

Visual Perception in Dogs (*Canis lupus familiaris*): Are Dogs Susceptible to
Visual Illusions?

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Abstract

Domestic dogs play many important roles in human lives and recently have garnered the attention of cognition researchers due to their unique socio-cognitive abilities. While studies of dog cognition have dramatically increased in the last two decades, inconsistencies in the results have often been observed. One potential reason for this is the use of visually based paradigms that may not be suited for dogs' visual capacities. To avoid experimental paradigms that may lead to inaccurate or opposing conclusions about cognition in dogs, it is important to understand dogs' visual perception. Thus, it is necessary to investigate the proposed mechanisms and underlying theories of visual processing in dogs. The purpose of this thesis is to improve current understanding of canine visual perception and provide a foundational framework of visual processing in a sample in which breed, facial morphology, genetics, and environment were extensively controlled. A novel approach of illusion susceptibility was implemented, which has been used across a variety of species to gauge similarities and differences in visual processing and perception. Two initial assessments were conducted to evaluate the appropriateness of the paradigm and optimise stimuli. In addition, four studies of illusion susceptibility, to the Ebbinghaus-Titchener, Delboeuf, Ponzo, and illusory contour (Ehrenstein and Kanizsa figures) illusions, were conducted. The results demonstrate that canine illusion susceptibility is dependent on the illusion, as human-like, null, and reversed susceptibility were all observed. Generally, however, the dogs tended to demonstrate an overall preference for local over global processing of visual stimuli. The complexity of the findings suggests that dogs do not visually process information as stimulus-response automatons in solely a bottom-up manner. Dogs utilised and applied information that was not visually present, suggestive that cognitive processes, such as top-down processing, adapt visual information after it enters the retina. This research highlights the importance of studying foundational aspects of canine vision, as well as the need to evaluate individual differences. Future studies are required to better understand the similarities and differences underlying the perception of illusory stimuli in dogs, as well as to clarify the generalisability of these findings to a broader population comprising different breeds and morphotypes.

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Statement of Authorship

This thesis includes work by the author that has been published or accepted for publication as described in the text. Except where reference is made in the text of the thesis, this thesis contains no other material published elsewhere or extracted in whole or in part from a thesis accepted for the award of any other degree or diploma. No other person's work has been used without due acknowledgment in the main text of the thesis. This thesis has not been submitted for the award of any degree or diploma in any other tertiary institution. All research reported in this thesis was approved by the La Trobe University Animal Ethics Committee (application numbers: AEC 15-18, 16-26, 16-49, 16-66, 17-14, 17-38).

Sarah-Elizabeth Byosiére

September 13th, 2018

Publications and Presentations Completed

Published and submitted works written during the course of this degree make up the majority of this dissertation. The research conducted over the course of this degree has been distributed via academic publications and presentations at relevant academic conferences. I also had the opportunity to be part of numerous other projects during my candidature, which were unrelated to the current thesis. All publications and presentations completed during this candidature are detailed below

Related publications

- Byosiére, S-E.**, Feng, L. C., Woodhead, J. K., Rutter, N. J., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). Visual perception in domestic dogs: susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions. *Animal cognition*, 20(3), 435-448.
- Byosiére, S-E.**, Feng, L. C., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). Relational concept learning in domestic dogs: Performance on a two-choice size discrimination task generalises to novel stimuli. *Behavioural Processes*.
- Byosiére, S-E.**, Feng, L. C., Rutter, N. J., Woodhead, J. K., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). "Do dogs see the Ponzo illusion." *Animal Behavior and Cognition*, 4(4) 396-412.
- Byosiére, S-E.**, Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). What do dogs (*Canis familiaris*) see? A review of vision in dogs and implications for cognition research. *Psychonomic Bulletin & Review*, 1-16.
- Byosiére, S-E.**, Feng, L. C., Wuister, J., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2018). Do dogs demonstrate susceptibility to a vertically presented Ponzo illusion? *Animal Behavior and Cognition*, 5(3), 254-267.
- Byosiére, S-E.**, Chouinard, P. A., Howell, T. J., & Bennett, P. C. (under review). Can domestic dogs (*Canis lupus familiaris*) perceive illusory contours? Submitted 7/2018 to Journal of Comparative Psychology.
- Byosiére, S-E.**, Chouinard, P. A., Howell, T. J., & Bennett, P. C. (under review). The effects of physical luminance on colour discrimination in dogs: A cautionary tale. Submitted 8/2018 to Applied Animal Behavior Science.

Related Conference Presentations

- Byosiére, S-E.**, Feng, L. C., Wuister J., Chouinard, P. A., Howell, T. J., & Bennett, P. C. Illusion or reality? Do dogs see the Ponzo illusion. The 25th International Conference on Comparative Cognition. (Melbourne, USA) April 2018.
- Byosiére, S-E.**, Chouinard, P. A., Howell, T. J., & Bennett, P. C. Can dogs discriminate between colours? Assessing perception of true colour and isoluminant stimuli. 35th Annual Meeting of the International Ethological Conference and the 2017 Summer Meeting of the Association for the Study of Animal Behaviour (Estoril, Portugal) July 2017.
- Byosiére, S-E.**, Feng, L. C., Rutter, N. J., Woodhead, J. K., Chouinard, P. A., Howell, T. J., & Bennett, P. C. Do dogs see the Ponzo illusion? 51st Annual Meeting of the International Society for Applied Ethology (Aarhus, Denmark) August 2017.
- Byosiére, S-E.**, Feng, L. C., Woodhead, J. K., Rutter, N. J., Chouinard, P. A., Howell, T. J., & Bennett, P. C. Visual perception in domestic dogs: susceptibility to the Ebbinghaus-Titchener and Delboeuf illusions. Canine Science Forum (Padova, Italy) June 2016.

Additional publications and conference presentations during this candidature

- Byosiére, S-E.**, Espinosa, J., Smith, B. P. Comparing the function of play bows in dingo puppies (*Canis dingo*) to dogs (*Canis lupus familiaris*) and wolf puppies (*Canis lupus occidentalis*). *Behaviour*.
- Byosiére, S-E.**, Espinosa, J., Marshall-Pescini, S. M., Smuts, B. B., Range, F. Investigating the Function of Play Bows in Dog and Wolf Puppies (*Canis lupus familiaris*, *Canis lupus occidentalis*). *PloS one*. 11 (12), e0168570.
- Byosiére, S-E.**, Espinosa, J., Smuts, B.B. Investigating the function of play bows in adult pet dogs (*Canis lupus familiaris*). *Behavioural Processes*. 125, 106-113.
- Byosiére, S-E.**, Espinosa, J., Smith, B. P. Comparing the function of play bows in dingo puppies (*Canis dingo*) to dogs (*Canis lupus familiaris*) and wolf puppies (*Canis lupus occidentalis*). Canine Science Conference (Tempe, Arizona) October 2017
- Byosiére, S-E.**, Range, F., Viranyi, Z. The Development of Attention to Social Cues. EthoDogs, (Erice, Sicily) November 2015.

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Chapter 1 – Introduction

As the first domesticated non-human animal species (Larson & Bradley, 2014; Larson et al., 2012; Perri, 2016), dogs (*Canis familiaris*) have co-existed with humans for thousands of years (Bensky, Gosling & Sinn, 2013; Clutton-Brock, 1995; Miklósi, 2015; Morey, 1994). Active domestication likely commenced around 14,000 years before present, resulting in numerous distinct dog breeds that were bred for a number of functional roles (Galibert, Quignon, Hitte & André, 2011) such as herding, hunting, and guarding (Cobb, Branson, McGreevy, Lill & Bennett, 2015; King, Marston & Bennett, 2012). Many dogs are still used for these roles or occupy modern working roles such as helping the physically impaired, identifying diseases, helping to maintain public safety and aiding in conservation efforts by detecting a variety of relevant scents (Bensky et al., 2013). Today, they also occupy a unique ecological niche in modern human society (Miklósi & Kubinyi, 2016). Dogs reside in a large percentage of modern western households (for an international review of pet ownership across 27,000 participants see *Global study: pet ownership*, 2016), and are frequently perceived as companions (Bennett & Rohlf, 2007; Blouin, 2013; Staats, Wallace & Anderson, 2008), family members, or even substitute children colloquially termed ‘fur babies’ (Greenebaum, 2004).

Given the selective pressures underlying their domestication and their unique inter-species relationships with humans (for examples see Payne, Bennett & McGreevy, 2015) dogs were long considered an ethologically ‘uninteresting’ species for study (Miklósi, Topál & Csányi, 2004). Some observational and experimental research (Fox, 1971a; Fox, 1971b; Frank, 1980; Frank & Frank, 1982) was conducted in the 1970s and

1980s, however, most behaviour and cognition research, at this time, focused on apes, monkeys, select mammals, and bird species (for review, see Shettleworth, 2010).

A (re) discovery of dogs as a research subject of interest began in the late-1990s when comparative cognition researchers (Hare, Call & Tomasello, 1998; Miklósi, Polgárdi, Topál & Csányi, 1998; Topál, Miklósi & Csányi, 1997) noted intriguing findings in regard to problem-solving using social cues. Dogs, rather than chimpanzees, humans' closest living primate relatives, outperformed all other animal species in locating hidden food based on human-given cues (Bräuer, Kaminski, Riedel, Call & Tomasello, 2006; Hare, Brown, Williamson & Tomasello, 2002b; Kaminski, 2009). Dogs appeared uniquely capable of understanding the underlying communicative intent behind these cues (Bräuer et al., 2006; Hare et al., 2002b; Kaminski, 2009; Kaminski, Schulz & Tomasello, 2012). Considering these remarkable social-cognitive abilities, it has since been suggested that dogs provide an interesting and unique model for understanding both social and non-social cognitive processes in non-human animals (from here on animals) (Hare & Tomasello, 1999; Miklósi et al., 1998; Soproni, Miklósi, Topál & Csányi, 2002; Soproni, Miklósi, Topál & Csányi, 2001; Udell, Dorey & Wynne, 2008; Udell & Wynne, 2008).

Dogs not only represent a unique model for investigating cognitive skills, their adaptability and economic practicality within everyday human life makes them a distinctively accessible research subject. Moreover, dogs represent the most morphologically diverse species on earth (Hart, 1995; Wayne, 1986a; Wayne, 1986b), representing the only species in which effects of morphology, size, and selective pressures can be extensively evaluated. Dogs have subsequently become a well-

researched species (Horowitz, 2014), although one might argue that they remain poorly understood. For example, while numerous studies have now evaluated various aspects of canine cognition, many of these provide conflicting reports. Perhaps the best-known example of this concerns problem-solving using social cues. Controversy has been observed in regard to the effects of life experience (Gácsi, Kara, Belényi, Topál & Miklósi, 2009a; Ittyerah & Gaunet, 2009; McKinley & Sambrook, 2000), shelter experience (Hare et al., 2010; Udell et al., 2008; Udell, Dorey & Wynne, 2010) morphology (Gácsi, McGreevy, Kara & Miklósi, 2009b; Helton & Helton, 2010; Wobber & Hare, 2009) and age (Dorey, Udell & Wynne, 2010; Gácsi et al., 2009a; Hare et al., 2002b; Riedel, Schumann, Kaminski, Call & Tomasello, 2008; Wynne, Udell & Lord, 2008) on canine comprehension of human-given communicative gestures. Additional examples in which conflicting reports have been observed include studies of object permanence, problem-solving, and means-end reasoning (for a thorough review of these examples see Bensky et al., 2013).

Many reasons likely exist to explain why these comparable studies, often with similar methodological paradigms, have yielded different results across assessments of dog cognition. One potential explanation, which has been largely neglected, is that variation in cognitive performance may arise due to diversity in dog visual processing and perception. To date, few studies have evaluated how dogs visually perceive and interpret their environment or whether visual capabilities are diverse (Byosiére, Chouinard, Howell & Bennett, 2017). This is perhaps surprising, as approximately 74% of canine cognition experiments using visually-based paradigms (Bensky et al., 2013). What remains uncertain is the appropriateness of these paradigms. Given that many of

these experiments are direct applications of well-established methodologies created for primates, including humans, it is possible that they have been applied to canines without adequate reflection (Byosiere et al., 2017). While humans and other primates share a similar visual system (Jacobs, 1996), the paucity of dog visual processing and perception research makes it difficult to determine whether or not these experiments can accurately assess dog cognitive skills. To gauge cognitive complexity in dogs, it is necessary to acknowledge not only their unique social cognitive capacities, but also to understand how these skills interact with and are affected by, fundamental components of perception.

While basic parameters of canine visual ability have been reported, they most often stem from older studies, employing small sample sizes, in which modern technologies (e.g. computers monitors, touch-screens), and methodologies are not utilised (Byosiere et al., 2017; Miller & Murphy, 1995). This has ultimately resulted in gaps in the literature (Byosiere et al., 2017). For example, what is a dog's typical visual acuity? How do they process light and changes in brightness? Can dogs perceive and discriminate between different colours? Are there systematic variations based on breed or morphology? These types of questions, underlying the fundamentals of dog vision, also lead us to question more complex components of perception. How do dogs visually process simple shapes and forms? Do they process stimuli globally or locally? How does their visual perception compare to humans and other animals? These questions represent a select handful of the many that have yet to be thoroughly investigated in dogs. They highlight that researchers must begin to evaluate overlooked but foundational aspects that may affect dog cognition, such as how dogs visually perceive their physical environment and to what extent their perception of the external world is similar to, or different from,

other animals.

One method used to explore visual perception in animals, which has yet to be applied in dogs, is illusion susceptibility. The notion of illusions in nature has endured since artist and amateur scientist, Thayer, noted: “the spectator seems to see right through the space really occupied by an opaque animal” (Thayer, 1909, p. 14). Explicitly referencing animal colouration and camouflage, Thayer and other researchers (Cott, 1940; Stevens & Merilaita, 2009; Stevens & Merilaita, 2011) suggested that animal colouration and patterns function to make the wearer undetectable to prey and predators. This concept is of particular interest to those evaluating illusion susceptibility in animals, as the elaborate, and potentially costly, development of this type of disguise would fail to occur were it not beneficial in an evolutionary sense. Therefore, it is conceivable that colouration and camouflage represents a naturalistic form of illusion in animals, indirectly indicating that prey and predators are likely to be susceptible to illusory properties. This, then, leads to the question ‘are animals, like humans, susceptible to non-naturalistic illusions and, if so, to what degree’?

While these observations were noted over a century ago, research evaluating illusory processes in animals has progressed slowly (Kelley & Kelley, 2014), and the question of whether animals are susceptible to illusions has mostly been overlooked. It is only recently that researchers have noted the benefits of evaluating illusion susceptibility in animals. By creating comparable paradigms that can be conducted in non-verbal species, illusion susceptibility can be used as a tool to reveal similarities and differences underlying psychological and cognitive processes of perception (Feng, Chouinard, Howell & Bennett, 2017; Kelley & Kelley, 2014). Given that humans have long been

intrigued with visual illusions, dating back to Ancient Greek philosophers (for a historical review see Coren & Girgus, 1978), the substantial literature available provides a detailed framework for assessing cognitive and neuropsychological mechanisms of visual processing, which can be used to, indirectly, understand perceptual processing in animals.

In summary, due to their socio-cognitive skills, accessibility, process of domestication, and immense within-species variation, dogs represent a unique model in which to explore and evaluate cognition. However, various controversies and gaps in the literature highlight the need to understand how cognition is affected by sensory perception, specifically vision (Byosiére et al., 2017; Miller & Murphy, 1995). To evaluate visual perception in dogs, this thesis aimed to apply the novel approach of using visual illusions to determine similarities and differences in susceptibility, specifically as compared to humans and other animals. The scope was necessarily limited by the constraints of the degree being undertaken. Hence, this thesis evaluates visual perception in dogs, with an exclusive focus on susceptibility to cognitive visual illusions that are geometrically and cognitively based. Illusions of other sensory modalities are not assessed. The thesis also evaluates specific foundational aspects of perception to optimise the methodologies and testing procedures for determining illusion susceptibility. The sample was restricted to one breed of dogs, Lagotto Romagnolos, of similar genetic and environmental experience, and to a small sample. Most subjects participated in multiple experiments, although naïve subjects were also added throughout experimentation as they became available. Due to this approach, a direct comparison of the findings across different breeds or morphotypes is not possible, although it is highly recommended for future studies. An overview of the thesis is presented next, which highlights the

innovative and exploratory nature of the research but also emphasises the specific predictions that were made on the basis of available theory and tested in the studies reported in the body of this thesis.

1.1 Overview of the thesis

Noteworthy to the structure of this thesis is that some of the published articles presented were published out of sequence and may not follow as logically as this summary suggests. Additionally, some of the experiments were conducted as a part of a larger collaborative endeavour. Therefore, certain publications presented in this thesis represent a joint effort involving other students. In these instances, it is clearly explained in advance which parts reflect my contribution to this thesis.

The thesis commences with Chapter 2, which reports on the available literature concerning how dogs perceive their environment, and includes the published theoretical review titled ‘What do dogs (*Canis familiaris*) see? A review of vision in dogs and implications for cognition research.’ The article provides an up to date account of dog vision research and highlights specific areas that require further investigation. It also stresses the immense diversity of dog physiology and morphology, and the effect this variation may have with regard to differences in perception. Chapter 2 expands on the literature review’s subsection of illusion susceptibility, highlighting the four cognitive geometric illusions to be addressed in this thesis, the Ebbinghaus-Titchener, Delboeuf, Ponzo, and illusory contour illusions. This portion of the thesis begins by summarising human-based theories that have been used to explain visual perceptual mechanisms of illusion susceptibility. It also highlights previous studies of vertebrate illusion

susceptibility, presenting information regarding which species have demonstrated susceptibility and the degree compared to humans. Finally, a theoretical framework of visual processing is proposed in which to evaluate the perceptual mechanisms underlying illusion susceptibility.

To appropriately address illusion susceptibility in dogs, the empirical component of the thesis began by probing basal aspects of visual processing and perception. This allowed for evaluation of the suitability of the proposed testing paradigm and methodology as well as the establishment of appropriate stimulus presentation. Chapters 3 and 4 report this work. Chapter 3 includes a published experiment titled ‘Relational concept learning in domestic dogs: Performance on a two-choice size discrimination task generalises to novel stimuli.’ This study expanded on an Honours project conducted by previous students, in which eight dogs were trained to touch the larger (or for some dogs, the smaller) of two circles presented on a screen. Once successful and well versed in this task, dogs were presented with novel presentations of pairs of stimuli varying in similarity to the circle stimuli the dogs were trained on (i.e. ovals, squares, rectangles, circles, diamonds, stars, and lines) to determine whether or not they would continue to apply their previously learned rule. In applied animal behaviour settings, it is commonly assumed that dogs are unsuccessful at generalising (for examples see Alexander, 2003; Cattet, 2013), however successful categorisation and generalisation have been observed in rather complex cognitive tasks (Range, Aust, Steurer & Huber, 2008). Therefore, it was predicted that the dogs would be able to successfully perform the two-choice discrimination task and generalise their previous learned rule to novel stimuli, barring instances in which physiological limitations, such as visual acuity, may alter

performance.

Chapter 4 evaluates colour discrimination capabilities in dogs, providing relevant information necessary for the creation of appropriate testing stimuli in which to embed illusions. The submitted manuscript ‘The effects of physical luminance on colour discrimination in dogs: A cautionary tale’ assessed whether or not dogs could distinguish maximum RGB (red, green, blue) values of red/green, and blue/yellow circle stimuli on a contrasting colour background. To measure the effects of physical isoluminance of the stimuli, colour contrasts with equal physical luminance were presented at varying degrees of intensity. The experiment identified what colour contrasts and intensities were suitable for testing illusion susceptibility. Due to differences in the number and structure of dog photoreceptor cells (compared to humans), and the widely held belief of red-green colour-blindness in dogs, it was predicted that dogs would demonstrate difficulty discriminating between red and green stimuli, but successfully discriminate between yellow and blue stimuli.

Chapter 5 presents one of the first studies ever reported to assess illusion susceptibility in dogs (see also Miletto Petrazzini, Bisazza & Agrillo, 2016). In the published article ‘Visual perception in domestic dogs: susceptibility to the Ebbinghaus-Titchener and Delboeuf illusions’, the foundations for appropriate stimuli presentation developed in Chapters 3 and 4 were implemented to create suitable illusory presentations of the Ebbinghaus-Titchener and Delboeuf illusions. This chapter aimed to determine if dogs demonstrated misperception, perceiving a size difference between stimuli that were truly identical in size, when presented with illusions. Dogs were presented with three kinds of illusions: a classical presentation (conducted as an Honours project) and an

illusory contour presentation of the Ebbinghaus-Titchener illusion, as well as its mechanistically similar counterpart, the Delboeuf illusion. At the onset of this thesis, no research into canine illusion susceptibility had been reported. As most animals have demonstrated human-like susceptibility of these illusions (Byosiére et al., 2016; Feng et al., 2017; Kelley & Kelley, 2014) and because there are human-like parallels observed in canine visual processing (Lind, Milton, Andersson, Jensen & Roth, 2017; Mongillo, Pitteri, Sambugaro, Carnier & Marinelli, 2016; Pitteri, Mongillo, Carnier & Marinelli, 2014; Siniscalchi, Ingeo, Fornelli & Quaranta, 2017), it was predicted that dogs would demonstrate human-like susceptibility to the illusions.

Following the exploration of dog susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions, Chapter 6 presents a published article titled ‘Do dogs see the Ponzo illusion?’. While representative of distorting illusions (as will be discussed in Chapter 2), like the Ebbinghaus-Titchener and Delboeuf, the mechanisms underlying susceptibility to the Ponzo illusion are thought to differ given that susceptibility is invoked by linear perspective or depth cues rather than size contrasts (however, relative size may function as a form of a depth cue). It was anticipated that investigation of this illusion might reveal, to a greater extent, the similarities and differences underlying possible perceptual mechanisms in dogs compared to humans and other animals. Dogs were evaluated on three presentations of the Ponzo illusion, for a total of three experiments and one re-test (the first version of which was conducted as a part of an Honours project). The purpose of this study was to assess whether or not dogs demonstrated susceptibility to the Ponzo illusion, as well as to evaluate susceptibility within the context of results from the Ebbinghaus–Titchener and Delboeuf illusions (discussed in Chapter 5). As all animals, to

date, have demonstrated human-like susceptibility to the Ponzo illusion (Barbet & Fagot, 2002; Bayne & Davis, 1983; Fujita, 1996; Fujita, 1997; Fujita, Blough & Blough, 1991; Imura, Tomonaga & Yagi, 2008; Nakagawa, 2002; Timney & Keil, 1996), it was expected that dogs would demonstrate human-like susceptibility to the Ponzo illusion.

Chapter 7 investigates further the equivocal results observed in Chapter 6. The published article ‘Do dogs demonstrate susceptibility to a vertically presented Ponzo illusion?’ focuses on exploring the effects of two variables that may have distorted the findings presented in Chapter 6. In addition to evaluating canine susceptibility to horizontally presented Ponzo illusions, susceptibility to a classic, vertical presentation was assessed. This decision was mainly driven by the fact that, in humans, vertical presentations of the Ponzo illusion have been proposed to invoke linear perspective cues necessary to induce susceptibility (Fujita, 1996). Additionally, a variety of size discriminations were conducted to determine if dogs are capable of perceiving the minimum size threshold required, in humans, to perceive the Ponzo (and other) illusions. Some of the size threshold experiments, with stimuli varying in percent differences in diameter from 60% different to 10% different, were conducted as part of a Masters thesis. In the current thesis, additional experiments were conducted to test the generalisability of the findings to stimuli that varied in absolute size (either small or large) but were identical in the percent size difference (20% and 40%). The purpose of the two experiments presented in Chapter 7 was to disentangle the findings observed in Chapter 6. Specifically, does the orientation of the Ponzo illusion affect illusory perception in dogs, and do dogs demonstrate a capacity to perceive the minimum size threshold required in humans to perceive illusions?

Chapter 8 presents the final empirical study included in this thesis, and comprises a submitted manuscript titled ‘Can domestic dogs (*Canis lupus familiaris*) perceive illusory contours?’. In this study, dog illusion susceptibility was evaluated within the context of illusion-invoking contours. Illusory contour perception is invoked when an individual perceptually completes a figure or shape that is physically missing connective contours in reality (Kanizsa, 1974). This experiment expands on preliminary findings reported in Chapter 5, in which dogs demonstrated a capacity to perceive the illusory contours of an Ebbinghaus-Titchener figure in much the same way as has been reported in humans and other animals (Bravo, Blake & Morrison, 1988; Fagot & Tomonaga, 2001; Fuss, Bleckmann & Schluessel, 2014; Kanizsa, Renzi, Conte, Compostela & Guerani, 1993; Nieder & Wagner, 1999; Sovrano & Bisazza, 2009; Wyzisk & Neumeyer, 2007; Zimmermann, 1962). The dogs were presented with two illusory figures, the Ehrenstein (1987) and Kanizsa (1955) figures, to determine if they perceived illusory stimuli in a similar manner to complete stimuli. Indirectly, these findings help ascertain whether dogs, like humans and other animals, experience a disassociation between what is depicted on the retina and what the brain processes. Given the findings observed in Chapter 5 and the fact that all animals tested to date have demonstrated human-like perception of illusory figures, it was predicted that dogs would perceive the fragmented stimuli in a human-like manner.

Finally, Chapter 9 provides an overall discussion of the results and presents theoretical and practical implications of the experiments reported in this thesis. This chapter also critically evaluates the limitations of the studies and gauges the extent to which these findings are generalisable to a broader population of dogs. The chapter

concludes with suggestions for future research directions, including the need to conduct similar studies on more dogs (e.g. breeds and morphological types), given the individual variation reported in this thesis and dog cognition in general.

1.2 Summary

The primary purpose of this chapter was to introduce a history of dog cognition research and discuss illusion susceptibility and misperception as a novel method to assess visual perception in dogs. It highlighted the trend in current canine cognition research to utilise primarily visual tasks, even though little is known about dog visual processing capabilities. Based on this discrepancy, a series of research questions were formulated, and the aims and scope of the thesis were presented. The chapter concluded with a roadmap for the remaining chapters presented in this thesis.

Chapter 2 – Literature Review

Over the last 20 years, dogs have re-emerged as a species of interest for behaviour and cognition researchers. While this curiosity has enhanced our understanding of dog cognition, the findings are limited by the fact that little is known about how dogs perceive the world. As briefly discussed in Chapter 1, it is imperative that fundamental visual assessments of dogs, specifically visual processing and perception, are investigated. The reason for this is that the majority of canine cognition studies have been conducted visually (Bensky et al., 2013), and mixed findings have been observed across and within dog cognition studies (Arden, Bensky & Adams, 2016). Future studies of visual perception in dogs may enhance our understanding of visual processing mechanisms and begin to clarify these mixed reports.

A literature review was conducted to document the current state of knowledge regarding dog vision and perception. This is presented below. The review begins with an overview of what is known regarding the dog's visual system, physiology, sensitivity to light, brightness discrimination, visual acuity and spatial resolution, depth perception, colour vision, and sensitivity to video monitors. Subsequently, a discussion of visual discrimination, form perception, global/local precedence, visual illusions, and face processing is presented, in which the objective is to determine how fundamental aspects of vision affect cognitively complex perceptual processes. The review concludes with an often-ignored postulation that there is evidence to suggest that morphological variation (e.g. facial morphology type, breed and or/individual differences) (Gácsi et al., 2009b; McGreevy, Grassi & Harman, 2004; Roberts, McGreevy & Valenzuela, 2010) may result in differences in perception in dogs.

The review was published as a theoretical review in *Psychonomic Bulletin and Review* in 2017 and is titled ‘What do dogs (*Canis familiaris*) see? A review of vision in dogs and implications for cognition research.’ Following presentation of the published review, Chapter 2 concludes with an introduction to illusions in subsection 2.3. This section provides a review of four types of illusions, which will be addressed in this thesis. The Ebbinghaus-Titchener, Delboeuf, Ponzo and illusory contour illusions are introduced as well as the proposed theories and mechanisms underlying susceptibility in humans. The section concludes with a history of illusion research in vertebrates and justification for using illusion susceptibility as a model of visual perception in dogs.

2.1 Declaration for thesis Chapter 2

In the case of Chapter 2, contributions to the work involved the following:

Name (authors in order)	Extent of contribution (%)	Nature of contribution
Sarah-Elizabeth Byosiene Corresponding author	70	Planning and executing literature search and interpretation, writing manuscript
Philippe Chouinard Co-author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Tiffani Howell Co-author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Pauleen Bennett Senior author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication

Declaration by co-authors

The undersigned hereby certify that:

- (1) the below declaration correctly reflects the nature and extent of the candidate's contribution to this work, and the nature of the contribution of each of the co-authors;
- (2) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (3) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (4) there are no other authors of the publication according to these criteria; and
- (5) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor or publisher of journals or other publications, and (c) the head of the responsible academic unit.

Signature 1	
Signature 2	
Signature 3	
Signature 4	

2.2 What do dogs (*Canis familiaris*) see? A review of vision in dogs and implications for cognition research

Byosiere, S. E., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2018). What do dogs (*Canis familiaris*) see? A review of vision in dogs and implications for cognition research. *Psychonomic bulletin & review*, 25(5), 1798-1813.

2.3 Illusion susceptibility

The published literature review, presented in section 2.1, provides a comprehensive summary of what is currently known regarding vision in dogs. However, it also stresses current gaps in the literature, which require additional investigation. One such gap begs an answer to the question ‘do dogs perceive the world differently than humans and other animals’? To begin to address this question, it is necessary to briefly review how visual information is processed, and what possible methods can be applied to evaluate perception in animals.

To make sense of the external world, organisms organise incoming sensations into meaningful information (Haber & Hershenson, 1973). Information that is received via the eye, more specifically the retina, is not only registered but can also be processed by the brain for further interpretation (Gregory, 2015). In humans, this has led to the creation and debate of various theories of perception. Typically, two theories are presented, Gibson’s (1966) 'bottom-up' theory, and Gregory’s (1970) 'top-down' theory of visual processing. Gibson’s (1966) bottom-up theory can be described as data-driven. More specifically, visual processing begins in the retina and proceeds to the cortex, in a unidirectional manner, involving more complex analysis at each successive stage of input. Gregory’s (1970) 'top-down' theory represents a constructive process, in which incoming visual input from the environment may be perceived ambiguously. To aid contextual understanding, the interpretation of a visual scene is likely to be mediated by previous experience (Gregory, 1970).

While these two theories were proposed almost 50 years ago, on-going controversy remains, and a lack of theoretical consensus exists (Itti & Borji, 2014). Both theoretical

accounts have their respective limitations (e.g. Awh, Belopolsky & Theeuwes, 2012). For example, Gibson's (1966) bottom-up theory readily explains the rapid interpretation of a visual scene (Nieder, 2002), however, it fails to provide an explanation for specific visual contexts, such as illusion susceptibility (Nieder, 2002). While Gibson strongly argued that this failure stemmed from the artificial nature of illusions (Gibson & Gibson, 1955), certain illusions do invoke realistic, naturally occurring, properties. Geometric cognitive illusions (also referred to as geometric illusions in this thesis) represent such an instance.

It has been proposed that susceptibility to geometric cognitive illusions is indicative that the brain adapts retinal information based on preconceptions (Gregory, 1970). While these 'corrections' are typically helpful and adaptive, illusions result when corrections are made in contexts in which they are unnecessary or inappropriate. Interestingly, geometric cognitive illusions are cognitively impenetrable (Pylyshyn, 1999), meaning we, as humans, cannot prevent ourselves from perceiving the illusion even when we are aware of its presence. This suggests that susceptibility does not originate in the retina, and likely arises post-retinally in the cortex (for an extensive review see Westheimer, 2008). Involuntary susceptibility and the fact that illusions persist even when someone is informed about the experience, suggests that susceptibility is based on perceptual knowledge and is likely affected by both conceptual and retinal input (Gregory, 1997). In other words, it is likely that susceptibility to geometric cognitive illusions represents an indirect measure of top-down processing.

To further evaluate these theories, this thesis reviews illusion susceptibility using an integrative lens of visual processing in which bi-directional exchange of both bottom-up and top-down processing is expected. This is illustrated in Figure 1. In this figure, a

bottom-up signal stemming from reality is sensed in the eye and is retinally processed. Top-down conceptual knowledge, meanwhile, likely influenced by previous experience, bi-directionally affects and is affected by perceptual knowledge. Together, these processes result in illusion susceptibility, which ultimately results in a behavioural output or indication of susceptibility.

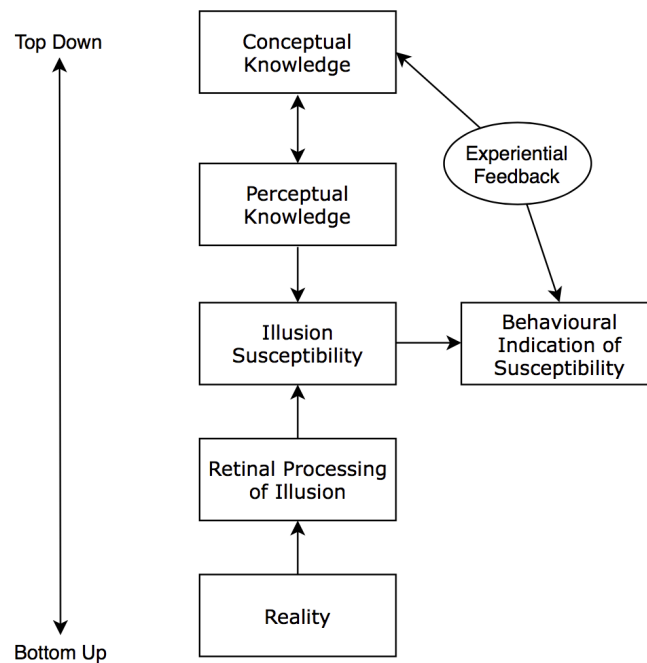


Figure 1. Proposed schematic of perceiving visual illusions including a dual approach of bottom-up and top-down visual processing. Adapted from “Knowledge in perception and illusion,” by R. L. Gregory, 1997, *Philosophical Transactions of the Royal Society*, 352, p. 1124.

Geometric cognitive illusions have been proposed to comprise of four distinct types (Gregory, 1997): ambiguous, paradox, distorting, and fictitious. Ambiguous illusions represent images that induce a perceptual shift between alternative interpretations (Bradley & Dumais, 1975). An example of this is the rabbit-duck illusion,

in which a duck or a rabbit can be seen depending on whether one sees a protruding beak or ears. Paradox illusions represent the perception of a normal image that in reality is not physically possible, for example, one might think of M.C Escher-like stairs (Gregory, 1968). A well-known example of this is the elephant-leg illusion, where an elephant's legs without feet and feet without the elephant's legs are drawn. While the feet and legs are not connected, one tries to make sense of the image by visually perceiving a connection that is not physically possible, in this case this results in the perception of five feet.

