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Do Dogs Demonstrate Susceptibility to a Vertically Presented Ponzo Illusion?

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Abstract – One way to uncover visual capabilities in animals is to assess perception of geometric illusions. Recently, we found that dogs did not demonstrate susceptibility to the Ponzo illusion when it was presented in a variety of contexts, a unique result as all other published reports of nonhuman animal species tested on the illusion have demonstrated human-like susceptibility. Two important variables were not considered in our previous study. First, the stimuli were presented horizontally, whereas the more traditional presentation is vertical. Second, it is not known whether dogs can differentiate physical size differences small enough to facilitate perception of the Ponzo illusion. To investigate these issues, we tested the same dogs from our previous study on a vertical version of the Ponzo illusion and on a size discrimination task. Dogs did not demonstrate illusion susceptibility at the group level, although one dog was susceptible. In general, they were better able to detect size differences when the absolute size of the stimuli was large. Nonetheless, with stimuli approximately the same size as those used to test susceptibility to the Ponzo illusion, all eight dogs were able to discriminate between circles that differed in length by 20%, with four discriminating 10% size differences and none able to discriminate 5% differences. These findings suggest that at least some dogs are capable of perceiving the average size difference that humans perceive when observing the Ponzo illusion, but that susceptibility to this illusion is variable and weak, regardless of whether it is presented in either a vertical or horizontal format.

Keywords – Dog, Ponzo illusion, Two-choice discrimination, Visual perception, Size, Sensitivity

Visual perception depends on interpretation of retinal information by the brain, and is important as it allows humans and non-human animals (hereafter animals) to perceive the external world and act upon it (Haber & Hershenson, 1973). However, visual perception does not always accurately reflect reality. The brain often adjusts visual information processed in the retina to fit adaptive preconceptions (Gregory, 2015). In these instances, illusions are said to occur, as there is a misrepresentation of physical reality and what the individual perceives. Therefore, one way to begin to uncover how animals see the world is to assess their misperception of geometric illusions, in which mechanisms that are normally helpful for accurately perceiving the environment trick the brain into applying 'corrections' to visual information in contexts where a correction is unnecessary.

While this sounds straightforward, in practice there is often variation in illusion susceptibility across species (for a review see Feng, Chouinard, Howell, & Bennett, 2017), including birds, fish, and primates. Some species demonstrate human-like susceptibility, some demonstrate no susceptibility, and some demonstrate reversed susceptibility (e.g., Agrillo, Parrish, & Beran, 2014; Fujita, 1996, 1997; Murayama, Usui, Takeda, Kato, & Maejima, 2012; Nakamura, Watanabe, & Fujita, 2008; Sovrano, Albertazzi, & Salva, 2014; Watanabe, Nakamura, & Fujita, 2011, 2013). Moreover, even within a species, mixed findings have been observed in susceptibility to the same illusion (e.g., Nakamura et al., 2008, 2014; Salva, Rugani, Cavazzana, Regolin, & Vallortigara, 2013). One species in which such findings have recently been observed is the domestic dog.

When presented with the Ebbinghaus-Titchener illusion, dogs demonstrate susceptibility to the illusion, but with marked individual differences and in the opposite direction observed in humans (Byosiere, Feng, Woodhead, et al., 2017) (Figure 1, images 1 and 2). In contrast, two studies have found that dogs do not demonstrate susceptibility to the Delboeuf illusion (Byosiere, Feng, Woodhead, et al., 2017; Miletto Petrazzini et al., 2017), although, in one of these studies, individual differences were again apparent (Byosiere, Feng, Woodhead, et al., 2017) (Figure 1, image 3). More recently, we assessed whether dogs demonstrate susceptibility to the Ponzo illusion (Byosiere, Feng, Rutter et al., 2017) (Figure 1, images 4 — 6). This illusion typically consists of two equally sized targets (e.g., circles or lines) that appear unequal when superimposed over converging lines that can be presented in a variety of contexts. Across these tests assessing susceptibility to the Ponzo illusion, our evidence converged on the conclusion that, as a group, dogs are not susceptible to the illusion. These findings are of particular interest as, to date, some individual pigeons (Fujita, Blough, & Blough, 1991), Sprague-Dawley rats (Nakagawa, 2002), horses (Timney & Keil, 1996), rhesus macaques (Bayne & Davis, 1983; Fujita, 1997), baboons (Barbet & Fagot, 2002), and chimpanzees (Fujita, 1997; Imura, Tomonaga, & Yagi, 2008), have all demonstrated human-like susceptibility to the Ponzo illusion.

