilities of domestic dogs (for a comprehensive review see Bensky et al. 2013). According to these studies, dogs appear uniquely capable in terms of their social-cognitive abilities. While dogs provide an interesting and unique model for understanding cognitive processes in non-human animals (Hare and Tomasello 1999; Soproni et al. 2002; Soproni et al. 2001;

Udell et al. 2008; Udell and Wynne 2008), little is known about how they visually perceive the physical environment and to what extent their perception is similar to, or different from, other mammals.

While a foundational understanding of dog vision has been available for over two decades (see Miller and Murphy 1995 for an extensive review of vision in dogs), advances since have been limited. One reason for this paucity can be attributed to the drastic physiological differences between breeds, as differences in facial morphology can affect even the most basic measures. However, we do know that the dog's visual system is highly adapted for dim light (Kemp and Jacobson 1992). Furthermore, a 'typical' dog has a total monocular field of view of 135 to 150°, with a binocular overlap of 30° to 116° depending on whether it is calculated behaviourally, or on the basis of ganglion cell density and optical considerations (Duke-Elder 1958; Peichlcu 1992; Sherman and Wilson 1975; Walls 1942). Less well established is the dog's visual acuity and their ability to distinguish different colours (Miller and Murphy 1995). While many early studies of colour vision suggested dogs lacked colour vision (Neitz et al. 1989; Rosengren 1969), there is now both behavioral and anatomic evidence that dogs have a potential to perceive colour (Jacobs 1983; Tanaka et al. 2000). However, colour vision capacities in dogs remain unclear.

At the level of visual perception, it has been reported that dogs are able to discern facial cues of both dogs and humans (Huber et al. 2013; Racca et al. 2010), discriminate smiling human faces from blank expressions (Nagasawa et al. 2011), and classify dog and landscape images according to a perceptual response rule (Nagasawa et al. 2011; Range et al. 2008). It has also been suggested that dogs typically process stimuli in a globally-oriented fashion although there appears to be much individual variation (Mongillo et al. 2016; Pitteri et al. 2014). These findings suggest that dogs process visual information cognitively, but additional research is required to understand the link between retinal input and perception.

If perceptual differences account for species differences in illusion susceptibility, practical implications are significant for both dogs and humans. Furthering our understanding of domestic dog visual processing, particularly if it differs from what is typically observed in humans, may have implications for dogs in roles that rely extensively on visual perceptions to aid themselves and humans. Considering that domestic dogs operate in a wide range of environments, such as acting as guardians, stock herders, detectors, guides, assistants, and companions, a functional understanding of how they perceive their environment may result in increased efficacy within their respective roles. For example, on average, only 50% of dogs across working industry sectors are successful (for a comprehensive review see Cobb et al. 2015). This high "wastage" problem suggests there is substantial room for improvement; a better understanding of dogs' psychophysical perceptions may facilitate this.

Furthermore, an accurate understanding of canine visual perception may aid in understanding behavioural outcomes in research settings. Most dog research utilizes behavioural outcomes to indirectly measure cognitive abilities. Understanding what dogs can and cannot see, and how their perception differs from humans, is integral to accurately representing their abilities. Many studies have reported that domestic dogs perform in a way suggestive of human-like visual processing abilities (Huber et al. 2013; Nagasawa et al. 2011; Racca et al. 2010; Range et al. 2008). However, how dogs visually perceive the physical environment, and to what extent this perception is similar to or different from other animals, remains unclear.

The aim in this study was to determine whether or not dogs demonstrate susceptibility to illusory stimuli. A positive-reinforcement based training protocol was used to teach companion dogs to discriminate between two solid circles, displayed on a computer screen, on the basis of relative size. After a learning criterion was reached, three experiments were conducted to test various aspects of their visual perception. In the first experiment, dogs were presented with the classical version of the Ebbinghaus-Titchener illusion. In the second, an illusory contour version of this illusion was used to clarify the unexpected results of experiment one, as it was thought that the inducer circles might have confounded perception of the target circle stimulus. Finally, the third experiment presented dogs with the Delboeuf illusion, an illusion suspected to be related to the Ebbinghaus-Titchener illusion in terms of its underlying mechanisms (Sherman and Chouinard 2016). It was predicted that the dogs would accurately detect the relative size of two differently sized circles following the appropriate training regimen, regardless of the background context in which these circles were presented. When presented with the illusions, with two target circles of the same size, the dogs were expected to demonstrate with their behaviour that they were susceptible to the illusions in the same manner as humans and most other animals (Murayama et al. 2012; Parron and Fagot 2007; Salva et al. 2013; Sovrano et al. 2014).

Methods

Participants

Eight companion dogs (*Canis familiaris*), six females and two males, were used as participants in this study (at the start of the study mean age = 1 year, 8 months; age range = 9 months to 6.5 years; see Table 1). All dogs were purebred Lagotto Romagnolos and sexually intact except for one, Gabbie, who was spayed during the period of data collection due to a medical condition. Neither the spaying nor the underlying medical condition was expected to affect the results of a visual processing study. The dogs were owned by the same individual and, as such, lived under the same environmental conditions. Having not participated in previous experiments, all dogs were completely experimentally naïve and had no previous formal training experience.

[Table 1]

Materials

Testing was conducted in the Canine Nose-Touch Testing Apparatus, a 1540mm x 600mm x 600mm wooden apparatus designed and manufactured specifically for the study (see Fig 2). This apparatus was implemented to reduce any experimenter-expectancy effect, and to decrease environmental distractions throughout the trials. The testing chamber was equipped with a 508mm Dell® widescreen computer monitor for stimulus presentation (1280 x 800 pixels; one pixel measures approximately 0.3 mm^2), which was located at approximately the height of the dogs' eyes, with the base of the screen being 24 cm above floor level. Below it, at ground level, was a remotely controlled treat dispenser (Treat & Train®) that distributed one piece of semi-moist dry dog food (Nature's Gift® Mini Kangaroo, or Good-o® treats) as positive reinforcement. Above the monitor, a video camera was mounted to record each trial.

[Figure 2]

Data acquisition was conducted through customized programs developed specifically for this study by the research team using Processing 2.2.1 on a Dell Latitude D531 LCD laptop. The program allowed the researcher operating it to control the presentation of stimuli, including trial commencement, trial duration, and the location of the target stimulus (left or right side) on the screen. Dog responses were recorded by the experimenter pressing either the up or down arrow (which indicated correct and incorrect choices, respectively) on the computer keyboard, which simultaneously ended the trial and commenced the inter-trial intermission while storing all data automatically. Order and side of stimuli presentation were randomly assigned using one of 44 left-right sequences designed by Gellerman (1933) to ensure that the most probable chance score in each round of ten trials would be 50%.

Pre-training Procedure

Dogs were trained based on their individual performance, beginning in April 2015 and continuing for four months. Pre-training was approached as if it was a game for the dogs, and involved two to three trainers working three hours per day for three days per week, with each dog receiving multiple short (4-6 min) pre-training sessions within this period. To begin, each dog was guided to target a black 80 mm diameter circle via a nose-touch. They were rewarded for doing so by an immediate 'click' sound, followed by rapid presentation of a small food treat. Target stimuli were first presented in a trainer's hand, and then glued to a wall (45cm above the ground). This behaviour was transferred to nose-touching a 62 mm circle presented on a computer monitor (on random locations on the screen) housed in an open shed (including the testing location, without the Canine Nose-Touch Testing Apparatus being present). Once this stimulus training was complete, the task was generalized to multiple stimulus pairs, each comprising a small and large circle.