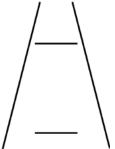
While ambiguous and paradox illusions are exceptionally interesting, they are quite complex. Therefore, the illusions presented in this thesis focus on distorting and fictitious illusions (Table 1). Distorting illusions can be characterised by misrepresentations of size, length, position etc., while fictitious illusions are characterised by the perception of an image that is physically not present (Gregory, 1968). The thesis specifically addresses susceptibility to distorting illusions such as the Ebbinghaus-Titchener, Delboeuf, and Ponzo, as well as fictitious illusions in the form of illusory contour illusions (Ehrenstein and Kanizsa figures). Each illusion is discussed extensively within its respective chapter; however, a brief review is provided here.

It is important to emphasise that these four illusions not only vary in type but also in modality driving the illusory effect. The Ebbinghaus-Titchener and Delboeuf illusions are distorted based on size, while the Ponzo illusion is distorted based on linear perspective. Human-like susceptibility to the Ebbinghaus-Titchener and Delboeuf illusions suggests that perception of the target stimulus is drastically influenced by its context, in other words, by the inducer circles or ring (Table 1). Similarly, human-like

susceptibility to the Ponzo illusion is invoked when the scene is misinterpreted as a three-dimensional figure rather than two-dimensional reality (Table 1). Human-like susceptibility to Ehrenstein and Kanizsa figures suggests an individual perceives a subjective figure that is not physically present (Gregory, 1997) (Table 1). While these geometric illusions vary in many ways, one similarity remains constant: susceptibility, in the form of perceptual error, is thought to occur when assumptions, typically stemming from previous experience, are applied.

Table 1

Description of the illusions evaluated in this thesis and the theoretical explanations for susceptibility in humans

<u>Illusion</u>	<u>Illusion Type</u>	<u>Modality</u>	<u>Human Theory</u>	<u>Theoretical Explanation</u>
Ebbinghaus-Titchener 	Distorting	Size	Inappropriate constancy scaling theory (Gregory, 1963)	The inducer circles surrounding the target are perceived as depth cues where none exist, which results in the two target circles being perceived at different distances, and therefore as different sizes
			Contour interaction theory (Jaeger, 1978)	The inducer circle contours that are close to the target perceptually attract while the contours of inducer targets that are further away perceptually repel, which results in the target stimuli being perceived as different sizes.
			Assimilation theory (Pressey, 1971)	The inducer circles are grouped with their respective target circle, perceptually rescaling the target circles to be more like the inducers.
			Angular size contrast theory (McCready, 1985)	Eye position is altered by depth cues, causing misperception of the apparent distance of the inducer circles, which make the target appear different in size.
			Size contrast theory (Coren & Enns, 1993)	The inducer circles are viewed as a standard and the target is misperceived in relation in size due to a comparison. The small inducers result in an overestimation of the target, while the large inducers cause an underestimation of the target.
Delboeuf 	Distorting	Size	Contour-interaction theory (Jaeger & Lorden, 1980)	The inducer circle contours that are close to the target perceptually attract while the contours of inducer targets that are further away perceptually repel, which results in the target stimuli being perceived as different sizes.
			Assimilation theory (Pressey, 1971)	The inducer circles are grouped with their respective target circle, perceptually rescaling the target circles to be more like the inducers.
Ponzo 	Distorting	Linear perspective	Inappropriate constancy scaling theory (Gregory, 1963)	The converging inducer lines induce depth cues, which results in the two target lines being at different distances, and therefore as different sizes
			Integration field-theory (Pressey & Epp, 1992)	The converging inducer lines provoke attentional demands to the space between the two target lines, which induces the target lines to be perceived as perceptually different.
			Tilt constancy theory (Prinzmetal & Beck, 2001)	Perception of size depends on the interpretation of the location of the end points of the converging lines. The interpretation of the location causes a misperception of size between the two targets.
Illusory Contours 	Fictitious	Brightness	Theory of amodal completion (Kanizsa, 1955)	The incomplete figure results in the emergence of a visual precept, which induces the perception of an illusory object superimposed on the gaps in the inducers.

Various theories have been proposed to explain susceptibility to the Ebbinghaus-Titchener, Delboeuf, Ponzo, and illusory contour illusions, in humans. These theories emphasise that susceptibility is largely driven by perceptual style. Global and local processing characterise two ways in which an individual may experience and interact with their surroundings (Navon, 1977). Humans tend to process stimuli globally, meaning that figures are integrated and perceived as a whole structure. Local processors, in contrast, emphasise individual local components within a stimulus and perceive them independently from one another (de Fockert, Davidoff, Fagot, Parron & Goldstein, 2007). Illusion susceptibility is thought to rely on the perception of multiple components within a visual array. For example, humans with increased global processing preference have been observed to demonstrate a higher degree of illusion susceptibility (e.g. Berry, 1968; Berry, 1971; Dawson, 1967; Witkin, 1967). Conversely, humans that demonstrate an increased preference for local processing appear to be less susceptible to illusory effects (e.g. Dakin & Frith, 2005; de Fockert et al., 2007; Happé, Frith & Briskman, 2001; Happé, 1996).

These findings raise a few questions. First, is illusion susceptibility uniquely human? Understanding the extent to which animals are susceptible to illusions may shed light onto various evolutionary and environmental influences of visual perception, which in turn, may help clarify the mechanisms underlying perceptual processing (Feng et al., 2017; Kelley & Kelley, 2014). It could also help researchers evaluate whether animals misperceive visual information, like humans, or process their environment identically to what is processed in the retina, more locally, like an automaton. Second, if animals are subject to illusion susceptibility, to what extent is this similar to human susceptibility?

Third, do animals demonstrate a perceptual style for visual processing information that is consistent with the global integration typically observed in humans? The answers to these kinds of questions can further our understanding of how animals perceive the world.

To date, research on susceptibility to visual illusions has been conducted across a variety of animals, yielding intriguing results that indicate clear differences at both the species and individual level (for detailed reviews see Feng et al., 2017; Kelley & Kelley, 2014). However, comprehensive assessments within a single species, across types of illusions, are limited. In Table 2 below, the main findings from 31 species are presented, in which vertebrate susceptibility to the Ebbinghaus-Titchener, Delboeuf, Ponzo and illusory contour illusions were evaluated.

Table 2

Overview of vertebrate susceptibility to illusions presented in this thesis

<u>Illusion</u>	<u>Species</u>	<u>Susceptibility?</u>	<u>Perceptual Style</u>
Ebbinghaus-Titchener	Baboons (<i>Papio papio</i>) (Parron & Fagot, 2007)	No	Local-processing
	Homing pigeons (<i>Columba livia</i>) (Nakamura, Watanabe & Fujita, 2008)	Reversed	Local-processing
	Bottlenose dolphin (<i>Tursiops truncatus</i>) (Murayama, Usui, Takeda, Kato & Maejima, 2012)	Yes	Global-processing
	Bantam chickens (<i>Gallus gallus</i>) (Salva, Rugani, Cavazzana, Regolin & Vallortigara, 2013)	Yes	Global-processing
	Bantam chickens (<i>Gallus gallus</i>) (Nakamura, Watanabe & Fujita, 2014)	Reversed	Local-processing
	Redtail splitfin fish (<i>Xenotoca eiseni</i>) (Sovrano, Albertazzi & Salva, 2014)	Yes	Global-processing
	Gray bamboo shark (<i>Chiloscyllium griseum</i>) and Teleost damselfish (<i>Chromis chromis</i>) (Fuss et al., 2014)	Damselfish, yes. Sharks, no.	Global-processing in Damselfish, Local-Processing in Sharks
Delbeouf	Chimpanzees (<i>Pan troglodytes</i>) (Parrish & Beran, 2014)	Yes	Global-processing
	Rhesus monkeys (<i>Macaca mulatta</i>) and Capuchin monkeys (<i>Cebus apella</i>) (Parrish, Brosnan & Beran, 2015)	Yes, reversed, depends on the task.	Global/Local-processing
	Gray bamboo shark (<i>Chiloscyllium griseum</i>) and Teleost damselfish (<i>Chromis chromis</i>) (Fuss & Schluessel, 2017)	Damselfish, yes. Sharks, no.	Global-processing in Damselfish, Local-Processing in Sharks
	Ring-tailed lemur (<i>Lemur catta</i>) (Santacà, Regaiolli, Miletto Petrazzini, Spiezio & Agrillo, 2017)	No	Methodological limitations with control performance
	Dogs (<i>Canis lupus</i>) (Miletto Petrazzini et al., 2016)	No	Local-processing
Ponzo	Rhesus monkeys (<i>Macaca mulatta</i>) (Bayne & Davis, 1983)	Yes	Global-processing
	Carneau pigeons (<i>Columba livia</i>) (Fujita et al., 1991)	Yes	Global-processing
	Rhesus monkeys (<i>Macaca mulatta</i>) (Fujita, 1996)	Yes	Global-processing
	Horses (<i>Equus caballus</i>) (Timney & Keil, 1996)	Yes	Global-processing
	Rhesus monkeys (<i>Macaca mulatta</i>) and Chimpanzees (<i>Pan troglodytes</i>) (Fujita, 1997)	Yes	Global-processing
	Baboons (<i>Papio papio</i>) (Barbet & Fagot, 2002)	Yes	Global-processing
	Sprague-Dawley rats (<i>Rattus norvegicus</i>) (Nakagawa, 2002)	Yes	Global-processing
	Chimpanzees (<i>Pan troglodytes</i>) (Imura et al., 2008)	Yes	Global-processing
Illusory Contours	Rhesus monkeys (<i>Macaca mulatta</i>) (Zimmermann, 1962)	Yes	Global-processing
	Cats (<i>Felis catus</i>) (Bravo et al., 1988)	Yes	Global-processing
	House mouse (<i>Mus musculus</i>) (Kanizsa et al., 1993)	Yes	Global-processing
	Barn owl (<i>Tyto alba</i>) (Nieder & Wagner, 1999)	Yes	Global-processing
	Chimpanzees (<i>Pan troglodytes</i>) (Fagot & Tomonaga, 2001)	Yes	Global-processing
	Goldfish (<i>Carassius auratus</i>) (Wyzisk & Neumeyer, 2007)	Yes	Global-processing
	Redtail splitfin fish (<i>Xenotoca eiseni</i>) (Sovrano & Bisazza, 2009)	Yes	Global-processing
	Gray bamboo shark (<i>Chiloscyllium griseum</i>) (Fuss et al., 2014)	Yes	Global-processing

As can be seen from Table 2, these studies demonstrate various differences in illusion susceptibility. First, not all animals demonstrate susceptibility to illusions. Susceptibility may be non-existent or reversed from what is typically observed in humans. Second, within an illusion, differences both between and within species exist. Animals do not demonstrate consistent or identical susceptibility both within and cross species. The Ebbinghaus-Titchener and Delboeuf illusions represent the two illusions in which considerable variation is observed. A single bottlenose dolphin, teleost damselfish, and red-tail splitfin fish have all demonstrated human-like susceptibility of the Ebbinghaus-Titchener illusion, while baboons and grey bamboo sharks have shown a lack of susceptibility, and homing pigeons have demonstrated reversed susceptibility compared to humans (See Table 2). Intriguingly, bantam chickens have been observed to perceive the illusion in *both* a human-like and reversed manner (Table 2).

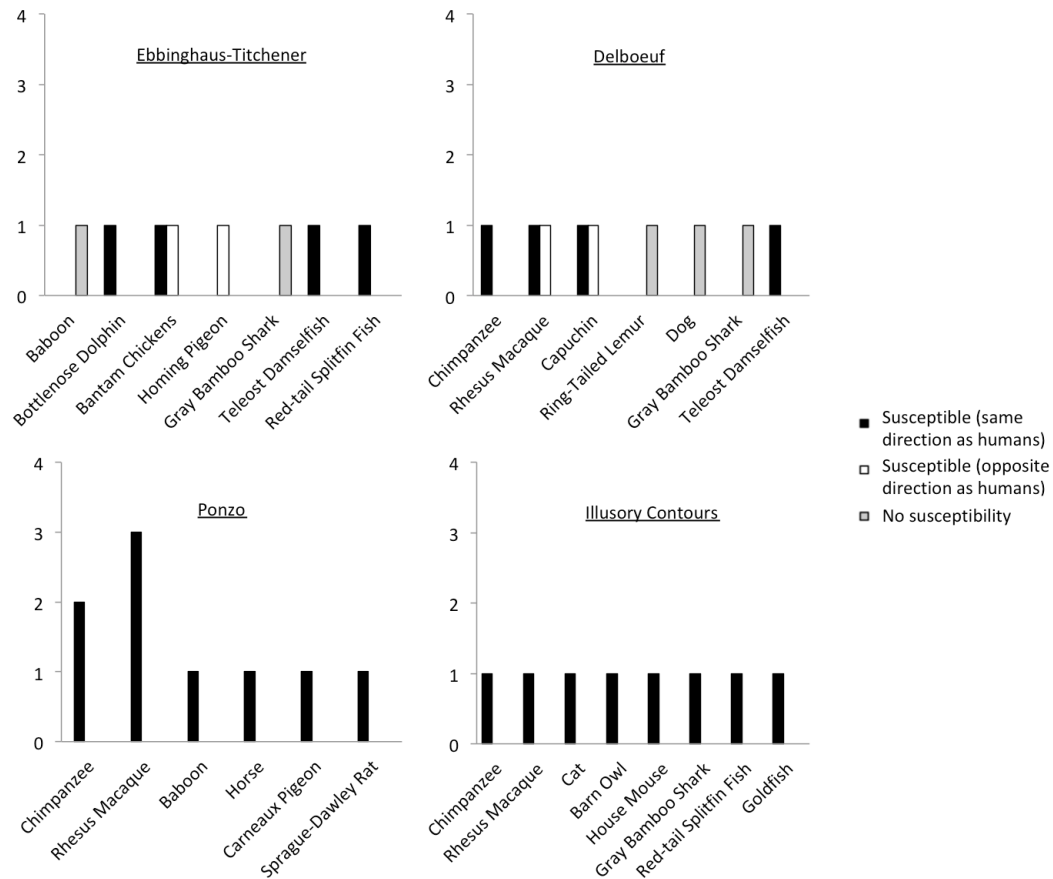


Figure 2. Direction of illusion susceptibility for each vertebrate species to the Ebbinghaus-Titchener, Delboeuf, Ponzo and illusory contour illusions. The bars indicate the number of studies showing human-like (black), reversed (white) and null illusion susceptibility (grey). Adapted from “Why do animals differ in their susceptibility to geometrical illusions?” by Feng et al., 2017, *Psychonomic Bulletin and Review*, 24(2), p. 270.

Mixed reports of illusion susceptibility within a species are not unique. Both rhesus macaques and capuchin monkeys have demonstrated human-like and reversed susceptibility to the Delboeuf illusion (Table 2). Chimpanzees and teleost damselfish have also been observed to demonstrate human-like perception of the Delboeuf illusion,

while ring-tailed lemurs, dogs (unpublished at the onset of this thesis, and using a vastly different methodology) and gray bamboo sharks have demonstrated a lack of susceptibility (Table 2). While these findings suggest both within and between species differences in illusion susceptibility, consistency has been observed across species in certain illusions. To date, *all* animals studied have demonstrated human-like susceptibility to the Ponzo and illusory contour illusions (Table 2).

While a large body of human illusion research exists, many of the theories and proposed mechanisms only explain human-like susceptibility to the illusion. Even within humans, there exists immense difficulty in extending common theoretical explanations, as presented in Table 1, across different illusions due to their visual variance (e.g. size, linear perspective and brightness) (Axelrod, Schwarzkopf, Gilaie-Dotan & Rees, 2017). Few studies have evaluated theoretical similarities across illusions (Carbon, 2014), and many of the theories described previously in Table 1 may not appropriately explain animal illusion susceptibility. Given these limitations, it is extremely difficult to apply these human-based theoretical accounts to animals, especially in instances where reversed or null susceptibility is observed. Moreover, such a comparison is only appropriate within illusions or across similar types of illusions.

However, collective assessments of illusion susceptibility, across a variety of illusion presentations, especially within a single species, may allow for a comparison of the similarities and differences of perceptual processing mechanisms. Animal illusion susceptibility, therefore, typically invokes discussion of perceptual style, specifically of local and global processing mechanisms. Within this framework, species that demonstrate human-like susceptibility are primarily classified as global processors, while species that

show null or reversed susceptibility are classified as local processors (Kelley & Kelley, 2014). It is important to note that existing studies are rarely directly comparable, due to vast differences (e.g. type of illusions, illusion modality, methodology, and training). Additionally, the evolution of these perceptual styles likely stems from differences in evolutionary pressures (Kelley & Kelley, 2014). It seems reasonable, given the ways in which an animal interacts within an environment (i.e. how they live, travel, eat, hunt, etc.), that certain perceptual styles may be more adaptive within certain ecological contexts (Kelley & Kelley, 2014). Despite all these factors, human-like susceptibility has been reported in 22 of the 31 experiments described above (Figure 2, Table 2). While this is a crude measure, it appears that animals, generally, have been observed to demonstrate human-like susceptibility to these cognitive geometric illusions. The immense variation emphasises that illusion susceptibility, as has been observed in humans, is a flexible experience.

While illusion susceptibility has been evaluated across a variety of animals, one neglected species is the domestic dog. Notwithstanding the ever-increasing amount of research conducted on canine cognition (for a comprehensive review see Bensky et al., 2013), no research at the onset of this thesis had been reported on canine illusion susceptibility. If perceptual differences can be observed in canine and human illusion susceptibility, the theoretical and practical implications are of paramount importance and potentially beneficial for both dogs and humans. An increased understanding is likely to further our knowledge of how dogs see the world, help researchers create more appropriate experimental paradigms, and may indirectly improve the many ways in which dogs co-interact with humans, including as companions, guides, or within various

working roles. Given the general pattern of human-like susceptibility in animals, it was expected that dogs would demonstrate human-like susceptibility to cognitive geometric illusions, demonstrative of dual processing of both bottom-up and top-down visual processing. However, to limit extraneous confounds, this thesis emphasises the need to evaluate perception in a single dog breed, in which facial morphology and eye structure are similar, and genetic and environmental conditions are controlled.

2.4 Summary

The primary aim of this chapter was to highlight and critically evaluate the current literature on canine vision, illusion susceptibility and visual processing. Despite the large amount of research conducted on canine cognition, primarily using visual paradigms, many questions remain unanswered. Specifically, how do fundamental aspects of dog vision affect more cognitively complex elements such as visual processing and perception? The literature review emphasised the need for more foundational vision research, as this may have broader implications for understanding how dogs see the world. This chapter also expanded on illusion susceptibility briefly discussed in the published review. In section 2.3, an overview of the four illusions to be addressed in this thesis was presented. Various proposed theoretical mechanisms from the human literature were discussed and evaluated within the context of animal illusion susceptibility. Finally, the significance of this line of research was applied to dogs, a species in which further exploration of visual perception is clearly pertinent.

Chapter 3 – Stimulus Generalisation in Dogs

In dog training, it is often, anecdotally, assumed that dogs are particularly poor at generalising their behaviours to novel situations. For instance, when teaching a dog the command ‘sit’ inside the house, it is generally believed that one must re-teach the command outside (e.g. Alexander, 2003; Cattet, 2013). These applied accounts contradict observations in canine cognition studies where researchers have observed successful generalisation within their paradigms (e.g. Range et al., 2008). As research explicitly assessing generalisation in dogs is limited, and given its particular relevance to the two-choice discrimination paradigm used to evaluate illusion susceptibility in this thesis, it was necessary to empirically evaluate if dogs could learn a rule and apply its properties across a variety of novel situations.

The nature of the two-choice discrimination paradigm utilised across the experiments in this thesis meant that dogs needed to be trained to learn a rule, which could be embedded into various novel contexts. Specifically, when presented with two solid circle stimuli, one on the left and one on the right, that differed in size (percent difference in diameter), the dogs were required to indicate which was the larger (or for some subjects, which was the smaller) one. This rule would then be generalised to novel presentations to evaluate their perceptual capabilities. To gauge the suitability of this paradigm, the study presented in this chapter set out to determine if dogs could generalise their previously learned rule (i.e. select or avoid a larger stimulus to obtain a reward) in a two-choice discrimination task when presented with pairs of shapes they had never seen.

The study was loosely based on Hanggi (2003) which evaluated relative size concepts across various 2-D and 3-D stimuli in horses. An assessment of relational concept learning in dogs is reported here, in the article titled 'Relational concept learning in domestic dogs: Performance on a two-choice size discrimination task generalises to novel stimuli', published in 2017 in Behavioural Processes.

3.1 Declaration for thesis Chapter 3

In the case of Chapter 3, contributions to the work involved the following:

Name (authors in order)	Extent of contribution (%)	Nature of contribution
Sarah-Elizabeth Byosiene Corresponding author	65	Study design, data collection and analysis, manuscript writing
Lynna Feng Co-author	5	Data collection and analysis
Philippe Chouinard Co-author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Tiffani Howell Co-author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Pauleen Bennett Senior author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication

Declaration by co-authors

The undersigned hereby certify that:

- (1) the below declaration correctly reflects the nature and extent of the candidate's contribution to this work, and the nature of the contribution of each of the co-authors;
- (2) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (3) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (4) there are no other authors of the publication according to these criteria; and
- (5) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor or publisher of journals or other publications, and (c) the head of the responsible academic unit.

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3.2 Relational concept learning in domestic dogs: Performance on a two-choice size discrimination task generalises to novel stimuli

Byosiere, S. E., Feng, L. C., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). Relational concept learning in domestic dogs: Performance on a two-choice size discrimination task generalises to novel stimuli. *Behavioural processes*, 145, 93-101.

3.3 Discussion

The objective of the study presented in this chapter was to ascertain if dogs could generalise a previously learned rule (i.e. select or avoid a large circle to obtain a reward) to novel stimuli. This was of particular relevance for this thesis as it was necessary to evaluate the appropriateness of using a two-choice discrimination in which novel illusory displays were embedded (Chapters 5 to 8). It was predicted that dogs would successfully be able to generalise their previously learned rule to novel stimuli. This prediction was confirmed; however, there were differences in dogs' generalisation capabilities across specific shapes, based on the degree of similarity to the trained discrimination.

In the experiment, dogs were presented with a two-choice size discrimination task in which they were trained to select either the larger or smaller of two circles. After successfully learning this task, pairs of eight novel shapes (ovals, squares, diamonds [a square tilted 45°], rectangles, triangles, stars, horizontal lines, and vertical lines) were presented. All dogs demonstrated successful generalisation of the rule to the shapes that were more or less similar to circles (ovals, squares, rectangles, diamonds, triangles, and stars), performing immediately at close to ceiling levels on the very first trial (for all shapes other than triangles). However, as a group, the dogs appeared unable to apply the rule to vertical or horizontal lines.

At first glance, the findings appear to indicate that dogs are capable of low-level stimulus generalisation, where generalisation is more likely to occur the more similar the novel stimulus is to the trained stimulus (Bouton, 2007). Upon further examination, the data revealed low-level stimulus generalisation could not solely explain the results. While a significant relationship was observed between the degree of similarity (how similar the

novel stimulus was to the trained stimulus) and performance, this effect was largely driven by the poor performance observed on the vertical and horizontal lines. When the line stimuli were removed from the analyses, no significant correlations were observed. This suggests that dogs successfully generalised their previously learned rule to novel stimuli, even as soon as the first presentation, regardless of the degree of similarity to the trained stimulus. In conclusion, while behavioural stimulus generalisation may be occurring, these findings also demonstrate a simplistic form of relational learning, where dogs not only compare the presented stimuli to one another but also apply an underlying concept developed through previous experience.

It is particularly curious that of all the shapes, the generalisation of the triangles did not transfer immediately. According to the Gabor-jet analysis that was performed to determine physical similarities between the different shapes, the triangles were deemed to be more similar to the trained circle shape than the stars. Yet, the dogs were more successful generalising to stars, a less similar shape, than triangles. While no significant correlation was observed between performance and area of the shape (both when the line stimuli were included and excluded), the triangle stimuli represented the greatest difference in area to the trained circle stimulus (excluding the line stimuli). Therefore, it is possible that difficulty in generalisation to the triangles stemmed from the combination of these two variables.

Of additional interest is the group performance when presented with the horizontal line stimuli in the first session. One explanation for the failure to generalise during this session is visual acuity. In the manuscript, it was proposed that perhaps the dogs, due to limitations in visual acuity, were unable to perceive the stimuli and thus

selected a stimulus at random. If this were the case, one would expect performance to be at chance. To the contrary, the dogs demonstrated a significant preference for selecting the *shorter* line (or for subjects trained to select the shorter, the longer line) when presented horizontally in the first session. Given the increased variation in this condition, the poor performance across the line stimuli, and the very limited number of trials, it appears that the most likely explanation for this result is that essentially this finding is random. Additional support for this conclusion can be drawn from the dogs' ophthalmological examination (Chapter 7), as well as a visual acuity test (that was not conducted as a part of this thesis). A co-authored manuscript (Graham et al., 2018) evaluated visual acuity (Table 3) through a forced-choice preferential looking task at 1 metre and 3 metre viewing distances. The study revealed no abnormalities such as myopia or hypermetropia (i.e. nearsightedness or farsightedness) that may have affected visual acuity (See Table 2 published in Graham et al., 2018). In conclusion, the findings from these chapter indicate the suitability of the two-choice discrimination paradigm, as well as identified optimally shaped stimuli which to embed within illusory displays.

Table 3

Highest estimated visual acuity recorded for each dog expressed in commonly reported notations

	<u>1m testing distance</u>					<u>3m testing distance</u>				
	LogMAR	Snellen (20ft)	Snellen (6m)	Decimal	Cycles per degree	LogMAR	Snellen (20ft)	Snellen (6m)	Decimal	Cycles per degree
Audrey	0.80	20/125	6/38	0.16	5.0	0.50	20/63	6/19	0.32	10.0
Baxter	0.45	20/56	6/17	0.36	11.25	0.30	20/39	6/12	0.51	15.0
Beth	0.54	20/69	6/21	0.29	9.0	0.47	20/58	6/17.5	0.34	10.75
Eliza	1.00	20/200	6/60	0.1	3.0	0.93	20/168	6/50.5	0.12	3.5
Gabbie	1.30	20/400	6/120	0.05	1.5	0.88	20/152	6/45	0.13	4.0
Hamish	1.15	20/283	6/85	0.07	2.25	1.08	20/238	6/71.5	0.08	2.6
Lulu	1.15	20/283	6/85	0.07	2.25	0.95	20/176	6/53	0.11	3.4
Molly	1.60	20/796	6/239	0.03	0.75	1.25	20/352	6/105	0.06	1.75

In order for stimuli to remain novel each experimental condition comprised only a few (10–20) trials per dog. This was necessary to evaluate relational concept transference of a previously learned rule to genuinely novel stimuli. While we observed striking results with such few trials, transposition paradigms are typically used to assess relational learning in animals. While this experiment was loosely based on Hanggi (2003), an extensive debate exists in regard to interpreting transposition task findings (for a review see Lazareva, 2012). Additional assessments of relational concept learning should, therefore, be conducted in dogs before overarching conclusions are made about relational learning. For the purpose of this thesis, these findings indicate the suitability of using a two-choice discrimination paradigm to evaluate illusion susceptibility, as dogs successfully generalised a previously trained rule to novel stimuli and contexts.

Chapter 4 – Colour Discrimination Capabilities in Dogs

One question that has long been a topic of interest for vision scientists is ‘do individuals see colours the same way’? Two (or more) individuals may agree that a certain object is yellow in terms of its focal colour, however, what remains unclear is whether their perception, specifically the subjective experience of perceiving the colour, is the same. In other words, is the subjective experience underlying my perception of yellow the same as another’s experience when they perceive yellow?

The perception of colour principally occurs due to the reflectance of light. Light in the form of wavelengths is either absorbed or reflected by the pigments on an object’s surface. Light, in the latter case, enters the eye and is processed by the photoreceptor cells in the retina. Specifically, cone and rod photoreceptor cells function to process and interpret visual information. Rods function in dim light conditions while cones aid perception of bright light and colour conditions. Humans have three types of cone photoreceptor cells: long-wave (red), medium-wave (green), and short-wave (blue), at spectral peaks of 558 nm, 531 nm, and 419 nm, respectively, indicating trichromatic colour perception. However, most mammals, dogs included, exhibit dichromatic colour perception, presumably comparable to red–green colour blindness in humans. Dogs possess photoreceptor cells equivalent to human short-wave and long-wave sensitivities (at spectral peaks of 555 nm and 429 nm) (Jacobs, Deegan, Crognale & Fenwick, 1993; Neitz, Geist & Jacobs, 1989). Given this physiological difference, it is often assumed that dogs are unable to perceive differences between green, yellow, and red colour cues (for a review see Rosengren, 1969). Behavioural studies have, however, provided conflicting reports with regard to colour perception in dogs. While some studies have found poor

colour discrimination capabilities (Neitz et al., 1989; Siniscalchi et al., 2017), others suggest that dogs can successfully discriminate a variety of colours across different brightness' (Rosengren, 1969; Tanaka, Watanabe, Eguchi & Yoshimoto, 2000).

These contradictory findings warrant further investigation, and concerning this thesis, this is justified by the need to understand optimal on-screen colour presentation(s). The findings presented in Chapter 3 suggest dogs can generalise their previously learned rule to novel *shapes*, however, what remains unknown is whether certain colour contrasts are optimal for on-screen presentations. Therefore, the purpose of the study reported in this chapter was to evaluate colour perception and physical luminance effects in dogs behaviourally. This unexamined interaction aims to clarify the discrepancies observed across previous behavioural assessments as well as to provide information in regard to the optimal colours for presenting visual stimuli to dogs. To our knowledge, the article presented in this chapter is one of the first to compare the discrimination of red and green, and blue and yellow colour cues in dogs across various degrees of physical luminance. The article is titled 'The effects of physical luminance on colour discrimination in dogs: A cautionary tale'. It was accepted for publication in the journal *Applied Animal Behavior Science* in January 2019.

4.1 Declaration for thesis Chapter 4

In the case of Chapter 4, contributions to the work involved the following:

Name (authors in order)	Extent of contribution (%)	Nature of contribution
Sarah-Elizabeth Byosiene Corresponding author	70	Study design, data collection and analysis, manuscript writing
Philippe Chouinard Co-author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Tiffani Howell Co-author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Pauleen Bennett Senior author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication

Declaration by co-authors

The undersigned hereby certify that:

- (1) the below declaration correctly reflects the nature and extent of the candidate's contribution to this work, and the nature of the contribution of each of the co-authors;
- (2) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (3) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (4) there are no other authors of the publication according to these criteria; and
- (5) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor or publisher of journals or other publications, and (c) the head of the responsible academic unit.

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4.2 The effects of physical luminance on colour discrimination in dogs: A cautionary tale

Byosiere, S. E., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2019). The effects of physical luminance on colour discrimination in dogs: A cautionary tale. *Applied Animal Behaviour Science*.

4.3 Discussion

The purpose of the study presented in this chapter was to understand colour discrimination capabilities in dogs and evaluate the effects of physical luminance within the two-choice discrimination task used to assess illusion susceptibility. Four experiments were conducted. In the first experiment, dogs discriminated between red and green, and between blue and yellow focal colours presented at their maximum RGB values, as well as between black and white controls. Results indicated that dogs were able to discriminate between red and green. This result was somewhat unexpected. However, because this initial experiment failed to address the effects of luminance, it was not possible to disentangle whether or not dogs used colour cues or brightness cues when discriminating between red and green. As they are not included in the published manuscript, Table 4 presents the effect sizes (Cohen's d) and degrees of freedom for the results presented in Chapter 4.

Table 4

<i>Effect sizes (Cohen's d) and degrees of freedom for results in Chapter 4</i>						
	Controls	Red on Green	Green on Red	Yellow on Blue	Blue on Yellow	df
Experiment 1	8.01	8.76	4.23	4.65	6.28	6
Experiment 2	23.3	8.34	7.29	10.0	6.16	5
Experiment 3	13.3	0.80	2.72	9.91	2.99	6
Experiment 4	21.2	6.51	14.23	7.40	2.89	5

To better understand why dogs were successful at discriminating between red and green in Experiment 1, Experiments 2 to 4 were conducted. In these experiments, the four focal colours (red, green, blue and yellow) were presented at equal physical luminance

levels across three different intensities. When the stimuli were presented at the lowest intensity, the dogs were successful at discriminating between red and green and between blue and yellow colours. As the stimuli increased in physical luminance, the task became more difficult. At the middle intensity, dogs demonstrated difficulty discriminating the red stimuli presented on a green background. When the stimuli were presented at the highest intensity, they demonstrated difficulty discriminating the blue stimuli presented on a yellow background. In summary, these findings suggest that dogs can discriminate between red and green, and blue and yellow focal colour contrasts at their maximum RGB values (Experiment 1), but in line with what was predicted, greater difficulty was observed when the physical luminance between the stimuli was identical (Experiment 3 and 4). This suggests that dogs appear to utilise colour cues, and performance between colour contrast combinations varies depending on the intensity of equally physical luminant stimuli.

These findings are particularly interesting considering dogs have been assumed to be red/green colour deficient like a human with deuteranopia. Dogs only have short-wave and long-wave spectral sensitivities, yet, behaviourally and under certain conditions, dogs are able to discriminate between red and green colours. In some cases, this behavioural indication of discrimination is possible even when stimuli have equal physical luminance. Moreover, it appears that under certain conditions, yellow and blue colour contrasts can also invoke difficulty in discrimination, even though the sensitivities for these wavelengths exist. These findings are in line with both physiological and behavioural evidence (Rosengren, 1969; Siniscalchi et al., 2017; Tanaka et al., 2000) and suggest that dogs likely perceive colour similarly to a deuteranope (Siniscalchi et al., 2017), a

red/green colour deficient human (Ishihara, 1918). Whether or not dogs subjectively perceive these colours similarly to humans is, of course, unanswerable at this time.

For the purpose of this thesis, the findings from Chapters 3 and 4 add to the foundational framework necessary to effectively evaluate illusion susceptibility in dogs. The conclusions from Chapter 3 suggest that dogs can successfully partake in the two-choice task implemented in the canine nose-touch apparatus, and can generalise previously learned rules to novel on-screen presented stimuli. The findings from this chapter are particularly instructive insofar as they allow for the creation of optimal stimuli to evaluate illusion susceptibility. Dogs were better at discriminating certain focal colour contrasts at specific intensities of physical isoluminance. Based on these conclusions, achromatic and blue/yellow focal colour contrasts (presented at the maximum RGB values in this experimental set-up) are ideal for stimulus presentation when testing illusion susceptibility. The following experiments presented in this thesis utilise these colour parameters.