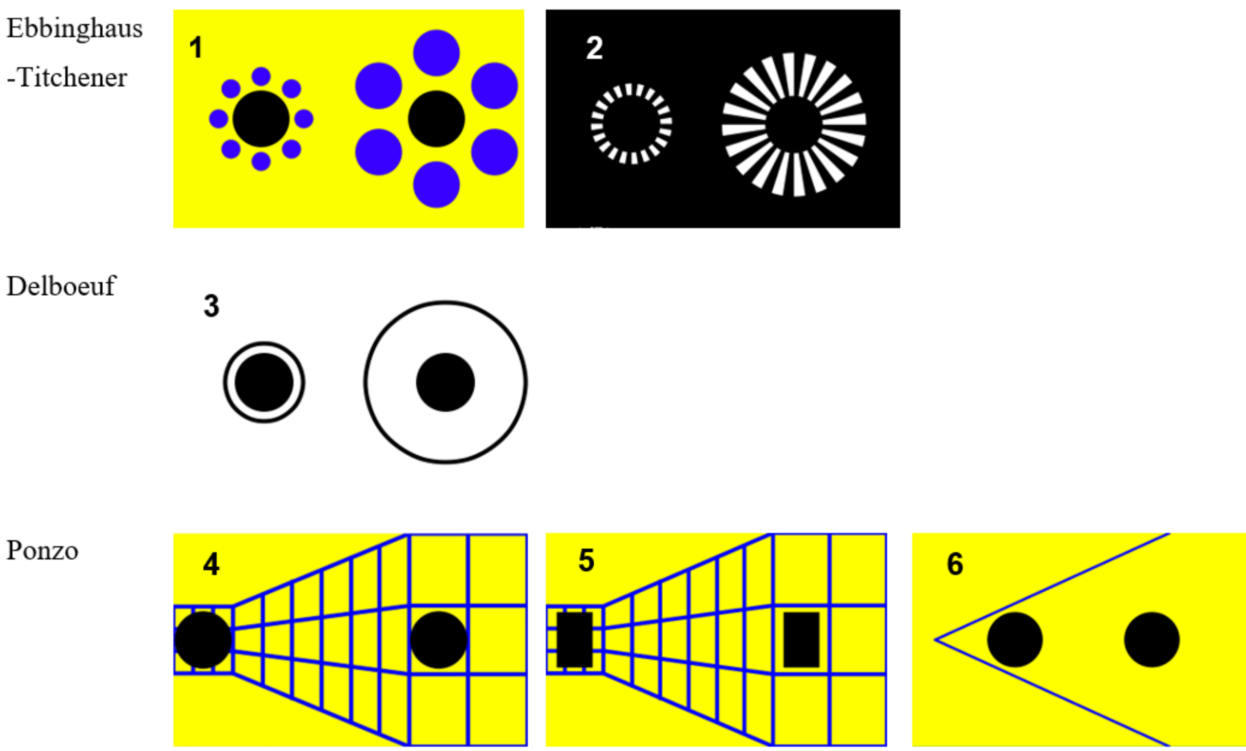


Figure 1. On-screen presented stimuli of the Ebbinghaus-Titchener (images 1 and 2), Delboeuf (image 3), and Ponzo (images 4-6) illusion that have been tested in dogs. In images 1-3, humans perceive the circle target stimulus located on the left in each presentation as larger. Ponzo images 4 and 5 are presentations using a 'grid inducer' context whereas image 6 is a presentation using a context 'converging lines' context. In the "grid inducer" context, the rectangle target stimulus located within the smallest grouping of rectangles is perceived by humans to be larger. In the 'converging lines' context, humans perceive the circle target stimulus located at the apex of the converging lines as larger.

It should be noted that two variables could potentially help explain the null findings observed in our previous study. Firstly, the illusory stimuli were presented horizontally. Gregory's (1963) Inappropriate Constancy-Scaling theory proposes that the Ponzo illusion is driven by a misapplication of size constancy arising from the brain's interpretation of the converging lines as depth cues (for review of multiple theories see Humphrey & Morgan, 1965; Newman & Newman, 1974; Sperandio & Chouinard, 2015). Thus, the stimulus nearest to the apex of the converging lines appears larger as it is perceived as being further away, which causes the viewer to inappropriately compensate for this distance in order to maintain size constancy. In humans, vertically presented stimuli, where the apex is at the top, produce greater perceived depth and size than stimuli presented in any other orientation (Miller, 1997). Therefore, one potential explanation for our previous findings is that the horizontally presented stimuli may not have induced the Ponzo illusion in dogs due to the fact that the illusory effect may have been weaker – although it should be noted that it did not appear weak to the human researchers.

Secondly, in order to be susceptible to illusions, one must be able to perceive, albeit incorrectly, a minimum size difference between two target stimuli (for a discussion of methodological issues in regards to discrimination abilities in primates see Agrillo et al., 2014; Santacà, Regaiolli, Miletto Petrazzini, Spiezio, & Agrillo, 2017). In humans, the average size difference for the Ponzo illusion has been demonstrated to be about 18% (Chouinard, Unwin, Landry, & Sperandio, 2016). Although it is generally assumed that dog visual acuity is worse than human acuity (Byosiere, Chouinard et al., 2017) recent research suggests that visual acuity thresholds in dogs may be higher than previously assumed; however, it is important to note that individual variation is high (Lind, Milton, Andersson, Jensen, & Roth, 2017). Taken together, it is possible that dogs may not perceive the illusion because they are not visually sensitive to small size differences, and this may account for our previous results.

Given the contradictory findings observed in previous studies of illusion susceptibility in dogs, canine illusion susceptibility warrants further investigation. Increasing our understanding of visual processing in the domestic dog, particularly if it deviates from what is typically observed in humans and other animal species, may have broad implications for research methodologies, working dog roles, and/or dog training methods, thereby indirectly improving the dog-human relationship. In this study, our aim was to extend our previous observations of when dogs were presented with the Ponzo illusion, in an attempt to clarify additional variables that were previously not considered. Eight dogs, previously trained on a simultaneous size discrimination task, participated in this two-part study. In Study 1, our aim was to examine if dogs demonstrated susceptibility to the Ponzo illusion when presented within a classical context that invokes vertical linear perspective cues. In Study 2, our aim was to measure size sensitivity thresholds by determining the dogs' ability to detect different size discrepancies.

General Methods

All procedures performed in the following experiments were in accordance with the ethical standards of La Trobe University Animal Ethics Committee (approval number: AEC16-66).

Participants. Eight purebred Lagotto Romagnolos (*Canis familiaris*), six females and two males, aged 12 months to 7 years (average age 2 years and 6 months) at the start of the experiments participated in this study. All dogs had previously participated in two other experiments assessing illusion susceptibility (for additional descriptive information on the participants see Byosiere et al., 2016). To assess visual competency, an ophthalmological examination by a registered veterinarian was performed on each dog. This included slit lamp biomicroscopy, an indirect ophthalmoscopy exam, rebound tonometry (TonoVet, iCare, Finland), and tear production (Schirmer Tear Test; Merck Animal Health, NJ, USA) tests. Results identified early age-related changes in the lens for the oldest dog in the study (Hamish, aged 7.8 years). No other abnormalities or clinical signs of ocular disease were evident.

Testing Apparatus and Training. Testing was conducted in the Canine Nose-Touch Testing Apparatus (Byosiere, Feng, Chouinard, Howell, & Bennett, 2017; Byosiere, Feng, Rutter et al., 2017; Byosiere, Feng, Woodhead, et al., 2017) (Figure 2), which was purposely built to eliminate effects such as potential cuing by the experimenters. The apparatus was equipped with a 508 mm Dell® widescreen computer monitor (1280 x 800 pixels; one pixel measures approximately 0.3 mm^2) positioned with the lower edge approximately 24 cm above ground level. Below it, at ground level, was a remotely controlled treat dispenser (Treat & Train®). When activated, it distributed one piece of semi-moist dry dog food (Nature's Gift® Mini Kangaroo, or Good-o® treats). A video camera was mounted above the monitor to record each trial. Data were collected through a customized program developed specifically for this study using Processing 2.2.1.