All dogs were trained to select the relatively larger circle, except for Baxter, who was trained to select the smaller circle. The reason for this distribution is as follows. Initially, the eight dogs were randomly assigned into two groups, Audrey, Gabbie, Hamish, and Molly being trained to select the larger circle and Baxter, Beth, Eliza, and Lulu being trained to select the smaller one. Each dog was trained on several combinations of circles S1-S12 for twelve weeks, following which they were tested for accuracy. It was observed throughout the training period that dogs being trained to select the small circle were less successful, appearing to have an existing preference for the larger stimulus that was difficult for them to overcome. Consistent with this, and despite previous reports that dogs do not show an innate preference for large over small stimuli (Tapp et al. 2004), only one dog in the small circle group, Baxter, met the criteria of 80% correct responses. All four dogs in the large circle group met the same criteria. Due to time constraints, our focus on dogs' susceptibility to visual illusions, and the wish to include as many dogs in the study as possible, we decided not to persist with training Beth, Eliza and Lulu to select the small circle. Rather than omitting them from the study entirely, we attempted to retrain them to select the large circle. When they were tested four weeks later, all three met the criteria of 80% correct responses.

All dogs were then familiarized within the Canine Nose-Touch Testing Apparatus. Dogs were trained to enter the apparatus via the rear door. This placed them in an enclosed tunnel from which they could observe the testing chamber through a central door made from horizontal iron bars, but could not observe the experimenters. The central door was raised after the dog was positioned properly inside the apparatus, allowing the dog to enter the testing chamber and select their response. Side panels could be removed from the testing chamber so that the dog was encouraged to face forward and could easily exit the chamber during the training process. Once testing commenced, the central door remained raised and the side panels were in place. Dogs entered the rear door, proceeded to the testing chamber, made their choice, received a treat if appropriate, and then exited via the rear door. This prevented them from forming side biases based on their exit point and positioned them at the rear of the apparatus, ready for the next trial.

Three experimenters (A, B, and C) were present at all times during testing. At the beginning of each trial, Experimenter A stood with the dog at the opening of the apparatus until the stimuli were presented on the computer monitor. Experimenter A did not look at the screen and was advised when to begin the trial. The dog was then permitted to enter the apparatus, walk up to the stimulus pair, and make a selection. Experimenter B could see the monitor, but could not see the dog before he or she made a response and, in addition, the dog could not see Experimenter B. If the dog chose correctly, Experimenter B quietly activated the remotely controlled treat dispenser located below the computer monitor. If the dog chose incorrectly, no reward was provided and Experimenter B relayed a non-verbal signal to Experimenter C to remove the stimuli. Experimenter C recorded the result (correct or incorrect) as indicated by

Experimenter B and removed the stimuli simultaneously. Experimenter A then signalled the dog to return to the entrance of the apparatus to resume the starting position for the next trial. Once the dog had returned to Experimenter A, he or she received a small treat randomly (regardless of whether the choice was correct or not) and began the next trial. Thus, some reward was provided to the dogs simply for participating in the experiments, which helped maintain motivation even when performance was suboptimal.

At the completion of this pre-training process, all dogs could reliably discriminate between two identical circle stimuli varying in pixel diameter size by 60% (106 pixels, 31.8mm, and 207 pixels, 62.1mm in diameter; 207 pixels, 62.1mm, and 403 pixels, 120.9mm in diameter) averaging an accuracy rate of 78.4% (65%-87%). When presented with two circles that were identical in size (207 pixels, 62.1mm, in diameter), each dog's performance was at chance levels of 54.7% (47.5%-72%). Importantly, the dogs clearly enjoyed playing the 'circle game' and were enthusiastic participants even if dozens of trials were administered in any given session.

Training & Testing Procedure

During the training and testing sessions described below, three circle sizes were presented in pairs to each dog to ensure that the dogs were not continually reinforced for choosing a stimulus of a given size. The circles sizes were based on an array of 12 circles used previously to test transpositions in pigeons (Lazareva et al. 2008; Lazareva et al. 2005; Lazareva et al. 2014) and labelled S_1 through S_{12} (16.2mm to 189mm, 54 to 630 pixels in diameter). We selected three intermediate circles from the array; S_4 (106 pixels, 31.8mm in diameter); S_7 (207 pixels, 62.1mm in diameter); and S_{10} (403 pixels, 120.9mm in diameter). S_4 and S_{10} differed in diameter from S_7 by 65% (Fig. 3). Visual angles were calculated for the target circle stimuli from the entrance of the apparatus; S_4 (3.1° of arc); S_7 (7.4° of arc); and S_{10} (9.5° of arc). However, due to the fact that the dogs were not restricted while entering the apparatus, this measure is imprecise.

[Figure 3]

Before each experiment, all dogs underwent several short training sessions, unique to each illusion, in which the circle stimuli were presented within novel background contexts (See Supplementary Material 1). These were used to acquaint the dogs with new images, such as inducers and/or colours, which would be present in the test condition. In these training sessions, circle pairs were presented in blocks of ten trials, with five comparisons of S_4-S_7 circles and five comparisons of S_7-S_{10} circles, all presented over the appropriate background images. The correct stimulus pseudo-randomly appeared on each side for an equal number of times in accordance with randomly selected Gellerman sequences (1933).

For each illusion, there were four to six types of training trials, depending on how many characteristics of the background context needed to be included, and to the extent that dogs were able to identify the correct target circle. Additionally, these served as controls to ensure dogs were not choosing stimuli based on overall stimulus size (see Supplementary Material 1 and 2). Each dog moved on to the next type of training trial only after reaching a criterion of either nine correct in a single ten-trial block or seven correct across each of two consecutive blocks. In order to participate in testing, each dog was required to successfully complete all training sessions. Most did this very easily, in just a small number of trials. In any case where a dog could not meet the criteria after seven attempts on any single stimulus type, the dog was excluded from participating further in that particular experiment.

Once a dog progressed through the relevant training sessions, illusion testing began. Circle pairs were presented in three sets: S_4-S_7 and S_7-S_{10} represented the control conditions, and S_7-S_7 represented the test trials. Each round of ten trials consisted of six control trials, including three S_4-S_7 pairs and three S_7-S_{10} pairs. Four experimental trials, comprising S_7-S_7 pairs, were randomly presented within the ten trials on the condition that the test presentation would not be presented within the first two trials. Ten blocks of ten trials were administered for each experiment, resulting in 100 trials per dog (60 control trials, 40 experimental trials) (See Supplementary Material 2 for video examples of testing sessions).

A response in the illusion condition was considered correct when the circle typically seen as 'perceptually larger' to humans was chosen. However, so as not to reinforce any particular way of responding, reinforcement for the experimental trials was pseudo-randomized using a Gellerman sequence to order the trials. If the Gellerman sequence dictated that the circle on the left for a particular experimental trial should be correct, it was deemed thus for the purposes of reinforcement. This was the case even though the circles were identical in size and even though the alternate circle may have been 'correct' in so far as humans perceived it as perceptually larger. In addition, throughout the session, the dog received intermittent food rewards directly from Experimenter A as the animal exited the testing apparatus, to maintain motivation to continue. Once all ten trials in a block were completed (this typically took less than two minutes), the dog was returned to his or her crate to await the next round, which occurred approximately 20 minutes later. Up to ten rounds were completed during a single testing day, with the dogs being tested on multiple days until sufficient trials were obtained for each experiment.

Classical Ebbinghaus-Titchener Stimuli

In the Classical Ebbinghaus-Titchener test, two black target circles (RGB values 0, 0, 0; Luminance 0.18 candela) were presented on a yellow background (RGB values 255, 255, 0; Luminance 163.6 cd) surrounded by six blue inducer circles (RGB values 0, 0, 255; Luminance 16.05 cd) (see Fig. 4). For this experiment, yellow and blue colours were used to create the stimuli as the difference between these has been suggested to be quite salient to dogs (Miller and Murphy 1995). For control conditions, same-sized inducer circles (110 pixels in diameter; 33mm) were placed around the two target circles of S_4-S_7, and S_7-S_{10} pairs. For experimental conditions, small (69 pixels in diameter; 20.7mm) and large (170 pixels in diameter; 50.1mm) inducer circles were placed around S_7-S_7 pairs.