Chapter 5 – Dog Susceptibility to the Ebbinghaus-Titchener and Delboeuf Illusions

In February 2015, the infamous photograph of “the dress” went viral, sparking a massive online debate about whether it was black and blue or white and gold. The phenomenon exposed differences in human perception of colour and has since been the subject of on-going scientific investigation (e.g. Lafer-Sousa, Hermann & Conway, 2015). This anecdote illustrates that it can be exceptionally challenging to evaluate perception even between humans, a verbal species that can easily communicate what they see. Therefore, it is not surprising that evaluating perception in non-verbal animals is problematic. Like “the dress,” one method, which has been proposed to evaluate perception comparatively, is visual illusion susceptibility (Feng et al., 2017; Fujita, 2004; Kelley & Kelley, 2014). Given that illusions occur when contexts trick the brain into misperceiving the environment, they offer an exclusive way to comparatively assess perception in verbal and non-verbal species alike (Fujita, 2004).

Since its introduction in 1901 (Titchener, 1901), susceptibility to the Ebbinghaus-Titchener illusion has been widely evaluated across humans of different ages (e.g. Doherty, Campbell, Tsuji & Phillips, 2010), cultures (e.g. de Fockert et al., 2007), and ability (e.g. Chouinard, Unwin, Landry & Sperandio, 2016). Its mechanistically similar counterpart (Sherman & Chouinard, 2016), the Delboeuf illusion has also been well-studied in humans (e.g. Coren & Girgus, 1978; Delboeuf, 1865; Nicolas, 1995), particularly recently in regard to plate size and human eating behaviour (e.g. Van Ittersum & Wansink, 2012).

As previously discussed in Chapter 2, the Ebbinghaus-Titchener and Delboeuf

illusions represent size-based distorting illusions. In most humans, and the majority of animals tested to date (Table 2, Chapter 2), the size of the target circle appears to increase when the inducers are small, or the ring is closer, and decrease when the inducers are large, or the ring is farther away (Pressey, Di Lollo & Tait, 1977; Zigler, 1960; Zigler & Phillips, 1960). Given dogs' unique co-evolution with humans (e.g. Clutton-Brock, 1995; Fox, 1978; Larson et al., 2012; Perri, 2016), specifically the convergence and similarities underlying the mechanisms of their unique socio-cognitive abilities (Bräuer et al., 2006; Hare, Brown, Williamson & Tomasello, 2002a; Hare et al., 2002b; Hare & Tomasello, 2005; Kaminski, 2009; Kaminski et al., 2012; Riedel et al., 2008; Udell et al., 2010), and human-like visual perception (Lind et al., 2017; Mongillo et al., 2016; Pitteri et al., 2014; Siniscalchi et al., 2017), it was predicted that dogs would demonstrate human-like susceptibility to both the Ebbinghaus-Titchener and Delboeuf illusions.

The article presented in this chapter was one of the first to assess illusion susceptibility in dogs (see also Miletto Petrazzini et al., 2016). The article is titled 'Visual perception in domestic dogs: susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions', and it was published in 2017 in *Animal Cognition*. It is important to note that the study design, data collection, and analysis for the Classical Ebbinghaus illusion was conducted as part of an Honours thesis completed by another student, while the study design for Illusory Contour Ebbinghaus-Titchener and Delboeuf illusions, data collection and analysis for Classical, Illusory Contour Ebbinghaus and Delboeuf illusions, and manuscript writing was conducted as part of this thesis.

5.1 Declaration for thesis Chapter 5

In the case of Chapter 5, contributions to the work involved the following:

Name (authors in order)	Extent of contribution (%)	Nature of contribution
Sarah-Elizabeth Byosiene Corresponding author	40	Study design for Illusory Contour Ebbinghaus-Titchener and Delboeuf illusions, data collection and analysis for Classical, Illusory Contour Ebbinghaus and Delboeuf illusions, manuscript writing
Lynna Feng Co-author	10	Study design for Classical Ebbinghaus illusion, data collection for Classical, Illusory Contour Ebbinghaus and Delboeuf illusions
Jessica Woodhead Co-author	15	Study design, data collection, and analysis for Classical Ebbinghaus illusion
Nicholas Rutter Co-author	10	Data collection for Classical Ebbinghaus illusion
Philippe Chouinard Co-author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Tiffani Howell Co-author	5	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Pauleen Bennett Senior author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication

Declaration by co-authors

The undersigned hereby certify that:

- (1) the below declaration correctly reflects the nature and extent of the candidate's contribution to this work, and the nature of the contribution of each of the co-authors;
- (2) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (3) they take public responsibility for their part of the publication, except for the

- responsible author who accepts overall responsibility for the publication;
- (4) there are no other authors of the publication according to these criteria; and
- (5) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor or publisher of journals or other publications, and (c) the head of the responsible academic unit.

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5.2 Visual perception in domestic dogs: susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions

Byosiere, S. E., Feng, L. C., Woodhead, J. K., Rutter, N. J., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). Visual perception in domestic dogs: susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions. *Animal cognition*, 20(3), 435-448.

5.3 Discussion

The purpose of the experiments presented in this chapter was to determine if dogs demonstrated human-like susceptibility when presented with the Ebbinghaus-Titchener and Delboeuf illusions. An additional aim was to compare the findings to those observed in other animals, highlighting similarities and differences in perception, or more specifically misperception. To do so, this chapter applied critical foundational components from Chapters 3 and 4, to create optimal illusory displays in which to embed two presentations of the Ebbinghaus-Titchener illusion and one presentation of the Delboeuf illusion.

Intriguing findings across the three presentations were observed. When presented with the classic presentation of the Ebbinghaus-Titchener illusion, dogs, as a group, demonstrated misperception, however, in a way opposite to that typically observed in humans. A second presentation of the illusion was conducted to clarify the findings. This presentation consisted of an illusory contour version of the Ebbinghaus-Titchener in which specific confounds (such as overall stimulus size) were systematically controlled. The findings once again revealed a reversed susceptibility to the Ebbinghaus-Titchener illusion. Finally, dogs were presented with a classic presentation of the Delboeuf illusion, a mechanistically similar illusion. As a group, the dogs performed at chance, demonstrating null susceptibility to the illusion.

The results from this experiment are unique, unexpected, and counter the original prediction. The reversed susceptibility to the Ebbinghaus-Titchener illusions suggests that dogs perceive the illusory stimuli differently from humans and most other animal species tested to date (Fuss & Schluessel, 2017; Murayama et al., 2012; Parron & Fagot, 2007;

Salva et al., 2013; Sovrano et al., 2014). While reversed susceptibility to this illusion is not unique, it has typically been explained by a preference for local processing (Nakamura et al., 2008; Nakamura et al., 2014). Originally, this explanation in dogs was reported to be unlikely as the only precedence study conducted on dogs observed a general preference for the global processing of stimuli (Mongillo et al., 2016). However, this general preference was not statistically significant, and more recent research suggests that there is evidence for a local processing preference in dogs (Kanizsár et al., 2018).

The null susceptibility observed towards the Delboeuf illusion is consistent with another behavioural assessment, which was published independently in *Animal Cognition* by a different group of researchers in tandem with this article. These two experiments provide converging evidence for null susceptibility to the Delboeuf illusion (Miletto Petrazzini et al., 2016). Given susceptibility to this illusion has been observed to be quite variable across species (Table 2, Chapter 2), and the illusory effects in humans are much weaker compared to the Ebbinghaus-Titchener (Sherman & Chouinard, 2016), these results are not completely surprising. However, additional research should be conducted to confirm these conclusions.

In regard to the theoretical mechanisms underlying the Ebbinghaus-Titchener and Delboeuf illusions, human-like susceptibility is typically explained by contour interaction theory (Jaeger, 1978), where the inducer circles close to the target perceptually attract while the contours of inducer targets further away perceptually repel. Given the reversed finding, this explanation cannot be applied to dogs. However, an alternative theoretical mechanism, assimilation theory (Pressey, 1971), can be applied. This theory suggests that target stimuli are perceptually rescaled to appear more similar to the inducers when

presented with the illusion. This theoretical explanation is supported by the Gestalt law of similarity, which purports that similar objects, close together in space, will perceptually be grouped and treated as different examples of the same object (Koffka, 1935). While assimilation theory represents the most suitable explanation for the findings presented in this chapter, additional assessments of canine illusion susceptibility are required to identify and compare the extent of these mechanistic similarities and differences.

Chapter 6 – Dog Susceptibility to the Ponzo Illusion

The experiment conducted in Chapter 5 was one of the first studies to evaluate illusion susceptibility in dogs (see also Miletto Petrazzini et al., 2016). Dogs demonstrated reversed susceptibility compared to humans and most other animal species (Fuss & Schluessel, 2017; Murayama et al., 2012; Parron & Fagot, 2007; Salva et al., 2013; Sovrano et al., 2014) when presented with two different versions of the Ebbinghaus-Titchener illusion and were not susceptible to the Delboeuf illusion (see also Miletto Petrazzini et al., 2016). Contrary to original predictions, these findings provide preliminary evidence that dogs and humans may differ in the mechanisms underlying illusion susceptibility. To comprehensively evaluate this claim, it was necessary to expand this line of inquiry to other illusions, particularly those in which different mechanisms and theoretical explanations have been proposed.

The Ponzo illusion, like the Ebbinghaus-Titchener and Delboeuf illusions, represents a distorting illusion. However, it differs in the theoretical mechanisms proposed to explain it as it is mediated by linear perspective cues. Typically, inappropriate constancy scaling theory (Gregory, 1963) is used to explain susceptibility to this illusion (Table 2, Chapter 2). This theoretical explanation suggests that two identically sized targets are perceived to be different in size due to the placement of converging inducer lines, which induce linear perspective cues. However, integration field-theory (Pressey & Epp, 1992) has also been proposed to explain this illusion, suggesting that converging inducer lines invoke attentional demands to the space in between, which results in misperception of the target lines. Unlike other geometric illusions, the Ponzo illusion is unique in the sense that human-like susceptibility has been

observed in every species tested to date (Barbet & Fagot, 2002; Bayne & Davis, 1983; Fujita, 1996; Fujita, 1997; Fujita et al., 1991; Imura et al., 2008; Nakagawa, 2002; Timney & Keil, 1996). The extent to which this is a by-product of a publishing bias against null findings remains unknown. Regardless, considering this consistency across animals, the purpose of this study was to assess canine susceptibility to the Ponzo illusion and to expand on the underlying theoretical mechanisms, specifically concerning the observations in Chapter 5.

The journal article, ‘Do dogs see the Ponzo illusion?’ was published in *Animal Behavior and Cognition* in 2017. Of particular relevance to this thesis, is that the study design, data collection, and analysis for Experiment 1 was conducted as an Honours thesis by another student, while the study design for Experiments 3 and 4, data collection and analysis, and manuscript writing for Experiments 1, 2, 3, and 4 was conducted as a part of this thesis.

6.1 Declaration for thesis Chapter 6

In the case of Chapter 6, contributions to the work involved the following:

Name (authors in order)	Extent of contribution (%)	Nature of contribution
Sarah-Elizabeth Byosiene Corresponding author	40	Study design for Experiments 3 and 4, data collection and analysis for Experiments 1, 2, 3, and 4, manuscript writing
Lynna Feng Co-author	10	Study design for Experiment 1, data collection for Experiments 1, 2, 3, and 4
Nicholas Rutter Co-author	15	Study design, data collection, and analysis for Experiment 1
Jessica Woodhead Co-author	10	Data collection for Experiment 1
Philippe Chouinard Co-author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Tiffani Howell Co-author	5	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Pauleen Bennett Senior author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication

Declaration by co-authors

The undersigned hereby certify that:

- (1) the below declaration correctly reflects the nature and extent of the candidate's contribution to this work, and the nature of the contribution of each of the co-authors;
- (2) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (3) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (4) there are no other authors of the publication according to these criteria; and

(5) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor or publisher of journals or other publications, and (c) the head of the responsible academic unit.

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6.2 Do dogs see the Ponzo illusion?



Do Dogs See the Ponzo illusion?

Sarah-Elizabeth Byosiere*, Lynna C. Feng, Nicholas J. Rutter, Jessica K. Woodhead,
Philippe A. Chouinard, Tiffani J. Howell, and Pauleen C. Bennett

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Citation – Byosiere, S-E., Feng, L.C., Rutter, N.J., Woodhead, J.K., Chouinard, P.A., Howell, T.J., & Bennett, P.C. (2017). Do dogs see the Ponzo illusion? *Animal Behavior and Cognition*, 4(4), 396 - 412.
<https://dx.doi.org/10.26451/abc/04.04.01.2017>

Abstract – While domestic dogs (*Canis familiaris*) play a large role in human daily lives, little is known about how they perceive the visual world. Recent research suggests that dogs may perceive certain visual illusions differently than humans. To further evaluate geometric illusion susceptibility, eight dogs were assessed on their susceptibility to the Ponzo illusion. Four experiments were conducted: 1) a presentation of the Ponzo illusion with target circles in a ‘grid inducer context’, 2) a re-test of Experiment 1 after additional training, 3) a presentation of the Ponzo illusion with target rectangles in a ‘grid inducer context’ and 4) a presentation of the Ponzo illusion with target circles in a ‘converging lines context.’ A one-sample t-test of the dogs’ responses to the Ponzo stimuli in Experiment 1 demonstrated illusion susceptibility at the group level; however, no individual dog performed significantly above chance in binomial tests. In Experiments 2, 3, and 4, one-sample t-tests found no significant results at the group level, although one or more dogs did demonstrate a small but significant effect. Taken together, then, there was limited evidence for dogs’ susceptibility to the Ponzo illusion in a two-choice discrimination paradigm. As most animals tested previously have demonstrated human-like susceptibility to the Ponzo illusion, these findings have implications for theoretical explanations. The divergence of results between dogs and humans/other animals suggest that mechanisms underlying perception of the Ponzo illusion may differ across species and that care should be taken when using visual paradigms to test dogs’ cognitive skills.

Keywords – Ponzo illusion; Geometric illusion; Domestic dog; Perception; Two-choice discrimination

Visual perception represents interpretation of retinal information by the brain, which 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 reflect reality, given that the brain often adapts visual information from the retina to fit preconceptions (Gregory, 2015). Geometric illusions provide an opportunity to examine perceptual processes by inducing these largely adaptive preconceptions, or ‘corrections’ to visual information, in contexts where visual corrections are unnecessary.

One of the most widely studied visual illusions is the Ponzo illusion. This illusion typically consists of two equally sized targets (e.g., circles or lines) that appear unequal when superimposed over converging lines (Figure 1). Several explanations for the Ponzo illusion have been proposed. One of the most popular, Gregory’s (1963) Inappropriate Constancy-Scaling theory proposes 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 circle nearest to the apex of the converging lines appears larger as it is perceived as

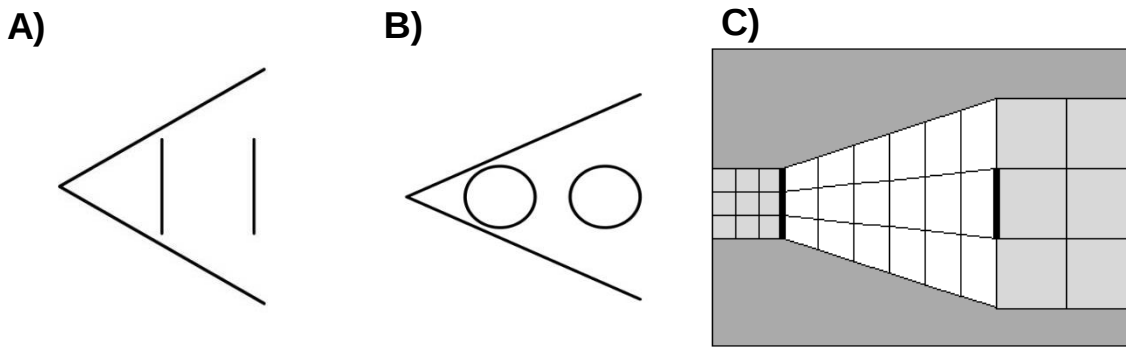


Figure 1. Three examples of the Ponzo illusion, where **A** and **C** utilize identically sized horizontal bars, and **B** utilizes identically sized circles. **A** and **B** are presentations using a ‘converging lines’ context whereas **C** is a presentation using a ‘grid inducer’ context. Here, the object closer to the apex of the converging lines, or in the smaller inducer grid, appears larger than the other object.

being further away, causing the viewer to inappropriately compensate for this distance in order to maintain size constancy. In contrast, Assimilation theory has been proposed by Pressey (1971) to explain the Ponzo illusion based on two main postulates, which are as follows:

- (1) Whenever judgments are made of a series of magnitudes, the smaller magnitudes in that series will be overestimated and the larger magnitudes will be underestimated. (2) Other things being equal, a context which falls within the attentive field will be more effective than a context outside that field (Pressey, 1971, p. 172).

Here, the target closest to the apex is said to appear larger as it is closer to the contextual lines than the alternative target. Furthermore, visually estimating the differences in stimuli size narrows the observer’s attentive field in a tunnel-vision like way, through which little of the surrounding context is considered, except that closest to the stimuli. Consequently, the stimulus closest to the context lines is ‘assimilated,’ thereby causing the perceiver to overestimate its size (Fujita, 1997).

Regardless of the specific mechanisms inducing the Ponzo illusion, research to date suggests that most humans are susceptible to the illusion. However, there is some evidence of cross-cultural differences in susceptibility (Brislin & Keating, 1976; Segall, Campbell, & Herskovits, 1963), in addition to the fact that susceptibility may be inversely correlated with the size of an individual’s primary visual cortex (Song, Schwarzkopf, & Rees, 2011). Furthermore, the Ponzo illusion has also been widely assessed across animal taxa (Feng, Chouinard, Howell, & Bennett, 2016). For instance, 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 been studied, with all species to date demonstrating susceptibility to the illusion in the same manner as humans.

Dogs represent a unique model for examining illusory susceptibility. However, to our knowledge their susceptibility to the Ponzo illusion has not yet been examined. Over the last 30,000 years, humans and dogs have evolved within similar ecological niches (Wang et al., 2013). Given this shared evolutionary development, it is plausible that certain evolutionary pressures, such as habitat, may have driven co-evolutionary processes (Geisler & Diehl, 2002). While little research has been conducted on the extent of visual perceptive abilities in domestic dogs, a basic understanding of how dogs detect light, process colors, and perceive motion, is available (Miller & Murphy, 1995). To our knowledge, however, only two studies have gauged susceptibility to geometrical illusions in dogs. These provided puzzling results. Byosiere et al. (2016) found that dogs misperceived the Ebbinghaus-Titchener illusory stimuli, but responded in a reversed manner compared to humans and most other mammals, indicating that the

stimulus humans perceive as being larger is perceived by dogs as being smaller. Furthermore, while dogs as a group appear not to be susceptible to the Delboeuf illusion, certain individuals may demonstrate susceptibility, also in a reversed direction than humans and other mammals (Byosiére et al., 2016; Miletto Petrazzini, Bisazza, & Agrillo, 2016).

Variation in illusion susceptibility is not unique to dogs. A variety of studies have found human-like susceptibility, no susceptibility, or reversed susceptibility in animals (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). Additionally, even within species mixed evidence has been observed in regards to susceptibility to the same illusion (e.g., Nakamura et al., 2008; Nakamura, Watanabe, & Fujita, 2014; Salva, Rugani, Cavazzana, Regolin, & Vallortigara, 2013). Therefore, the intriguing findings observed in previous studies of dogs warrant further investigation of dogs' illusory susceptibility.

The aim of this study was to determine whether dogs demonstrate susceptibility to the Ponzo illusion. We predicted that dogs would accurately indicate the relative size of two differently sized target stimuli, following an appropriate training regimen, regardless of the background context in which these stimuli were presented. However, we had no a-priori predictions in regards to performance in the illusion condition. While susceptibility to the Ponzo illusion is widespread and has been observed in humans and other mammals (Barbet & Fagot, 2002; Bayne & Davis, 1983; Fujita, 1996, 1997; Fujita et al., 1991; Imura et al., 2008; Nakagawa, 2002; Timney & Keil, 1996), the fact that dogs have previously demonstrated reversed susceptibility or no susceptibility when presented with other geometric illusions (Byosiére et al., 2016; Miletto Petrazzini et al., 2016) meant that we were unable to predict if dogs would perceive the illusion at all and, if they did, whether this would be in the same or opposite manner to humans.

General Methods

Subjects

Eight companion dogs (*Canis familiaris*), six females and two males, participated in this study (at the start of Experiment 1, mean age = 1 year, 8 months; age range = 9 months to 6.5 years). All dogs were purebred Lagotto Romagnolos and sexually intact except for two (Gabbie and Baxter) who were spayed or neutered respectively during the period of data collection. All dogs had previously participated in an experiment assessing illusion susceptibility (Byosiére et al., 2016) as well as one testing relational class concepts (Byosiére et al., under review).

Apparatus

Testing was conducted in the Canine Nose-Touch Testing Apparatus, a 1540 mm x 600 mm x 600 mm wooden apparatus designed for a different study (Byosiére et al., 2016), in order to reduce experimenter-expectancy effects and environmental distractions. The testing chamber was equipped with a 508 mm Dell® widescreen computer monitor for stimulus presentation (1280 x 800 pixels; one pixel measures approximately 0.3 mm²), positioned with the lower edge approximately 24 cm above ground level. Below it, at ground level, was a remotely controlled treat dispenser (Treat & Train®) that, when activated, 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 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.

Training Procedure

Dogs were initially trained based on their individual performance, beginning in April 2015 and continuing for four months, to target a black 80-mm diameter circle via a nose-touch. Target stimuli were

first presented in a trainer's hand, and then glued to a wall (45cm above the ground). This behavior was transferred to nose-touching a 62-mm circle presented in random locations on a computer monitor housed in an open room. Once this stimulus training was complete, the dogs were familiarized with the Canine Nose-Touch Testing Apparatus and 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 one (Baxter), who was trained to select the smaller circle. This is due to the fact that the dogs were originally 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 for 12 weeks, following which he or she was tested for accuracy. 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. We decided that rather than exclude Beth, Eliza and Lulu from the study, we would retrain them to select the large circle. When tested four weeks later, all three met the criteria of 80% correct responses.

At the conclusion of the pre-training process, all dogs could reliably discriminate between two identical circle stimuli varying in pixel diameter size by 60% (106 pixels, 31.8 mm, and 207 pixels, 62.1 mm in diameter; 207 pixels, 62.1 mm, and 403 pixels, 120.9 mm in diameter) averaging an accuracy rate of 78.4% (65 – 87%). When presented with two circles that were identical in size (207 pixels, 62.1 mm, in diameter), each dog's performance was at chance levels of 54.7% (47.5 – 72%). The dogs typically participated in the experiments enthusiastically. Although data were recorded manually, the dog's responses were typically very easy to distinguish. In our previous study, we assessed inter-observer reliability using a random sample of the video-recorded data ($n = 150$) and found it was 99.3% (Byosiére et al., 2016).

Testing 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. This person presented and removed the stimuli, while recording the data. Exp B was positioned at the front-right side of the apparatus, 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 remotely controlled treat dispenser located below the computer monitor and signaled to Exp A to record a correct choice. If the dog chose incorrectly, and 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. Once the dog returned to Exp A, the dog received occasional food rewards. This meant that the dogs were rewarded simply for participating in the experiment, which helped to maintain motivation even when performance was suboptimal.

Before each experiment, all dogs underwent familiarization sessions in which the target stimuli were presented over a non-illusory background (Figure 2) to acquaint the dogs with new images, such as inducers and/or colors, which would be present in the experimental trials. In these sessions, target stimulus pairs were presented in blocks of ten trials, with five presentations each of S₄-S₇ and S₇-S₁₀ stimuli being included in random order. The correct stimulus pseudo-randomly appeared on each side for an equal number of times in accordance with randomly selected Gellerman (1933) sequences. Six types of familiarization trials were conducted for Experiments 1 and 3, and one type for Experiments 2 and 4 (Figure 2). Type 6 was the only familiarization type conducted for Experiment 2 as this was a re-test of Experiment 1. Dogs progressed to the next type of familiarization trial 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 testing 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, the dog was excluded from participating in the testing condition.

Experiment 1 and 2

Type 1				
Type 2				
Type 3				
Type 4				
Type 5				
Type 6				

Experiment 3

Type 1				
Type 2				
Type 3				
Type 4				

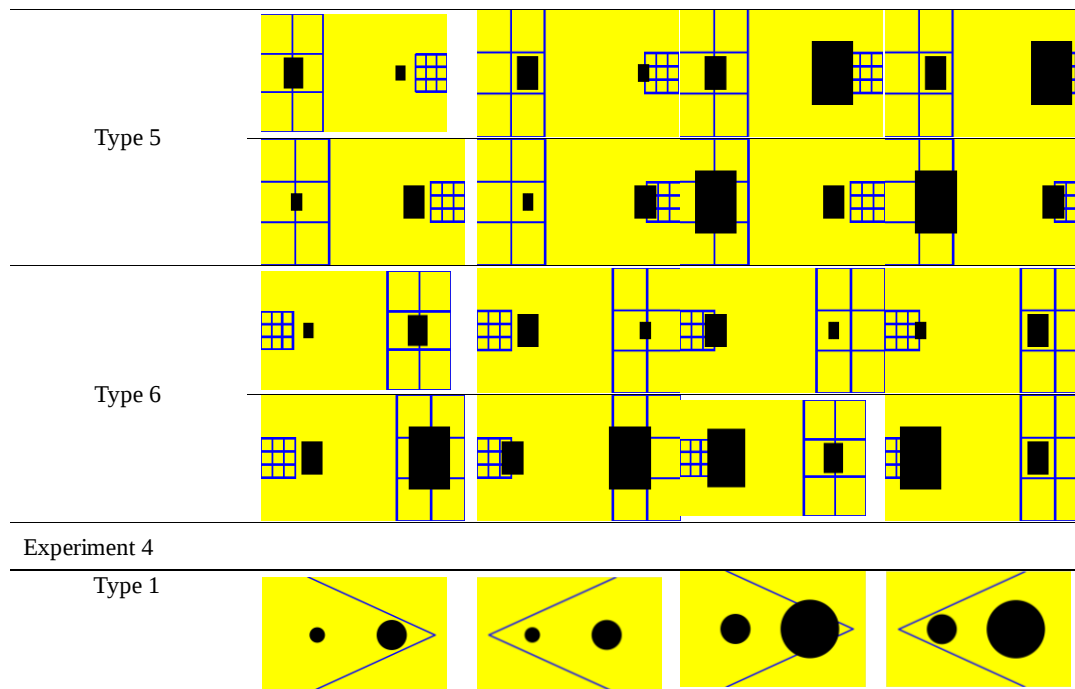


Figure 2. Familiarization stimuli used in Experiment 1 and 2 employing the circle ‘grid inducer context’, Experiment 3 employing the rectangle ‘grid inducer context’, and Experiment 4 employing the ‘converging lines context.’

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. Ten blocks of ten trials were administered for each experiment, resulting in 100 trials per dog (60 control trials, 40 experimental trials). Each round of ten trials consisted of six control trials, including three comparisons of S₄-S₇ and three comparisons of S₇-S₁₀ (control condition), and four experimental trials of S₇-S₇ comparisons (illusion condition).

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 sequence to order the trials. If the Gellerman sequence dictated that the target stimulus 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 target stimuli were identical in size, and even though a particular target stimulus may have been ‘correct’ insofar 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 and are notated in the data presented below.

Compliance with Ethical Standards

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in the following experiments were in accordance with the ethical standards of La Trobe University Animal Ethics Committee (approval number: AEC15-18 and AEC16-26). This article does not contain any studies with human participants performed by any of the authors. Informed consent was obtained from all dog owners included in the study.

Experiment 1

Experiment 1 was conducted to determine whether dogs demonstrated susceptibility to the Ponzo illusion. Target stimuli consisted of black (RGB values 0, 0, 0; Luminance 0.18 c/m²) circles presented on a highly contrasting yellow background (RGB values 255, 255, 0; Luminance 163.6 c/m²) with blue

contextual grids (RGB values 0, 0, 255; Luminance 16.05 c/m²) (Figure 3). The colors used were determined based on the fact that dogs are dichromatic, with two types of cone photoreceptor cells, for blue and yellow (Jacobs, Deegan, Crognale, & Fenwick, 1993; Neitz, Geist, & Jacobs, 1989) and based on previous research suggesting dogs are capable of perceiving differences between yellow and blue stimuli (Kasparson, Badridze, & Maximov, 2013).

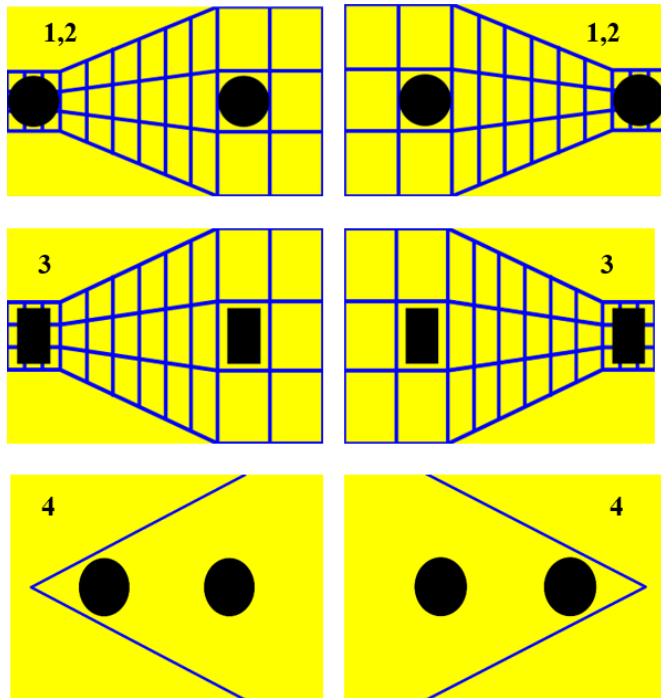


Figure 3. Ponzo illusion used in Experiments 1, 2, and 3 employing the ‘grid inducer context’ and the classic presentation in Experiment 4 employing the ‘converging lines context.’ The perceptually larger target stimulus appears on the left in the image on the left, and on the right in the image on the right.

The circles sizes were based on 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 in this same group of dogs (Byosiére et al., 2016). Three circle stimuli were used: S₄ circles were 106 pixels or 31.8 mm in diameter; S₇ circles were 207 pixels or 62.1 mm in diameter; S₁₀ stimuli were 403 pixels or 120.9 mm in diameter (Figure 4). 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.

Experiment 2

Due to the significant group effect observed in Experiment 1, but the lack of an individual effect, Experiment 2 was conducted to replicate Experiment 1. Therefore, the stimuli and procedure were identical to those listed above.

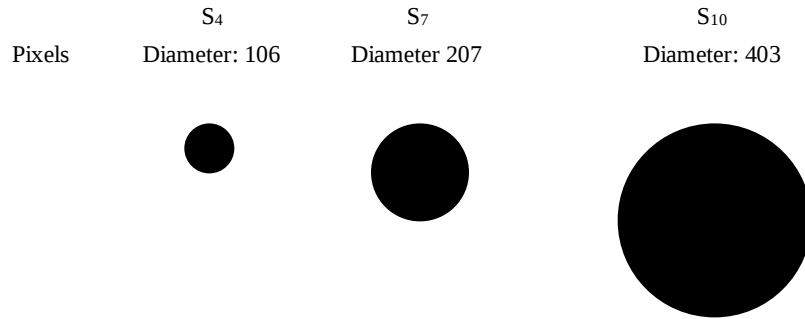


Figure 4. Schematic representation of circle stimuli implemented in the study with pixel values representing the diameter. Circles are provided to aid conceptual understanding only and are not actual size.

Experiment 3

In Experiment 3, we aimed to clarify the findings observed in Experiments 1 and 2. To determine if the results of the replication experiment (Experiment 2) were due to familiarity with the stimuli, we adapted the experiment and used novel target stimuli. Experiment 3 was identical to Experiments 1 and 2, barring the fact that rectangles were used as target stimuli instead of circles (Figure 5). Target stimuli consisted of black (RGB values 0, 0, 0; Luminance 0.18 c/m²) rectangles presented on a highly contrasting yellow background (RGB values 255, 255, 0; Luminance 163.6 c/m²) with blue contextual grids (RGB values 0, 0, 255; Luminance 16.05 c/m²) (Figure 3). Rectangle stimuli were chosen based on previous research conducted in our lab that indicated successful generalization from circles to novel rectangle shapes by the dogs in this study (Byosiére et al., under review). Three rectangle stimuli were presented in pairs of approximately S₄-S₇ and S₇-S₁₀. S₄ rectangles were 68.9 pixels in width and 106 pixels in height (20.6 x 31.8 mm). S₇ rectangles were 134.5 pixels in width and 207 pixels in height (40.3 x 62.1 mm). S₁₀ rectangles were 261.9 pixels in width and 403 pixels in height (478.5 x 120.9 mm).

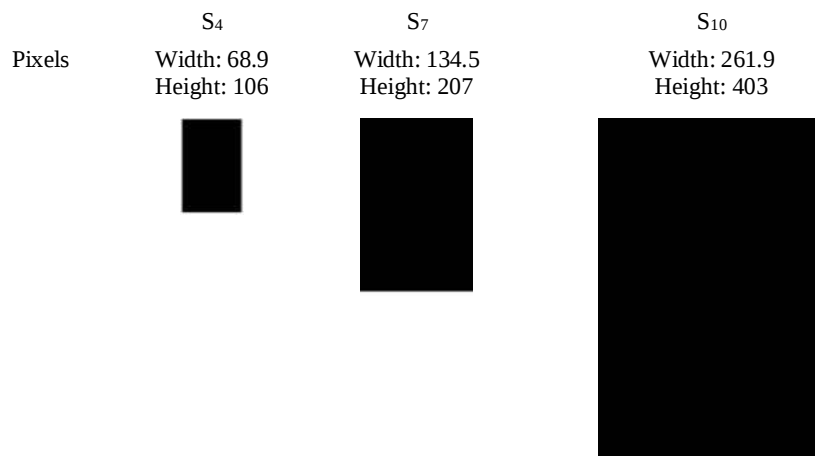


Figure 5. Schematic representation of rectangle stimuli implemented in the study with pixel values representing the width and height. Rectangles are provided to aid conceptual understanding only and are not actual size.

Experiment 4

Due to the differences observed in the results across Experiments 1, 2, and 3, we aimed to verify if these findings were due to the context in which the stimuli were presented. Therefore, in Experiment 4 we utilized the classic presentation in which the Ponzo illusion is usually presented. Target stimuli once again consisted of black (RGB values 0, 0, 0; Luminance 0.18 c/m²) circles presented on a highly contrasting 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).

Data Analysis

To determine if dogs were performing significantly above chance, two-tailed binomial tests were conducted on each dog's individual 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. Effect sizes were calculated for each illusion condition based on the means of the group. To examine group performances each illusion was analyzed using a two-tailed, one-sample *t*-test, conducted on the dogs' average proportion correct. Effect sizes (Cohen's *d*) are also reported.