Dogs were initially trained to target a single black circle stimulus. This training was then transferred to circles presented in pairs in a two-choice discrimination task. Most did this by targeting the larger circle, except Baxter who did so by selecting the smaller circle (for an explanation see Byosiere, Feng, Woodhead, et al., 2017).

Design and Procedure. Two experimenters (Exp A, Exp B) were present at all times during testing. Exp A sat to the left of the Canine Nose-Touch Testing Apparatus and controlled a laptop computer (Figure 2). This person presented and removed the stimuli, while recording the data. Exp B was positioned at the front-right side of the apparatus, also out of sight from the dog. The trial began when the stimuli were presented on the screen and the dog was positioned at the entrance of the apparatus. Once in the apparatus and unable to see either experimenter, the dog moved to the screen and selected one stimulus by nose-touching the image. If the dog chose correctly, Exp B, watching the dog through the top of the apparatus, activated the remote-controlled treat dispenser located below the computer monitor and signaled to Exp A to record a correct choice. If the dog chose incorrectly, Exp B relayed a signal to Exp A to remove the stimuli and thereby end the trial. Exp A then called the dog to return to the entrance of the apparatus to resume the starting position for the next trial. Between trials, the dog received occasional food rewards from Exp A, which happened 2-3 times during each ten-trial session.

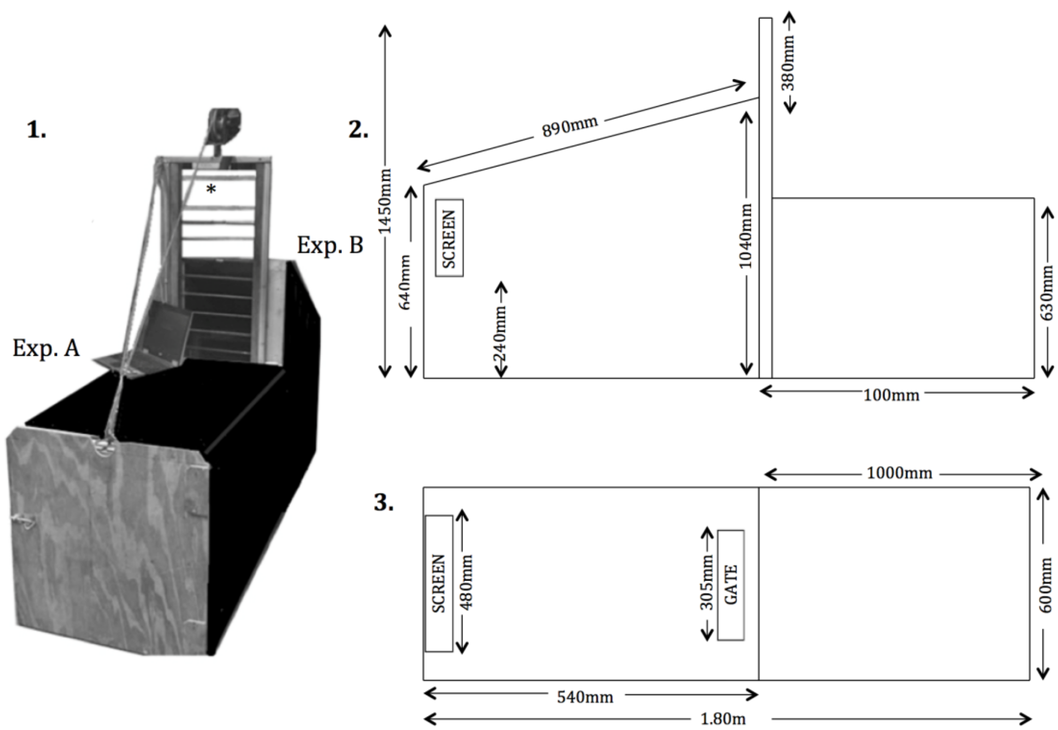


Figure 2. Schematic representation of the testing apparatus implemented in the experimental paradigm (1) with the side (2) and aerial (3) diagram. The figure provides a photographic representation of the Canine Nose-Touch Testing Apparatus used during training and testing phases, as well as the position of Experimenters A and B during the testing process (indicated as Exp. A and Exp. B in the figure). The asterisk represents the location of the camera.

Experiment 1

The purpose of Experiment 1 was to assess whether or not the dogs demonstrated susceptibility to the Ponzo illusion when it was presented vertically, presumably invoking linear perspective cues. Our previous study (Byosiere, Feng, Rutter et al., 2017) provided no evidence of an illusory effect when the illusion was presented horizontally.

Stimuli. Stimuli were pairs of black circles (RGB values 0, 0, 0; Luminance 0.18 c/m2), presented on a yellow background (RGB values 255, 255, 0; Luminance 163.6 c/m2) with blue converging lines (RGB values 0, 0, 255; Luminance 16.05 c/m2) (Figure 3). These colors were chosen based on dogs' dichromatism, as they demonstrate wavelength sensitivities of blue at a spectral peak of 555 nm and yellow at 429 nm (Jacobs et al., 1993; Neitz, Geist, & Jacobs, 1989). Three circle stimuli were used, which were constructed from an array of 12 circles used previously to test transpositions in pigeons (Lazareva, Miner, Wasserman, & Young, 2008; Lazareva, Wasserman, & Young, 2005; Lazareva, Young, & Wasserman, 2014) and illusion susceptibility in this same group of dogs (Byosiere, Feng, Rutter et al., 2017; Byosiere, Feng, Woodhead, et al., 2017). These specific stimuli were chosen as they represented a systematic array of figures. S4 circles were 106 pixels or 31.8 mm in diameter, S7 circles were 207 pixels or 62.1 mm in diameter, and S10 stimuli were 403 pixels or 120.9 mm in diameter. The circles were presented in pairs of S4 -S7 and S7 -S10, to ensure that the dogs were not continually reinforced for choosing a single stimulus. The blue converging lines were 10 pixels or 3 mm wide. This width was chosen based on unpublished research in this specific subset of dogs that suggested they could discriminate between pairs of outlined circle stimuli similarly to filled-in circle stimuli.