[Figure 4]

Illusory Contour Ebbinghaus-Titchener Stimuli

For the Illusory Contour Ebbinghaus-Titchener test, white rays (RGB values 255, 255, 255; Luminance 175.5 cd) were presented on a black background (RGB values 0, 0, 0; Luminance 0.18 cd) (adpated from Ninio 1998). Twenty rays were placed around each circle (Fig. 4). Because this Ebbinghaus-Titchener presentation represents an alternative and less widely utilized version of the illusion in humans, colours were not added in order to preserve the illusory effect. For control conditions, same size inducer rays (S_4-S_7: approximately 48mm by 9.9mm, and 37.3mm by 9.9mm; S_7-S_{10}: approximately 37.3mm by 9.9mm, and 15.2mm by 9.9mm) were placed around the two target circles of S_4-S_7, and S_7-S_{10} pairs. For the experimental condition, small (S_7: 10.1mm by 6.35mm) and large (S_7: 37.3mm by 9.9mm) inducer rays were placed around two target circles (S_7-S_7 pairs).

Delboeuf Stimuli

In the Delboeuf condition, black rings (RGB values 0, 0, 0; Luminance 0.18 cd), 15 pixels wide, were situated around each black target circle on a white background (RGB values 255, 255, 255; Luminance 175.5 cd) (Fig. 4). For control conditions, same sized inducer rings (580 pixels in diameter; 174mm) were placed around the two target circles of S_4-S_7, and S_7-S_{10} pairs. For experimental conditions, inducers were placed around S_7-S_7 pairs, however one ring was placed close to the target circle (290 pixels in diameter; 87mm) whereas the other ring was left at the control distance (580 pixels in diameter; 174mm).

Data Analysis

To examine group performances, all illusions were analysed using two-tailed one-sample *t*-tests conducted on the dogs' average proportion correct. Alpha was set at 0.05 and chance levels were considered to be 0.5. Effect sizes were calculated for each illusion condition. Additionally, to examine individual performances, two-tailed binomial tests were conducted on each dog's individual responses in the control conditions and the illusion condition. In order to assess session effects, potentially caused by variables such as learning, binomial logistic regressions were conducted on the illusion condition for each illusion presentation. Finally, in order to assess reliability of the scoring, two coders assessed a selection of videos from the test conditions. Each coder independently scored the same 150 trials, with high inter-observer reliability of 99.3%. As Baxter was the only subject trained to select the smaller target stimulus, his results have been reversed (and notated) in the data presented below.

Results

Classical Ebbinghaus-Titchener

The number of attempts that each dog required to reach criterion in the Classical Ebbinghaus-Titchener training sessions varied only marginally across the six stimulus types. On average, it took 1.89 blocks of ten trials for the group as a whole to progress to the next type, with Stage Two appearing to be the most difficult at 2.25 blocks. Eliza was removed from this experiment at Stage Six for exceeding the maximum number of attempts permitted to reach criterion.

Results of the two-tailed *t*-test for the group in the Classical Ebbinghaus-Titchener illusion were significant [$t(6) = 8.74$, $P = .0001$, $SD = 8.86$, Cohen's $d = 3.30$]. Binomial tests for each dog are presented in Figure 5a and indicate that, in the control conditions, all dogs performed, as expected, significantly above the chance score of 50%. For the illusion condition, all dogs recorded response accuracies that were again significantly different from chance, but in the direction opposite to what would be expected with human participants. The dogs consistently perceived the target circle that appears larger to humans as smaller, and the target circle that appears smaller to humans as larger. Results of the binary logistic regression indicated no effect of session on performance in the illusion condition (P = 0.70).

Illusory Contour Ebbinghaus-Titchener

The number of attempts that each dog required to reach criterion in the Illusory Contour Ebbinghaus-Titchener training sessions varied only marginally across the four stages. On average it took 2.25 trials as a group to continue to the testing phase, with Stage Four being the most difficult at 4.13 trials. Lulu and Beth were removed at Stage Four for exceeding the maximum attempts to reach criterion and were therefore excluded from participating in the testing phase. Eliza was removed from the results post-hoc, as she failed to perform above chance on control conditions (58%, z = 1.29).

Results of the two-tailed t-test for the group in the Illusory Contour Ebbinghaus-Titchener illusion were significant [$t(4)$ = 3.44, P = .026, SD = 12.67, Cohen's d = 1.53]. Binomial tests for each dog are presented in Figure 5b and indicate that, for overall response accuracy in control conditions, all dogs were significantly above the chance score of 50%. It should be noted, however, that the dogs typically performed more poorly on the control conditions for this experiment than they did on the control conditions for the previous one. For the illusion condition Audrey, Gabbie and Hamish recorded response accuracies that differed significantly from chance. As in the previous experiment, the dogs misperceived the circle sizes in the illusion condition, but in the opposite direction to that typically observed in humans. Results of the binary logistic regression indicated no effect of session on performance in the illusion condition (P = 0.12).

Delboeuf Illusion

The number of attempts that each dog required to reach criterion in the Delboeuf training sessions varied across five stages. On average, it took 1.32 blocks of 10 trials as a group to continue to the testing phase, with Stage Five being the most difficult at 1.37 blocks.

Results of the two-tailed *t*-test for the group for the Delboeuf illusion were not significant [$t(7) = 1.8$, $P = .106$, $SD = 10.97$, Cohen's $d = 0.65$]. Binomial tests for each dog are presented in Figure 5c and indicate that, for overall response accuracy in control conditions, all dogs were significantly above the chance score of 50%. However, only two dogs were significantly different from chance in the illusory condition of this experiment and, overall, the effect was not significant. Thus, dogs did not show susceptibility to the Delboeuf illusion overall, although it is instructive that two dogs did exhibit a performance which was significantly different from chance and, for these two dogs (Beth and Lulu), the results were again in the opposite direction than what would be expected based on human studies. Results of the binary logistic regression indicate no effect of session on performance in the illusion condition ($P = 0.44$).

[Figure 5]

Discussion

The current study examined susceptibility to the Ebbinghaus-Titchener and Delboeuf illusions in dogs. It was predicted that dogs would demonstrate susceptibility to each of the illusions investigated, in the same direction as humans. Contrary to our predictions, the results of the experiments demonstrate that dogs do not experience the illusions in this manner. The *t*-tests on the group data, and the binomial tests on the individual data, indicated that the dogs were responding to stimuli significantly differently from chance in both the Classical and Illusory Contour Ebbinghaus-Titchener conditions. The results indicate however, that, for these illusions, target circles typically perceived as larger by humans were perceived as smaller by dogs. When presented with the Delboeuf illusion, the t-tests on the group data and the binomial tests on the individual data indicated that the dogs overall were responding at chance. While these results demonstrate a lack of susceptibility to the Delboeuf illusion as a group, it is instructive that two dogs did appear to demonstrate susceptibility. Also informative is that, again, this was in the opposite direction to humans. This null finding for the Delboeuf illusion is consistent with a behavioral preference paradigm, also testing susceptibility of dogs to the Delboeuf illusion (Agrillo et al. in press).

In humans, the prevailing theory to explain susceptibility to the Ebbinghaus-Titchener illusion is size contrast theory. According to this theory, high-level cognitive processes compare relative sizes between objects and create a perceptual accentuation of apparent size differences (Coren and Miller 1974; de Fockert et al. 2007; Gold 2014; Massaro and Anderson 1971). Thus, a target appears smaller than it physically is in the context of large inducers and, conversely, larger than it physically is in the context of small inducers. However, size contrast theory cannot be used to explain the perceptual rescaling of the target circles we observed in the Ebbinghaus-Titchener illusion in dogs. Considering, the dogs perceived the target circle as being more like the inducer circles, they therefore did not accentuate the size difference between the stimuli. Instead, the results suggest that the dogs cognitively grouped, or assimilated, all circles as being more similar, perceptually rescaling the target circles to be more like the inducers.