Results

Experiment 1

The dogs generally performed extremely well in the familiarization sessions. On average, it took 1.27 blocks of ten trials for the group as a whole to progress to the next level, with stimulus types Two and Six appearing to be the most difficult, averaging 1.38 blocks each.

Figure 6 shows individual performance data for each dog in the test sessions. It is evident that performance in the control conditions was uniformly high, as the average level of performance was 82.7% $\pm$ 6.7. Binomial tests indicated that all dogs were significantly above the chance score of 50%. In contrast,

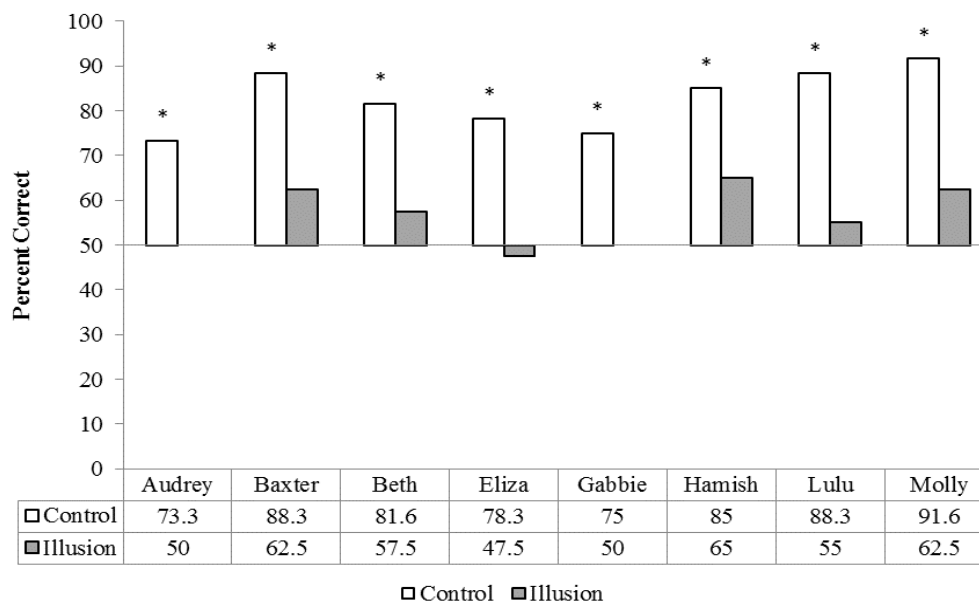


Figure 6. Individual percent correct for control and illusion conditions in Experiment 1.

*Indicates that the binomial result significantly differed from chance level at $p < 0.05$. Correct trials in the illusion condition were defined as those in which the dog selected the stimulus that, to humans, would appear larger (or smaller in the case of Baxter).

dogs averaged $56.25\% \pm 6.7$ in the illusion condition. Despite this, the result of the two-tailed one-sample *t*-test conducted on the dogs' average proportion correct for the illusion condition in Experiment 1 was significant, indicating susceptibility to the illusion in a human-like direction [$t(7) = 2.65$, $p = 0.033$, $SD = 6.68$, Cohen's $d = 0.9328$]. 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, there was insufficient evidence to suggest that any individual dog was susceptible to the illusion above chance levels at $\alpha = 0.05$ ($p \geq 0.06$ for all tests). Interestingly, the effect size was extremely large considering dogs averaged only 56.25% and no individual performed significantly above chance. This likely reflects the small standard deviation observed across trials.

Experiment 2

Given that, as a group, the dogs demonstrated significant susceptibility to the Ponzo illusion in Experiment 1, while no dog performed significantly above chance individually, it was decided to repeat the experiment. Unfortunately, in the intervening period the dogs had been used in an additional study testing their sensitivity to size differences of various magnitudes (Byosiére et al., in prep). They were therefore extremely practiced at the discrimination task. Regardless, the dogs performed extremely well in the repeat presentation of familiarization Type 6. On average, it took 1.25 blocks of ten trials for the group as a whole to progress from the single familiarization session to the test session.

Figure 7 shows individual performance data for each dog. Performance in the control conditions was again uniformly high, as the average level of performance was $94.7\% \pm 6.9$. Binomial tests indicated that all dogs were significantly above the chance score of 50%. In contrast, dogs as a group averaged only $48.1\% \pm 12.5$ in the illusion condition. Results of the two-tailed, one-sample *t*-test for the illusion condition of the group in Experiment 2 were not significant [$t(7) = 0.42$, $p = 0.685$, $SD = 12.52$, Cohen's $d = -0.1498$]. Only one dog, Baxter, performed significantly above chance level, demonstrating human-like susceptibility to the illusion (72.5% , $p < 0.01$). All other dogs recorded responses that did not significantly differ from chance levels ($p \geq 0.11$).

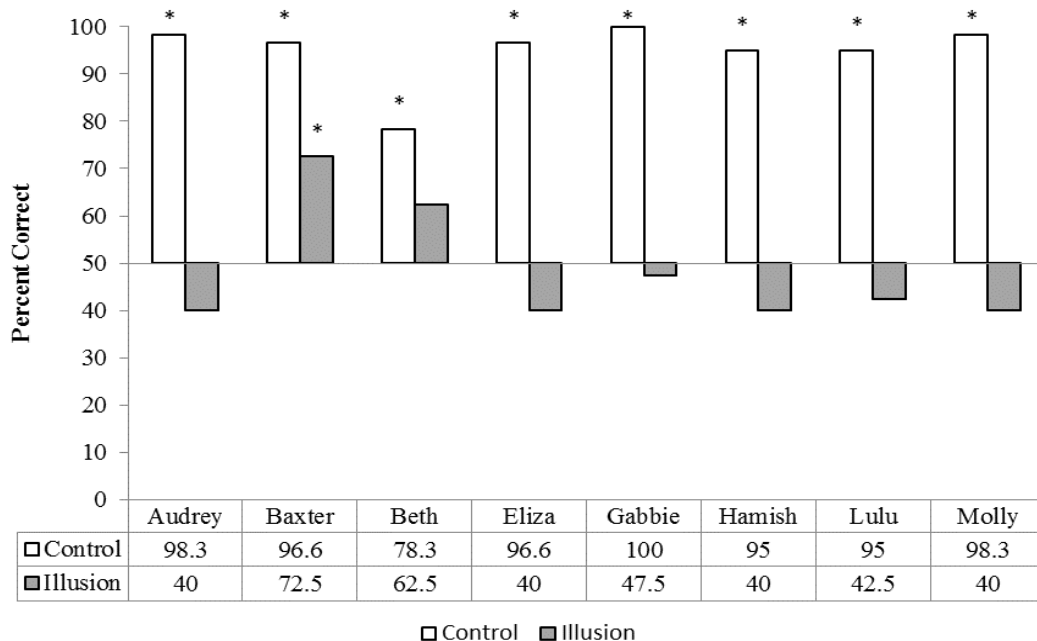


Figure 7. Individual percent correct for control and illusion conditions in Experiment 2.

*Indicates that the binomial result significantly differed from chance level at $p < 0.05$. Correct trials in the illusion condition were defined as those in which the dog selected the stimulus that, to humans, would appear larger (or smaller in the case of Baxter).

Experiment 3

Given the differences observed in the results of Experiment 1 and 2, we conducted Experiment 3 in order to present the dogs with a novel target stimulus, rectangles. Once again, the dogs performed extremely well in the familiarization sessions. On average, it took 1.81 blocks of ten trials for the group as a whole to progress to the next level, with Type 1, 3, 4 and 6 stimuli (see Figure 2) being the most difficult and requiring an average of 2 blocks of ten trials. Performance between dogs was more variable in this experiment, however, with Beth and Eliza being excluded from testing as they reached the maximum seven attempts in Type 1 and 4, respectively.

Figure 8 shows individual performance data for each dog. Performance in the control conditions was once again uniformly high, as the average level of performance was $85\% \pm 7$. Binomial tests indicated that all dogs were significantly above the chance score of 50%. In contrast, dogs as a group averaged only $45.8\% \pm 15.5$ in the illusion condition. Results of the two-tailed, one-sample *t*-test for the illusion condition of the group in Experiment 3 were not significant [$t(5) = 0.66$, $p = 0.53$, $SD = 15.46$, Cohen's $d = -0.269$]. Again, individuals varied greatly in the illusion condition. Consistent with his performance in Experiment 2, Baxter performed significantly above chance level, indicating susceptibility to the illusion in the same direction as humans ($p = 0.03$). Gabbie and Lulu performed significantly below chance level, indicating susceptibility in the opposite direction to humans ($p \leq 0.03$). The three remaining dogs performed at chance ($p \geq 0.21$).

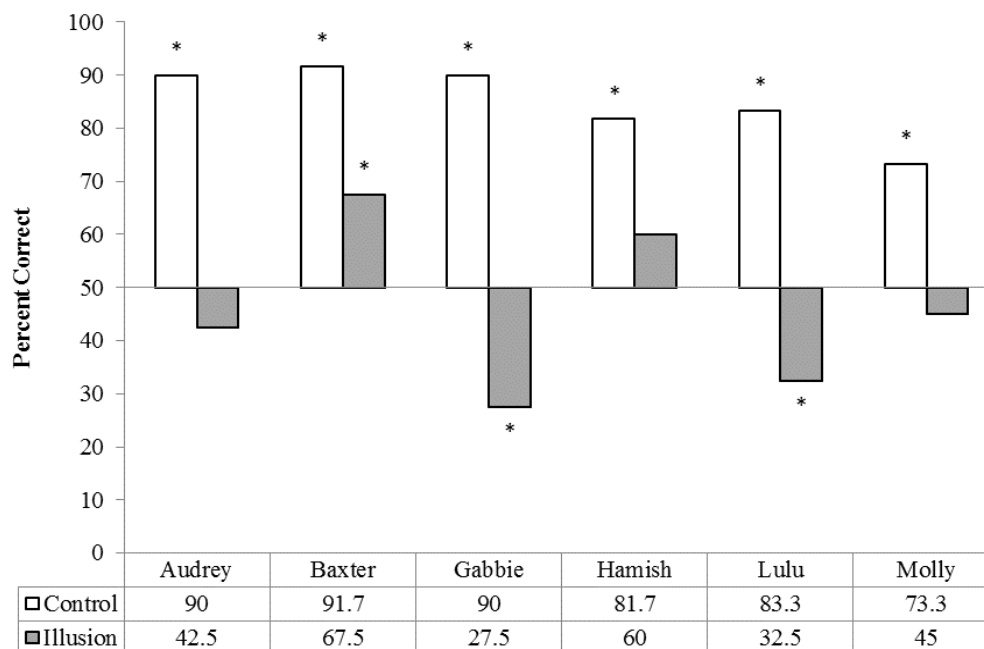


Figure 8. Individual percent correct for control and illusion conditions in Experiment 3.

*Indicates that the binomial result significantly differed from chance level at $p < 0.05$. Correct trials in the illusion condition were defined as those in which the dog selected the stimulus that, to humans, would appear larger (or smaller in the case of Baxter).

Experiment 4

In order to assess illusion susceptibility in a commonly presented Ponzo context, we conducted Experiment 4. Once again, dog performed extremely well in the familiarization sessions. All dogs performed at 90% or above (average of 97.14%) and therefore passed through to the illusion condition. Lulu was excluded from participating in this experiment, as she was pregnant at the time of testing.

Figure 9 shows individual performance data for each dog. Performance in the control conditions was once again uniformly high, as the average level of performance was $95.2\% \pm 4.7$. Binomial tests indicated that all dogs were significantly above the chance score of 50%. In contrast, dogs as a group averaged only $56.4\% \pm 18.6$ in the illusion condition. Results of the two-tailed one-sample *t*-test for the illusion condition of the group in Experiment 4 were not significant [$t(6) = 0.95$, $p = 0.37$, $SD = 18.64$, Cohen's $d = 0.34$]. Performance in the illusion condition was similar to the previous three experiments. Baxter and Gabbie performed significantly above chance level, indicating illusion susceptibility in the same direction as humans ($p \leq 0.01$). The remaining five dogs performed at chance levels ($p \geq 0.06$).

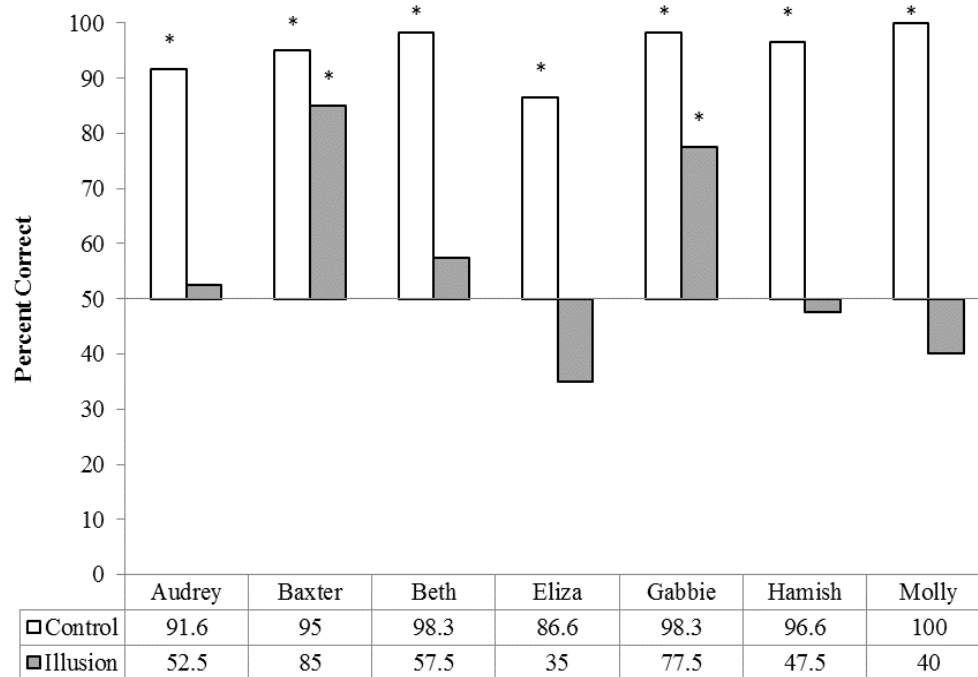


Figure 9. Individual percent correct for control and illusion conditions in Experiment 4.

*Indicates that the binomial result significantly differed from chance level at $p < 0.05$. Correct trials in the illusion condition were defined as those in which the dog selected the stimulus that, to humans, would appear larger (or smaller in the case of Baxter).

Summary of Results

To summarize group performance across Experiments 1-4, the dogs generally performed at or around chance when presented with the varying presentations of the Ponzo illusion. Dogs only performed significantly above chance, as a group, when presented with the circle 'grid inducer' context in Experiment 1, demonstrating (weak) susceptibility in the same direction as humans ($p = 0.033$) (Figure 10). Dogs performed at chance as a group across Experiments 2 ($p = 0.685$), 3 ($p = 0.53$), and 4 ($p = 0.37$) (Figure 10). There were exceptions in each experiment, however. While some dogs performed significantly above chance in either both a human-like and reversed direction, only one dog, Baxter, showed a weak but consistent tendency towards human-like susceptibility. These instances are discussed in more detail below.

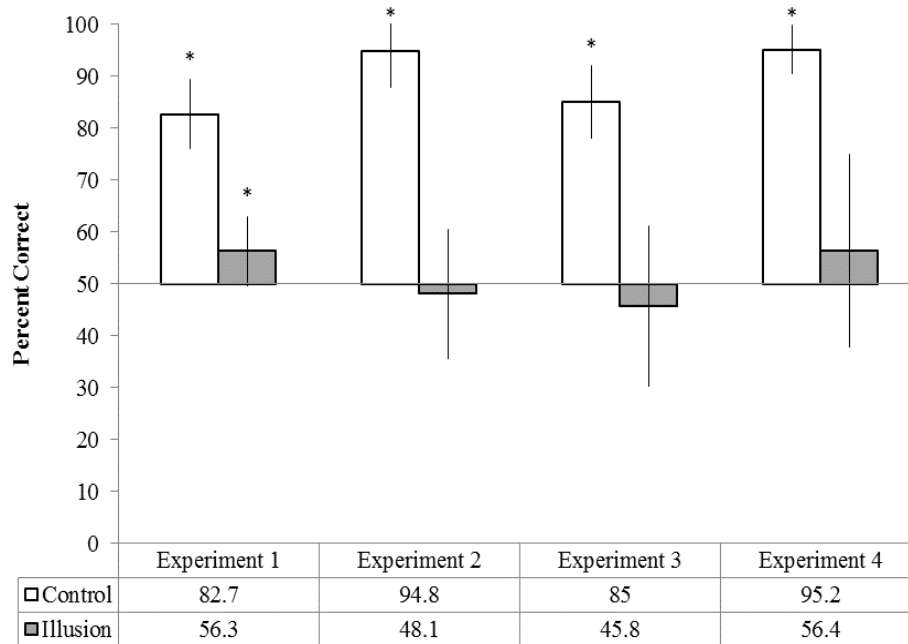


Figure 10. Percent of correct choices at the group level for the control and illusion condition for Experiments 1, 2, 3, and 4, with group standard deviations for each experiment.

*Indicates that the *t*-test at the group level, comparing correct responses against chance, was significant at $p < 0.05$. Error bars indicate standard deviation.

Discussion

The current study examined susceptibility to the Ponzo illusion in dogs across a variety of presentations, utilizing both ‘grid inducer’ and ‘converging lines’ contexts. While the *t*-test on the group data for Experiment 1 was suggestive that the dogs were responding to illusory stimuli significantly above chance and in the same direction as humans and other animals, no individual dog performed significantly above chance. However, when the exact same experiment was run again, as Experiment 2, no significant group result was found. The results of Experiments 3 and 4 also indicated that the dogs, as a group, were responding to illusory stimuli at chance. Taken together, there was a lack of compelling evidence for discernible susceptibility to the Ponzo illusion in a two-choice discrimination paradigm when utilizing both ‘grid inducer’ and ‘converging lines’ contexts.

Despite this overall conclusion, a number of anomalies indicate that additional testing may be required before it can be concluded with certainty that dogs are not susceptible to the Ponzo illusion. First, the dogs, as a group, did perform significantly above chance in Experiment 1, even though no single individual dog demonstrated performance significantly above chance. This result can be explained by the fact that most dogs were trending just above chance performance (at approximately 56%). Additionally, the standard deviation for the dogs as a group was quite small in Experiment 1, which resulted in a relatively large effect size.

Furthermore, while we were unable to replicate the outcome of Experiment 1 in Experiment 2, and the converging evidence across the four experiments suggests there is very limited evidence for canine susceptibility to the Ponzo illusion, it remains possible that dogs are weakly susceptible to this illusion. Perhaps the dogs were originally susceptible to the illusion in Experiment 1 and then developed a dissociation between sensation and perception over time, as they underwent additional familiarization and testing trials. This could have led to more veridical responses. In a forthcoming paper we show that this same group of dogs are able to discriminate between two circles that differ in size by 20%, with some able to discern differences of 15% and others differences of 10% (Byosiére et al., in prep). This may be

instructive, as in the Ponzo illusion the two stimuli are physically identical, but appear slightly different to humans because of the illusory effect. In humans, this magnitude has been suggested to be about 18%, however this is for line stimuli in a ‘converging line’ context (Chouinard, Unwin, Landry, & Sperandio, 2016). Considering we used circle and square stimuli we cannot draw comparisons or make inferences about the degree of misperception in dogs. However, in a species not visually sensitive to small size differences, the illusion may be invisible, or very weak.

Additionally, it could be that illusion susceptibility in dogs may have been reduced in Experiments 2, 3, and 4 due to the repeated exposure to the illusory presentations. However, Parrish, Agrillo, Perdue, and Beran (2016) observed that both experimentally naïve and veteran capuchin monkeys performed similarly when presented with the Solitaire illusion (although with increased intra and inter individual variation than humans). It should be noted that the dogs were not rewarded for any particular choice in the test trials. Thus, perhaps in the absence of reinforcement, they were motivated to ‘try out’ different strategies and this prevented the results from being more coherent. An alternative explanation could be that of global precedence. Research suggests that dogs process stimuli in a globally oriented fashion, although there appears to be much individual variation (Pitteri, Mongillo, Carnier, & Marinelli, 2014). It appears that individual global/local preferences are stable over time and there is an overall global bias observed in dogs (Mongillo, Pitteri, Sambugaro, Carnier, & Marinelli, 2016). We suspect that susceptibility to geometrical illusions can be affected by preferential processing of local versus global aspects of a visual stimulus. While our familiarization processes were methodical, well controlled, and randomized, and we believed them necessary to introduce the dogs to the novel background images, it is possible that this extra training influenced the dogs to preferentially focus on local features, affecting their susceptibility to inducer cues in the global environment of the target object. However, additional research is needed to further assess this hypothesis. Studies of global/local precedence in dogs are largely based on performance in one precedence task (Navon, 1977), and it is clear from a number of experiments in humans that global processing should not be considered a singular construct, but rather an umbrella term to represent multiple independent mechanisms (Chouinard, Noulty, Sperandio, & Landry, 2013; Chouinard et al., 2016).

Also of particular interest was the performance of specific individuals. Baxter consistently performed above 62% on the illusion trials across all four experiments, and this was significantly above chance in Experiments 2, 3, and 4. This may suggest individual variation in illusion susceptibility, as was observed in our previous study investigating susceptibility to the Ebbinghaus-Titchener illusion. Interestingly, Baxter is the only one of our subjects that we were able to successfully train to select the smaller stimulus. He is also extremely impulsive and confident in his choices, tending to choose quickly and decisively without pausing to consider options. We are currently training other dogs to select the smaller of two circles, and we are testing Baxter, as well as the other subjects on additional Ponzo stimuli.

Gabbie and Lulu performed significantly differently from chance in Experiment 3; however, their performance was in the opposite direction than observed in humans, demonstrating reversed illusion susceptibility. This reversed susceptibility was found in this same group of dogs when they were presented with the Ebbinghaus-Titchener illusion (Byosiére et al., 2016). Gabbie’s performance was especially variable across Experiments, as she performed significantly different from chance, in Experiment 4, demonstrating illusion susceptibility in the same direction as humans. This may indicate that Gabbie and Lulu (in Experiment 3) were confused by the identically sized stimulus circles and used some aspect of the surrounding context to inform their choices, such that their errors were systematic but due to a confound rather than to illusion susceptibility. It is possible that they were demonstrating a preference for selecting the larger grid as opposed to the larger stimulus, although their performance in the familiarization trials showed that they were able to ignore the background image when the circles were different in size.

While these anomalies require further investigation, the results overall are particularly intriguing because they indicate that dogs may not be susceptible to the Ponzo illusion. To our knowledge, all animals previously tested have demonstrated susceptibility to this illusion in the same direction as humans (Feng et al., 2016). Therefore, if dogs are not susceptible, these findings have implications for

underlying theoretical explanations. Recent research suggests that dogs may perceive illusory stimuli differently than humans (Byosiere et al., 2016; Miletto Petrazzini et al., 2016). These findings, together with the results of the current study, suggest that visual processing mechanisms may differ between humans, and dogs.

Clearly, additional research should be conducted to further assess Ponzo illusion susceptibility in dogs before more general conclusions are drawn. In order to maintain consistencies in facial morphology and, thus, ocular similarities, dogs of the same breed were used as participants in this study. They were also closely related and lived in the same environment, meaning that the results we observed may be breed-specific, specific to this genetic line, or the environmental context. In dogs, it appears that morphological diversity may be related to visual processing and eye structure (McGreevy, Grassi, & Harman, 2003; Roberts, McGreevy, & Valenzuela, 2010). McGreevy et al. (2003) observed that, while dog eye size is variable, it is strongly correlated with skull dimension, and that retinal ganglion cell distribution is highly variable and correlated with nose length. Considering the wide variety of morphological differences in dogs, future research should attempt to discern if breeds with flat faces (such as Boxers, Pugs, and Bulldogs) have different illusion susceptibility when compared to longer-nosed breeds (such as Labrador retrievers, German shepherds, and Border collies).

As discussed previously, additional investigation into whether training or testing methods influence the demonstration of direction of susceptibility to visual illusions is required, as is research establishing basic visual capabilities of dogs. Studies that find no apparent susceptibility often base that conclusion on the animal selecting the ‘larger’ or ‘smaller’ circle/line at chance levels. While this is a reasonable conclusion, other confounding factors (e.g., visual acuity, experimental stimuli) may be affecting these results. It would be instructive to see what happens when animals are taught to indicate a ‘same size’ option, in addition to the ‘larger’ or ‘smaller’ option on which they are normally trained. This is challenging from a training perspective, however, and is potentially limited to species capable of comprehending and demonstrating the abstract concept of same or different. We could find no studies testing this conceptual understanding in dogs.

Lastly, future research should extend this study to assess canine susceptibility to the Ponzo illusion in additional contexts. We were limited in the stimuli we could present, as the dogs were already well trained to select the larger (or smaller) of two circles presented in a horizontal plane on a computer monitor. This was assumed to be satisfactory because the illusions were robust when viewed by the researchers. However, future research should examine Ponzo illusion susceptibility using a presentation with vertical alignment, which may provide stronger linear perceptive cues, in both a classical and pictorial form. Such stimuli would more closely approximate those used with rhesus macaques (Fujita, 1996), horses (Timney & Keil, 1996), and rats (Nakagawa, 2002).

To the best of our knowledge, this study is the first to examine canine susceptibility to the Ponzo illusion. Recent research in dogs suggests that they may perceive certain illusions in an opposite manner than humans and most other animal species (Byosiere et al., 2016), or may not demonstrate susceptibility at all (Byosiere et al., 2016; Miletto Petrazzini et al., 2016). Across four presentations of the Ponzo illusion, we could not find evidence for discernible susceptibility to the Ponzo illusion in a two-choice discrimination paradigm. In Experiment 1, susceptibility to the Ponzo illusion was observed at the group level; however, no individual dog performed significantly above chance. In Experiments 2, 3, and 4, no significant results were observed at the group level, although individual dogs did show some evidence of susceptibility. This was sometimes in the same direction as humans but, at other times, was in the reverse direction. These findings require replication but potentially have implications for theoretical explanations of the Ponzo illusion. Several other animal species have demonstrated susceptibility to the Ponzo illusion in the same direction as humans, but we could find no other reports of any animal not being susceptible. Considering that susceptibility to the Ponzo illusion has been suggested to require high levels of visual processing in humans, this divergence in findings may suggest that the mechanisms underlying perception of the Ponzo stimuli differ across species, resulting in only some experiencing the illusion.

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Conflict of Interest: The authors declare that they have no conflict of interest.

References

- Agrillo, C., Parrish, A. E., & Beran, M. J. (2014). Do primates see the solitaire illusion differently? A comparative assessment of humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 128, 402 – 413.
- Barbet, I., & Fagot, J. (2002). Perception of the corridor illusion by baboons (*Papio papio*). *Behavioural Brain Research*, 132, 111 – 115.
- Bayne, K. A. L., & Davis, R. T. (1983). Susceptibility of rhesus monkeys (*Macaca mulatta*) to the Ponzo illusion. *Bulletin of the Psychonomic Society*, 21, 476 – 478.
- Brislin, R. W., & Keating, C. F. (1976). Cultural differences in the perception of a three-dimensional Ponzo illusion. *Journal of Cross-Cultural Psychology*, 7, 397 – 412.
- Byosiére, S.-E., Feng, L. C., Woodhead, J. K., Rutter, N. J., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2016). Visual perception in domestic dogs: Susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions. *Animal Cognition*, 20, 435 – 448.
- Chouinard, P. A., Noulty, W. A., 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, P. A., Unwin, K. L., 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.
- Feng, L. C., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2016). Why do animals differ in their susceptibility to geometrical illusions? *Psychonomic Bulletin & Review*, 24, 262 – 276.
- Fujita, K. (1996). Linear perspective and the Ponzo illusion: A comparison between rhesus monkeys and humans. *Japanese Psychological Research*, 38, 136 – 145.
- Fujita, K. (1997). Perception of the Ponzo illusion by rhesus monkeys, chimpanzees, and humans: Similarity and difference in the three primate species. *Perception & Psychophysics*, 59, 284 – 292.
- Fujita, K., Blough, D. S., & Blough, P. M. (1991). Pigeons see the Ponzo illusion. *Animal Learning & Behavior*, 19, 283 – 293.
- Geisler, W. S., & Diehl, R. L. (2002). Bayesian natural selection and the evolution of perceptual systems. *Philosophical Transactions of the Royal Society B*, 357, 419 – 448.
- Gellermann, L. W. (1933). Chance orders of alternating stimuli in visual discrimination experiments. *The Pedagogical Seminary and Journal of Genetic Psychology*, 42, 206–208.
- Gregory, R. L. (1963). Distortion of visual space as inappropriate constancy scaling. *Nature*, 199, 678 – 680.
- Gregory, R. L. (2015). *Eye and brain: The psychology of seeing*. Princeton, NJ: Princeton University Press.
- Haber, R. N., & Hershenson, M. (1973). *The psychology of visual perception*. Oxford, UK: Holt, Rinehart, & Winston.
- Humphrey, N. K., & Morgan, M. J. (1965). Constancy and the geometric illusions. *Nature*, 206, 744 – 745.
- Imura, T., Tomonaga, M., & Yagi, A. (2008). The effects of linear perspective on relative size discrimination in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). *Behavioural Processes*, 77, 306 – 312.
- Jacobs, G. H., Deegan, J. F., Crognale, M. A., & Fenwick, J. A. (1993). Photopigments of dogs and foxes and their implications for canid vision. *Visual Neuroscience*, 10, 173 – 180.
- Kasparson, A. A., Badridze, J., & Maximov, V. V. (2013). Colour cues proved to be more informative for dogs than brightness. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20131356.
- Lazareva, O. F., Miner, M., Wasserman, E. A., & Young, M. E. (2008). Multiple-pair training enhances transposition in pigeons. *Learning & Behavior*, 36, 174 – 187.

- Lazareva, O. F., Wasserman, E. A., & Young, M. E. (2005). Transposition in pigeons: Reassessing Spence (1937) with multiple discrimination training. *Animal Learning & Behavior*, 33, 22 – 46.
- Lazareva, O. F., Young, M. E., & Wasserman, E. A. (2014). A three-component model of relational responding in the transposition paradigm. *Journal of Experimental Psychology: Animal Learning and Cognition*, 40, 63 – 80.
- McGreevy, P., Grassi, T. D., & Harman, A. M. (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.
- Miletto Petrazzini, M. E., Bisazza, A., & Agrillo, C. (2016). Do domestic dogs (*Canis lupus familiaris*) perceive the Delboeuf illusion? *Animal Cognition*, 20, 427 – 434.
- Miller, P. E., & Murphy, C. J. (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*, 20, 257 – 265.
- 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 – 342.
- Nakagawa, E. (2002). Rats respond to configurations of stimuli. *The Psychological Record*, 52, 531 – 558.
- 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 – 387.
- 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, G. H. (1989). Color vision in the dog. *Visual neuroscience*, 3, 119 – 125.
- Newman, C. V., & Newman, B. M. (1974). The Ponzo illusion in pictures with and without suggested depth. *The American Journal of Psychology*, 87, 511 – 516.
- Parrish, A. E., Agrillo, C., Perdue, B. M., & Beran, M. J. (2016). The elusive illusion: Do children (*Homo sapiens*) and capuchin monkeys (*Cebus apella*) see the Solitaire illusion? *Journal of Experimental Child Psychology*, 142, 83 – 95.
- Pitteri, E., Mongillo, P., Carnier, P., & Marinelli, L. (2014). Hierarchical stimulus processing by dogs (*Canis familiaris*). *Animal Cognition*, 17, 869 – 877.
- Pressey, A. (1971). An extension of assimilation theory to illusions of size, area, and direction. *Perception & Psychophysics*, 9, 172 – 176.
- Roberts, T., McGreevy, P., & Valenzuela, M. (2010). Human induced rotation and reorganization of the brain of domestic dogs. *PLoS One*, 5, e11946.
- Salva, O. R., 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.
- Segall, M. H., Campbell, D. T., & Herskovits, M. J. (1963). Cultural differences in the perception of geometric illusions. *Science*, 139, 769 – 771.
- Song, C., Schwarzkopf, D. S., & Rees, G. (2011). Interocular induction of illusory size perception. *BMC Neuroscience*, 12, 27.
- Sovrano, V. A., Albertazzi, L., & Salva, O. R. (2014). The Ebbinghaus illusion in a fish (*Xenotoca eiseni*). *Animal Cognition*, 18, 533 – 542.
- Sperandio, I., & Chouinard, P. A. (2015). The mechanisms of size constancy. *Multisensory Research*, 28, 253-283.
- Tapp, P. D., Siwak, C. T., Head, E., Cotman, C. W., Murphey, H., Muggenburg, B. A., ...Milgram, N. W. (2004). Concept abstraction in the aging dog: Development of a protocol using successive discrimination and size concept tasks. *Behavioural Brain Research*, 153, 199 – 210.
- Timney, B., & Keil, K. (1996). Horses are sensitive to pictorial depth cues. *Perception*, 25, 1121 – 1128.
- Wang, G.-d., Zhai, W., Yang, H.-c., Fan, R.-x., Cao, X., Zhong, L., ...Cheng, L.-g. (2013). The genomics of selection in dogs and the parallel evolution between dogs and humans. *Nature Communications*, 4, 1860.
- Watanabe, S., Nakamura, N., & Fujita, K. (2011). Pigeons perceive a reversed Zöllner illusion. *Cognition*, 119, 137 – 141.
- Watanabe, S., Nakamura, N., & Fujita, K. (2013). Bantams (*Gallus gallus domesticus*) also perceive a reversed Zöllner illusion. *Animal Cognition*, 16, 109 – 115.

6.3 Discussion

The objective of this chapter was two-fold. One, to determine whether dogs demonstrated susceptibility to the Ponzo illusion and two, to expand on the findings presented in Chapter 5 by evaluating susceptibility to a distorting illusion with different proposed theoretical mechanisms. This was accomplished by presenting the dogs with three illusory displays, specifically ‘grid inducer’ and ‘converging lines’ contexts, which previously have been observed to induce susceptibility in both humans (Jackson & Shaw, 2000) and animals (Barbet & Fagot, 2002; Bayne & Davis, 1983; Fujita, 1996; Fujita, 1997; Fujita et al., 1991; Imura et al., 2008; Nakagawa, 2002; Timney & Keil, 1996).