Design and Procedure. All dogs had previously been trained on a horizontally presented two-choice size discrimination task, with the correct stimulus located randomly on either the left or right side. As the task in the current study utilized vertically presented stimuli (where the computer monitor was rotated 90 degrees to a portrait orientation) we began by presenting the dogs with the same discrimination task presented vertically. In this task, each block consisted of ten trials, comprising five pairs of S4-S7 and S7-S10 black circles, presented on a white background (RGB values 255, 255, 255; Luminance 175.5 c/m2). The correct stimulus pseudo-randomly appeared in the top or bottom section of the monitor, based on a Gellerman (1933) sequence. All dogs participated in a minimum of two blocks. Dogs progressed only after reaching a criterion of > 90% correct in a single ten-trial block, or > 70% correct across each of two consecutive blocks (Byosiere, Feng, Chouinard et al., 2017; Byosiere, Feng, Rutter et al., 2017; Byosiere, Feng, Woodhead, et al., 2017). The dogs generally performed extremely well in transferring their left/right choices to up/down choices, taking an average of 4.25 blocks of ten trials to progress to the next stage of the study.

Once the dogs were successfully able to perform the size discrimination task presented vertically, familiarization sessions took place. These sessions presented the target stimuli over non-illusory backgrounds to acquaint the dogs with new images, such as inducers and/or colours that would be present in the test sessions (Figure 3). In these sessions, target stimulus pairs were presented in blocks of ten trials, with five presentations each of S4-S7 and S7-S10 stimuli randomly presented up or down for an equal number of times in accordance with randomly selected Gellerman (1933) sequences. Four types of familiarization sessions were conducted. Dogs progressed to the next type of familiarization session only after reaching a criterion of > 90% correct in a single ten-trial block, or > 70% correct across each of two consecutive blocks. In order to continue onto test sessions, the dogs were required to successfully complete all familiarization sessions. In any case where a dog did not meet the criteria after seven attempts of a ten-trial block the dog was excluded from participating in the testing condition.

In the test sessions, stimulus pairs were presented in three sets: S4-S7 and S7-S10 represented control conditions, and S7-S7 represented experimental trials. Each block of ten trials consisted of six control trials, comprising three comparisons each of S4-S7 and S7-S10, and four experimental trials of S7-S7 comparisons. Ten blocks were conducted, resulting in 100 trials per dog (60 control trials, 40 experimental trials).

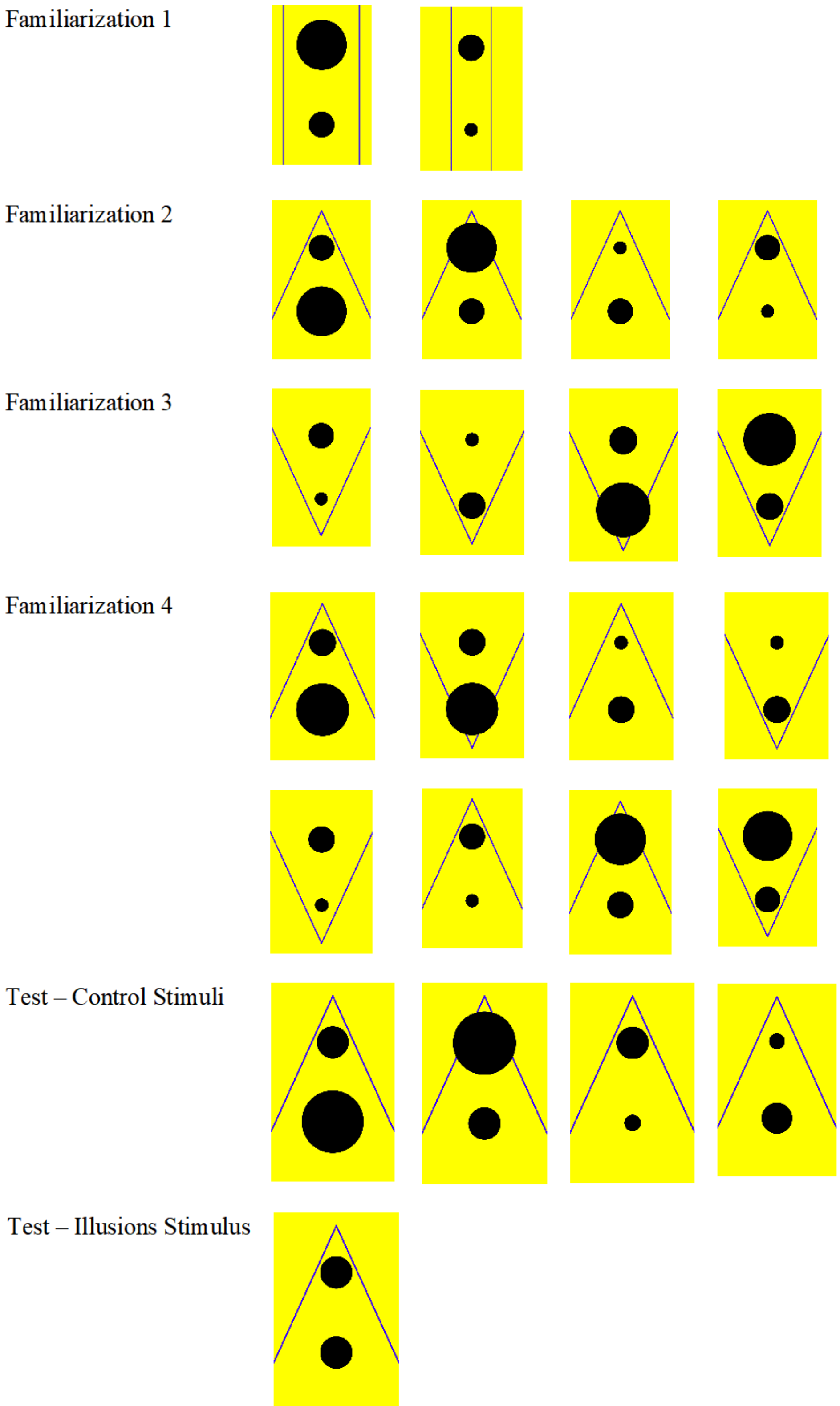


Figure 3. Stimuli used in the Familiarization and Test trials for the Ponzo illusion.