The results of both the Classical and Illusory Contour Ebbinghaus-Titchener circles are not unique, but they are remarkable, as they go in the opposite direction to humans, and also contrary to results yielded in studies conducted on other animals, particularly other mammals (Murayama et al. 2012; Parron and Fagot 2007; Salva et al. 2013). However, Nakamura and colleagues (2008; 2014) have consistently reported that homing pigeons and Bantam chicks perceive the Ebbinghaus-Titchener illusion in the opposite direction as humans. The authors proposed an assimilation account to explain these results, whereby the birds tend to perceptually rescale the target circles in the Ebbinghaus-Titchener display so that they appear more like the other circles.

While this explanation cannot apply to humans, given that the size contrast between the target and the inducers is accentuated rather than reduced, it can be applied to explain dogs' susceptibility to the illusion. When presented with the Ebbinghaus-Titchener display, the dogs in this study perceptually rescaled the target stimulus so that it was perceived to be more similar to the inducers. This finding is consistent with the Gestalt law of similarity, a school of thought that suggests humans are naturally capable of perceiving objects as orderly and organized forms and patterns. The law of similarity holds that objects that look similar and are physically close together will perceptually be grouped together and treated as different examples of the same object (Koffka 1935). Given the divergence in the illusory effects between dogs and humans, the mechanisms underlying perception of the Ebbinghaus-Titchener stimuli must differ in terms of the perceptual rescaling of objects between species. Identifying what these mechanisms are will require further comparative research between the species.

We speculate that susceptibility to both the Ebbinghaus-Titchener and Delboeuf illusions in dogs requires cortical processing. Our reasoning is that it is difficult to invoke low-level processing at the level of the retina to explain assimilation effects if one considers that multiple stimuli in a visual scene fall within the receptive fields of different retinal ganglion cells (e.g. Hubel and Wiesel 1962). Given the known properties of receptive fields at different stages of visual processing, it is conceivable that this convergence of information takes place in higher-order areas of the visual cortex (Livingstone and Hubel 1988). In addition, assimilation effects would require a conceptual understanding of context in order for the size of the target circle to appear more similar in size as the inducer circles. Conceptual understanding requires knowledge, which is mediated by higher-order processes at the level of the cortex (Caramazza and Mahon 2006). Taken together, we believe that high-level processes as opposed to low-level processes explain our results.

In addition to revealing the nature of dogs' susceptibility to common illusions, our results also provide preliminary evidence and, to our knowledge, the first evidence that dogs may perceive illusory contours. One possible interpretation of this finding is that the dogs demonstrated modal completion abilities, where they perceived a physical border around a given stimulus even when parts of the contextual cues were physically missing. The target stimuli presented in the Illusory Contour Ebbinghaus-Titchener illusion utilized inducer rays to create the image of a circle that, in actuality, was not there, similar to the 'phantom' edge phenomenon observed in the Kanizsa triangle illusion

(Kanizsa et al. 1993). However, further investigation is required to substantiate this claim. Specifically, future studies may consider confirming that dogs can see contour illusions, such as the Kanizsa triangle illusion, and varying parameters that are known to affect the strength of contour illusions in humans.

If it is the case that dogs can mentally perceive a whole circle structure when only certain parts of the stimulus are physically present, then this could lend support to previous claims that dogs are "global processors" with perceptual cognitive styles favouring global over local processing (Mongillo et al. 2016; Pitteri et al. 2014). However, one should consider that these claims are largely based on dogs' performance on the Navon task (Navon 1977). It is clear from a number of experiments in humans that global processing should not be considered a singular construct that is invoked by the same cognitive operations across all types of global tasks, but rather an umbrella term to denote multiple independent mechanisms (Chouinard et al. 2013; Chouinard et al. 2016). To fully determine whether or not dogs are "global processors", one should perform multiple global tasks; such as we did in this study with three different geometrical illusions that require one to process multiple components in a visual scene in order for a target stimulus to be perceptually rescaled. As it turned out, the dogs were susceptible to two of the three illusions and some (two) dogs appeared susceptible to the third. Thus, dogs may be "global processors" in some tasks, which invoke certain mechanisms, but not in others, which invoke different mechanisms. Only future research can address this issue.

Methodological Considerations of Present Investigation

It will be necessary to confirm our results in other dogs before more general conclusions can be drawn. In dogs, certain morphological differences, such as nose length and face shape, may have an impact on brain structure and visual processing (McGreevy et al. 2003; Roberts et al. 2010). In order to avoid possible variations in vision caused by facial morphology, dogs of the same breed were used as participants in this study. They were also closely related and lived in the same environment, many since birth. This means that the results may be breed-specific or specific to this genetic line or environmental context. It would be interesting for future research to discern if breeds with flat faces (such as Boxers, Pugs, and Bulldogs) have different or varying illusion susceptibility compared to longer-nosed breeds (such as Labrador retrievers, German shepherds, and Border collies). It would also be of interest to test additional Lagotto Romagnolos, particularly those who live in very different environments.

Of great interest is the observation that, following twelve weeks of training, only one dog out of four was able to reach criteria in the group being trained to select the smaller of two circles, while all four in the large circle group were successful. This was not due to any learning deficits on the part of the dogs, since all three who were unable to reach criteria when selecting the smaller circles, quickly did so when they were retrained to select larger circles. This suggests, therefore, that most, but perhaps not all, dogs may have an innate preference for selecting larger versus smaller targets. Resolving this issue was beyond the scope of this study, and requires further investigation. In terms of susceptibility to visual illusions, the fact that seven of the eight dogs were trained to select the stimulus perceived to be larger was inconsequential, particularly since the one dog trained to select the smaller circle was equally susceptible.

Additionally, while our training sessions attempted to control for the potential confound of overall stimulus size, future research should attempt to determine exactly what parameters dogs use to make their decisions. This should include additional assessments of the effect of overall stimulus size, in case our controls were insufficient. If the dogs had failed to be susceptible to the illusory stimuli, it could be argued that this was because we trained them to ignore the inducers, such that they were 'blind' to overall stimulus size. This could have occurred through the training process of gradually darkening the inducers in the Classical Ebbinghaus-Titchener illusion in the training stages. However, the fact that dogs were susceptible to the illusions, albeit in the opposite direction to what was predicted, argues against this possibility. If the dogs had been trained to ignore the inducers, they should not have demonstrated susceptibility in either direction and should have performed at chance levels. Furthermore, the training with fading occurred in the version of the Ebbinghaus-Titchener illusion, which showed the strongest effect sizes. Had the fading trained the dogs to ignore the cues, these effect sizes should have been lower than effect sizes in the other illusions, where the inducers were not faded in.

It is plausible that the null findings in the Delboeuf illusion, when the dogs are evaluated as a group, could be because it is a weaker illusion than the Ebbinghaus-Titchener illusion. In the current study the effect size for the Classical Ebbinghaus-Titchener illusion (Cohen's d = 3.30) was much larger than the effect size for the Delboeuf illusion (Cohen's d = 0.65). This is not surprising given that others have consistently shown that the Ebbinghaus-Titchener is one of the strongest illusions in humans when compared to other illusions (Aglioti et al. 1995; Choplin and Medin 1999;

Coren and Enns 1993; de Grave et al. 2005; Girgus et al. 1972; Weintraub 1979), while effect sizes in the Delboeuf illusion in human are typically halved relative to the Ebbinghaus-Titchener illusion (Sherman and Chouinard 2016). Of course, given that dogs perceive both illusions differently than do humans, it is difficult to argue that one is likely to be stronger or weaker in dogs on the basis of how humans are affected. Nonetheless, considering that dogs' susceptibility to both variants of the Ebbinghaus-Titchener illusion was similar, it is possible that the Delboeuf illusion has an overall weaker effect even when this effect is reversed. This explanation is consistent with the observation that, of those dogs that did show some susceptibility to this illusion, including the two that performed significantly differently from chance, the direction of susceptibility was in the same direction as with the other two illusions, but generally quite weak (Fig. 5c).