In Experiment 1, dogs, as a group, demonstrated significant human-like susceptibility to the Ponzo illusion, however, no individual dog performed significantly above chance. While group performance was significant, it was low at only 56% and appeared to be largely driven by a small and consistent standard deviation. To clarify this result, and evaluate the extent to which the number of trials may have affected the outcome, Experiment 2 comprised a re-test of Experiment 1. When re-tested, no significant group effect was observed. To ascertain whether the familiarity of the presentation reduced the illusory effect in the re-test, Experiment 3 embedded novel target stimuli within the ‘grid inducer’ context. Dogs, as a group, responded to the illusory stimuli at chance. Finally, given that inappropriate constancy scaling theory (Gregory, 1963) highlights the importance of linear perspective cues, a classic presentation of a ‘converging lines’ context was presented in Experiment 4. Once again, the dogs, as a group, performed at chance, providing a lack of convincing evidence for

discernible susceptibility to the Ponzo illusion in dogs, and converging on the result of null susceptibility.

Of particular interest was the variation in performance amongst individuals. In addition to the group analysis, statistics for each individual were also conducted. Baxter consistently performed above chance on the illusion trials across all four experiments, demonstrating consistent individual susceptibility to the Ponzo illusion. Gabbie and Lulu performed significantly below chance in Experiment 3, demonstrating a reversed susceptibility compared to humans. Gabbie's performance was especially variable across the Experiments, as she performed significantly above chance in Experiment 4, demonstrating illusion susceptibility in the same direction as humans. The marked individual variation suggests that dogs, as individuals, can differ in their illusion susceptibility, even when extensively controlling for breed, genetics, and environment. Moreover, susceptibility is flexible and can vary within subjects across presentational contexts and perhaps even over time. These findings suggest that dogs do not visually process stimuli identically, as would be expected for a stimulus-response automaton. They suggest that, like humans (Coren & Porac, 1987), within species differences at the individual level are present, specifically in terms of the degree and direction of susceptibility, and that genetics or environment cannot exclusively explain such variation.

Considering dogs did not demonstrate human-like susceptibility to the Ebbinghaus-Titchener and Delboeuf illusions, it is not surprising that the dogs did not demonstrate human-like susceptibility towards the Ponzo illusion. While different theoretical mechanisms have been proposed to explain these illusions, there is consistency in the dogs' dissimilarity from humans. The results from this chapter provide additional support

for the preliminary observations presented in Chapter 5 that indicate dogs and humans might differ in the mechanisms underlying their visual perception. While the results from Chapter 5 provide support for an alternative mechanism, specifically assimilation theory, the null susceptibility to the Ponzo illusion does not allow for such interpretation. As all species previously assessed on the Ponzo illusion have demonstrated human-like susceptibility (Barbet & Fagot, 2002; Bayne & Davis, 1983; Fujita, 1996; Fujita, 1997; Fujita et al., 1991; Imura et al., 2008; Nakagawa, 2002; Timney & Keil, 1996), it is necessary to exhaust all potential confounds (discussed in detail in the next chapter), such as presentation orientation and size sensitivity thresholds, before confident conclusions about canine susceptibility and the underlying theoretical mechanisms can be made.

Chapter 7 – Illusion or Reality: Are Dogs Susceptible to the Ponzo Illusion?

Chapter 6 comprised the first study to examine canine susceptibility to the Ponzo illusion, and provided additional evidence, following Chapter 5, that the mechanisms underlying canine perception of illusions may differ from humans. Despite this broad interpretation, a number of irregularities were observed across the four illusory presentations. Thus, additional investigation and evidence are required before it can be confidently suggested that dogs are not susceptible to the Ponzo illusion.

The illusory displays presented in Chapter 6 represent well-studied scenes, yet it is important to note that they were presented horizontally. While this orientation has been observed to invoke susceptibility in humans (e.g. Jackson & Shaw, 2000; Whitwell, Buckingham, Enns, Chouinard & Goodale, 2016), only one horizontal Ponzo presentation has been tested in animals (Fujita et al., 1991). Using a two-choice size discrimination task with horizontal converging lines, pigeons demonstrated difficulty selecting the larger bar when it was further from the apex, providing preliminary evidence of susceptibility to the Ponzo illusion. In supplementary vertically presented contexts, additional support for pigeon susceptibility was observed. While the non-significant findings presented in Chapter 6 converge with the results observed from the Ebbinghaus-Titchener and Delboeuf illusions presented in Chapter 5, interpretation of the theoretical mechanisms underlying susceptibility to the Ponzo is limited. According to inappropriate constancy scaling theory (Gregory, 1963), the theoretical mechanism most often used to explain susceptibility to the Ponzo illusion, linear perspective cues invoke linear perspective cues to induce the illusory display. Consequently, the weak susceptibility observed as a group in Experiment 1, and the individual variation observed in susceptibility across

Experiments 2, 3, and 4, may reflect the need to evaluate the Ponzo illusion in a vertically presented context.

To further explore this notion, the research questions presented in Chapter 6 were extended to Chapter 7. Identical methodologies to Experiment 4 were employed, barring the fact that the screen and ‘converging line’ stimuli were re-positioned 90 degrees to create a vertical display. It was expected that, if the findings observed in Chapter 6 were demonstrative of weak susceptibility, the dogs would perform significantly different from chance, in a human-like manner, when presented with a vertical presentation of the illusion.

Upon careful reflection, it was also realised that the findings observed in Chapter 6 might be demonstrative of a canine inability to perceive illusions based on small perceptual (not actual) differences in size. It has been hypothesised that to be susceptible to illusions, subjects must be able to perceive a minimum size difference between stimuli (for a discussion of methodological issues in regards to discrimination abilities in primates see Agrillo, Parrish & Beran, 2014; Santacà et al., 2017). Thus, certain unknown limitations, such as poor visual acuity, may unknowingly affect canine illusion susceptibility. While this is a particularly unlikely explanation, given the significant reversed susceptibility to the Ebbinghaus-Titchener illusions presented in Chapter 5, it remains a possibility. Humans, on average, perceive an 18% size difference between illusory stimuli (Chouinard et al., 2016). However, an equivalent in dogs is unknown. Previous research suggests that dogs can correctly identify size differences of approximately 20% when presented with 3-D stimuli (Tapp et al., 2004), yet there is no information applicable to 2-D on-screen presented stimuli. Given conflicting reports of

canine visual acuity across breeds and individuals (Byosiere et al., 2017; Lind et al., 2017), it was deemed necessary to further explore size sensitivities in dogs.

In this chapter, dogs' susceptibility to the Ponzo illusion was evaluated in a vertical context to clarify whether linear perspective cues are necessary to invoke susceptibility to the illusion. To determine whether the non-significant findings observed in Chapter 6 were demonstrative of an inability to perceive the minimum size threshold required to perceive the illusion, performance across various size sensitivities, ranging from 5%-60% different in diameter, was evaluated. The results are presented in an article titled 'Do dogs demonstrate susceptibility to a vertically presented Ponzo illusion?' published in *Animal Behavior and Cognition* in August 2018. It is important to note that Experiment 1 and Experiment 2 - Phase 2 were conducted as a part of this thesis, while Experiment 2 - Phase 1 was conducted as part of a Masters thesis conducted by a different student.

7.1 Declaration for thesis Chapter 7

In the case of Chapter 7, contributions to the work involved the following:

Name (authors in order)	Extent of contribution (%)	Nature of contribution
Sarah-Elizabeth Byosiene Corresponding author	50	Study design for Experiments 1 and Experiment 2 – Phase 2, data collection and analysis for Experiments 1 and 2.
Lynna Feng Co-author	10	Study design for Experiment 2 Phase 1, data collection for Experiments 1 and 2.
Joyce Wuister Co-author	20	Study design for Experiment 2 Phase 1, data collection for Experiments 1 and 2.
Philippe Chouinard Co-author	5	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Tiffani Howell Co-author	5	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Pauleen Bennett Senior author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication

Declaration by co-authors

The undersigned hereby certify that:

- (1) the below declaration correctly reflects the nature and extent of the candidate's contribution to this work, and the nature of the contribution of each of the co-authors;
- (2) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (3) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (4) there are no other authors of the publication according to these criteria; and
- (5) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor or publisher of journals or other publications, and (c) the head of the

responsible academic unit.

Signature 1	
Signature 2	
Signature 3	
Signature 4	
Signature 5	
Signature 6	

7.2 Do dogs demonstrate susceptibility to a vertically presented Ponzo illusion?



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

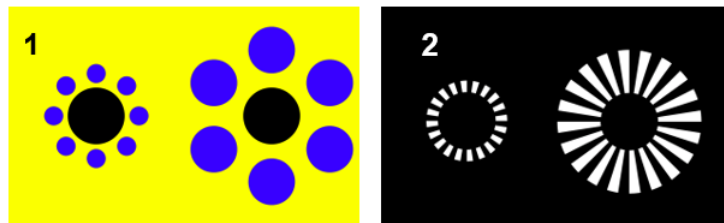
Visual perception depends on interpretation of retinal information by the brain, and is important as it allows humans and non-human animals (hereafter animals) to perceive the external world and act upon it (Haber & Hershenson, 1973). However, visual perception does not always accurately reflect reality. 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,

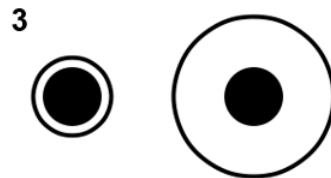
Albertazzi, & Salva, 2014; Watanabe, Nakamura, & Fujita, 2011, 2013). Moreover, even within a species, mixed findings have been observed in susceptibility to the same illusion (e.g., Nakamura et al., 2008, 2014; Salva, Rugani, Cavazzana, Regolin, & Vallortigara, 2013). One species in which such findings 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 (Byosiére, 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 (Byosiére, Feng, Woodhead, et al., 2017; Miletto Petrazzini et al., 2017), although, in one of these studies, individual differences were again apparent (Byosiére, Feng, Woodhead, et al., 2017) (Figure 1, image 3). More recently, we assessed whether dogs demonstrate susceptibility to the Ponzo illusion (Byosiére, 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.

Ebbinghaus
-Titchener



Delboeuf



Ponzo

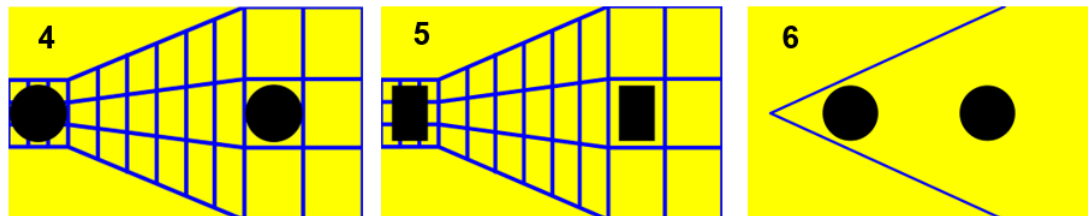


Figure 1. On-screen presented stimuli of the Ebbinghaus-Titchener (images 1 and 2), Delboeuf (image 3), and Ponzo (images 4-6) illusion that have been tested in dogs. In images 1-3, humans perceive the circle target stimulus located on the left in each presentation as larger. Ponzo images 4 and 5 are 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 (Byosiére, 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 Byosiére 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 (Byosiére, Feng, Chouinard, Howell, & Bennett, 2017; Byosiére, Feng, Rutter et al., 2017; Byosiére, 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 mm²) 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 Byosiére, 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.

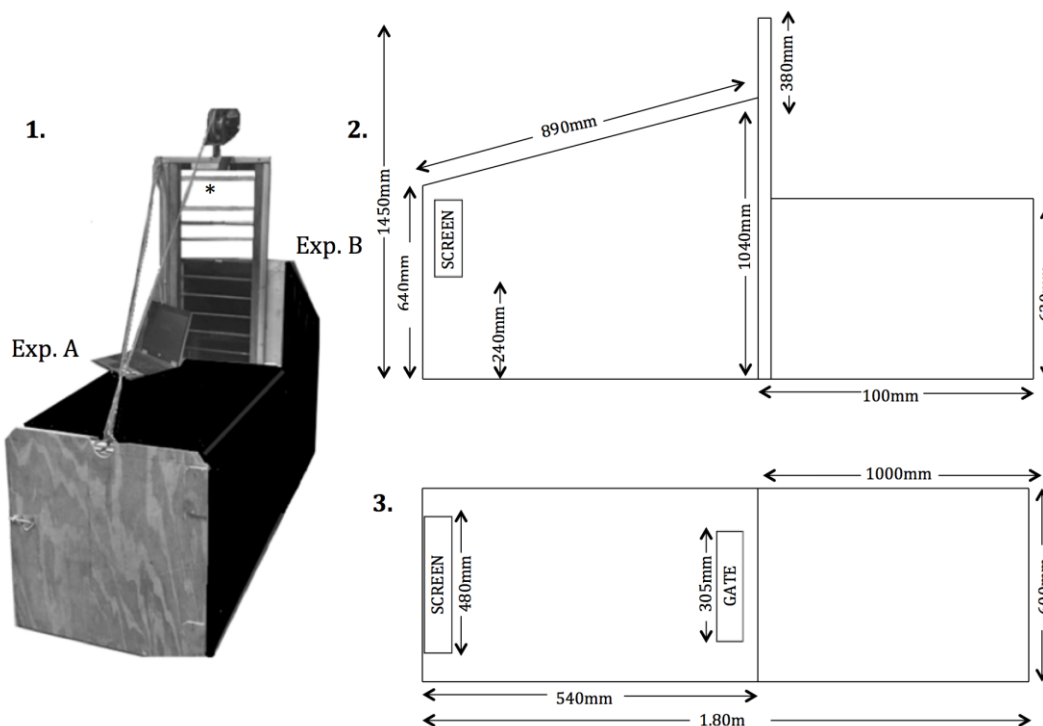


Figure 2. Schematic representation of the testing apparatus implemented in the experimental paradigm (1) with the side (2) and aerial (3) diagram. The figure provides a photographic representation of the Canine Nose-Touch Testing Apparatus used during training and testing phases, as well as the position 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 (Byosiére, Feng, Rutter et al., 2017) provided no evidence of an illusory effect when the illusion was presented horizontally.

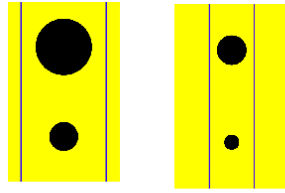
Stimuli. Stimuli were pairs of black circles (RGB values 0, 0, 0; Luminance 0.18 c/m²), presented on a yellow background (RGB values 255, 255, 0; Luminance 163.6 c/m²) with blue converging lines (RGB values 0, 0, 255; Luminance 16.05 c/m²) (Figure 3). These colors were chosen based on dogs' dichromatism, 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 (Byosiére, Feng, Rutter et al., 2017; Byosiére, 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 (Byosiére, Feng, Chouinard et al., 2017; Byosiére, Feng, Rutter et al., 2017; Byosiére, 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.

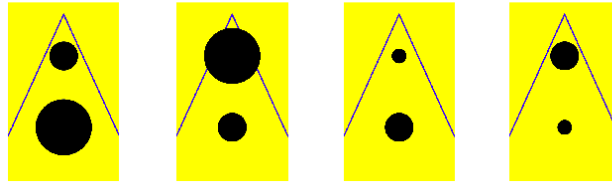
Once the dogs were successfully able to perform the size discrimination task presented vertically, familiarization sessions took place. These sessions presented the target stimuli over non-illusory backgrounds to acquaint the dogs with new images, such as inducers and/or colours that would be present 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).

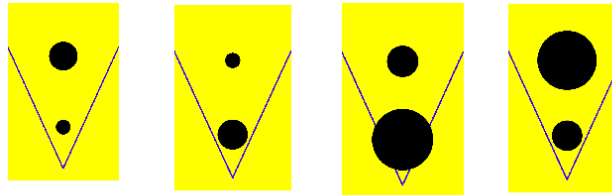
Familiarization 1



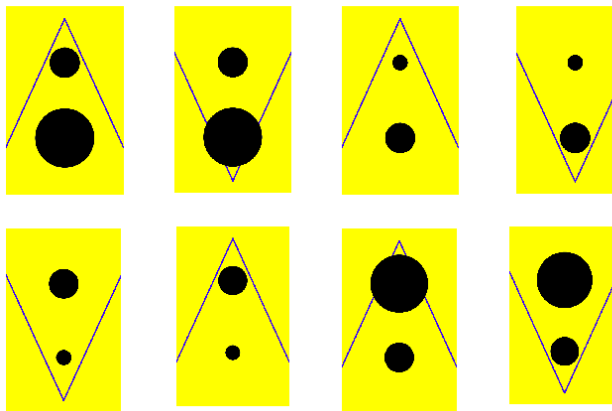
Familiarization 2



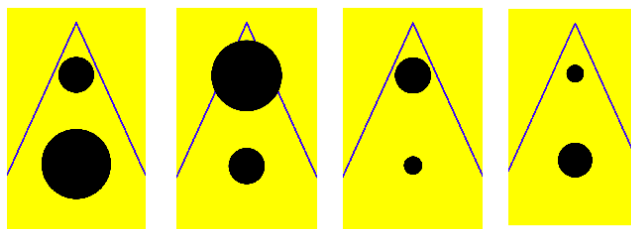
Familiarization 3



Familiarization 4



Test – Control Stimuli



Test – Illusions Stimulus

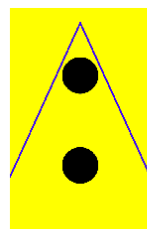


Figure 3. Stimuli used in the Familiarization and Test trials for the Ponzo illusion.

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 BF₁₀ 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 $90.3\% \pm 4.77$ ($t(5) = 15.48$, $p < .001$, $BF_{10} = 841.52$). In contrast, dogs averaged $61.25\% \pm 6.52$ 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 ($t(5) = 2.25$, $p = .074$, $BF_{10} = 1.58$). 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.

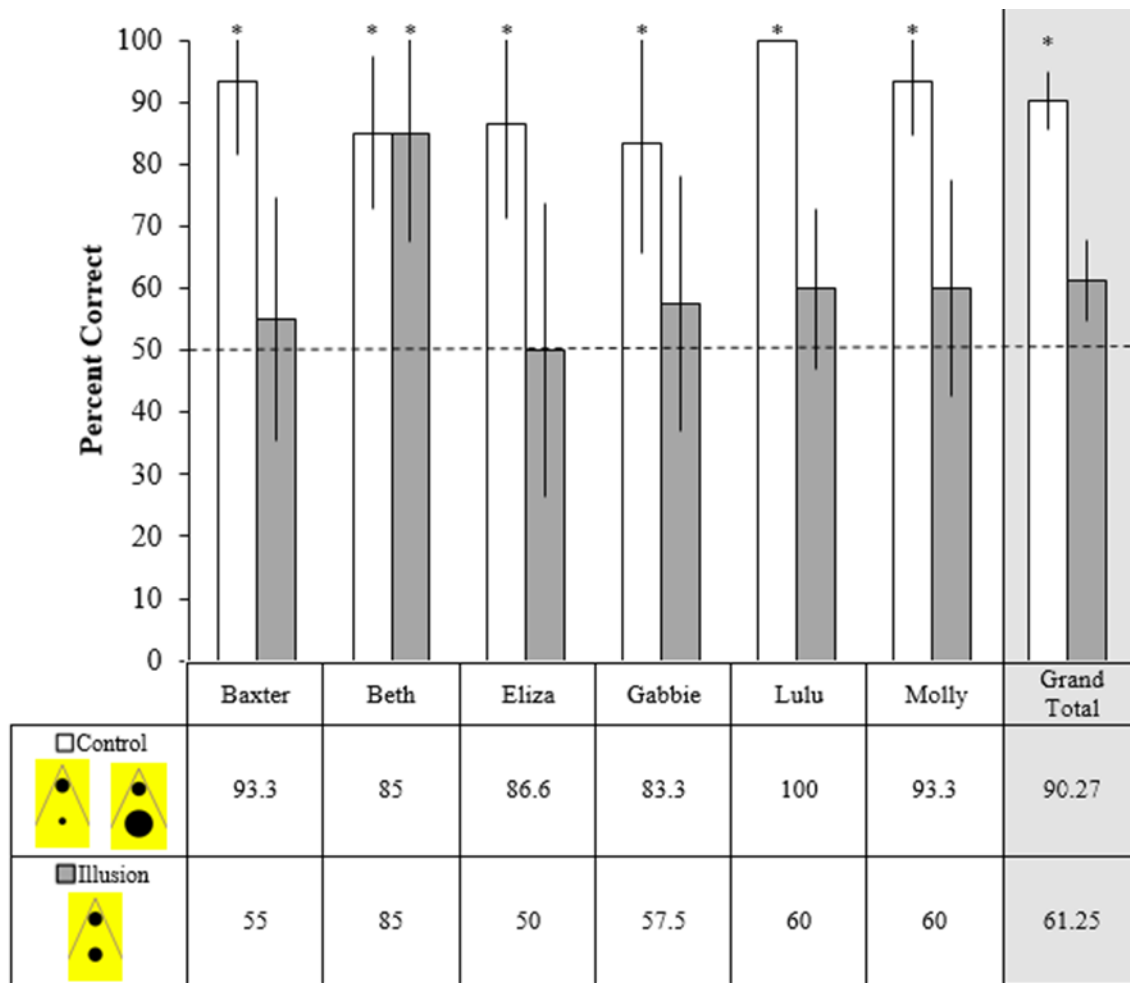


Figure 4. Individual and group percent correct (and standard deviations) for control and illusion conditions. Correct trials in the illusion condition were defined as those in which the dog selected the larger stimulus. The perceptually larger target stimulus appears on the top in the illusion condition. 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/m²) 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 ($\geq 37/60$ 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 ($\geq 37/60$ 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, $p = .47$.

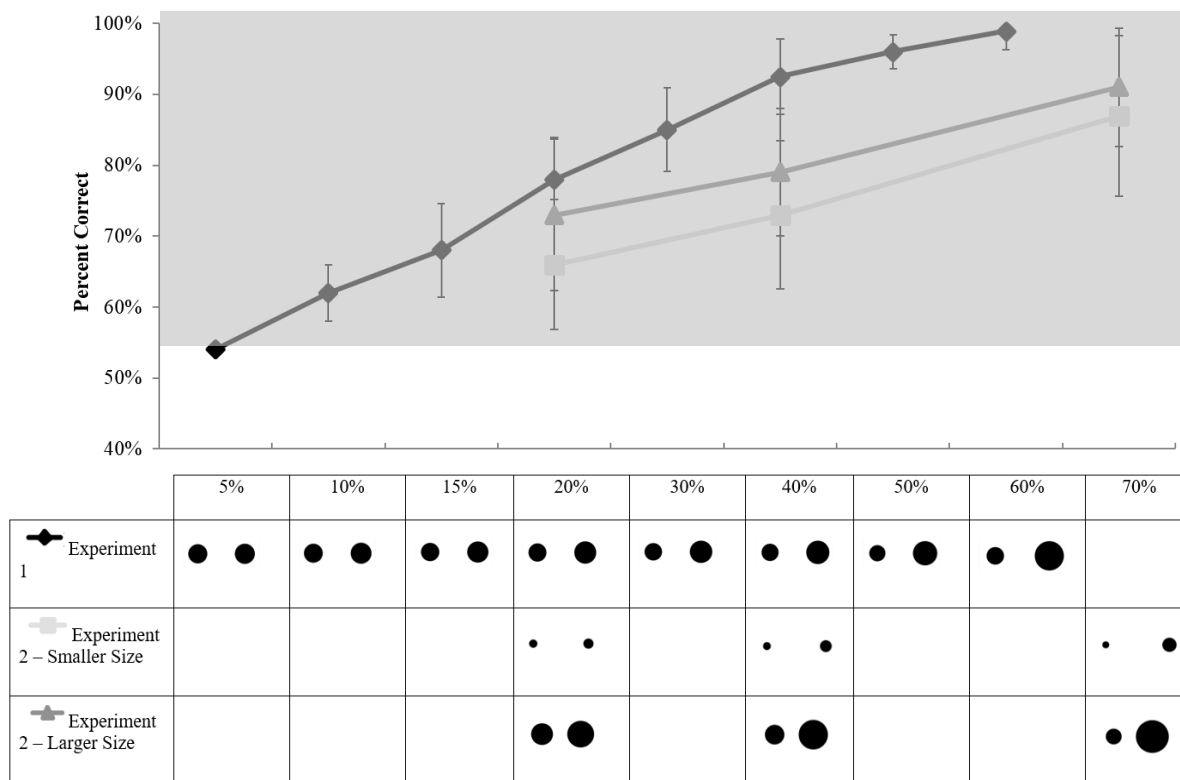


Figure 5. Group average percent correct (and standard deviations) by percent difference in diameter for Experiments 1 and 2. Grey area indicates that the binomial result significantly differed from chance at $p < .05$.

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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References

- Agrillo, C., Parrish, A. E., & Beran, M. J. (2014). Do primates see the solitaire illusion differently? A comparative assessment of humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 128, 402–413.
- Barbet, I., & Fagot, J. (2002). Perception of the corridor illusion by baboons (*Papio papio*). *Behavioural Brain Research*, 132, 111–115.
- Bayne, K. A. L., & Davis, R. T. (1983). Susceptibility of rhesus monkeys (*Macaca mulatta*) to the Ponzo illusion. *Bulletin of the Psychonomic Society*, 21, 476–478.
- Byosiére, S.-E., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). What do dogs (*Canis familiaris*) see? A review of vision in dogs and implications for cognition research. *Psychonomic Bulletin & Review*. Advance online publication. doi:10.3758/s13423-017-1404-7
- Byosiére, S.-E., Feng, L. C., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). Relational concept learning in domestic dogs: Performance on a two-choice size discrimination task generalises to novel stimuli. *Behavioural Processes*, 145, 93–101.
- Byosiére, S.-E., Feng, L. C., Rutter, N. J., Woodhead, J. K., Chouinard, P. A., ...Bennett, P. C. (2017). Do dogs see the Ponzo illusion? *Animal Behavior and Cognition*, 4, 396–412.
- Byosiére, S.-E., Feng, L. C., Woodhead, J. K., Rutter, N. J., Chouinard, P. A., ...Bennett, P. C. (2017). Visual perception in domestic dogs: Susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions. *Animal Cognition*, 20, 435–448.
- Chouinard, P. A., Unwin, K. L., 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.
- Chouinard, P. A., Noulty, W. A., 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.
- Feng, L. C., Chouinard, P. A., Howell, T. J., & Bennett, P. C. (2017). Why do animals differ in their susceptibility to geometrical illusions? *Psychonomic Bulletin & Review*, 24, 262–276.
- Fujita, K. (1996). Linear perspective and the Ponzo illusion: A comparison between rhesus monkeys and humans1. *Japanese Psychological Research*, 38, 136–145.
- Fujita, K. (1997). Perception of the Ponzo illusion by rhesus monkeys, chimpanzees, and humans: Similarity and difference in the three primate species. *Perception & Psychophysics*, 59, 284–292.
- Fujita, K., Blough, D. S., & Blough, P. M. (1991). Pigeons see the Ponzo illusion. *Animal Learning & Behavior*, 19, 283–293.
- Gellermann, L. W. (1933). Chance orders of alternating stimuli in visual discrimination experiments. *The Pedagogical Seminary and Journal of Genetic Psychology*, 42, 206–208.
- Gregory, R. L. (1963). Distortion of visual space as inappropriate constancy scaling. *Nature*, 199, 678–680.
- Gregory, R. L. (2015). *Eye and brain: The psychology of seeing*. Princeton, NJ: Princeton University Press.
- Haber, R. N., & Hershenson, M. (1973). *The psychology of visual perception*. Oxford, England: Holt, Rinehart & Winston.
- Humphrey, N. K., & Morgan, M. J. (1965). Constancy and the geometric illusions. *Nature*, 206, 744–745.
- Imura, T., Tomonaga, M., & Yagi, A. (2008). The effects of linear perspective on relative size discrimination in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). *Behavioural Processes*, 77, 306–312.
- Jacobs, G. H., Deegan, J. F., Crognale, M. A. & Fenwick, J. A. (1993). Photopigments of dogs and foxes and their implications for canid vision. *Visual Neuroscience*, 10, 173–180.
- Lazareva, O. F., Miner, M., Wasserman, E. A., & Young, M. E. (2008). Multiple-pair training enhances transposition in pigeons. *Learning & Behavior*, 36, 174–187.
- Lazareva, O. F., Wasserman, E. A., & Young, M. E. (2005). Transposition in pigeons: Reassessing Spence (1937) with multiple discrimination training. *Animal Learning & Behavior*, 33, 22–46.
- Lazareva, O. F., Young, M. E., & Wasserman, E. A. (2014). A three-component model of relational responding in the transposition paradigm. *Journal of Experimental Psychology: Animal Learning and Cognition*, 40, 63–80.
- Lind, O., Milton, I., Andersson, E., Jensen, P., & Roth, L. S. V. (2017). High visual acuity revealed in dogs. *PLoS One*, 12, e0188557.
- McGreevy, P., Grassi, T. D., & Harman, A. M. (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.

- Miletto Petrazzini, M. E., Bisazza, A., & Agrillo, C. (2017). Do domestic dogs (*Canis lupus familiaris*) perceive the Delboeuf illusion? *Animal Cognition*, 20, 427—434.
- Miller, R. J. (1997). Pictorial depth cue orientation influences the magnitude of perceived depth. *Visual Arts Research*, 23, 97—124.
- Mongillo, P., Pitteri, E., Sambugaro, P., Carnier, P. & Marinelli, L. (2017). Global bias reliability in dogs (*Canis familiaris*). *Animal Cognition*, 20, 257-265.
- 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—342.
- Nakagawa, E. (2002). Rats respond to configurations of stimuli. *The Psychological Record*, 52, 531—558.
- 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—387.
- Nakamura, N., Watanabe, S., & Fujita, K. (2014). A reversed Ebbinghaus–Titchener illusion in bantams (*Gallus gallus domesticus*). *Animal Cognition*, 17, 471—481.
- Neitz, J., Geist, T. & Jacobs, G. H. (1989). Color vision in the dog. *Visual Neuroscience*, 3, 119-125.
- Newman, C. V., & Newman, B. M. (1974). The Ponzo illusion in pictures with and without suggested depth. *The American Journal of Psychology*, 87, 511—516.
- Parrish, A. E., & Beran, M. J. (2014). When less is more: Like humans, chimpanzees (*Pan troglodytes*) misperceive food amounts based on plate size. *Animal Cognition*, 17, 427—434.
- Parrish, A. E., Brosnan, S. F., & Beran, M. J. (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, 395-405.
- Pitteri, E., Mongillo, P., Carnier, P. & Marinelli, L. (2014). Hierarchical stimulus processing by dogs (*Canis familiaris*). *Animal Cognition*, 17, 869-877.
- Roberts, T., McGreevy, P., & Valenzuela, M. (2010). Human induced rotation and reorganization of the brain of domestic dogs. *PLoS One*, 5, e11946.
- Salva, O. R., 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.
- Santacà, M., Regaiolli, B., Miletto Petrazzini, M., Spiezio, C., & Agrillo, C. (2017). Preliminary study to investigate the Delboeuf illusion in ring-tailed lemurs (*Lemur catta*): Methodological challenges. *Animal Behavior and Cognition*, 4, 365—377.
- Sovrano, V. A., Albertazzi, L., & Salva, O. R. (2014). The Ebbinghaus illusion in a fish (*Xenotoca eiseni*). *Animal Cognition*, 18, 533—542.
- Sperandio, I., & Chouinard, P. A. (2015). The mechanisms of size constancy. *Multisensory Research*, 28, 253—283.
- Timney, B., & Keil, K. (1996). Horses are sensitive to pictorial depth cues. *Perception*, 25, 1121—1128.
- Watanabe, S., Nakamura, N., & Fujita, K. (2011). Pigeons perceive a reversed Zöllner illusion. *Cognition*, 119, 137—141.
- Watanabe, S., Nakamura, N., & Fujita, K. (2013). Bantams (*Gallus gallus domesticus*) also perceive a reversed Zöllner illusion. *Animal Cognition*, 16, 109—115.
- Wetzels, R., Matzke, D., Lee, M. D., Rouder, J. N., Iverson, G. J. & Wagenmakers, E. J. (2011). Statistical evidence in experimental psychology: An empirical comparison using 855 t tests. *Perspectives on Psychological Science*, 6, 291-298.

7.3 Discussion

The primary objective of this study was to extend research conducted in Chapter 6 to clarify whether potential confounds such as presentation orientation and size sensitivity could explain dogs' lack of susceptibility to the Ponzo illusion. In Experiment 1, group performance when presented with the vertical Ponzo illusion was generally higher than the performance observed in horizontal presentations (see Chapter 6). However, the findings were not significant, suggesting that dogs do not demonstrate susceptibility to the Ponzo illusion, even when it is presented vertically. Consistent with findings reported in Chapters 5 and 6, individual variation of performance and susceptibility was present, with one dog, Beth, demonstrating human-like susceptibility to the Ponzo illusion.

In Experiment 2, a size discrimination task of various circle stimuli, differing in diameter (percent different), was used to assess whether dogs could perceive the minimum size difference hypothesised to be necessary for humans to see geometric illusions. It was observed that all dogs could successfully discriminate between circles varying in size by 20%. Most dogs were capable of perceiving 15% size differences and half of the dogs were capable of perceiving 10% size differences. No dog could successfully perceive 5% size differences. When the study was extended to evaluate identical percent size differences in stimuli differing in absolute size, the dogs typically performed worse when the absolute size of the stimuli was smaller. Generally, the dogs were successful at discriminating 40% size differences for both the smaller and larger absolute sized stimuli, yet more dogs were successful at discriminating 20% size differences when the absolute size of the stimulus was larger. These findings indicate that

dogs can perceive the minimum size difference required in humans to perceive the Ponzo illusion and that the null susceptibility observed in Chapters 6 and 7 is not an artefact of a physical inability.

The collection of experiments presented in Chapters 6 and 7 converge on the conclusion that dogs do not demonstrate susceptibility to the Ponzo illusion, even when vertical linear perspective cues are present. Even though the findings observed in this study were not significant, the group's average performance was higher than those observed in Chapter 6 when the illusion was presented horizontally. Thus, it is possible that dogs may demonstrate susceptibility to the Ponzo illusion when stimuli are further enhanced with additional linear perspective cues. Future research should attempt to present the Ponzo illusion embedded within pictorial stimuli as has been done in horses (Timney & Keil, 1996) and rhesus macaques (Fujita, 1996).

If the findings observed in Chapters 6 and 7 genuinely represent a lack of susceptibility to the Ponzo illusion, they might suggest that dogs differ, from humans, in their underlying mechanisms of perception. A lack of susceptibility may indicate that dogs do not process this visual scene post-retinally, but that it is perceived identically to the retinal projection. If so, bottom-up processing alone would suffice to explain the lack of susceptibility to the illusion. In addition to mechanistic accounts, evolutionary interpretations also exist. Given the environment in which a dog experiences its surroundings, it is possible that linear perspective cues are irrelevant in the perception of a visual scene. While this explanation is unlikely, given that dogs, like other terrestrial beings, live in similar environments, it remains a possibility that, perhaps, no evolutionary benefit or past experiences induce this perception (Feng et al., 2017; Kelley

& Kelley, 2014). If this is the case, it is likely that the majority of dogs, when presented within a Ponzo context, or any other linear perspective distorting illusions, would fail to demonstrate any susceptibility. Based on the immense individual variation presented in Chapters 6 and 7, such a conclusion seems far-fetched, however this hypothesis does exist and remains to be evaluated.