For the purpose of analysis, a response in the illusion condition was considered correct when the target stimulus 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 (1933) sequence. If the Gellerman sequence dictated that the target stimulus on the top of the screen for a particular experimental trial should be correct, it was deemed to be correct. In order to maintain a rewarding scheme while evaluating susceptibility in this specific paradigm, subjects were rewarded randomly based during illusion presentations dictated by a randomly selected Gellerman sequence. This was the case even though the target stimuli were identical in size, and even though a particular target stimulus may or may not have been ‘correct’ in so far as humans perceived it as perceptually larger. As Baxter was the only subject trained to select the smaller target stimulus, his results indicate which stimulus he perceived as smaller.

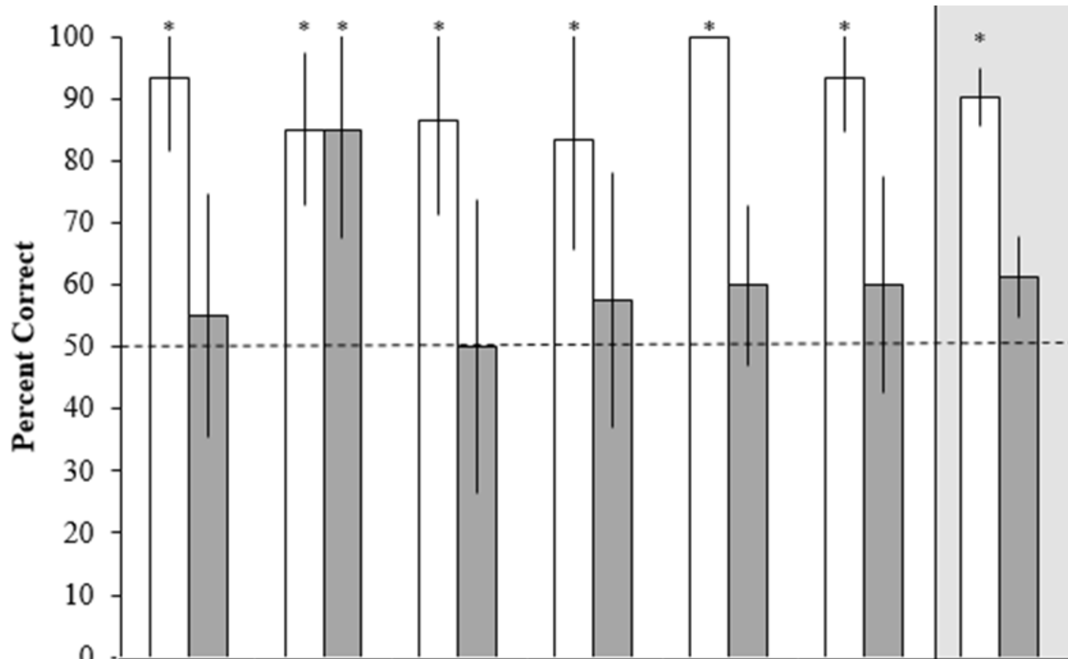
Data Analysis. The data were analyzed using the Statistical Package for Social Sciences (SPSS) version 24 (IBM Corporation; Armonk, NY, USA), JASP software version 0.8 (University of Amsterdam, Amsterdam, Netherlands). To determine if individual dogs were performing significantly above chance, two-tailed binomial tests were conducted on their responses in the control conditions and the illusion condition. Alpha was set at 0.05 and chance levels of performance were considered to be 0.5. To examine group performances, the illusion was analyzed using a two-tailed one-sample t-test, conducted on the dogs’ average percent correct, or in the case of equal stimuli, on the basis of the proportion of trials in which the stimulus was selected that would match the human-based illusion. In addition to null hypothesis statistical testing, Bayes factors were calculated for the control and illusion conditions in order to quantify evidence in support for either the null or alternative hypothesis relative to the other (Wetzels et al., 2011). Bayes factors (BF10) reported below denote the likelihood of the alternative over the null hypothesis. Therefore, a BF_{10} value greater than 3 was considered to provide substantial support for the alternative hypothesis.

Results. The dogs generally performed extremely well in the familiarization sessions. On average, it took 1.73 blocks of ten trials for the group as a whole to progress to the next level, with familiarizations sessions 1 and 3 appearing to be the most difficult, averaging 1.875 and 2 blocks respectively. Six of the eight dogs participated in the experiment. Audrey was unable to continue onto testing after reaching the maximum 7 attempts during the familiarization sessions and Hamish was excluded as he developed a bias for the “up” stimulus.

Figure 4 shows individual performance data for each dog in the test sessions. Performance in the control conditions was uniformly high, as the average level of performance was 90.3% ± 4.77 ($t(5) = 15.48$, $p < .001$, BF10 = 841.52). In contrast, dogs averaged 61.25% ± 6.52 in the illusion condition. The results of the two-tailed one-sample t-test and the Bayesian approach conducted on the group percent correct for the illusion condition was not significant ($t(5) = 2.25$, $p = .074$, BF10 = 1.58). While most dogs, individually, showed a slight susceptibility to the illusion in that their score was above, rather than below, the chance level performance of 50% correct, only one individual, Beth, demonstrated human-like susceptibility to the illusion ($p < .001$).

Experiment 2

Experiment 2 consisted of two phases to establish size sensitivity thresholds in the dogs. Phase 1 analyzed performance across various percent size differences in a two choice size discrimination task where the stimuli varied relative to the circles used in the illusion tests. The second phase evaluated changes in performance when the dogs were presented with size differences taken from Phase 1, but using stimuli of smaller and larger absolute sizes.