It is also possible that the lower effect size for the Illusory Contour version stems from differences in the colours used in the presentation. The Classical version was chromatic, with blue contextual cues placed over a yellow background. In contrast, the Illusory Contour Ebbinghaus-Titchener Illusion was achromatic, with white cues placed over a black background. The former was stronger than the latter in terms of illusory strength, perhaps indicating that the introduction of colours, specifically yellow and blue, may have contributed to the strength of the illusion. Indeed, yellow and blue colours might create stronger perceptual contrasts for dogs relative to other colour combinations, considering the retinal composition of their cone photoreceptors (Miller and Murphy 1995). The differences in chromatic composition between the two versions were due to constraints imposed by the context. In order to consistently test the dogs using a black target circle (the only colour they had been trained to target), a black background had to be used in the illusory contour version of the Ebbinghaus-Titchener illusion and the Delboeuf illusion. Only the Classical version of the Ebbinghaus-Titchener lends itself to introduction of a coloured background, although we are currently testing the Ponzo illusion using coloured stimuli and will report the results in a subsequent manuscript.

Yet another possibility is that the differences in effect sizes we reported for the two versions of the Ebbinghaus-Titchener illusion stem from a difference in luminance contrast. This explanation is unlikely since the luminance contrast between the background and contextual cues in the Ebbinghaus-Titchener illusion displays was stronger in the black and white (difference = 175.32 cd) than the yellow and blue (difference = 147.55 cd) version. Yet the former created a less powerful illusion than the latter.

Conclusions

This study is one of the first, to our knowledge, to examine geometrical illusion susceptibility in dogs (see Agrillo et al. in press for an additional study completed at approximately the same time). Dogs were found to perceive two different versions of the Ebbinghaus-Titchener illusion in a manner that is in the opposite direction to how humans and most other animals perceive this illusion. The results from the illusory contour display also demonstrate preliminary evidence that dogs may be able to detect illusory contours and therefore possess modal completion abilities, although this requires confirmation in a more focused study. Dogs as a group were not susceptible to the

Delboeuf illusion, although individual differences were apparent and two of eight dogs tested did appear to be susceptible. We propose that assimilation theory, rather than the size contrast theory, which is typically applied to explain human susceptibility, best explains canine susceptibility to the reversed Ebbinghaus-Titchener illusion. Additionally, since dogs perceive a stimulus different from the physical one presented on the screen in the Ebbinghaus-Titchener conditions, these results suggest that dogs use conceptual formations beyond the visual system to make decisions based on concept rather than on receptor sensory input.

References

Aglioti S, DeSouza JF, Goodale MA (1995) Size-contrast illusions deceive the eye but not the hand Current biology 5:679-685

Bensky MK, Gosling SD, Sinn DL (2013) The world from a dog's point of view: a review and synthesis of dog cognition research Adv Study Anim Behav 45:209-406

Caramazza A, Mahon BZ (2006) The organisation of conceptual knowledge in the brain: The future's past and some future directions Cognitive Neuropsychology 23:13-38

Choplin JM, Medin DL (1999) Similarity of the perimeters in the Ebbinghaus illusion Perception & Psychophysics 61:3-12

Chouinard PA, Noulty WA, Sperandio I, Landry O (2013) Global processing during the Müller-Lyer illusion is distinctively affected by the degree of autistic traits in the typical population Experimental brain research 230:219-231

Chouinard PA, Unwin KL, Landry O, Sperandio I (2016) Susceptibility to Optical Illusions Varies as a Function of the Autism-Spectrum Quotient but not in Ways Predicted by Local–Global Biases Journal of autism and developmental disorders 46:2224-2239

Cobb M, Branson N, McGreevy P, Lill A, Bennett P (2015) The advent of canine performance science: Offering a sustainable future for working dogs Behavioural processes 110:96-104 doi:http://dx.doi.org/10.1016/j.beproc.2014.10.012

Coren S, Enns JT (1993) Size contrast as a function of conceptual similarity between test and inducers Perception & Psychophysics 54:579-588

Coren S, Miller J (1974) Size contrast as a function of figural similarity Perception & Psychophysics 16:355-357

de Fockert J, Davidoff J, Fagot J, Parron C, Goldstein J (2007) More accurate size contrast judgments in the Ebbinghaus Illusion by a remote culture Journal of Experimental Psychology: Human Perception and Performance 33:738

de Grave DD, Biegstraaten M, Smeets JB, Brenner E (2005) Effects of the Ebbinghaus figure on grasping are not only due to misjudged size Experimental brain research 163:58-64

Duke-Elder S (1958) System of Ophthalmology Vol. 1 The Eye in Evolution. Henry Kimpton,

Eagleman DM (2001) Visual illusions and neurobiology Nature Reviews Neuroscience 2:920-926

Feng LC, Chouinard PA, Howell TJ, Bennett PC (2016) Why do animals differ in their susceptibility to geometrical illusions? Psychonomic Bulletin & Review:1-15

Girgus JS, Coren S, Agdern M (1972) The interrelationship between the Ebbinghaus and Delboeuf illusions Journal of Experimental Psychology 95:453

Gold JM (2014) Information processing correlates of a size-contrast illusion Frontiers in psychology 5

Gregory RL (1980) Perceptions as hypotheses Philosophical Transactions of the Royal Society B: Biological Sciences 290:181-197

Gregory RL (2015) Eye and brain: The psychology of seeing. Princeton university press, Haber RN, Hershenson M (1973) The psychology of visual perception. Holt, Rinehart & Winston,

Hare B, Tomasello M (1999) Domestic dogs (Canis familiaris) use human and conspecific social cues to locate hidden food Journal of Comparative Psychology 113:173

Hubel DH, Wiesel TN (1962) Receptive fields, binocular interaction and functional architecture in the cat's visual cortex The Journal of physiology 160:106

Huber L, Racca A, Scaf B, Virányi Z, Range F (2013) Discrimination of familiar human faces in dogs (Canis familiaris) Learning and motivation 44:258-269

Jacobs GH (1983) Colour vision in animals Endeavour 7:137-140

Kanizsa G, Renzi P, Conte S, Compostela C, Guerani L (1993) Amodal completion in mouse vision Perception 22:713-721

Kelley LA, Kelley JL (2014) Animal visual illusion and confusion: the importance of a perceptual perspective Behavioral Ecology 25:450-463

Kemp C, Jacobson S (1992) Rhodopsin levels in the central retinas of normal miniature poodles and those with progressive rod-cone degeneration Experimental eye research 54:947-956

King DL (1988) Assimilation is due to one perceived whole and contrast is due to two perceived wholes New Ideas in Psychology 6:277-288 doi:http://dx.doi.org/10.1016/0732-118X(88)90039-6

Koffka K (1935) Principles of Gestalt Psychology, International Library of Psychology, Philosophy and Scientific Method. Harcourt Brace, New York,

Lazareva OF, Miner M, Wasserman EA, Young ME (2008) Multiple-pair training enhances transposition in pigeons Learning & Behavior 36:174-187

Lazareva OF, Wasserman EA, Young ME (2005) Transposition in pigeons: Reassessing Spence (1937) with multiple discrimination training Animal Learning & Behavior 33:22-46

Lazareva OF, Young ME, Wasserman EA (2014) A three-component model of relational responding in the transposition paradigm Journal of Experimental Psychology: Animal Learning and Cognition 40:63

Livingstone M, Hubel D (1988) Segregation of form, color, movement, and depth: anatomy, physiology, and perception

Massaro DW, Anderson NH (1971) Judgmental model of the Ebbinghaus illusion Journal of Experimental Psychology 89:147

McGreevy P, Grassi TD, Harman AM (2003) A strong correlation exists between the distribution of retinal ganglion cells and nose length in the dog Brain, Behavior and Evolution 63:13-22

Miller PE, Murphy CJ (1995) Vision in dogs Journal-American Veterinary Medical Association 207:1623-1634