Chapter 8 – Dog Susceptibility to Illusory Contours

The experiments conducted in Chapters 5 through 7 suggest that illusion susceptibility in dogs differs from what has previously been observed in humans and other animals (Table 2, Chapter 2). The null, and/or reversed susceptibility observed across the Ebbinghaus-Titchener, Delboeuf, and Ponzo illusions suggest that more research is needed to further understand the underlying mechanisms of illusion susceptibility in dogs and the indirect effects these may have on how dogs perceive their environment.

Therefore, the framework presented in this thesis was expanded to include illusory contour illusions, a variety of illusion that occurs when individuals recognise and complete figures or shapes that are missing connective contours (Kanizsa, 1974; Schumann, 1900). This process, termed the theory of amodal completion (Kanizsa, 1955), is the result of a visual experience where an individual perceives superimposed edges due to brightness, colour or texture boundary even though a physical counterpart is not present. Perception of illusory contours emphasises a disconnect between what is presented on the retina and what is interpreted by the brain. While illusory contour susceptibility has not yet been evaluated in dogs, preliminary evidence was indirectly presented in Chapter 5. The fact that dogs demonstrated little difficulty generalising and misperceiving the illusory contour Ebbinghaus-Titchener illusion suggests that dogs interpret the illusory contours similarly to humans and other animals (Bravo et al., 1988; Fagot & Tomonaga, 2001; Fuss et al., 2014; Kanizsa et al., 1993; Nieder & Wagner, 1999; Sovrano & Bisazza, 2009; Wyzisk & Neumeyer, 2007; Zimmermann, 1962).

The most famous and well-studied examples of illusory contours are Ehrenstein (1987) and Kanizsa (1955) figures. While the Ehrenstein is well known, no studies of animal susceptibility exist. On the other hand, the Kanizsa figure is well-studied in animals, with chimpanzees (Fagot & Tomonaga, 2001), rhesus macaques (Zimmermann, 1962), cats (Bravo et al., 1988), mice (Kanizsa et al., 1993), barn owls (Nieder & Wagner, 1999), bamboo sharks (Fuss et al., 2014), redbellied splitfin fish (Sovrano & Bisazza, 2009), and goldfish (Wyzisk & Neumeyer, 2007) all demonstrating human-like perception of the figure.

The purpose of this chapter was to assess canine perception of illusory contours in the forms of the Ehrenstein and Kanizsa figures to substantiate the preliminary findings observed in Chapter 5. Given that susceptibility to illusions generally appears to differ between dogs, as presented in Chapters 5 to 7, it is of particular relevance to pursue the one parallel that has been observed. The preliminary findings of the illusory contour Ebbinghaus-Titchener illusion suggest that dogs may perceive illusory contours in a manner similar to humans and other animals (Bravo et al., 1988; Fagot & Tomonaga, 2001; Fuss et al., 2014; Kanizsa et al., 1993; Nieder & Wagner, 1999; Sovrano & Bisazza, 2009; Wyzisk & Neumeyer, 2007; Zimmermann, 1962). Making this deduction is somewhat problematic and controversial given that susceptibility to the figure presented has yet to be empirically evaluated in humans (Byosiere et al., 2016; Ninio, 1998). Thus, further exploration of these results in well-studied figures may provide additional insight into canine perception and the characteristics of shared and or/non-shared underlying theoretical mechanisms. The journal article, 'Can domestic dogs

(*Canis lupus familiaris*) perceive illusory contours?’ was submitted to the Journal of Comparative Psychology in July 2018 and is currently under review.

8.1 Declaration for thesis Chapter 8

In the case of Chapter 8, contributions to the work involved the following:

Name (authors in order)	Extent of contribution (%)	Nature of contribution
Sarah-Elizabeth Byosiene Corresponding author	70	Study design, data collection and analysis, manuscript writing
Philippe Chouinard Co-author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Tiffani Howell Co-author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication
Pauleen Bennett Senior author	10	Advising on literature search and interpretation, and contributing in the editing of the manuscript for publication

Declaration by co-authors

The undersigned hereby certify that:

- (1) the below declaration correctly reflects the nature and extent of the candidate's contribution to this work, and the nature of the contribution of each of the co-authors;
- (2) they meet the criteria for authorship in that they have participated in the conception, execution, or interpretation, of at least that part of the publication in their field of expertise;
- (3) they take public responsibility for their part of the publication, except for the responsible author who accepts overall responsibility for the publication;
- (4) there are no other authors of the publication according to these criteria; and
- (5) potential conflicts of interest have been disclosed to (a) granting bodies, (b) the editor or publisher of journals or other publications, and (c) the head of the responsible academic unit.

Signature 1	
Signature 2	
Signature 3	
Signature 4	

8.2 Can domestic dogs (*Canis lupus familiaris*) perceive illusory contours?

Can domestic dogs (*Canis lupus familiaris*) perceive illusory contours?

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Abstract

One way to better understand visual perception in animals is to assess misperception with illusion displays. Domestic dogs represent a unique species to evaluate misperception as recent findings suggest there may be mechanistic differences underlying their illusion susceptibility. In addition, to date, dogs, in general, have demonstrated human-like, reversed, and null susceptibility depending on the type of geometric illusion under investigation. To further evaluate illusion susceptibility in dogs, eleven dogs were assessed on their susceptibility to two illusory contour figures, the Ehrenstein illusory contour and Kanizsa figures, in a two-choice size discrimination task. For both illusions, dogs, as a group, demonstrated perception of the illusory contours, yet evidence for susceptibility was weaker for the Ehrenstein than the Kanizsa figures. To our knowledge, no animal species has been assessed on susceptibility to the Ehrenstein figure. However, these findings are consistent with those observed in animal species and humans with the Kanizsa illusion. Together, these findings provide preliminary evidence that dogs perceive illusory contour illusions and improve the current understanding of canine visual perception capabilities. Additional research is needed to substantiate these claims.

Keywords: Dog, Ehrenstein, Kanizsa, Perception, Illusory contour

Introduction

Visual perception represents an inventive process. Not only does the brain receive information from a visual scene from the retina, but it also interprets this information and adapts it to fit preconceptions (Gregory, 2015). Therefore, the perception of a visual scene may not accurately reflect reality, but instead, the most likely scene based on an individual's previous experiences and neural wiring (Kandel & Schwartz, 2000). It is in these instances that misperceptions, or illusions, can occur when mechanisms that are generally helpful for accurately perceiving the environment trick the brain into applying preconceptions to visual information in situations where they are inappropriate.

Illusory contour illusions represent one such misperception, which occurs when individuals recognise and mentally complete figures or shapes that are missing connective contours (Kanizsa, 1974) (Figure 1). Initially described by Schumann (1900), perhaps the most famous examples of illusory contours are the Ehrenstein illusory contour (1987) and Kanizsa (1955) figures. These illusions involve amodal completion, also known as the perceptual filling of gaps in a visual scene, through mentally perceiving boundaries that are not there. The process makes use of available information such as foreground/background brightness, colour, and textures so that when an object in its entirety is incomplete, the missing components are imagined.

The ability to perceive illusory contours indicates that the visual system is capable of deducing information about the world beyond present retinal input. Much debate exists concerning whether the neuronal processing of illusory contours is purely driven by bottom-up processing (Paradiso, Shimojo & Nakayama, 1989; von der Heydt, Peterhans & Baumgartner, 1984) or high-level cognitive mechanisms (Gregory, 1972; Rock &

Anson, 1979). Several findings indicate that bottom-up processing may be the most parsimonious explanation of illusory contour perception (for in depth explanation see Larsson et al., 1999). However, this does not exclude the involvement of high-level cognitive factors. For example, in humans, it has been reported that processing of illusory contours, specifically the Ehrenstein illusory contour and Kanizsa figures, takes place at higher levels in the visual system, post-retinally, perhaps cortically (Sugawara & Morotomi, 1991). Considering this equivocal debate and the fact that illusory contour stimuli can be easily used comparatively, they offer a unique way to evaluate evolutionary and environmental effects on perception.

To date, illusory contour susceptibility has been assessed in a variety of non-human animals (hereafter animals) (Bravo, Blake & Morrison, 1988; Fagot & Tomonaga, 2001; Fuss, Bleckmann & Schluessel, 2014; Kanizsa, Renzi, Conte, Compostela & Guerani, 1993; Nieder & Wagner, 1999; Sovrano & Bisazza, 2009; van Hateren, Srinivasan & Wait, 1990; Wyzisk & Neumeyer, 2007; Zimmermann, 1962; Zylinski, Darmaillacq & Shashar, 2012) to improve our understanding of how they perceive the world and to determine similarities and/or differences between humans. The majority of studies have done so by evaluating perception of Kanizsa figures. Chimpanzees (Fagot & Tomonaga, 2001), rhesus macaques (Zimmermann, 1962), cats (Bravo et al., 1988), mice (Kanizsa et al., 1993), barn owls (Nieder & Wagner, 1999), bamboo sharks (Fuss et al., 2014), redbtail splitfin fish (Sovrano & Bisazza, 2009), and goldfish (Wyzisk & Neumeyer, 2007) have all indicated human-like misperception of illusory contours. Taken together, these findings suggest that there may be similarities in the development

of visual processing and the shared and/or non-shared neural mechanisms regarding illusory contour perception (Banica & Schwarzkopf, 2016).

While many species demonstrate human-like susceptibility to visual illusions (Feng, Chouinard, Howell & Bennett, 2016), one species, in particular, the domestic dog, has demonstrated multifaceted findings (Byosiere et al., 2017b; Byosiere et al., 2016; Miletto Petrazzini, Bisazza & Agrillo, 2016). Two studies have found that dogs are not susceptible to the Delboeuf illusion (Byosiere et al., 2016; Miletto Petrazzini et al., 2016). Additionally, while all animal species tested to date have demonstrated susceptibility to the Ponzo illusion, dogs failed to demonstrate susceptibility across different presentational contexts (Byosiere et al., 2017b). Furthermore, when presented with the Ebbinghaus-Titchener illusion, dogs appear to be susceptible, however in the opposite direction observed in humans, indicating the target circle appears larger and not smaller when surrounded by larger contextual circles (Byosiere et al., 2016). Susceptibility in humans across different illusions likely represents multiple independent mechanisms rather than a single construct invoked by the same cognitive processes (Chouinard, Noulty, Sperandio & Landry, 2013; Chouinard, Unwin, Landry & Sperandio, 2016), which may explain the variation seen in dogs' susceptibility. However, the deviation from findings in other animal species warrants additional explanation, particularly given the evolutionary and domestication pressures on domestic dogs, as they have co-existed with humans for thousands of years (Bensky, Gosling & Sinn, 2013; Clutton-Brock, 1995; Miklósi, 2015; Morey, 1994), ultimately having been selectively bred for a variety of functional roles (Galibert, Quignon, Hitte & André, 2011).

Given their unique relationship with humans and the ever-increasing rise of canine cognition research in the last two decades (Bensky et al., 2013), it is essential to better understand the underlying mechanism(s) of how dogs perceive their external environment. Such findings may consequently have broader implications, especially if the mechanisms underlying dog visual processing diverge from those observed in humans and other animals. Given the prevalence of dogs in modern human society, an increased understanding of their perception may increase the efficacy of research methodologies and training methods, which ultimately affect the dog-human relationship. Therefore, the current research aimed to evaluate the perception of illusory contours in domestic dogs. Two experiments were conducted; Experiment 1, which evaluated perception of the Ehrenstein illusory contour figure and Experiment 2, which evaluated the perception of illusory Kanizsa squares.

General Methods

The procedures performed and presented in the subsequent experiments were conducted and evaluated in accordance with the ethical policies instated under La Trobe University's Animal Ethics Committee under applications AEC17-14 and AEC17-38.

Subjects

Eleven purebred Lagotto Romagnolos (*Canis familiaris*), nine females and two males, participated in two separate experiments. Six subjects participated in each experiment. Some of the dogs had previously participated in other experiments assessing illusion susceptibility (Byosiére et al., 2017b; Byosiére et al., 2016; Gellermann, 1933)

and colour discrimination (Byosiére et al., under review), while others were completely naïve, having not participated in any previous experiments (Table 1).

Testing apparatus and training

Dogs were first trained to target a single black circle stimulus. They were then transferred to circles of different sizes presented in pairs in a two-choice discrimination task. The majority were trained to target the larger circle, except for Baxter, Cricket, Isabelle, and Daisy, who were trained to select the smaller circle. Testing was conducted in the Canine Nose-Touch Testing Apparatus (Byosiére et al., 2017b; Byosiére et al., 2016; Byosiére et al., in press), which was used to minimise potential experimenter cues and distractions. The apparatus was equipped with a 508mm Dell® widescreen computer monitor (1280 x 800 pixels; one pixel measures approximately 0.3mm²) positioned with the lower edge approximately 24 cm above ground level. At ground level, directly below, was a remotely controlled treat dispenser (Treat & Train®), which when activated, 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. Microsoft PowerPoint was used to create and present stimuli, and data were collected via analysing and coding videos after testing.

Procedure

One experimenter was present at all times during testing, out of sight from the dog. The experimenter sat to the left of the Canine Nose-Touch Testing Apparatus and controlled a laptop computer (presenting and removing the stimuli) and activated the remote-controlled treat dispenser. The first trial in each block of ten trials 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 the experimenter, the dog moved to the screen and selected one stimulus by nose-touching the image.

Experiment 1 was conducted before Experiment 2. Before participating in test trials for any experiment, each dog completed the necessary familiarisation phases to ensure they were able to identify the correct target. All dogs participated in the familiarisations, and progressed only after reaching a criterion of > 90% correct in a single ten-trial block, or > 70% correct across each of two consecutive blocks. To partake in testing, each dog was required to complete all familiarisation phases successfully. Subjects were excluded from continuing after failing to successfully pass the criteria after a maximum of seven block attempts. During familiarisations, if the dog chose correctly, the remote-controlled treat dispenser was activated and delivered a food reward. If the dog chose incorrectly, the stimuli were removed thereby ending the trial. The dog then returned to the entrance of the apparatus to resume the starting position for the next trial. So as not to reinforce any particular way of responding, reinforcement for the experimental trials that evaluated illusory contour perception, occurred regardless of whether or not their choice was correct or incorrect, however, the location of the correct stimulus was dictated by a randomly selected Gellermann (1933) sequence. The reward was delivered once the stimuli were removed from the screen.

Stimuli

All stimuli were presented in black (RGB values 0, 0, 0; Luminance 0.18 c/m²) and white colours (RGB values 255, 255, 255; Luminance 175.5 c/m²) on an LCD screen. The target stimuli used were based on those previously used to evaluate illusion susceptibility, size sensitivity thresholds, and various discrimination tasks in this same

group of dogs (Byosiére et al., 2017b; Byosiére et al., 2016). The small circle and square stimuli were 207 pixels in diameter (62.1mm), while the large stimulus was 403 pixels in diameter (120.9mm).

Data analysis

Descriptive statistics for the familiarisation sessions were conducted to ensure passing criteria were met before each experiment. To determine if dogs were performing significantly above chance, one-tailed binomial tests were conducted at the group level to examine the discrimination performance of the various stimulus presentations, including standard deviations. To evaluate whether there were any differences between the stimulus presentations, a non-parametric Friedman test of differences among repeated measures was conducted. In cases of a significant Friedman result, Dunn's tests for multiple comparisons were conducted. Alpha was set at 0.05 and chance levels were considered to be 0.5, barring the multiple comparisons for Dunn's test in which a Bonferonni correction was applied, and significance was set at 0.0125.

In addition to null hypothesis statistical testing, Bayes factors were calculated for the control and illusion conditions for each experiment to quantify evidence in support for either the null or alternative hypothesis relative to the other (Wetzels et al., 2011). Bayes factors (BF_{10}) denote the likelihood of the alternative over the null hypothesis. Therefore, a BF_{10} value greater than three was considered to provide substantial support for the alternative hypothesis.

Experiment 1

The purpose of Experiment 1 was to assess canine perception of illusory contours of the Ehrenstein illusory contour figures in a two-choice size discrimination task.

Procedure

Before participating in the test, the dogs completed three familiarisation phases. Blocks consisted of ten total trials, where the first two trials always consisted of a previously trained stimulus. Familiarisation 1 consisted of two presentations of a size discrimination task of solid circles and was followed by eight presentations of a ring-like stimulus (Figure 2). Familiarisations 2 and 3 also consisted of two presentations of a size discrimination task of solid circles but were followed by eight presentations of a ring-like stimulus with lines or rays protruding from it. However, to ensure the dogs were selecting based on ring size and not overall figure size, the rays protruding from the smaller circle in Familiarisation 2 resulted in an overall larger figure. In Familiarisation 3, this was not the case.

In the test, the first two trials were familiar and consisted of the ring-like stimuli previously seen in Familiarisation 1 (Figure 2 (a)). The eight remaining trials consisted of two presentations of each stimulus presented in Familiarisations 2 and 3 (Figure 2 (b) and (c)), and four presentations of the Ehrenstein illusory contour illusion (Figure 2 (c)). Each dog completed 100 trials, 20 for each previously seen stimulus, and 40 for the illusion.

Results

Nine dogs participated in Experiment 1, most of which successfully completed Familiarisation 1 in the first block. However, one dog (Isabelle) required two blocks to continue to Familiarisation 2. In Familiarisation 2, the dogs averaged 4.56 blocks (ranging 1 to 7) before successfully meeting criteria in order to continue on to

Familiarisation 3. During this phase, three dogs (Beth, Eliza and Hamish) were unable to meet passing criteria within seven total blocks successfully and were excluded from continuing in the experiment. In Familiarisation 3, the six dogs averaged two blocks (ranging from 1 to 5) before successfully moving onto the test.

Figure 3 shows individual and group performance for each dog in the test sessions. Performance when presented with the ring-like control was high, as the average level of performance was $95\% \pm 5.5$ ($t(5) = 20.13$, $p < .001$, $BF_{10} = 2347.71$, Cohen's $d = 8.18$). When presented with the stimulus presented in Familiarisation 2, where the rays of the smaller ring extended beyond that of the larger ring (S7 long controls), performance was $77.5\% \pm 14.4$ ($t(5) = 4.7$, $p = .005$, $BF_{10} = 10.92$, Cohen's $d = 1.91$). When presented with the stimulus presented in Familiarisation 3, where the rays of the larger ring extended beyond that of the smaller ring (S10 long controls), performance was $83.3\% \pm 8.2$ ($t(5) = 10$, $p < .001$, $BF_{10} = 158.02$, Cohen's $d = 4.06$). However, when presented with the Ehrenstein illusory contour illusion, performance decreased and variability increased, with the dogs averaging $59.2\% \pm 21.1$ ($t(5) = 1.07$, $p = .34$, $BF_{10} = .572$, Cohen's $d = 0.44$).

To determine whether performance differed across the stimulus presentations, a non-parametric Friedman's test was conducted. All possible comparisons were made, which rendered a significant finding ($\chi^2(4) = 13.07$, $p < 0.01$). Upon further analysis of Dunn's test for multiple comparisons, no significant differences between the ring-like controls and the S7 long controls ($p = 0.34$), or the ring-like controls and the S10 long controls ($p = 0.56$) were observed, however a significant difference was found between the ring-like controls and Ehrenstein illusory contour illusion ($p = 0.002$). This significant

difference suggests that the dogs were not equally proficient at discriminating the control stimulus presentations from the test stimulus presentations. However, it is important to also note that Dunn's test for multiple comparisons did not indicate any significant differences between the S7 long controls and the Ehrenstein illusory contour illusion ($p = 0.6$), and the S10 long controls and the Ehrenstein illusory contour illusion ($p = 0.3$). While the dogs performed worse when presented with the Ehrenstein illusory contour illusion than when presented with the ring-like controls, the dogs did not perform significantly different when presented with the Ehrenstein illusory contour illusion compared to any other stimuli.

Experiment 2

The purpose of Experiment 2 was to assess canine perception of illusory contours of illusory Kanizsa squares in a two-choice size discrimination task.

Procedure

Before participating in the test, each dog participated in four familiarisation phases. Once again, blocks consisted of ten total trials. The first two trials (unless stated otherwise) consisted of a previously trained stimulus or, as the familiarisations progressed, the preceding familiarisation stimulus. Familiarisation 1 consisted of ten size discrimination presentations of solid circles to re-familiarise dogs with their previously learned rule (Figure 4). Familiarisation 2 consisted of two presentations of a size discrimination task of solid circles and was followed by eight presentations of a size discrimination task of solid squares. Familiarisation 3 began with two presentations of a size discrimination task of solid squares but was followed by eight presentations of an

empty or outline square shape. Finally, Familiarisation 4 consisted of two presentations of empty or outline squares followed by eight presentations of empty squares enclosed with Pac-Man-like figures to create a shape similar to that of a Kanizsa figure.

In the test, the first two trials were termed blank controls and consisted of the unfilled squares previously seen in Familiarisations 3 and 4 (Figure 4 (a)). Two presentations of the unfilled squares surrounded by Pac-Man-like shapes, termed Kanizsa controls (Figure 4 (b)) previously presented in Familiarisation 4, were randomly presented across the remaining eight trials. Included in the remaining six trials were two presentations of three novel Kanizsa-like stimuli (Figure 4 (c), (d), and (e)), in which at least one of the stimuli in the pair represented an illusory contour (Figure 4). Each dog completed 200 total trials, a total of 40 trials for each stimulus presentation.

Note that correct trials in the Kanizsa stimulus condition were defined as those in which the dog selected the larger (or for those trained to select the smaller) illusory stimulus. Correct trials in the Trained stimulus condition were defined as those in which the dog selected the larger (or for those trained to select the smaller) trained stimulus they had previously seen in familiarisations.

Results

The dogs generally performed well in the familiarisation sessions. The eight dogs successfully completed Familiarisation 1 in the first block; however, three dogs (Cricket, Daisy and Hamish) required two blocks to continue to Familiarisation 2. In Familiarisation 2, the dogs averaged 2.75 blocks (ranging 1 to 7) before successfully meeting criteria to continue to Familiarisation 3. During this phase, one dog (Beth) was unable to meet passing criteria within seven total blocks successfully and was excluded

from continuing the experiment. In Familiarisation 3, the seven remaining dogs averaged 3.41 blocks (ranging from 2 to 4) before successfully moving onto the final familiarisation. In Familiarisation 4, the dogs averaged 4.86 blocks (ranging from 4 to 7) before successfully moving onto the final familiarisation. During this phase, one dog (Cricket) to meet passing criteria within seven total blocks successfully and was excluded from continuing in the experiment. Therefore, six dogs continued to the test phase.

Figure 5 shows individual and group performance data for the dogs in the test sessions. Performance in the blank control (Figure 4 (a)) and Kanisza control (Figure 4 (b)) conditions was high, as the average level of performance was $84.6\% \pm 10.2$ ($t(5) = 8.3$, $p < .001$, $BF_{10} = 80.02$, Cohen's $d = 3.39$) and $82.5\% \pm 9.9$ ($t(5) = 8.1$, $p < .001$, $BF_{10} = 71.2$, Cohen's $d = 3.28$) respectively. Performance remained consistently high across the three novel presentations. Dogs averaged $74.5\% \pm 8.7$ ($t(5) = 7.1$, $p < .001$, $BF_{10} = 45.9$, Cohen's $d = 2.83$) in the Kanisza stimulus condition (Figure 4 (e)), $82.1\% \pm 13.5$ in the trained stimulus condition ($t(5) = 5.8$, $p = .002$, $BF_{10} = 22.8$, Cohen's $d = 2.38$) (Figure 4 (c), (d)), and $75\% \pm 11.8$ in the illusion condition ($t(5) = 5.2$, $p < .004$, $BF_{10} = 15.2$, Cohen's $d = 2.12$).

To determine whether performance differed across the stimulus presentations, a non-parametric Friedman's test was conducted. All possible comparisons were made, which rendered a non-significant finding ($\chi^2(5) = 7.1$, $p = .13$) suggesting that the dogs were equally proficient at discriminating the control stimulus presentations from the test stimulus presentations.

Discussion

To assess whether or not dogs demonstrate the perception of illusory contours we conducted two experiments. Experiment 1 examined dogs' susceptibility to illusory contours when presented with a size discrimination version of Ehrenstein illusory contour figures. Experiment 2 assessed dogs' susceptibility to illusory contours when presented with a size discrimination version of Kanizsa figures, a well-studied illusion in both humans and animals.

In Experiment 1, the dog's perception of illusory contours of Ehrenstein illusory contour figures was equivocal. As a group, the dogs performed significantly above chance when presented with the illusory stimulus, and certain individuals, such as Audrey, Baxter, and Cricket, appeared to demonstrate perception of the figure. However, the average group performance was only 59.2%, and performance differed significantly from controls, suggesting that the dogs were not equally proficient at discriminating between stimuli when presented with the illusion than discriminating the stimuli when presented with the ring-like controls. It is important to note that no significant difference in performance was observed between the illusion and either the S7 long controls or S10 long controls. Taken together, these inexplicit findings provide weak evidence that dogs perceive illusory contours.

In Experiment 2, the dogs, as a group, did demonstrate perception of illusory contours of Kanizsa figures, performing significantly above chance. The average group performance was 75%, and performance was not significantly different between any of the stimulus presentations, suggesting that the dogs were equally proficient at discriminating the control, and familiar presentations from the illusion. Additionally, all subjects (except for Daisy) performed above chance, demonstrating individual perception

of illusory contours. These findings indicate that dogs perceive illusory contours when presented with Kanizsa figures.

The findings from Experiment 1 and 2 are consistent with those observed in other animal species as well as in humans and provide preliminary information in regards to canine illusory contour perception. Specifically, these findings suggest that dogs, like humans and many other animals, experience a separation between what is projected on the retina and what the brain processes. The observed susceptibility to illusory contours most likely indicates that the canine brain applies existing underlying preconceptions to contexts in which they are not necessary. It is unlikely that contour-detecting cells in primary visual cortex solely facilitate this perception, as edge detection can be characterised as a complex and multidimensional process in which various cells analyse and extrapolate information from the visual field across the stage(s) of visual processing (Hubel & Wiesel, 1962). Therefore, it appears that the perception of illusory contours is demonstrative of the creation of an imaginative figure, produced by a visual system with a proclivity to complete figural components (Gerbino & Salmaso, 1987; Kanizsa, 1974; Purghé & Coren, 1992). Whether or not the underlying mechanism facilitating this perception in dogs is demonstrative of bottom-up processing or high-level cognitive mechanisms remains a question.

Methodological considerations of the present investigation

It is important to highlight that any conclusions drawn from this study are preliminary and additional investigation is required. This is due to the inherent difficulties of verifying that decisions are made by dogs, or any other nonhuman animal species, on the basis of seeing contours rather than adopting other strategies. For example, our subjects

may have based their decisions on the amount of white space in the Ehrenstein illusory contour stimulus in Experiment 1 and the separation of the corners in the Kanizsa figure presented in Experiment 2. While we attempted to rule out as many alternative explanations as possible with different control conditions, we could not think of any definitive litmus test that could be used to demonstrate with certainty that the dogs were basing their decisions on perception of illusory contours. Some authors have created Kanizsa control stimuli where the Pac-Man inducer mouths face outward by 180 degrees, and have tested these in other animal species (e.g. Fuss et al., 2014; Sovrano & Bisazza, 2009; Wyzisk & Neumeyer, 2007). However, it seems likely to us that our dogs, trained to detect relative size, would continue to choose the stimulus with the larger amount of space between the inducers in a non-illusory condition, regardless of whether or not they were capable of perceiving the illusory contours.

These limitations are not unique to animal perception research. In humans, the development of illusory contour perception is highly contested (Nayar, Franchak, Adolph & Kiorpes, 2015). While object recognition is generally considered to be a hierarchical process, progressing from elemental and local function to more complex integrative global processing with age, a number of studies provide conflicting reports (for a review see Nayar et al., 2015). In a study of 4-month old infants, Freeseaman, Colombo and Coldren (1993) observed that global processing is evident *before* local processing.

Given such wide-ranging controversies, further testing, using additional control conditions, is required to clarify these preliminary observations in dogs. We reason that alternative strategies are less likely to underlie the results we obtained, given that these alternative strategies may often require more cognate analytical reasoning than basing

370 decisions on perceiving illusory contours. For example, basing decisions on the
371 separation of the corners in the Kanizsa figure in Experiment 2 may require a cognate
372 understanding of local elements and distance. Ultimately, convergence between
373 independent studies would make our conclusions less equivocal.

374 An interesting observation is that some dogs were incapable of completing the
375 relevant familiarisation phases to meet the criteria for testing. This begs an answer to the
376 question, ‘why is it that certain dogs could not complete the familiarisation task?’ One
377 dog, Beth, failed to pass through familiarisation phases of both experiments successfully,
378 yet has previously demonstrated an aptitude for this paradigm, participating in previous
379 studies of illusion susceptibility (although her performance has often been variable). In
380 previous experiments, it has been observed that Hamish has a reduced size sensitivity
381 threshold, meaning that his ability to determine smaller percent size differences between
382 stimuli is worse than those observed in the other dogs. Thus, Hamish’s failure in
383 Experiment 1 may have been due to an inability to perceive the stimuli. Finally, Cricket
384 was unsuccessful in completing the last familiarisation phase in Experiment 2. Even
385 though she was trained to identify the smaller stimulus, she demonstrated a clear
386 preference for the overall larger stimulus during this phase. This may have been due to a
387 misapplication of her trained ‘rule’. While each subject is trained to select the larger or
388 smaller stimulus, it is possible that the dogs use additional ‘rules’ that we are unaware of.
389 Thus, Cricket may have failed because she was selecting stimuli based on a different
390 strategy.

391 Additionally, it is interesting to note the variation in performance between
392 Experiment 1 and 2. The lack of an illusory effect in Experiment 1 may be due to a

variety of reasons, for example, it may be possible that the stimuli were not salient enough to induce proper perception (i.e., maybe the dogs were unable to see the lines). Research conducted in our lab, and in this same group of dogs, has found that dogs are less successful when generalising their two-choice size discrimination task to line stimuli (Byosiére, Feng, Chouinard, Howell & Bennett, 2017a). However, if the lines were difficult to discriminate one would expect to see poor performance across familiarisation and control tests conducted in Experiment 1, which was not the case.

It is important to note that these findings may, therefore, be specific to this specific population of dogs. To control for specific factors, all dogs tested were purebred Lagotto Romagnolos who were genetically related and living in similar living conditions. Morphological consistency was maintained as morphological variations may affect brain structure and visual processing (McGreevy, Grassi & Harman, 2003; Roberts, McGreevy & Valenzuela, 2010). Even so, individual differences were apparent, which highlights the need to study individual differences within dogs in addition to breed and environmental effects. Such research, within genetically and environmentally similar or dissimilar dogs, could not only enhance our understanding of dog perception and cognition but also aid in more applied settings.

Conclusion

It has previously been observed that immense variation exists across illusion susceptibility in domestic dogs. Dogs have demonstrated human-like, reversed, and null susceptibility. While this may be due to variation in the mechanisms underlying illusory perception, the variation and deviation in susceptibility from other animal species are

particularly interesting. To date, perception of illusory contours has not been studied in dogs. Therefore we conducted two experiments assessing canine susceptibility to both Ehrenstein illusory contour and Kanizsa figures. Dogs, as a group, demonstrated perception of subjective contours, a finding consistent with those observed in other animal species as well as humans, which indicate that additional processing occurs in the brain after visual information enters the retina. However, additional research is needed to substantiate these claims and rule out alternative accounts more definitely.

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References

Banica, T. & Schwarzkopf, D. S. (2016). Induction of Kanizsa Contours Requires Awareness of the Inducing Context. *PLOS ONE*, 11(8), e0161177.

- 437 Bensky, M. K., Gosling, S. D. & Sinn, D. L. (2013). The world from a dog's point of
438 view: a review and synthesis of dog cognition research. *Advances in the Study of*
439 *Behaviour*, 45, 209-406.
- 440 Bravo, M., Blake, R. & Morrison, S. (1988). Cats see subjective contours. *Vision*
441 *Research*, (28), 861-865.
- 442 Byosiére, S.-E., Feng, L. C., Chouinard, P. A., Howell, T. J. & Bennett, P. C. (2017a).
443 Relational concept learning in domestic dogs: Performance on a two-choice size
444 discrimination task generalises to novel stimuli. *Behavioural Processes*.
- 445 Byosiére, S.-E., Feng, L. C., Rutter, N. J., Woodhead, J. K., Chouinard, P. A., Howell, T.
446 J. & Bennett, P. C. (2017b). Do dogs see the Ponzo illusion? *Animal Behavior*
447 *and Cognition*.
- 448 Byosiére, S.-E., Feng, L. C., Woodhead, J. K., Rutter, N. J., Chouinard, P. A., Howell, T.
449 J. & Bennett, P. C. (Byosiére2016). (2016). Visual perception in domestic dogs:
450 susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions. *Animal*
451 *Cognition*, 1-14.
- 452 Byosiére, S.-E., Feng, L. C., Wuister, J., Chouinard, P. A., Howell, T. J. & Bennett, P. C.
453 (in press). Do dogs demonstrate susceptibility to a vertically presented Ponzo
454 illusion? *Animal Behavior and Cognition*.
- 455 Chouinard, P. A., Noulty, W. A., Sperandio, I. & Landry, O. (2013). Global processing
456 during the Müller-Lyer illusion is distinctively affected by the degree of autistic
457 traits in the typical population. *Experimental brain research*, 230(2), 219-231.
- 458 Chouinard, P. A., Unwin, K. L., Landry, O. & Sperandio, I. (2016). Susceptibility to
459 Optical Illusions Varies as a Function of the Autism-Spectrum Quotient but not in

- 460 Ways Predicted by Local–Global Biases. *Journal of autism and developmental*
461 *disorders*, 46(6), 2224-2239.
- 462 Clutton-Brock, J. (1995). Origins of the dog: domestication and early history. In J.
463 Serpell (Ed.), *The domestic dog: Its evolution, behaviour and interactions with*
464 *people* (1st ed., pp. 7-20).
- 465 Ehrenstein, W. (1987). Modifications of the Brightness Phenomenon of L. Hermann. In
466 S. Petry & G. E. Meyer (Eds.), *The Perception of Illusory Contours* (pp. 35-39).
467 New York, NY: Springer New York.
- 468 Fagot, J. & Tomonaga, M. (Fagot2001). (2001). Effects of element separation on
469 perceptual grouping by humans (*Homo sapiens*) and chimpanzees (*Pan*
470 *troglodytes*): perception of Kanizsa illusory figures. *Animal Cognition*, 4(3), 171-
471 177.
- 472 Feng, L. C., Chouinard, P. A., Howell, T. J. & Bennett, P. C. (2016). Why do animals
473 differ in their susceptibility to geometrical illusions? *Psychonomic Bulletin &*
474 *Review*, 1-15.
- 475 Freeseaman, L. J., Colombo, J. & Coldren, J. T. (1993). Individual differences in infant
476 visual attention: Four-month-olds' discrimination and generalization of global and
477 local stimulus properties. *Child Development*, 64(4), 1191-1203.
- 478 Fuss, T., Bleckmann, H. & Schluessel, V. (2014). The brain creates illusions not just for
479 us: sharks (*Chiloscyllium griseum*) can “see the magic” as well. *Frontiers in*
480 *Neural Circuits*, 8, 24.