	Baxter	Beth	Eliza	Gabbie	Lulu	Molly	Grand Total
Control	93.3	85	86.6	83.3	100	93.3	90.27
Illusion	55	85	50	57.5	60	60	61.25

Figure 4. Individual and group percent correct (and standard deviations) for control and illusion conditions. Correct trials in the illusion condition were defined as those in which the dog selected the larger stimulus. The perceptually larger target stimulus appears on the top in the illusion condition. Control conditions also included the inverse presentation of stimuli depicted here. *Indicates that the binomial result significantly differed from chance level at $p < .05$.

Stimuli. Stimuli were pairs of black circles (RGB values 0, 0, 0; Luminance 0.18 c/m^2) presented on a white background (RGB values 255, 255, 255; Luminance 175.5 c/m2) on an LCD screen. In Phase 1, the circles varied in percent size difference, in diameter, ranging from 5% different to 60% different, and were presented in eight sets of varying percent size differences (Figure 5). In Experiment 2, the circles varied in percent size difference but, unlike in Experiment 1, the stimuli also differed in absolute size. Here, the purpose was to determine if and how size discrimination performance was influenced by the absolute size of the stimuli. Three size differences (20%, 40%, 70%) were assessed using stimuli both smaller than and larger than the ones used in Experiment 1 (Figure 5).

Design and Procedure. *Phase 1*. Each dog was presented with 20 blocks of ten trials, in which the size of two circles varied by 10%, 30% or 50% in diameter. The first trial was used as a familiarization trial, and consisted of a presentation in which the two circles differed by 100% in diameter. The nine remaining trials consisted of test trials, three pseudo-randomized presentations of each percent size difference. A total of 60 trials for each percent size difference were administered for each dog.

The subsequent test consisted of fifteen blocks of ten trials of 20% and 40% diameter size differences. The first two trials were used as familiarization trials, and consisted of presentations in which the two circles differed in diameter by 100%. The eight remaining trials consisted of test trials, four pseudo-randomized presentations of each percent size difference. Once again, a total of 60 trials for each percent size difference stimulus were administered for each dog.

Based on the dog's individual performance, additional tests were conducted. If the dog performed successfully above chance (≥ 37/60 trials correct) when presented with circles varying in diameter size by 20%, that dog was then tested on twelve blocks of ten trials of circles varying in diameter size by 15% and 60%. If a dog performed successfully above chance (≥ 37/60 trials correct) on the 10% diameter size discrimination, twelve blocks of ten trials of 5% and 60% diameter size differences were presented. In these follow-up tests, the first trial was always a presentation of a 60% diameter size difference stimulus to facilitate dogs' motivation to participate. The remaining nine trials constituted four additional presentations of 60% diameter size differences and five presentations of 5% or 15% diameter size differences. A total of 60 trials for each percent size difference stimulus were administered for each dog.

Phase 2. Each dog was presented with 20%, 40%, and 70% diameter size differences, which were either smaller or larger in absolute size than the stimuli presented in Phase 1. The first two trials were used as control trials, and consisted of a 70% size difference stimuli, based on the findings in Phase 1, which suggested that all dogs were successful at circles that varied in size by 60%. The eight remaining trials consisted of test trials, four pseudo-randomized presentations of each percent and absolute size difference (20%, 40%). Each dog participated in ten blocks of ten trials of both 20% and 40% stimuli at both the larger and smaller size, for a total of 40 trials for each percent size difference of each absolute size.

Data analysis. To determine if dogs were performing significantly above chance, one-tailed binomial tests were conducted at the group level to examine their discrimination of various size sensitivities. A one-tailed binomial test, rather than a two-tailed binomial test was conducted due to the nature of the research question, as there was no reason to conduct an analysis that looked at performance significantly less than chance. Alpha was set at 0.05 and chance levels were considered to be 0.5. Three binary logistic regressions were then performed to assess the effect of the size difference of stimuli presented in Phases 1 and 2 (both the larger and smaller absolute sizes) on performance. The model contained two independent variables 1) dog and 2) the percent size difference (i.e. 5%-70%) nested within dog.

Results. *Phase 1*. All dogs performed above chance when discriminating between circles that differed in diameter by 20% (42 pixels, approximately 12.6 mm; group average: 78%, $p < .001$) or larger (Figure 5). Four of the eight dogs were able to discriminate between circles that were 10% different in diameter (21 pixels, approximately 6.3 mm; group average: 62%, $p < .001$), but none of the dogs was able to discriminate circles that were 5% different in diameter (10 pixels, approximately 3 mm; group average; 54.2%, $p = .10$).

The model for the logistic regression was statistically significant when controlling for percent size difference nested within dog, Wald χ^2 (8, N = 60) = 359.26, $p < .001$, indicating a significant relationship between performance and the percent size difference of the stimuli. There was no significant effect when controlling simply for dog Wald χ^2 (7, N = 60) = 4.36, $p = .74$.

Phase 2. When presented with the smaller absolute size stimuli, all dogs except Hamish performed above chance when discriminating between circles that differed in diameter by 70% (74 pixels, approximately 22.2 mm; accuracy range: 65% — 100%), as shown in Figure 5. Similarly, all dogs but Hamish performed above chance when discriminating between circles that differed in diameter by 40% (42 pixels, approximately 12.6 mm; accuracy range: 65% — 87.5%). Four of the eight dogs were able to discriminate between circles that were 20% different in diameter (22 pixels, approximately 6.6 mm; accuracy range: 65% — 85%). As a group, dogs could discriminate all three size differences; 72.5% ($p <$ .001) at 20%, 79.1% ($p < .001$) at 40% and 91.3% ($p < .001$) at 70%. The model for the logistic regression was statistically significant when controlling for percent size difference nested within dog, Wald χ^2 (8, N = 24) = 44.54, $p < .001$, indicating a significant relationship between performance and the percent size difference of the stimuli. There was no significant effect when controlling simply for dog Wald χ^2 (7, N = 24) = 9.20, $p = .24$.