Mongillo P, Pitteri E, Sambugaro P, Carnier P, Marinelli L (2016) Global bias reliability in dogs (Canis familiaris) Animal Cognition:1-9 doi:10.1007/s10071-016-1044-8

Murayama T, Usui A, Takeda E, Kato K, Maejima K (2012) Relative size discrimination and perception of the Ebbinghaus illusion in a bottlenose dolphin (Tursiops truncatus) Aquatic Mammals 38:333

Nagasawa M, Murai K, Mogi K, Kikusui T (2011) Dogs can discriminate human smiling faces from blank expressions Animal cognition 14:525-533

Nakamura N, Watanabe S, Fujita K (2008) Pigeons perceive the Ebbinghaus-Titchener circles as an assimilation illusion Journal of Experimental Psychology: Animal Behavior Processes 34:375

Nakamura N, Watanabe S, Fujita K (2014) A reversed Ebbinghaus–Titchener illusion in bantams (Gallus gallus domesticus) Animal cognition 17:471-481

Navon D (1977) Forest before trees: The precedence of global features in visual perception Cognitive psychology 9:353-383

Neitz J, Geist T, Jacobs GH (1989) Color vision in the dog Visual neuroscience 3:119-125

Ninio J (1998) La science des illusions. Odile Jacob,

Parrish AE, Beran MJ (2014) When less is more: like humans, chimpanzees (Pan troglodytes) misperceive food amounts based on plate size Animal cognition 17:427-434

Parrish AE, Brosnan SF, Beran MJ (2015) Do you see what I see? A comparative investigation of the Delboeuf illusion in humans (Homo sapiens), rhesus monkeys (Macaca mulatta), and capuchin monkeys (Cebus apella) Journal of Experimental Psychology: Animal Learning and Cognition 41:395

Parron C, Fagot J (2007) Comparison of grouping abilities in humans (Homo sapiens) and baboons (Papio papio) with the Ebbinghaus illusion Journal of Comparative Psychology 121:405

Peichlcu L (1992) Topography of ganglion cells in the dog and wolf retina Journal of Comparative Neurology 324:603-620

Pitteri E, Mongillo P, Carnier P, Marinelli L (2014) Hierarchical stimulus processing by dogs (Canis familiaris) Animal cognition 17:869-877

Pressey AW, Di Lollo V, Tait RW (1977) Effects of gap size between shaft and fins and of angle of fins on the Müller-Lyer illusion Perception 6:435-439

Pylyshyn Z (1999) Is vision continuous with cognition?: The case for cognitive impenetrability of visual perception Behavioral and brain sciences 22:341-365

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) Animal cognition 13:525-533

Range F, Aust U, Steurer M, Huber L (2008) Visual categorization of natural stimuli by domestic dogs Animal Cognition 11:339-347

Roberts T, McGreevy P, Valenzuela M (2010) Human induced rotation and reorganization of the brain of domestic dogs PLoS One 5:e11946

Rosengren A (1969) Experiments in colour discrimination in dogs. Societas pro fauna et flora Fennica,

Salva OR, Rugani R, Cavazzana A, Regolin L, Vallortigara G (2013) Perception of the Ebbinghaus illusion in four-day-old domestic chicks (Gallus gallus) Animal cognition 16:895-906

Sherman JA, Chouinard PA (2016) Attractive Contours of the Ebbinghaus Illusion Perceptual & Motor Skills 122:88-95

Sherman SM, Wilson JR (1975) Behavioral and morphological evidence for binocular competition in the postnatal development of the dog's visual system Journal of Comparative Neurology 161:183-195

Soproni K, Miklósi A, Topál J, Csányi V (2002) Dogs'(Canis familaris) responsiveness to human pointing gestures Journal of Comparative Psychology 116:27

Soproni K, Miklósi Á, Topál J, Csányi V (2001) Comprehension of human communicative signs in pet dogs (Canis familiaris) Journal of Comparative Psychology 115:122

Sovrano VA, Albertazzi L, Salva OR (2014) The Ebbinghaus illusion in a fish (Xenotoca eiseni) Animal cognition 18:533-542

Tanaka T, Watanabe T, Eguchi Y, Yoshimoto T (2000) Color Discrimination in Dogs Nihon Chikusan Gakkaiho 71:300-304 doi:10.2508/chikusan.71.300

Tapp PD et al. (2004) Concept abstraction in the aging dog: development of a protocol using successive discrimination and size concept tasks Behavioural Brain Research 153:199-210 doi:http://dx.doi.org/10.1016/j.bbr.2003.12.003

Udell MA, Dorey NR, Wynne CD (2008) Wolves outperform dogs in following human social cues Animal behaviour 76:1767-1773

Udell MA, Wynne CD (2008) A review of domestic dogs' (canis familiaris) human-like behavior: or why behavior analysts should stop worrying and love their dogs Journal of the experimental analysis of behavior 89:247-261

Von Helmholtz H (1867) Handbuch der physiologischen Optik vol 9. Voss,

Walls GL (1942) The vertebrate eye and its adaptive radiation

Weintraub DJ (1979) Ebbinghaus illusion: context, contour, and age influence the judged size of a circle amidst circles Journal of Experimental Psychology: Human Perception and Performance 5:353

Zigler E (1960) Size estimates of circles as a function of size of adjacent circles Perceptual and Motor Skills 11:47-53

Zigler E, Phillips L (1960) Social effectiveness and symptomatic behaviors The Journal of Abnormal and Social Psychology 61:231

Table 1 Participant demographics at the time of testing

Name	Sex	Age
Audrey[1,2,3]	Female	9 months
Baxter[1,2,3]	Male	12 months
Beth[1,3]	Female	3 year, 2 months
Eliza[2,3]	Female	1 year, 8 months
Gabbie[1,2,3]	Female	1 year, 3 months
Hamish[1,2,3]	Male	6 years, 6 months
Lulu[1,3]	Female	1 year, 8 months
Molly[1,2,3]	Female	2 years, 6 months

Note. Eliza, Hamish and Lulu have the same sire, and Eliza and Lulu the same dam. Hamish is the sire of Audrey, Beth, Gabbie and Molly, whose dams are also closely related to one another

[1]Participated in Classical Ebbinghaus-Titchener condition

[2]Participated in Illusory Contour Ebbinghaus-Titchener condition

[3]Participated in Delboeuf condition

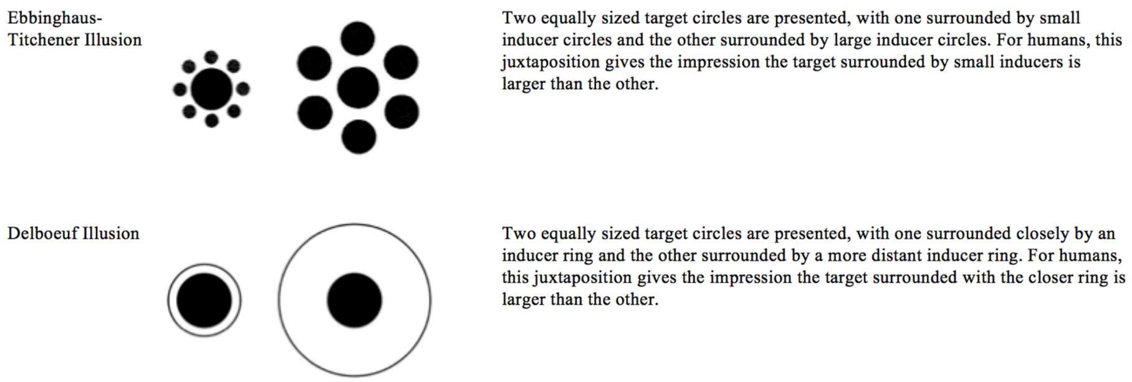


Figure 1 Schematic representation of the Ebbinghaus-Titchener and Delboeuf illusions The figure provides classic representations of the both the Ebbinghaus-Titchener and Delboeuf illusions, with descriptions explaining the expected illusory phenomena typically observed in humans.