- 481 Galibert, F., Quignon, P., Hitte, C. & André, C. (2011). Toward understanding dog
482 evolutionary and domestication history. *Comptes Rendus Biologies*, 334(3), 190-
483 196.
- 484 Gellermann, L. W. (1933). Chance orders of alternating stimuli in visual discrimination
485 experiments. *The Pedagogical Seminary and Journal of Genetic Psychology*,
486 42(1), 206-208.
- 487 Gerbino, W. & Salmaso, D. (1987). The effect of amodal completion on visual matching.
488 *Acta Psychologica*, 65(1), 25-46.
- 489 Gregory, R. L. (1972). Cognitive Contours. *Nature*, 238, 51.
- 490 Gregory, R. L. (2015). *Eye and brain: The psychology of seeing*: Princeton university
491 press.
- 492 Hubel, D. H. & Wiesel, T. N. (1962). Receptive fields, binocular interaction and
493 functional architecture in the cat's visual cortex. *The Journal of physiology*,
494 160(1), 106.
- 495 Kanizsa, G. (1955). Margini quasi-percettivi in campi con stimolazione omogenea.
496 *Rivista di psicologia*, 49(1), 7-30.
- 497 Kanizsa, G. (1974). Contours without gradients or cognitive contours? *Italian journal of*
498 *Psychology*, 1(1), 93-112.
- 499 Kanizsa, G., Renzi, P., Conte, S., Compostela, C. & Guerani, L. (1993). Amodal
500 completion in mouse vision. *Perception*, 22(6), 713-721.
- 501 Larsson, J., Amunts, K., Gulyás, B., Malikovic, A., Zilles, K. & Roland, P. E. (1999).
502 Neuronal correlates of real and illusory contour perception: functional anatomy
503 with PET. *European Journal of Neuroscience*, 11(11), 4024-4036.

- 504 McGreevy, P., Grassi, T. D. & Harman, A. M. (2003). A strong correlation exists
505 between the distribution of retinal ganglion cells and nose length in the dog.
506 *Brain, Behavior and Evolution*, 63(1), 13-22.
- 507 Miklósi, Á. (2015). *Dog behaviour, evolution, and cognition* (2nd ed.). New York, NY:
508 Oxford University Press.
- 509 Miletto Petrazzini, M. E., Bisazza, A. & Agrillo, C. (Miletto Petrazzini2016). (2016). Do
510 domestic dogs (*Canis lupus familiaris*) perceive the Delboeuf illusion? *Animal*
511 *Cognition*, 1-8.
- 512 Morey, D. F. (1994). The Early Evolution of the Domestic Dog. *American Scientist*,
513 82(4), 336-347.
- 514 Nayar, K., Franchak, J., Adolph, K. & Kiorpes, L. (2015). From local to global
515 processing: The development of illusory contour perception. *Journal of*
516 *Experimental Child Psychology*, 131, 38-55.
- 517 Nieder, A. & Wagner, H. (1999). Perception and neuronal coding of subjective contours
518 in the owl. *Nature Neuroscience*, 2, 660.
- 519 Paradiso, M. A., Shimojo, S. & Nakayama, K. (1989). Subjective contours, tilt
520 aftereffects, and visual cortical organization. *Vision Research*, 29(9), 1205-1213.
- 521 Purghé, F. & Coren, S. (Purghé1992). (1992). Subjective contours 1900–1990: Research
522 trends and bibliography. *Perception & Psychophysics*, 51(3), 291-304.
- 523 Roberts, T., McGreevy, P. & Valenzuela, M. (2010). Human induced rotation and
524 reorganization of the brain of domestic dogs. *PLoS One*, 5(7), e11946.
- 525 Rock, I. & Anson, R. (1979). Illusory Contours as the Solution to a Problem. *Perception*,
526 8(6), 665-681.

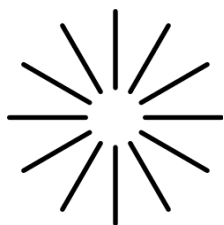
- 527 Schumann, F. (1900). Beiträge zur Analyse der Gesichtswahrnehmungen. Erste
528 Abhandlung. Einige Beobachtungen über die Zusammenfassung von
529 Gesichtseindruecken zu Einheiten. *Zeitschrift für Psychologie und Physiologie*
530 *der Sinnesorgan*, (23), 1–32.
- 531 Sovrano, V. A. & Bisazza, A. (2009). Perception of Subjective Contours in Fish.
532 *Perception*, 38(4), 579-590.
- 533 Sugawara, M. & Morotomi, T. (1991). Visual evoked potentials elicited by subjective
534 contour figures. *Scandinavian Journal of Psychology*, 32(4), 352-357.
- 535 van Hateren, J. H., Srinivasan, M. V. & Wait, P. B. (1990). Pattern recognition in bees:
536 orientation discrimination. *Journal of Comparative Physiology A*, 167(5), 649-
537 654.
- 538 von der Heydt, R., Peterhans, E. & Baumgartner, G. (1984). Illusory contours and
539 cortical neuron responses. *Science*, 224(4654), 1260-1262.
- 540 Wetzels, R., Matzke, D., Lee, M. D., Rouder, J. N., Iverson, G. J. & Wagenmakers, E.-J.
541 (2011). Statistical Evidence in Experimental Psychology: An Empirical
542 Comparison Using 855 t Tests. *Perspectives on Psychological Science*, 6(3), 291-
543 298.
- 544 Wyzisk, K. & Neumeyer, C. (2007). Perception of illusory surfaces and contours in
545 goldfish. *Visual Neuroscience*, 24(3), 291-298.
- 546 Zimmermann, R. R. (1962). Form generalization in the infant monkey. *Journal of*
547 *Comparative and Physiological Psychology*, 55(6), 918-923.

- 548 Zylinski, S., Darmaillacq, A.-S. & Shashar, N. (2012). Visual interpolation for contour
549 completion by the European cuttlefish and its use in dynamic camouflage.
550 *Proceedings of the Royal Society B: Biological Sciences*, 279(1737), 2386.

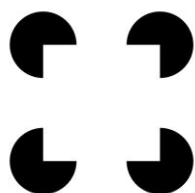
551 **Figure Captions**

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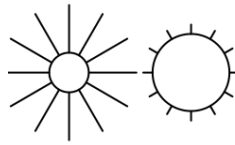
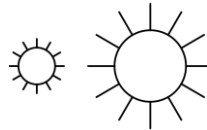
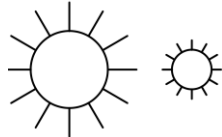
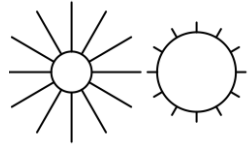
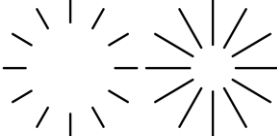


553

554 **Figure 1.** Schematic representations of the (1) Ehrenstein illusory contour and (2)

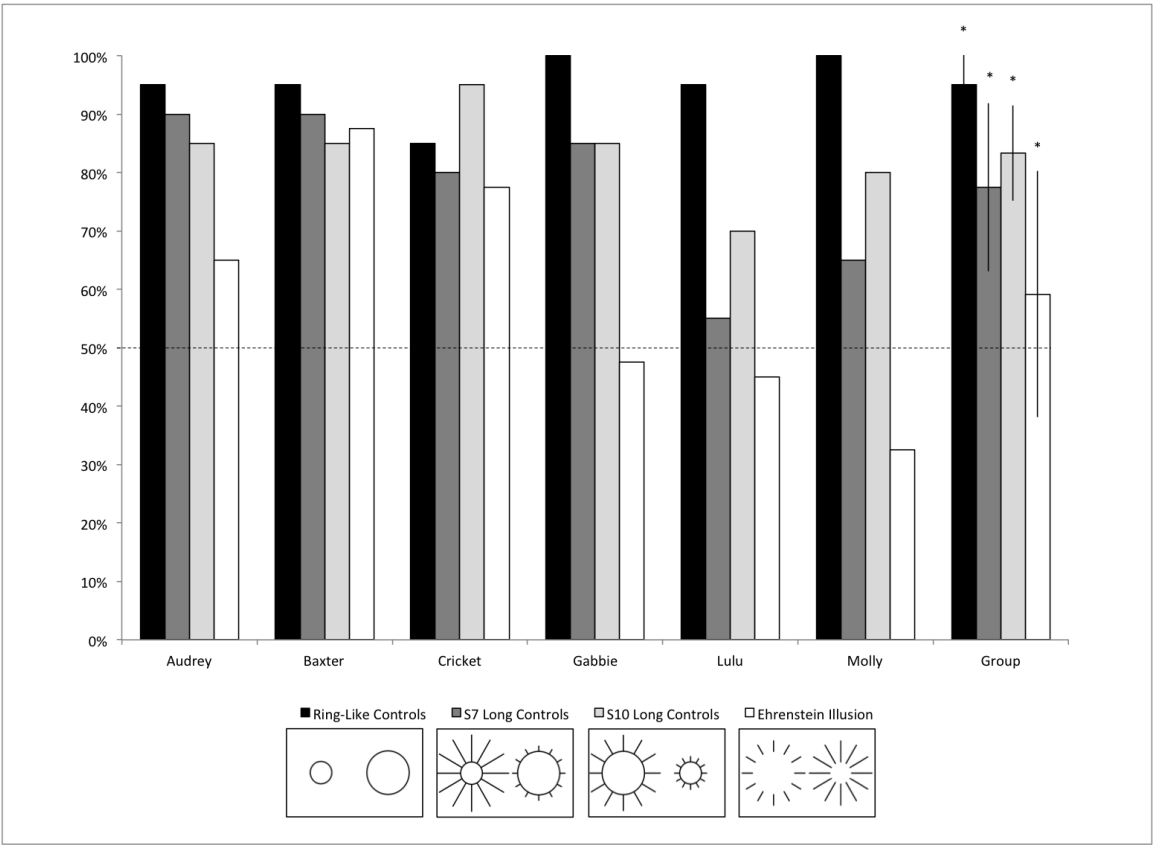
555 Kanizsa figures.

556

Familiarisation 1				
Familiarisation 2				
Familiarisation 3				
Test	a. 	b. 	c. 	d. 

557

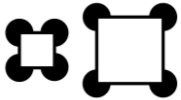
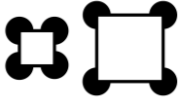
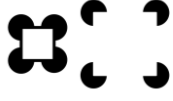
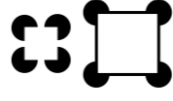
558 **Figure 2.** Schematic representations of the stimuli presented in Experiment 1,
559 specifically in familiarisation 1, 2, and 3, as well as during the test.



561

562 **Figure 3.** Individual and group percent correct (and standard deviations) for
563 control and illusion conditions. * Indicates that the binomial result significantly differed
564 from chance level at $p < 0.05$.

565

Familiarisation 1					
Familiarisation 2					
Familiarisation 3					
Familiarisation 4					
Test	a. 	b. 	c. 	d. 	e. 

566

567 **Figure 4.** Schematic representations of the stimuli presented in Experiment 2,
568 specifically in Familiarisation 1, 2, and 3, as well as during the test.

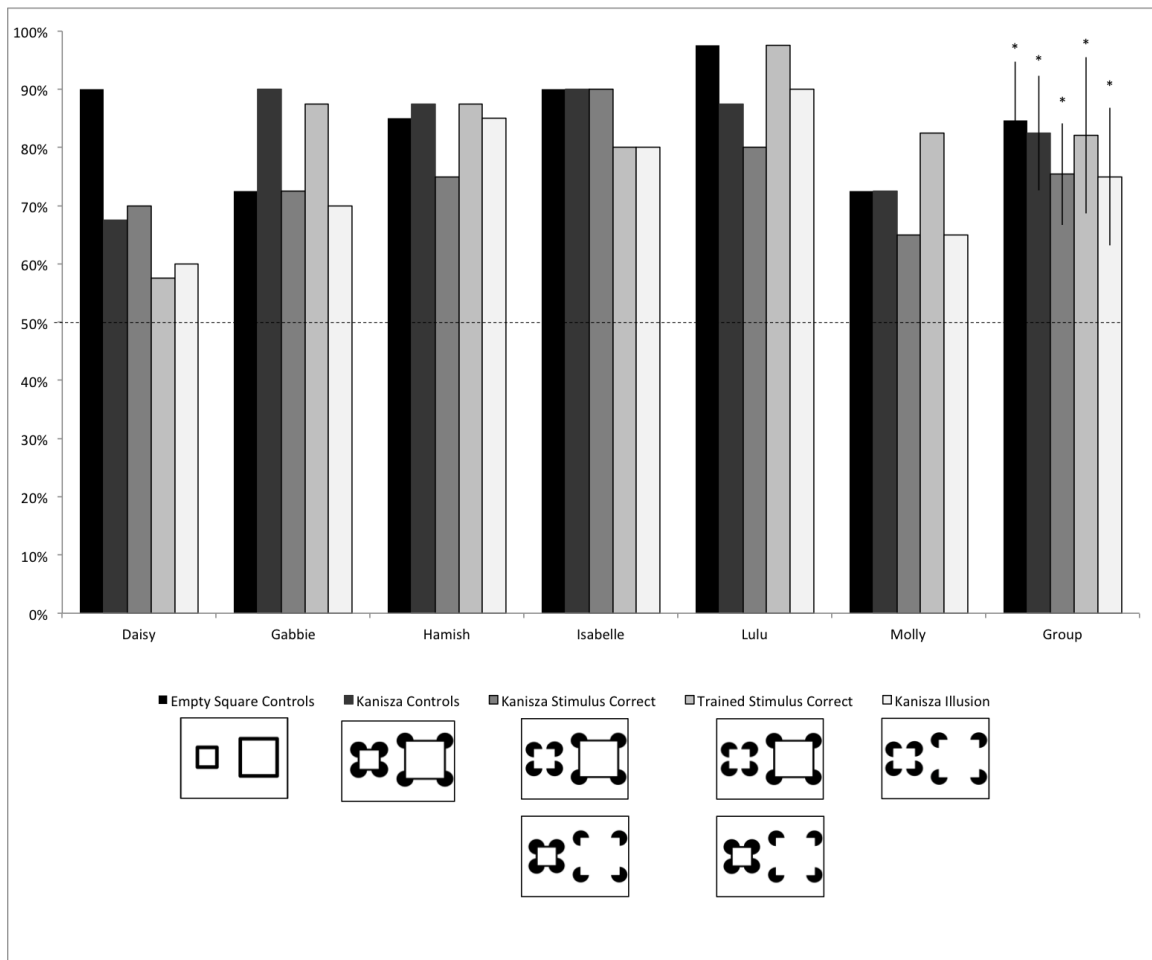


Figure 5. Individual and group percent correct (and standard deviations) for control and illusion conditions. * Indicates that the binomial result significantly differed from chance level at $p < 0.05$.

Table 1

Subject demographics at the time of testing

Name	Sex	Age (years)	Experiment(s) participated
Audrey ¹	Female	2.3	1
Baxter ^{1, 2, *}	Male	3	1
Beth ^{1, 3}	Female	5.5	1 (failed), 2 (failed)
Cricket [*]	Female	10 months	1, 2 (failed)
Daisy [*]	Female	1	2
Eliza ¹	Female	4	1 (failed)
Gabbie ^{1, 2}	Female	3.6	1, 2
Hamish ^{1, 3}	Male	7.8	1 (failed), 2
Isabelle [*]	Female	1.1	2
Lulu ¹	Female	4	1, 2
Molly ¹	Female	5	1,2

Note.

¹ Participated in previously published experiments² Subject desexed before Experiment 1 and 2³ Subject desexed after Experiment 1^{*} Subject trained to select small stimulus

8.3 Discussion

This study is one of the first to examine canine susceptibility to illusory contours. The goal of this chapter was to evaluate illusory contour perception in dogs across two figural presentations, the Ehrenstein and Kanizsa figures, to further probe the preliminary findings reported in Chapter 5. Specifically, the aim was to address if dogs, like humans and several other animals (Bravo et al., 1988; Fagot & Tomonaga, 2001; Fuss et al., 2014; Kanizsa et al., 1993; Nieder & Wagner, 1999; Sovrano & Bisazza, 2009; Wyzisk & Neumeyer, 2007; Zimmermann, 1962), integrate figural fragments and perceive them similarly to figures in which physical contours are present.

When presented with the Ehrenstein figure, dogs demonstrated an equivocal result. Dogs, as a group, performed significantly above chance in a human-like manner, but performance in this condition significantly differed from the ring-like controls. This difference was only present between these two conditions, and no difference was observed between the illusion condition and two other familiar presentations. Thus, the findings provide some, albeit weak, evidence that dogs perceive illusory contours.

Additional evidence for illusory contour perception in dogs was observed when the dogs were presented with Kanizsa figures. Dogs, as a group, performed significantly above chance, performing equally well across the control and the illusion conditions. These findings suggest that dogs demonstrate perception of the illusory figures when presented with the incomplete illusory stimuli, in a human-like manner.

These findings, specifically those observed in regard to the Kanizsa figure, parallel results observed in other animal species as well as in humans (Bravo et al., 1988; Fagot & Tomonaga, 2001; Fuss et al., 2014; Kanizsa et al., 1993; Nieder & Wagner,

1999; Sovrano & Bisazza, 2009; Wyzisk & Neumeyer, 2007; Zimmermann, 1962). It appears that dogs experience a disjuncture between the information received in the retina and what the brain processes. This is likely explained by the theory of amodal completion (Kanizsa, 1955) and the application of underlying preconceptions to contexts in which they are not necessary. Whether or not this difference is due to bottom-up processing or high-level cognitive mechanisms remains unknown. The convergence of similar findings across animal species would indicate that the perception of illusory contours is likely a conserved trait, potentially facilitated by bottom-up processing. However, this does not exclude the possibility that high-level cognitive factors are involved. While this question is particularly intriguing, it is beyond the scope of this thesis, and further investigation is required.

Chapter 9 – General Discussion and Future Directions

9.1 Thesis background

In the last two decades, there has been a rapid and ever-growing interest in canine behaviour and cognition (Bensky et al., 2013). Relevant studies have primarily focused on social-cognition (e.g. Bräuer et al., 2006; Hare et al., 2002b; Kaminski, 2009), and have led researchers to believe that dogs may represent an important model for understanding social-cognitive processes in animals (Hare & Tomasello, 1999; Miklösi et al., 1998; Soproni et al., 2002; Soproni et al., 2001; Udell et al., 2008; Udell & Wynne, 2008). While this has markedly improved our current understanding of dog behavior and cognition, it has also exponentially increased our curiosity and desire to understand humans' best friend.

Consequently, dogs have now participated in a variety of cognitive assessments. Across these tasks, conflicting findings and observations often have muddled interpretations of canine cognition research. For example, unpredictable findings have been observed across a range of social and non-social cognition paradigms that employ similar methodologies (e.g. Bell & Fox, 1997; Collier-Baker, Davis & Suddendorf, 2004; Dorey et al., 2010; Fiset, Beaulieu & Landry, 2002; Gagnon & Doré, 1992; Gagnon & Doré, 1994; Hare & Tomasello, 2005; Miller, Gipson, Vaughan, Rayburn-Reeves & Zentall, 2009; Range, Hentrup & Virányi, 2011; Soproni et al., 2002; Tauzin, Csík, Kis & Topál, 2015; Udell et al., 2008; Virányi et al., 2008; Wynne et al., 2008). While multiple explanations for these conflicting reports likely exist, this thesis addresses one potential variable that has largely been overlooked.

Differences in dog visual processing and perception may begin to explain why similar studies with almost identical methodologies have observed such contradictory results (Byosiere et al., 2017). Visual tasks currently comprise the principal method to assess cognition in dogs (Bensky et al., 2013). This appears to be a consequence of accessibility, driven by human and non-human primate cognition research, rather than deliberate rationale. The use of these paradigms in dogs may be problematic as they have often been adapted and applied without critical evaluation (Byosiere et al., 2017). Although human and non-human primate visual capacities are quite comparable (Jacobs, 1996), the application of human-centric paradigms in dogs may not be justified.

This issue is exacerbated by the fact that few studies of visual processing and perception have been conducted in dogs. The current state of literature regarding fundamental components of dog vision is incomplete (Byosiere et al., 2017; Miller & Murphy, 1995). Accurate measures of visual acuity, colour perception, processing precedence and more remain unknown. Moreover, given the vast intra-specific variation observed in dogs (Byosiere et al., 2017; Miller & Murphy, 1995), morphological differences in terms of body size, height, facial structure, and eye placement may all affect the way dogs process visual stimuli (Byosiere et al., 2017; Gácsi et al., 2009b; McGreevy et al., 2004; Roberts et al., 2010). Under these circumstances, it seems plausible that the variation observed across canine cognition studies may stem from differences in the sample, primarily dog's physiology both within and between breeds. It is of the utmost importance that research into dog behaviour and cognition fully understand the effects of these variables before conclusions about cognitive skills and competence are confirmed. To appropriately do so, it is necessary to thoroughly

investigate this line of inquiry systematically within a single breed, in which facial morphology is consistent, and genetic and environmental controls are in place.

Even within humans, a verbal species capable of describing and communicating what they can see, it is exceptionally challenging to evaluate visual perception. It is, therefore, not surprising that gauging perception in non-verbal animals is a particularly complex task. One method used to assess visual processing in humans is illusion susceptibility. As it is possible to evaluate illusion susceptibility non-verbally, this method has been proposed to function as an innovative tool to indirectly and comparatively assess perception in animals (Fujita, 2004; Kelley & Kelley, 2014). Given the substantial body of human illusion literature available, and the feasibility of generalising these paradigms to non-verbal species, researchers have evaluated illusion susceptibility across a variety of animals (Byosiére et al., 2017; Feng et al., 2017; Kelley & Kelley, 2014). In doing so, similarities and differences underlying psychological and cognitive processes of perception can be compared, both within and across species (Kelley & Kelley, 2014).

One species in which illusion susceptibility had not yet been evaluated was the domestic dog. The purpose of this thesis was to gain insight and understanding into canine perception by applying this unique approach to a well-studied, but not well-understood, species. The comprehensive body of work presented in this thesis represents many firsts for gauging illusion susceptibility in dogs. Consequently, predictions at the onset were rudimentary, limited, and were adapted as various results were observed throughout this thesis. These predictions were not necessarily composed in the order in which the studies are presented. Initially, there was no reason to predict dogs would

demonstrate anything but human-like susceptibility to visual illusions. It was predicted that dogs would demonstrate human-like susceptibility to the first illusions assessed, the Ebbinghaus-Titchener and Delboeuf illusions. This prediction was not supported, and the purpose of the thesis was transformed to not only evaluate susceptibility to visual illusions but also to identify similarities and differences that might reveal insights regarding mechanisms of visual processing. This final chapter summarises and collectively interprets the findings from the results reported in this thesis, and evaluates the broad theoretical and practical implications of this research. Various limitations and proposed future directions to this line of research are discussed. The thesis concludes with final remarks, in which a summary of the thesis is presented.

9.2 Thesis summary

Throughout the thesis, numerous findings were reported. These findings, both individually, and as a collective assessment, provide a significant contribution to the current understanding of canine visual perception and cognition. Although some of the published works contain projects conducted both, by myself as well as with others, my contribution to these projects has been substantial as indicated by the authorship of the articles. Here I provide a concise review of the results presented in each chapter.

Before canine illusion susceptibility could be evaluated, it was essential to gauge the suitability of the proposed two-choice discrimination paradigm. Chapters 3 and 4 provide this fundamental assessment. In Chapter 3, dogs' generalisation capacities were discussed. While it is often assumed that dogs are not capable of generalising in applied settings (Alexander, 2003; Cattet, 2013), it was of utmost importance to this thesis to

ascertain whether or not dogs could learn a rule and apply its properties to novel contexts. This was largely due to the nature of the experimental design, in which dogs were required to generalise previously learned rules to novel illusion-invoking displays. It was observed that dogs could easily be trained to select the larger (or in a few instances, the smaller) of two solid circle stimuli in a two-choice size discrimination task. Once successful, dogs were presented with novel on-screen stimuli that varied in degree of similarity to the trained and familiar circle. The stimuli represented shapes in the form of ovals, squares, rectangles, diamonds, triangles, stars, as well as horizontal and vertical lines. Results indicated that dogs were quite adept at generalising, performing above chance for many of the shapes upon the first test session, particularly for ovals, squares, diamonds, stars, and to some extent triangles. Generalisation was not successful for all novel stimuli; some shapes were noticeably more difficult. Specifically, performance on the horizontal and vertical lines proved to be quite variable.

In continuation of the foundational assessment in Chapter 3, Chapter 4 reported on colour discrimination capabilities in dogs and the effects of physical isoluminance on performance. Physiological assessments indicate dichromatic vision in dogs, suggesting that they are incapable of perceiving colour contrasts of red and green (Miller & Murphy, 1995). However, behavioural assessments of colour discrimination conflict with these physiological reports (Kasparson, Badridze & Maximov, 2013; Neitz et al., 1989; Rosengren, 1969; Siniscalchi et al., 2017; Tanaka et al., 2000). In order to ascertain optimal colour contrasts in which to embed illusory stimuli, contrasts of blue and yellow, and red and green, were presented in a two-choice size discrimination task. Across a variety of experiments, it was observed that dogs were able to discriminate between all

colour contrasts, and that physical luminance affected performance. The results fail to disentangle whether or not dogs perceive colours in the same way as humans, but they suggest that dogs use both colour cues and/or brightness cues when discriminating between contrasts, and performance is dependent on the physical luminance of the stimuli.

Chapter 5 reported one of the first studies to assess illusion susceptibility in dogs, evaluating canine perception of two presentations of the Ebbinghaus-Titchener illusion and one presentation of the Delboeuf illusion. Dogs as a group demonstrated reversed susceptibility compared to humans, to both versions of the Ebbinghaus-Titchener illusion. No susceptibility was demonstrated when presented with the Delboeuf illusion. In humans, susceptibility to the Ebbinghaus-Titchener and Delboeuf size illusions is most often explained by contour interaction theory (Jaeger, 1978). This theory cannot explain the reported results as they fail to account for reversed and null susceptibility. The best theoretical explanation for the findings is assimilation theory (Pressey, 1971), which conforms to the Gestalt law of similarity, in which items or objects with similar visual characteristics (e.g. shape, size, colour, texture) are grouped together (Koffka, 1935). These results suggest that dogs preferentially process visual stimuli locally, rather than globally, as observed in humans. Given this divergence, and the manner in which illusions can be used to evaluate global and local processing preferences, it was deemed necessary to further explore the similarities and differences underlying the mechanisms of canine perception by assessing canine susceptibility to other geometric visual illusions.

The intriguing findings reported in Chapter 5, particularly the reversed susceptibility to the Ebbinghaus-Titchener illusion, warrant additional investigation. The

study conducted in Chapter 6 presented dogs with the various presentations of the Ponzo illusion for two main reasons. First, the Ponzo illusion, like the Ebbinghaus-Titchener and Delboeuf, represents a distorting illusion, albeit one in which the modality and theoretical explanations differ. Second, the illusion has been evaluated across a variety of animals, with all species to date demonstrating human-like susceptibility (Barbet & Fagot, 2002; Bayne & Davis, 1983; Fujita, 1996; Fujita et al., 1991; Imura et al., 2008; Nakagawa, 2002; Timney & Keil, 1996), although this may represent a bias for significant results within the publishing industry. Three presentational contexts, encompassing four experiments (in which one presentation was re-tested) were conducted. Although individual variation was observed, with some dogs demonstrating susceptibility in both a human-like and reversed manner, equivocal findings were observed across the four experiments. The results converged on the conclusion that dogs do not demonstrate susceptibility to the Ponzo illusion. In addition to the reversed and null findings observed in Chapter 5, these results reveal an example in which dogs and humans differ in their perception of stimuli. However, it is difficult to interpret whether the lack of susceptibility to the Ponzo illusion is indicative of a difference in visual processing, or whether the findings can be explained by other confounding variables related to the presentational context.

To further investigate and clarify the potential reasons why dogs did not appear susceptible to the Ponzo illusion, the study presented in Chapter 6 was extended to Chapter 7. Susceptibility to the Ponzo illusion is typically explained by inappropriate constancy scaling theory (Gregory, 1963), which proposes that linear perspective cues facilitate the illusory effects. While well-studied and evaluated illusion displays were

presented in Chapter 6, it seemed possible that the results were demonstrative of weak susceptibility and that a stronger effect may have been invoked had the stimuli been presented vertically with more salient linear perspective cues. Upon reflection, it was also noted that the lack of susceptibility might have been driven by an inability to perceive the minimum size difference between stimuli. In humans, a minimum percent size difference is required to perceive illusory effects (Sperandio & Chouinard, 2015). However, this explanation is unlikely given the reversed susceptibility observed in Chapter 5 (in regard to the Ebbinghaus-Titchener illusion). Consistent with the findings presented in Chapters 5 and 6, dogs did not demonstrate human-like susceptibility to the vertically presented Ponzo illusion, and this did not appear to be the result of an inability to perceive the illusory effects. While the null results limit specific interpretation of the visual processing mechanisms in dogs, they do provide additional support for Chapters 5 and 6. Specifically, they highlight that dogs and humans differ in their perception of cognitive geometric illusions and indirectly suggest that these differences may stem from variation in how information is visually processed and interpreted.

In contrast to evaluating various differences of illusion susceptibility between dogs and humans, Chapter 8 focused on the single comparative parallel observed in this thesis. Preliminary results from the Illusory Contour Ebbinghaus-Titchener illusion (discussed in Chapter 5) suggested that dogs perceive figural fragments as complete structures in a manner similar to humans. The perception of illusory contours is most often explained by the theory of amodal completion (Kanizsa, 1955), in which a disconnect is observed between the information received by the retina and interpretation of this information by the brain. To date, all animals assessed have demonstrated human-like susceptibility to

Kanizsa figures (Bravo et al., 1988; Fagot & Tomonaga, 2001; Fuss et al., 2014; Kanizsa et al., 1993; Nieder & Wagner, 1999; Sovrano & Bisazza, 2009; Wyzisk & Neumeyer, 2007; Zimmermann, 1962), the most widely recognised and studied illusory contour illusion. The results presented in Chapter 8 indicated that dogs perceive the figural fragments of illusory contours in a manner consistent with humans and other animals. Across two presentations, the Ehrenstein (1987) and Kanizsa (1955) figures, dogs performed significantly above chance when presented with the illusion. These findings are particularly intriguing as they represent the single instance in which similarity was observed between dog and human perception.

9.3 Theoretical implications

The results from the studies conducted as part of this thesis comprise a thorough investigation of illusion susceptibility within a single species. The findings contribute to various theoretical debates, which are discussed individually in their respective chapters, as well as briefly summarised above in section 9.2. However, it is important to note the broader theoretical implications of this research. More specifically, the method of using illusion susceptibility to evaluate perception allows for a systematic and readily generalisable approach (Kelley & Kelley, 2014) in which new theories can be developed and existing theories can be tested beyond what is conceivably possible in a human population (Feng et al., 2017). By evaluating susceptibility across multiple illusory displays, it is possible to evaluate and interpret similarities and differences underlying perceptual processing, indirectly yielding a comprehensive account of perceptual and psychophysical mechanisms, which can be compared and contrasted across species.

Before illusion susceptibility could be addressed, the thesis emphasised the need to establish a foundational framework of illusion susceptibility in a morphologically consistent breed in which environmental and genetic factors were controlled. As discussed in Chapter 2, the illusions reported in this thesis can be categorised as cognitive geometric illusions, in which the illusory effect is elicited by an interaction of perceived reality and prior knowledge. Within these illusions, the modality, or way perception is affected (e.g. size, linear perspective, shape, brightness), can vary (Table 5). To appropriately compare illusion susceptibility in dogs, it is important to analyse the results reported in this thesis based on this classification. Initially, it was useful to consider the group results, as if all dogs in a group were consistent. Given that this was not the case, however, the topic of individual differences will be revisited at a later stage in this chapter.

Table 5

Overview of the illusions and the results observed in dogs presented in this thesis

<u>Illusion</u>	<u>Chapter</u>	<u>Type of Illusion</u>	<u>Modality</u>	<u>Canine Susceptibility</u>	<u>Theory</u>	<u>Perceptual Style</u>
Classical Ebbinghaus-Titchener	5	Distorting	Size	Reverse	Assimilation	Local
Illusory Contour Ebbinghaus-Titchener	5	Distorting	Size	Reverse	Assimilation	Local
Delboeuf	5	Distorting	Size	Null	Assimilation?	Local
Horizontal Ponzo Grid Inducer (Circles)	6	Distorting	Linear Perspective	Human-like?	Inappropriate size constancy scaling?	Global?
Re-test Horizontal Ponzo Grid Inducer (Circles)	6	Distorting	Linear Perspective	Null	N/A	Local
Horizontal Ponzo Grid Inducer (Rectangles)	6	Distorting	Linear Perspective	Null	N/A	Local
Horizontal Ponzo Converging Lines	6	Distorting	Linear Perspective	Null	N/A	Local
Vertical Ponzo Converging Lines	7	Distorting	Linear Perspective	Null	N/A	Local
Ehrenstein	8	Fictitious	Brightness	Human-like?	Amodal completion	Global
Kanizsa	8	Fictitious	Brightness	Human-like	Amodal completion	Global

By analysing canine perception of these illusions in a more structured context, interesting and consistent patterns come to light. When presented with distorting illusions, based on size and linear perspective, dogs appear to differ from humans regarding their perception. In the case of the Ebbinghaus-Titchener and Delboeuf illusions, perceptually distorted by size, dogs tended to demonstrate reversed susceptibility compared to humans. In both presentations of the Ebbinghaus-Titchener illusion, dogs performed significantly above chance in a way opposite to what is typically observed in humans. While dogs did not demonstrate significant susceptibility to the

Delboeuf illusion, there was evidence to suggest this may be due to a lack of power and a weaker effect of the illusion itself (see Chapter 5). Additional evidence for this conclusion can be drawn from the limited evidence of canine susceptibility to the Ponzo illusion. When presented with the Ponzo illusion, across a variety of presentational contexts, dogs failed to demonstrate any susceptibility. Moreover, this result was consistent. Across eight illusory presentations, dogs only once demonstrated significant human-like susceptibility (Ponzo 1) and, even in this presentation, group performance was practically at chance (56.2%).