When presented with the larger absolute size stimuli, all dogs performed above chance when discriminating between circles that differed in diameter by 70% (282 pixels, approximately 84.6 mm; accuracy range: 75% — 100%) or 40% (162 pixels, approximately 18.6 mm; accuracy range: 65% — 87.5%). Six of the eight dogs were also able to discriminate between circles that were 20% different in diameter (82 pixels, approximately 24.6 mm; accuracy range: 67.5% — 85%). As a group, dogs could discriminate all three size differences; 66.3% ($p < .001$) at 20%, 73.4% ($p < .001$) at 40% and 86.9% ($p < .001$) at 70%. The model for the logistic regression was statistically significant when controlling for percent size difference nested within dog, Wald χ^2 (8, $N = 24$) = 38.84, $p < .001$, indicating a significant relationship between performance and the percent size difference of the stimuli. There was no significant effect when controlling simply for dog Wald χ^2 (7, $N = 24$) = 6.64, $p = .47$.

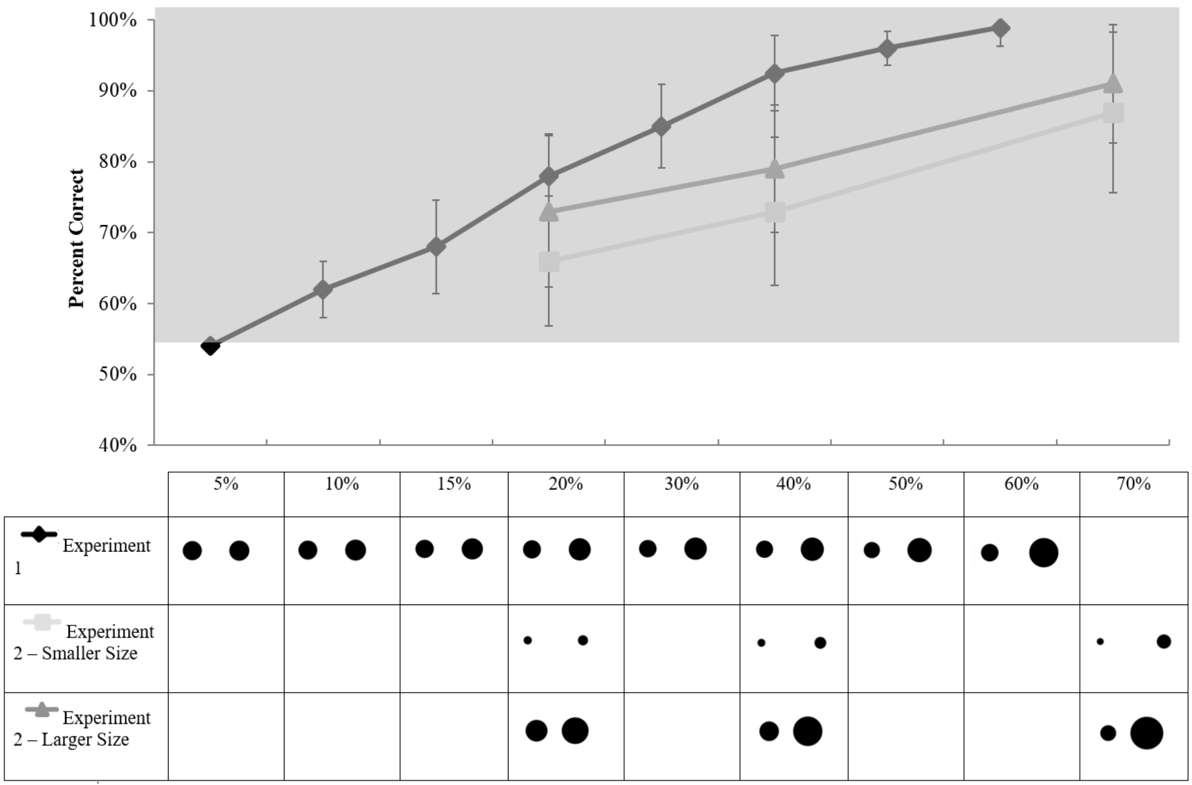


Figure 5. Group average percent correct (and standard deviations) by percent difference in diameter for Experiments 1 and 2. Grey area indicates that the binomial result significantly differed from chance at $p < .05$.

General Discussion

In order to extend previous findings that suggest dogs may not be susceptible to the Ponzo illusion, we conducted two experiments. Experiment 1 examined dogs' susceptibility to the Ponzo illusion when it was presented in a vertical format, hypothesized to invoke linear perspective cues. Experiment 2 evaluated size sensitivities, in order to determine whether the same dogs were capable of perceiving the size difference hypothesized to be required to perceive the Ponzo illusion in humans.

In Experiment 1, the dogs, as a group, did not demonstrate susceptibility in the same direction as humans when presented with a vertical presentation of the Ponzo illusion. Only one dog, Beth, performed significantly above chance, in a human-like manner, when presented with the illusion. Additional testing is therefore required in order to determine whether other contexts (e.g., in which pictorial cues are presented), when presented vertically, invoke susceptibility to the illusion. In humans, orientation of the presentation affects the perceived depth and size of the stimuli and pictorial depth increases the perceived size of the stimuli (Miller, 1997). It is possible that similar effects could be observed in at least some dogs.

In Experiment 2's first phase, all dogs were successfully able to discriminate between circles varying in size by 20%, but marked individual differences were present when the percent size difference was smaller than this. Some individuals could not discriminate 15% size differences, half of the sample could not discriminate 10% size differences, and none could successfully discriminate between circles varying in size by 5%. Thus, dogs appear to be able to perceive the minimum size difference required in humans in order to perceive the Ponzo illusion (approximately 18% difference), although it is of interest that there was no evidence to suggest that dogs that successfully discriminated between smaller size differences also demonstrated susceptibility to the illusion. Given the observed variation in performance in this relatively similar population of dogs, these findings may have implications for future studies of dogs' visual performance.

Using different absolute-sized stimuli (Experiment 2, Phase 2), it was found that dogs' performance generally worsened when the absolute size was smaller. Dogs were successful at discriminating 40% size differences regardless of absolute size. However, more dogs were successful at discriminating 20% size differences when the stimulus was larger than when it was smaller. One factor that may affect performance is age and eye condition. One of the dogs, Hamish, failed to perform above chance when presented with the discrimination task for the smaller absolute sized stimulus for all percent size differences presented (*i.e.*, 20%, 40% and 70% difference in diameter). His ophthalmological examination suggested early age-related changes in his lens. Therefore, it is possible he was unable to perceive the percent size differences when the absolute size of the stimuli was smaller because of reduced visual acuity.