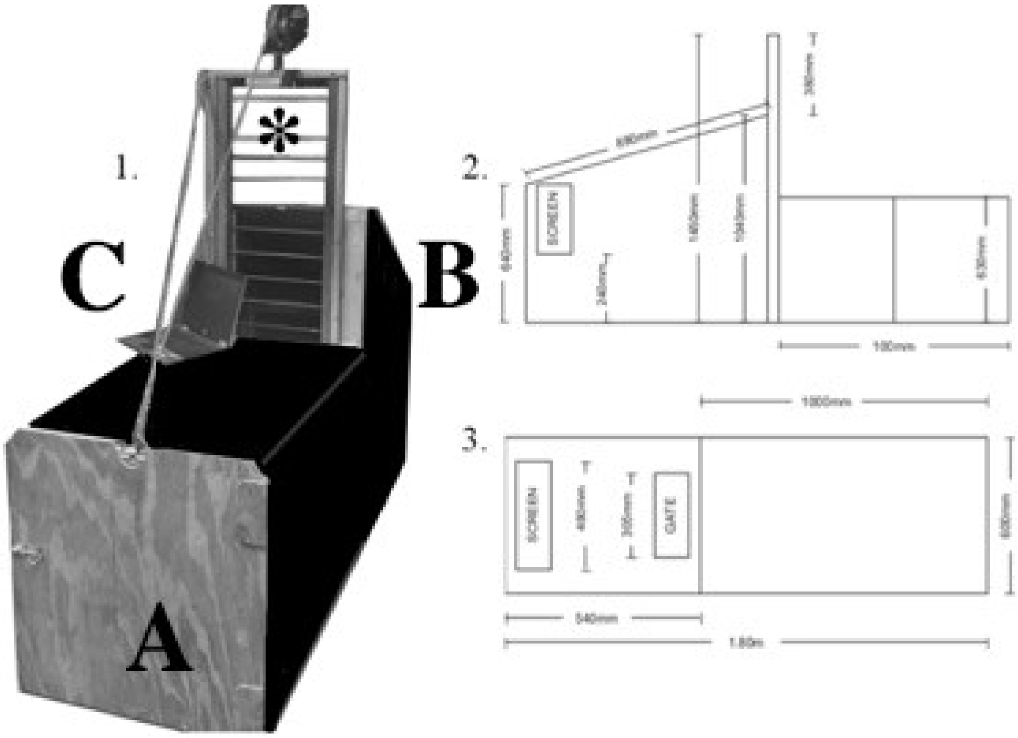


Figure 2 Schematic representation of the testing apparatus implemented in the experimental paradigm (1) with the side (2) and aerial (3) diagram The figure provides a photographic representation of the Canine Nose-Touch Testing Apparatus used during training and testing phases, as well as the position of Experimenters A, B, and C during the testing process. The asterisk represents the location of the camera. The schematics on the right include information to the size and placement of integral components within the apparatus.

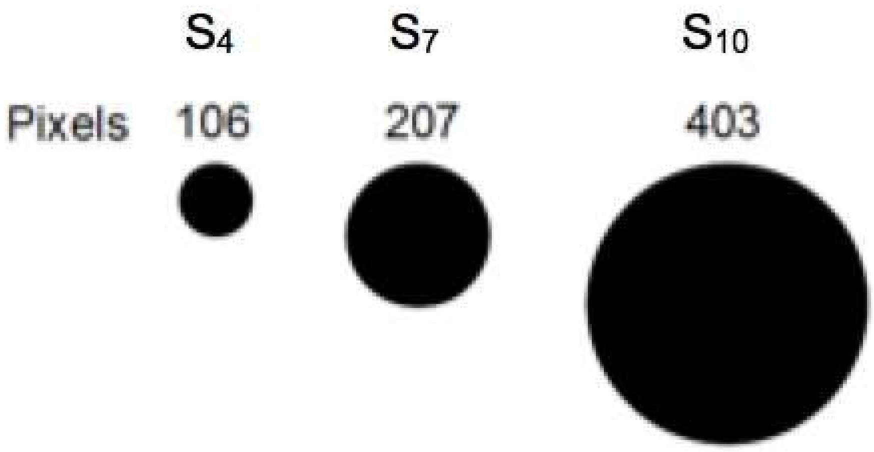


Figure 3 Schematic representation of circle stimuli implemented in the study with pixel values representing the diameter. Circles are provided to aid conceptual understanding only and are not actual size but are relative to scale The figure provides a photographic representation of the stimuli used during both size discrimination training and testing phases.

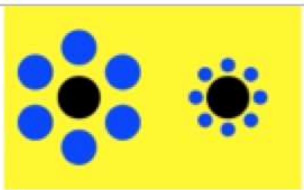
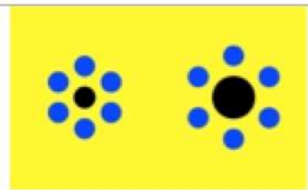
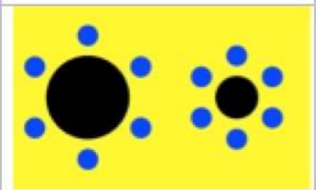
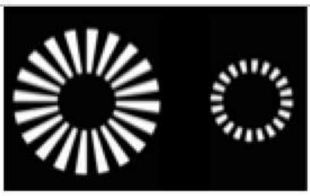
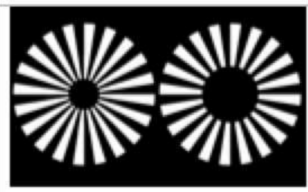
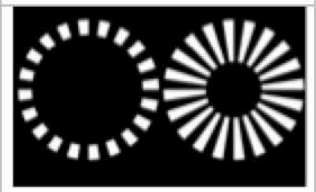
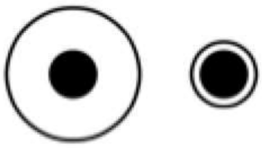
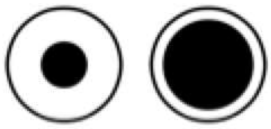
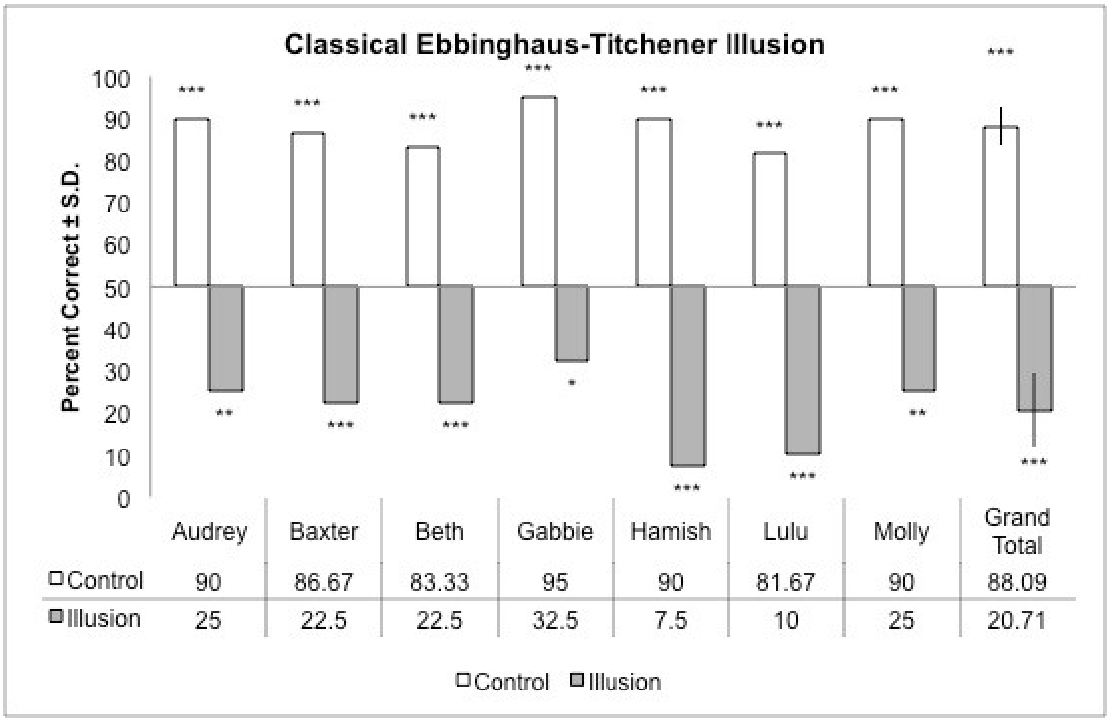
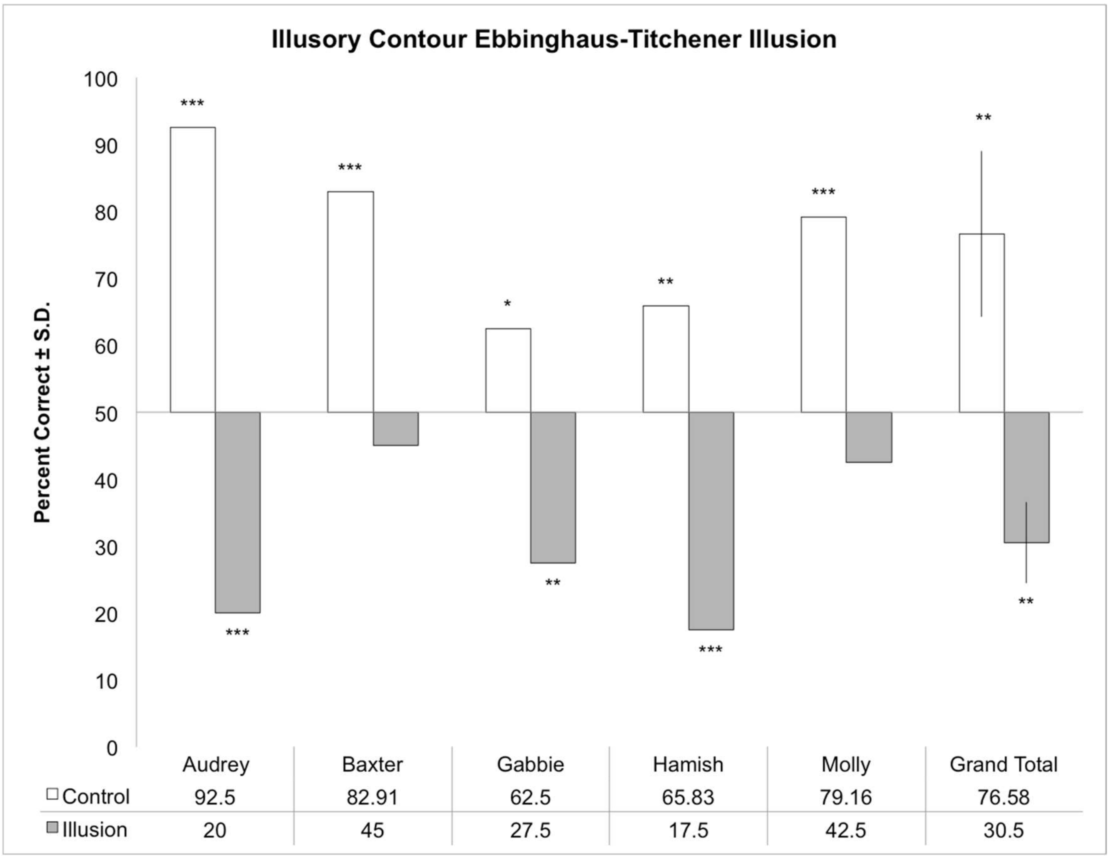
	Illusion condition	Control condition (S_4-S_7)	Control condition (S_7-S_{10})
Classical Ebbinghaus-Titchener			
Illusory Contour Ebbinghaus-Titchener			
Delboeuf			

Figure 4 Schematic depictions of the Illusion and control stimuli utilized in investigating the perception of the Classical Ebbinghaus-Titchener, Illusory Contour Ebbinghaus-Titchener, and Delboeuf Illusions The figures provided present examples control and illusory stimuli displayed in the three illusion presentations.

A


Classical Ebbinghaus-Titchener Illusion
Percent Correct ± S.D.
100
90
80
70
60
50
40
30
20
10
0
Audrey
Baxter
Beth
Gabbie
Hamish
Lulu
Molly
Grand Total
Control 90 86.67 83.33 95 90 81.67 90 88.09
Illusion 25 22.5 22.5 32.5 7.5 10 25 20.71
Control Illusion

B


Illusory Contour Ebbinghaus-Titchener Illusion
Percent Correct ± S.D.
100
90
80
70
60
50
40
30
20
10
0
Audrey
Baxter
Gabbie
Hamish
Molly
Grand Total
Control 92.5 82.91 62.5 65.83 79.16 76.58
Illusion 20 45 27.5 17.5 42.5 30.5

C

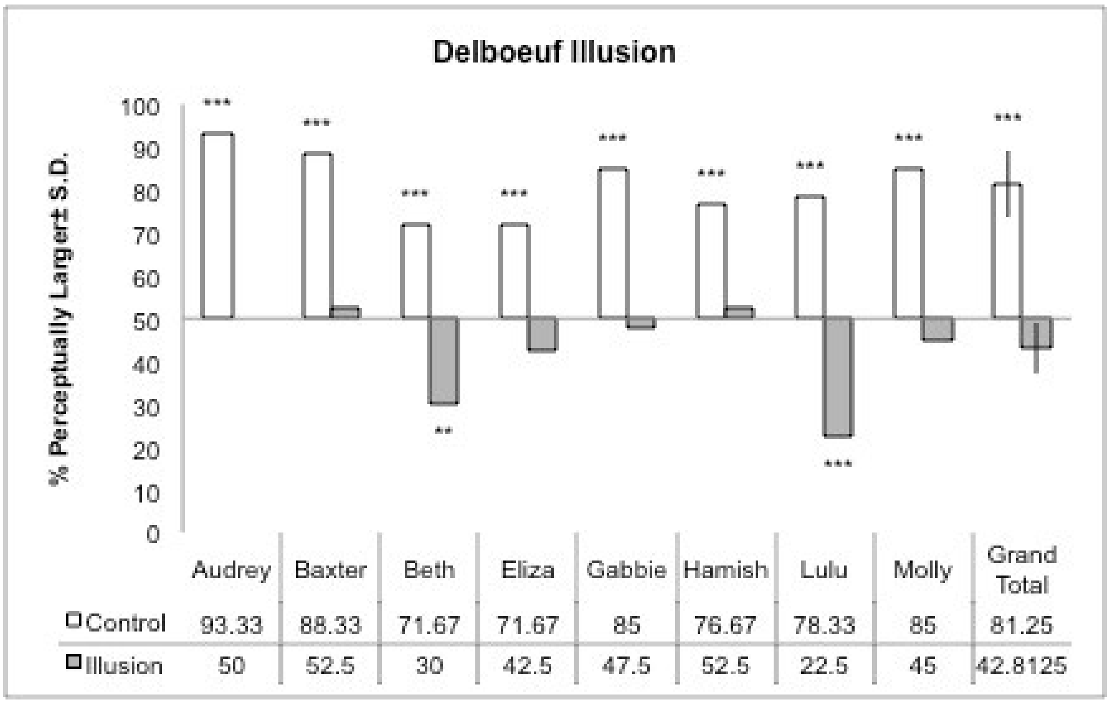


Figure 5 Individual response accuracy for Control and Illusion conditions. The result significantly differed from chance level at: * p< .05. **p < .01. ***p <.001 The three graphs represent the percent of correct choices (for control conditions) or percent perceptually larger stimulus chosen (for the illusion conditions) at both an individual and group level. Note that as Baxter was the only subject trained to select the smaller target stimulus, his results have been reversed.