The findings reported above provide evidence complimentary to that reported previously (Byosiere, Feng, Rutter et al., 2017) in suggesting that dogs may not be susceptible to the Ponzo illusion. In previous assessments of the Ponzo illusion conducted in these same dogs, only one illusory presentation (Experiment 1 in Byosiere, Feng, Rutter et al., 2017) resulted in a significant result, however group performance was low at only 56.25%. Group performance across all other presentations, including a re-test of the single significant presentation, has consistently been at chance; (48.1% in Experiment 2, 45.8% in Experiment 3 and 56.4% in Experiment 4 as presented in Byosiere, Feng, Rutter et al., 2017). While the results observed in the current experiment are generally higher than the findings reported across all other Ponzo presentations, convergence of the findings supports the conclusion that dogs do not demonstrate susceptibility to the Ponzo illusion.

Although it has been previously proposed that terrestrial animals may consistently share the same perceptual experiences of geometrical illusions as humans (Feng et al., 2017), the results from this study and others in domestic dogs (Byosiere, Feng, Rutter et al., 2017; Byosiere, Feng, Woodhead, et al., 2017; Miletto Petrazzini et al., 2017) suggest this may not be the case. In a previous study assessing susceptibility to the Ebbinghaus-Titchener illusion, reversed susceptibility was found in this same group of dogs when presented with two different illusory contexts (Byosiere, Feng, Woodhead, et al., 2017), and two studies have failed to observe canine susceptibility to the Delboeuf illusion (Byosiere, Feng, Woodhead, et al., 2017; Miletto Petrazzini et al., 2017). Baboons, the only other terrestrial species to have been assessed on the Ebbinghaus-Titchener illusion, failed to demonstrate susceptibility to the illusion (Barbet & Fagot, 2002), and while some terrestrial species, such as chimpanzees, macaques and capuchin monkeys (Parrish & Beran, 2014; Parrish, Brosnan, & Beran, 2015), have demonstrated human-like susceptibility to the Delboeuf illusion, others, like ring-tailed lemurs, have not (Santacà et al., 2017). Yet, it is important to note that these studies emphasize the methodological constraints and confounds that arise when evaluating illusion susceptibility in animals. Presentation style, training procedures, stimuli design, the kind of paradigm used, and failure to reliably differentiate control stimuli have all been observed to affect the perception of the Ebbinghaus-Titchener and Delboeuf illusions in animals (Barbet & Fagot, 2002; Parrish & Beran, 2014; Parrish et al., 2015; Santacà et al., 2017). Future research should examine vertical Ponzo illusion susceptibility using additional pictorial linear perspective cues, as has been done in horses (Timney & Keil, 1996), or within alternative testing paradigms (e.g., absolute classification, same-different tasks).

If it is correct that dogs are not susceptible to the Ponzo illusion, this has implications for underlying theoretical explanations for illusion susceptibility, as five terrestrial species, ranging from rats to chimpanzees, have all demonstrated susceptibility (Barbet & Fagot, 2002; Bayne & Davis, 1983; Fujita, 1997; Fujita et al., 1991; Imura et al., 2008; Nakagawa, 2002; Timney & Keil, 1996). It is possible that dogs differ from these other species in terms of their perceptual cognitive style, preferring to focus on local cues (individual components of a stimulus) rather than global cues (viewing the stimulus as a whole). Recent findings in regards to canine illusion susceptibility indicate that many dogs may favor local over global processing, at least in some circumstances (Byosiere, Feng, Woodhead, et al., 2017). Considering the Ponzo illusion is thought to be caused by a global precedence, susceptibility to the Ponzo illusion may not occur if dogs consistently demonstrate a preference for local processing. Arguing against this explanation, previous reports claim that dogs demonstrate perceptual cognitive styles favoring global over local processing (Mongillo et al,. 2017; Pitteri et al., 2014) and rhesus macaques, a known local processor, have demonstrated susceptibility to the Ponzo illusion (Parrish et al., 2015). However, in humans, it has been suggested that precedence functions as an umbrella term to denote multiple independent mechanisms rather than a singular construct invoked by the same cognitive operations across all types of global tasks (Chouinard, Noulty, Sperandio & Landry, 2013; Chouinard, Unwin, Landry & Sperandio, 2016). Therefore, the variation across individuals and across tasks in dogs may not be surprising. Multiple global versus local tasks should be conducted to further investigate this issue.

In order to control for morphological variations that may affect brain structure and visual processing (McGreevy, Grassi, & Harman, 2003; Roberts, McGreevy, & Valenzuela, 2010), all dogs tested were purebred Lagotto Romagnolos. However, considering the drastic differences in facial morphologies between breeds, future research should replicate this study in a larger and more diverse sample, including brachycephalic dog breeds, as their visual processing capacities may differ (Byosiere, Chouinard et al., 2017). Furthermore, while many of the dogs tested in this study were genetically related and living in similar living conditions, individual differences were observed. These findings highlight the need to study individual differences within dogs in addition to breed and environmental effects. Further research into factors that contribute to these differences could not only enhance our understanding of dog perception and cognition, but also aid in more applied scenarios.

In conclusion, while canine research has increased greatly over the last two decades, very little is known about dogs' visual perception. This is a serious omission, considering the primary sensory mode underlying many studies is vision. We evaluated misperception by assessing the susceptibility of eight dogs to a vertically presented Ponzo illusion. As a group, the dogs did not perceive the illusion, even though it was demonstrated that they could perceive the minimum size difference required in humans for the illusion to occur. However, there did appear to be a small, non-significant effect with all dogs scoring above rather than below chance, and one individual, Beth, clearly demonstrating illusion susceptibility. These findings are intriguing and should prompt further research examining illusion susceptibility in other breeds and other presentations, particularly those in which the stimuli are presented in a way that invokes strong linear perspective cues.

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