Evaluating all distorting illusions as a whole (i.e. size and linear perspective), in two instances dogs demonstrated reversed susceptibility (Classic and Illusory Contour Ebbinghaus-Titchener), and in four cases the dogs failed to demonstrate any kind of susceptibility at all. The convergence of these findings across the Ebbinghaus-Titchener, Delboeuf and Ponzo illusion suggest that dogs likely visually process distorting illusions using local precedence, meaning that emphasis is drawn to the individual components presented in a scene rather than the perceptual grouping of elements. In summary, these findings suggest that dogs do not visually perceive size distorting illusions like humans.

In light of the findings described in Chapters 5 to 7, the results presented in Chapter 8 promote discussion of what this single parallel might mean in the context of the consistent divergence observed in earlier chapters. When presented with illusory contour illusions, also known as fictitious illusions (in this case, distorted by luminance contrast), the dogs demonstrated preliminary human-like susceptibility to the Ehrenstein figure and human-like susceptibility to the Kanizsa figure. These findings indicate that dogs visually perceive these illusory contour illusions in a human-like manner, consistent with findings

reported in other animals (Bravo et al., 1988; Fagot & Tomonaga, 2001; Fuss et al., 2014; Kanizsa et al., 1993; Nieder & Wagner, 1999; Sovrano & Bisazza, 2009; Wyzisk & Neumeyer, 2007; Zimmermann, 1962). It is somewhat surprising that similarities in visual perception were noted within the experiments reported in this thesis, particularly because of the divergence (from humans) observed within distorting illusions. One question that now remains is ‘is it possible to reconcile this human-like susceptibility observed in fictitious illusions with respect to the reversed and null susceptibility observed in the distorting illusions’?

The human literature has proposed that visual processing should not be considered to be a singular construct (Chouinard, Noulty, Sperandio & Landry, 2013; Chouinard et al., 2016), but instead should be identified as an umbrella term in which various independent mechanisms are involved in cognitive operations. For example, in humans, a preference for global precedence is generally more common than local precedence, however, cultural (e.g. de Fockert et al., 2007) and psychological (e.g. Chouinard et al., 2013; Chouinard et al., 2016; King, Hodgekins, Chouinard, Chouinard & Sperandio, 2017) effects have been observed to elicit variation in perceptual styles. Moreover, these individual differences have been associated with illusion susceptibility. Specifically, increased global processing preferences have been linked to increased illusion susceptibility (e.g. Berry, 1968; Berry, 1971; Dawson, 1967; Witkin, 1967), and increased local processing preferences have been linked to decreased illusion susceptibility (e.g. Dakin & Frith, 2005; de Fockert et al., 2007; Happé et al., 2001; Happé, 1996). These results suggest that tests of illusion susceptibility can be used in addition to more conventional tasks of global/local precedence to determine perceptual

style. Moreover, they confirm previous findings that it is necessary to conduct multiple assessments to adequately evaluate a perceptual style and gauge convergence amongst the findings (Chouinard et al., 2013; Chouinard et al., 2016), as performance on a single task, or illusion, may inaccurately depict a species' preferential processing style.

Under this interpretation, visual processing tasks, such as different illusion types presented in this thesis, might be expected to yield different results. Given that illusions vary in type and modality, it is not unexpected that different underlying mechanisms and perceptual and cognitive operations are involved. What does this mean for the findings reported in this thesis, specifically the mechanisms underlying canine visual processing? The results presented in this thesis suggest that the perceptual mechanisms underlying illusion susceptibility in dogs depend on the type of illusion and modality that is affected. Dogs generally demonstrated a reversed susceptibility to size-distorting geometric illusions, null susceptibility to linear perspective distorting illusions, and human-like susceptibility to fictitious illusions (Figure 3). More crudely, across the ten illusion presentations evaluated in this thesis, dogs demonstrated null susceptibility to five, human-like susceptibility to three, and reversed susceptibility to two. These findings suggest an overall local preference for visual processing in dogs, as seven instances of local and three cases of global processing were observed. Nonetheless, it is necessary to highlight that a conventional assessment, such as the Navon's task, of global/local precedence was not conducted as a part of this thesis. One avenue for future research is to further evaluate these conclusions by assessing the relationship between global/local precedence and illusion susceptibility in dogs.

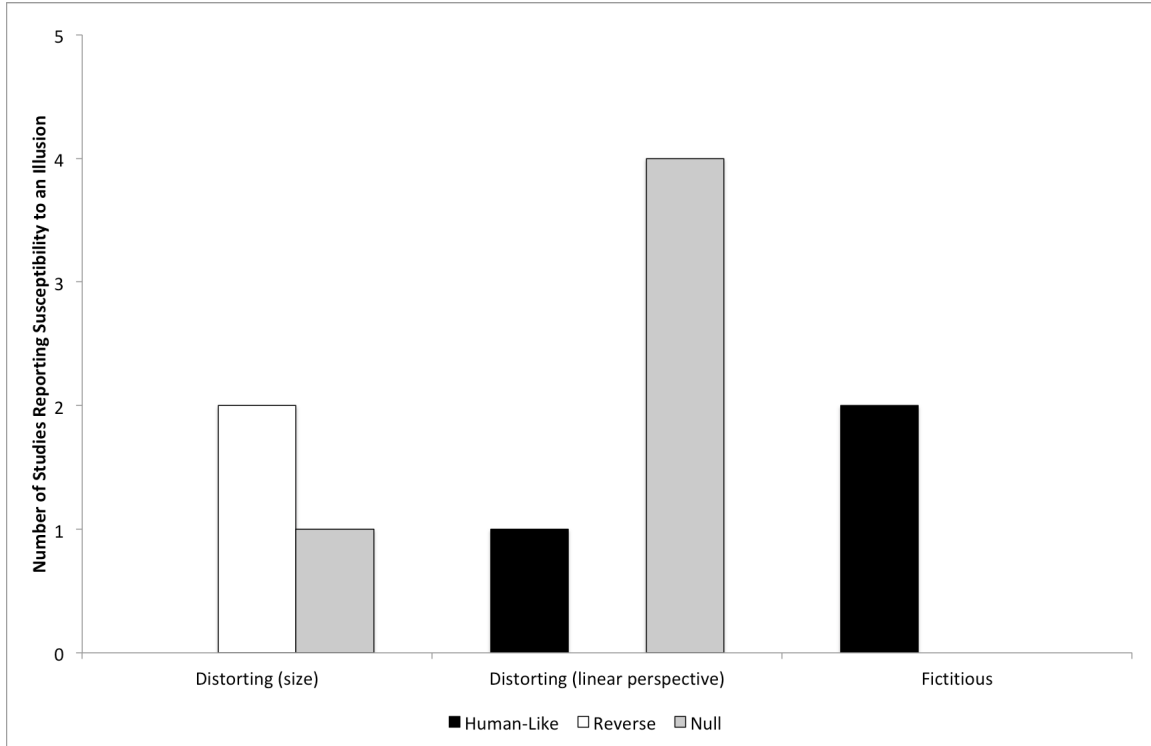


Figure 3. Graphical representation of illusion susceptibility, showing human-like (black) and reversed (white) and null illusion susceptibility (grey), for each experiment conducted as a part of this thesis. The bars indicate the number of experiments while the x-axis divides the experiments by type of illusion and modality.

In addition to the ten illusion assessments reported in this thesis, four other studies have also evaluated canine perceptual style. One study evaluated illusion susceptibility to the Delboeuf illusion (Miletto Petrazzini et al., 2016), two evaluated global-local precedence in a Navon's task (Mongillo et al., 2016; Pitteri et al., 2014), and another assessed motion perception (Kanizsár et al., 2018). In the study of illusion susceptibility, dogs demonstrated null susceptibility to the Delboeuf illusion (Miletto Petrazzini et al., 2016) suggestive of a preference for local processing. Support for this finding can be

drawn from a recent study evaluating motion perception in dogs, which reported that dogs locally integrate elements (Kanizsár et al., 2018). However, two of the studies specifically evaluating global-local precedence in dogs, suggest dogs may prefer to process stimuli globally. It is important to note that these two studies used the same sample of dogs, and while a global processing preference in dogs was identified, this trend was non-significant (Mongillo et al., 2016; Pitteri et al., 2014). Given these limitations, various concerns arise from the conclusions reported (Byosiére et al., 2017). Regardless, the findings reported in other studies, together with the results presented in this thesis, suggest that dogs demonstrate an overall local preference for visual processing. Dogs demonstrate local processing on nine out of fourteen perceptual style tasks. However, this is a gross oversimplification of the data as it is possible that visual style can be depicted as a spectrum. In this case, dogs as well as other animals may simply be less efficient in grouping visual stimuli compared to humans (Deruelle & Fagot, 1998; Fagot & Deruelle, 1997; Spinozzi, De Lillo & Truppa, 2003).

The interpretation of the findings reported in this thesis, clarify visual processing mechanisms in dogs by maintaining consistency in variables such as breed and facial morphology, and controlling for genetics and environment. The research reported represents a necessary building block, which can be refined and advanced in future research to develop a more complete theory of dog visual processing. While it is difficult to ascertain whether the differences in illusion susceptibility observed between dogs, humans, and other animals stem from differences in perception or cognitive factors, the susceptibility observed suggests dogs likely process illusions at a higher-level than the retina, invoking top-down processing mechanisms. The reversed susceptibility observed

in distorting illusions, and the human-like susceptibility seen in fictitious illusions, suggest that dogs visually process scenes using both bottom-up and top-down mechanisms (Figure 4). Dogs demonstrated evidence of bottom-up processing when presented with the Delboeuf and Ponzo illusions, and both top-down and bottom-up processing when presented with the Ebbinghaus-Titchener and illusory contour illusions.

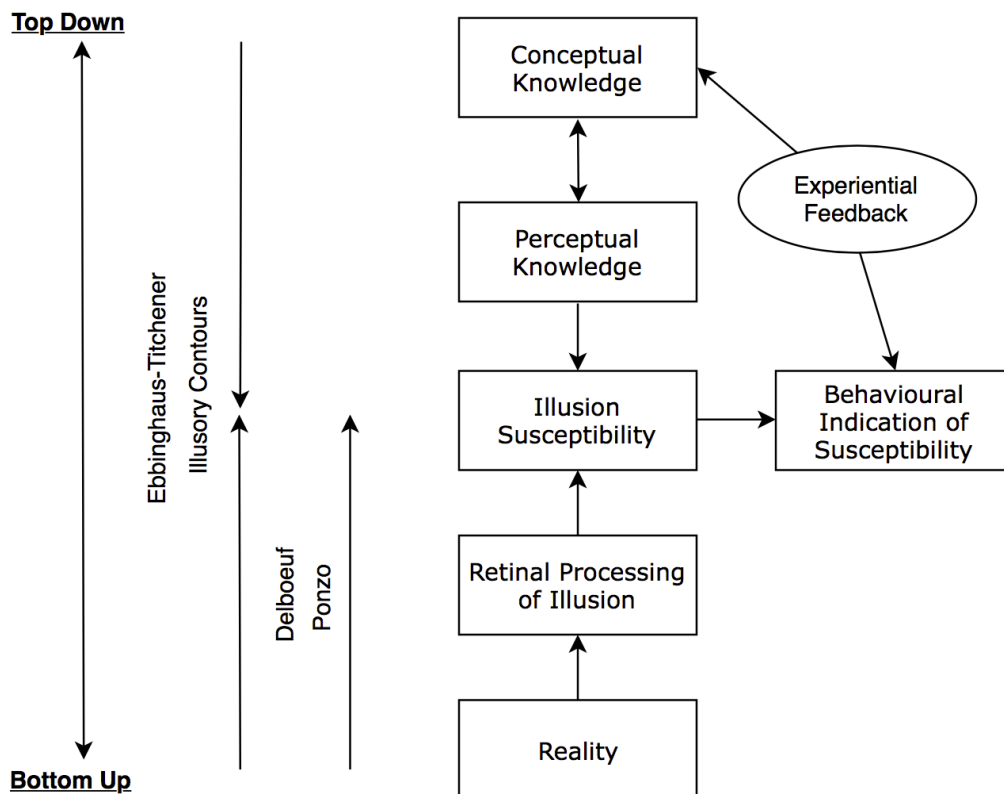


Figure 4. Revised schematic of illusion perception, as initially presented in Chapter 2, to include the four illusion types presented in this thesis using a dual approach framework of bottom-up and top-down processing. Adapted from “Knowledge in perception and illusion,” by R. L. Gregory, 1997, *Philosophical Transactions of the Royal Society*, 352, p. 1124.

Additional support for this conclusion can be inferred from the tremendous

individual variation observed in this sample of dogs. While the conclusions presented above address the results at the level of the group, variation was observed both within and across subjects and illusions. It is intriguing that subjects differed vastly in their perception of visual stimuli, some of them demonstrating consistent susceptibility to different illusions. This is particularly remarkable, as all dogs were Lagotto Romagnolos, from similar genetic lines, all reared and living under generally similar environmental conditions. However, it is important to note that this result is not unexpected given the small sample size and the fact that some dogs participated in multiple studies (see section 9.5. for a discussion of this limitation). Regardless, these findings reveal a cognitive component underlying perception, facilitated by experience that varies on an individual level – and perhaps even from day to day. To summarise, these findings suggest that dogs are not stimulus-response automatons, as their responses to stimuli are variable and not fixed.

Finally, these findings have broader implications, beyond what is discussed and presented in this thesis. The illusion susceptibility reported not only provides invaluable assessments of visual processing in dogs, but also contributes to various on-going theoretical debates. While an in-depth discussion of this is beyond the scope of this thesis, I identify two such matters. First, the illusion susceptibility observed in dogs, begs for additional research into the sense of sight in animals. Specifically, whether or not dogs experience ‘qualia’, individual instances of subjective and/or conscious experience (for a comprehensive review of qualia and consciousness see Chalmers, 1996). If so, do animals have visual awareness and consciousness? Second, the within- and between-species variation underlying the mechanisms of illusion susceptibility question the

current proposed theories of illusion susceptibility in humans. While many of these theories are well established, debate and individual variation in humans still exists (e.g. Chouinard et al., 2013; Chouinard et al., 2016; de Fockert et al., 2007; King et al., 2017). Given this variation has been extended to include animals, it begs an answer to the question ‘are there other theoretical mechanistic explanations of illusion susceptibility that more accurately account for illusion susceptibility in humans and animals’? It is important that future research into illusion susceptibility begin to propose new, potentially all-encompassing, theories as it is possible that current understanding of animal perception is simply a by-product of the existing theoretical framework. By redeveloping theoretical accounts of the mechanisms underlying illusion susceptibility, a more optimal and inclusive account of illusion susceptibility may become apparent.

9.4 Practical implications

While the primary purpose of this thesis was to evaluate and improve the current understanding of visual perception in dogs, indirect practical applications for this research also exist. These practical implications may help benefit and improve the unique human-dog relationship. By employing better methodologies in cognition and vision tasks, researchers can more accurately understand humans’ best friend. The thesis collectively emphasises the need for more canine visual processing research and provides various descriptive examples of the potential complications that may occur when evaluating perception via visually-based tasks. Furthermore, various advances and recommendations are proposed to allow for the implementation of more appropriate methodologies to minimise conceivable variables that may alter interpretations of dogs’

cognitive abilities.

This research not only aids cognition researchers but also attempts to bridge a gap with vision scientists as well. The research presented in this thesis describes a collaborative interdisciplinary endeavour in which the purpose was to join two fields of research to evaluate visual and cognitive processing in dogs. Much of the research conducted as a part of thesis was consistent with paradigms currently utilised in the field of dog cognition. However, it is of the utmost importance that vision scientists and cognition researchers collaborate to advance current understanding. Considering the interest in dogs as a research subject, additional foundational investigation is needed before more substantiated claims about dog perception can be made.

These detailed accounts of visual capacities may, in turn, allow for an accessible summary of how dogs see the world. By implementing this knowledge into applied settings, such as the service, working, and pet dog industries, it is possible these findings may inform various training methods. For example, the results reported in Chapter 3 suggest that dogs are adept at generalising in certain contexts. Extending these generalisation capabilities to training methodologies, such as the ‘Do As I Do’ method (e.g. Fugazza & Miklósi, 2014; Fugazza & Miklósi, 2015), may result in faster, more successful acquisition of complex commands. In turn, these findings have consequences in improving training procedures and may result in ancillary benefits, such as reducing behavioural problems and facilitating a positive dog-owner relationship. This is of paramount importance as thousands of dogs are relinquished to shelters each year as a result of perceived behavioural problems (Bennett & Rohlf, 2007; Clark & Boyer, 1993; Kutsumi, Nagasawa, Ohta & Ohtani, 2013), which consequently increase the risk of

euthanasia (Marston, Bennett & Coleman, 2004). While it remains unknown whether certain kinds of training may reduce or alter these outcomes (Marston et al., 2004; Salman et al., 2000; Segurson, Serpell & Hart, 2005), the research presented in this thesis may help optimise techniques to further clarify this on-going debate.

9.5 Limitations and future directions

The research discussed in this thesis extensively explores illusion susceptibility and perception in dogs. It is essential to keep in mind that potential overarching strengths and limitations of this line of inquiry exist. While experiment-specific limitations are addressed in each chapter, select universal limitations and future directions also exist. These require explanation while viewing this thesis as a whole and are discussed in detail below.

To appropriately control for as many external variables as possible, dogs of the same breed, closely related and living in similar environments, were used as participants in these experiments. While this served as a control for environmental, genetic, and optical similarities, the specificity of this sample can be seen as a limitation to the generalisation of this research. The breed selected, Lagotto Romagnolos, were used for two main reasons: (1) they were continuously available across the three years of experimentation and (2) they represent a mesocephalic breed where the eye-placement is typical unlike brachycephalic and dolichocephalic breeds. It may be the case that the results observed are breed-specific, specific to this genetic line, or the environment in which they lived. Therefore, these studies must be extended to other samples before more

general conclusions about the canine population are drawn.

Given the lack of foundational research into canine perception and variation, this control was deemed necessary for several reasons. Considering that dogs differ in size, body type, facial morphology and behaviour, it is possible that such differences could be associated with, effect, or perhaps even be caused by, different visual processing capacities (Blackwell, Twells, Seawright & Casey, 2008; Deldalle & Gaunet, 2014; Herron, Shofer & Reisner, 2009). It has been common practice to collectively pool dogs together within a single sample, disregarding breed, facial morphology, age, and sex (McGreevy, Grassi & Harman, 2003; Roberts et al., 2010), yet given mixed findings across canine cognition studies, in which similar or identical methodologies have been employed, it may be the case that breed differences are more robust than previously expected. This is not unforeseen, as dogs have been selectively bred to occupy specific, and often unique, roles. Due to this selective process of domestication, dogs now vary drastically in their size, shape, and eye placement. Thus, it seems plausible that this variation may extend to visual processing in certain breeds or facial morphology types. These findings urge for the study of breed, facial morphology type, and individual differences in dogs (Bensky et al., 2013; Byosiére et al., 2016). Future research should attempt to discern if breeds with flat faces (such as Boxers, Pugs, and Bulldogs) and dogs with relatively long skulls (such as Greyhounds and Whippets) process visual stimuli differently than longer-nosed breeds (such as Labrador retrievers, German shepherds, and Border collies), as well as evaluate the individual variation within and across these breeds.

Moreover, to compare performance across this sample, the same dogs were

presented with multiple illusory displays. This allowed for appropriate control(s) of individual differences as well as cross-comparison of the experiments in this thesis, although it may also explain the high rates of individual variation were observed in concert with often surprising and intriguing results (Chapters 5 to 7, in particular). Certain methodologies were employed to minimize confounds related to the repeated exposure to stimuli. While it is currently unknown whether multiple presentations affect illusion susceptibility, it was important to minimize unnecessary exposure to stimuli as long as the dog demonstrated successful understanding of the task. Therefore, a double criteria in familiarization and training session allowed for variation in learning capacities, limiting unnecessary and potential confounding exposure to stimuli. Additionally, power analyses were conducted at the start of experimentation to determine the appropriate number of trials for each experiment (as indicated in certain respective chapters). However, post-hoc evaluations of power achieved are presented in Table 6. Using the conventional power of .80 and alpha of 0.05 this analysis suggests that the significant findings observed in this thesis are, in fact, statistically powerful enough, and align with the conclusions drawn from the null-hypothesis testing and Bayes factors reported.

Table 6

Effect sizes observed in thesis and post-hoc power analyses

<u>Illusion</u>	<u>Chapter</u>	<u>Effect Size</u>	<u>Sample Size</u>	<u>Critical t</u>	<u>Sample Size Needed</u>	<u>Actual Power</u>	<u>Post-Hoc Power Achieved</u>	<u>Susceptibility</u>
Classical Ebbinghaus- Titchener	5	3.3	7	4.3	3	0.8	1.0	Reverse
Illusory Contour Ebbinghaus- Titchener	5	1.5	5	2.6	6	0.8	0.7	Reverse
Delboeuf	5	0.7	8	2.1	21	0.8	0.4	Null
Horizontal Ponzo Grid Inducer (Circles)	6	0.9	8	2.2	12	0.8	0.6	Maybe
Re-test Horizontal Ponzo Grid Inducer (Circles)	6	-0.2	8	2.0	356	0.8	0.1	Null
Horizontal Ponzo Grid Inducer (Rectangles)	6	-0.3	6	2.0	119	0.8	0.1	Null
Horizontal Ponzo Converging Lines	6	0.3	7	2.0	70	0.8	0.1	Null
Vertical Ponzo Converging Lines	7	1.7	6	2.8	5	0.8	0.9	Null
Ehrenstein	8	0.4	6	2.0	43	0.8	0.1	Maybe
Kanizsa	8	2.1	6	2.7	5	0.9	1.0	Yes

While many of the experiments conducted utilised novel stimuli, subjects may have become complacent over time, or the stimuli (such as the illusions presented) may have become less salient due to repeated exposure. To evaluate these concerns, some of the experiments included naïve and veteran subjects, in which very few differences were

observed in performance. Given that within-species variation in illusion assessments is not uncommon (see also Arden et al., 2016), and there is no evidence to suggest experimentally naïve and veteran participants perform differently when presented with illusions (Nakamura et al., 2008; Nakamura et al., 2014; Salva et al., 2013), I believe these concerns have been properly addressed. Additional investigation into the effects of repeated use of these training and/or testing methods is advised.

One potential line of inquiry would be to extend these experiments to different methodological paradigms. It would be particularly instructive to see what happens when dogs are taught to indicate a ‘same size’ option, as utilised in ‘same/different’ paradigms. Research suggests that monkeys perform differently on illusion assessments depending on the type on task (Beran et al., 2016). When presented with the Delboeuf illusion, rhesus macaques and capuchin monkeys demonstrated null and reversed susceptibility on a discrimination task, but demonstrated human-like susceptibility when presented with an absolute classification task (Parrish et al., 2015). Furthermore, animal illusion researchers have recently adopted a novel spontaneous-choice paradigm, which requires minimal training. To date, this methodological paradigm has been used to evaluate illusion susceptibility in dogs (Miletto Petrazzini et al., 2016), lemurs (Santacà et al., 2017), and chimpanzees (Parrish & Beran, 2014). This approach is subject to certain limitations (e.g. assuming an inherent ability for the species to discriminate and demonstrate a preference for a larger food quantity), but its practicality makes this task an alternative to heavily training-dependent paradigms. Given these alternative methodologies, it is possible that additional investigation into illusion susceptibility in dogs may find task dependent variation. Additional investigation is therefore needed to clarify this possibility.

9.6 Final remarks

The thesis at hand constitutes one of the most comprehensive examinations of illusion susceptibility in a single species. More specifically, the studies reported contribute to the current understanding of dog perception in a variety of ways. First, two foundational experiments (Chapters 3 and 4) were conducted to better understand how dogs process and generalise simple visual stimuli in the form of shapes and colours. Second, these primary aspects of vision were incorporated to more appropriately evaluate cognitively complex forms of perception, specifically illusion susceptibility (Chapters 5 to 8). Dogs were assessed on their susceptibility to a variety of illusions, such as the Ebbinghaus-Titchener, Delboeuf, Ponzo, Ehrenstein and Kanizsa, and follow up experiments evaluated alternative hypotheses for the sometimes unique and often equivocal findings observed. The studies conducted in this thesis are some of the first, and only, to assess illusion susceptibility in dogs, and to highlight that the underlying visual processing mechanisms between dogs and humans may differ. It is crucial that future research attempt to evaluate foundational aspects of vision in a larger sample of dogs.

In conclusion, while canine research has drastically increased in the last two decades, many gaps still exist in the literature. Surprisingly, many of these poorly understood components are critical to interpreting cognitively complex processes. In this thesis, I addressed the lack of an interdisciplinary approach to understanding perception and cognition in dogs. While there is no shortage of canine cognition research, the majority of these studies are conducted visually. Yet, very little research has been conducted on the canine visual system, making it impossible to evaluate whether

paradigms and methodologies are appropriate measures of cognitive ability. This thesis demonstrates the critical need to understand foundational aspects of vision before assessing dogs in visually complex tasks and making conclusions about their cognitive abilities. The findings presented highlight that dogs may see the world in a manner quite different than humans, and therefore emphasise the need for such factors to be taken into consideration when evaluating cognition in dogs. Not only are these findings relevant for academic and theoretical reasons, but also for improving specific practical benefits such as dog training, and dog-human relationships.

References

- Agrillo, C., Parrish, A. E. & Beran, M. J. (2014). Do primates see the solitaire illusion differently? A comparative assessment of humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 128(4), 402-413. doi:10.1037/a0037499
- Alexander, M. (2003). *Generalization*. Retrieved from <http://www.clickersolutions.com/articles/2003/generalization.htm>
- Arden, R., Bensky, M. K. & Adams, M. J. (2016). A Review of Cognitive Abilities in Dogs, 1911 Through 2016: More Individual Differences, Please! *Current Directions in Psychological Science*, 25(5), 307-312.
- Awh, E., Belopolsky, A. V. & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: a failed theoretical dichotomy. *Trends in cognitive sciences*, 16(8), 437-443. doi:10.1016/j.tics.2012.06.010
- Axelrod, V., Schwarzkopf, D. S., Gilaie-Dotan, S. & Rees, G. (2017). Perceptual similarity and the neural correlates of geometrical illusions in human brain structure. *Scientific Reports*, 7, 39968. doi:10.1038/srep39968
- Barbet, I. & Fagot, J. (2002). Perception of the corridor illusion by baboons (*Papio papio*). *Behavioural brain research*, 132(1), 111-115.
- Bayne, K. A. L. & Davis, R. T. (1983). Susceptibility of rhesus monkeys (*Macaca mulatta*) to the Ponzo illusion. *Bulletin of the Psychonomic Society*, 21(6), 476-478. doi:10.3758/BF03330013
- Bell, M. A. & Fox, N. A. (1997). Individual differences in object permanence performance at 8 months: Locomotor experience and brain electrical activity. *Developmental Psychobiology*, 31(4), 287-297.
- Bennett, P. C. & Rohlf, V. I. (2007). Owner-companion dog interactions: Relationships between demographic variables, potentially problematic behaviours, training engagement and shared activities. *Applied Animal Behaviour Science*, 102(1), 65-84. doi:<https://doi.org/10.1016/j.applanim.2006.03.009>
- Bensky, M. K., Gosling, S. D. & Sinn, D. L. (2013). The world from a dog's point of view: a review and synthesis of dog cognition research. *Advances in the Study of Behaviour*, 45, 209-406. doi:<https://doi.org/10.1016/B978-0-12-407186-5.00005-7>
- Beran, M. J., Menzel, C. R., Parrish, A. E., Perdue, B. M., Sayers, K., Smith, J. D. & Washburn, D. A. (2016). Primate cognition: attention, episodic memory, prospective memory, self-control, and metacognition as examples of cognitive control in nonhuman primates. *Wiley Interdisciplinary Reviews: Cognitive Science*, n/a-n/a. doi:10.1002/wcs.1397
- Berry, J. W. (1968). Ecology, Perceptual Development and the Müller-Lyer Illusion. *British Journal of Psychology*, 59(3), 205-210. doi:10.1111/j.2044-8295.1968.tb01134.x
- Berry, J. W. (1971). Müller-Lyer Susceptibility: Culture, Ecology or Race? *International Journal of Psychology*, 6(3), 193-197. doi:10.1080/00207597108246682
- Blackwell, E. J., Twells, C., Seawright, A. & Casey, R. A. (2008). The relationship between training methods and the occurrence of behavior problems, as reported

- by owners, in a population of domestic dogs. *Journal of Veterinary Behavior: Clinical Applications and Research*, 3(5), 207-217.
- Blouin, D. D. (2013). Are Dogs Children, Companions, or Just Animals? Understanding Variations in People's Orientations toward Animals. *Anthrozoös*, 26(2), 279-294. doi:10.2752/175303713X13636846944402
- Bouton, M. E. (2007). *Learning and behavior: A contemporary synthesis*: Sinauer Associates.
- Bradley, D. R. & Dumais, S. T. (1975). Ambiguous cognitive contours. *Nature*, 257, 582. doi:10.1038/257582a0
- Bräuer, J., Kaminski, J., Riedel, J., Call, J. & Tomasello, M. (2006). Making inferences about the location of hidden food: social dog, causal ape. *Journal of Comparative Psychology*, 120(1), 38.
- Bravo, M., Blake, R. & Morrison, S. (1988). Cats see subjective contours. *Vision Research*, (28), 861-865. doi:[https://doi.org/10.1016/0042-6989\(88\)90095-8](https://doi.org/10.1016/0042-6989(88)90095-8)
- Byosiére, S.-E., Chouinard, P. A., Howell, T. J. & Bennett, P. C. (Byosiére2017). (2017). What do dogs (*Canis familiaris*) see? A review of vision in dogs and implications for cognition research. *Psychonomic Bulletin & Review*. doi:10.3758/s13423-017-1404-7
- Byosiére, S.-E., Feng, L. C., Woodhead, J. K., Rutter, N. J., Chouinard, P. A., Howell, T. J. & Bennett, P. C. (Byosiére2016). (2016). Visual perception in domestic dogs: susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions. *Animal Cognition*, 1-14. doi:<https://doi.org/10.1007/s10071-016-1067-1>
- Carbon, C.-C. (2014). Understanding human perception by human-made illusions. *Frontiers in Human Neuroscience*, 8, 566. doi:10.3389/fnhum.2014.00566
- Cattet, J. (2013). Generalization in dogs and humans – the difference is in the brain. Retrieved from <http://blog.smartanimaltraining.com/2013/12/03/generalization-in-dogs-and-humans-the-difference-is-in-the-brain/>
- Chalmers, D. J. (1996). *The conscious mind: In search of a fundamental theory*: Oxford university press.
- Chouinard, P. A., Noulty, W. A., 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(2), 219-231. doi:<https://doi.org/10.1007/s00221-013-3646-6>
- Chouinard, P. A., Unwin, K. L., 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(6), 2224-2239. doi:<https://doi.org/10.1007/s10803-016-2753-1>
- Clark, G. I. & Boyer, W. N. (1993). The effects of dog obedience training and behavioural counselling upon the human-canine relationship. *Applied Animal Behaviour Science*, 37(2), 147-159.
- Clutton-Brock, J. (1995). Origins of the dog: domestication and early history. In J. Serpell (Ed.), *The domestic dog: Its evolution, behaviour and interactions with people* (1st ed., pp. 7-20).

- 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>
- Collier-Baker, E., Davis, J. M. & Suddendorf, T. (2004). Do dogs (*Canis familiaris*) understand invisible displacement? *Journal of Comparative Psychology*, 118(4), 421.
- Coren, S. & Enns, J. T. (1993). Size contrast as a function of conceptual similarity between test and inducers. *Perception & Psychophysics*, 54(5), 579-588.
- Coren, S. & Girgus, J. S. (1978). *Seeing is deceiving: The psychology of visual illusions*. Oxford, England: Lawrence Erlbaum.
- Coren, S. & Porac, C. (1987). Individual differences in visual-geometric illusions: Predictions from measures of spatial cognitive abilities. *Perception & Psychophysics*, 41(3), 211-219.
- Cott, H. B. (1940). *Adaptive coloration in animals*: Methuen; London.
- Dakin, S. & Frith, U. (2005). Vagaries of Visual Perception in Autism. *Neuron*, 48(3), 497-507. doi:<https://doi.org/10.1016/j.neuron.2005.10.018>
- Dawson, J. L. (1967). Traditional versus Western attitudes in West Africa: The construction, validation, and application of a measuring device. *British Journal of Social and Clinical Psychology*, 6(2), 81-96.
- 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(3), 738.
- Delboeuf, F. J. (1865). Note sur certaines illusions d'optique: Essai d'une théorie psychophysique de la manière dont l'oeil apprécie les distances et les angles. *Bulletins de l'Académie Royale des Sciences, Lettres et Beaux-arts de Belgique*, 19, 195-216.
- Deldalle, S. & Gaunet, F. (2014). Effects of 2 training methods on stress-related behaviors of the dog (*Canis familiaris*) and on the dog-owner relationship. *Journal of Veterinary Behavior: Clinical Applications and Research*, 9(2), 58-65.
- Deruelle, C. & Fagot, J. (Deruelle 1998). (1998). Visual search for global/local stimulus features in humans and baboons. *Psychonomic Bulletin & Review*, 5(3), 476-481. doi:10.3758/bf03208825
- Doherty, M. J., Campbell, N. M., Tsuji, H. & Phillips, W. A. (2010). The Ebbinghaus illusion deceives adults but not young children. *Developmental Science*, 13(5), 714-721. doi:doi:10.1111/j.1467-7687.2009.00931.x
- Dorey, N. R., Udell, M. A. & Wynne, C. D. (2010). When do domestic dogs, *Canis familiaris*, start to understand human pointing? The role of ontogeny in the development of interspecies communication. *Animal Behaviour*, 79(1), 37-41.
- Ehrenstein, W. (1987). Modifications of the Brightness Phenomenon of L. Hermann. In S. Petry & G. E. Meyer (Eds.), *The Perception of Illusory Contours* (pp. 35-39). New York, NY: Springer New York. doi:https://doi.org/10.1007/978-1-4612-4760-9_3
- Fagot, J. & Deruelle, C. (1997). Processing of global and local visual information and hemispheric specialization in humans (*Homo sapiens*) and baboons (*Papio papio*).

- Journal of Experimental Psychology: Human Perception and Performance*, 23(2), 429.
- Fagot, J. & Tomonaga, M. (Fagot2001). (2001). Effects of element separation on perceptual grouping by humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*): perception of Kanizsa illusory figures. *Animal Cognition*, 4(3), 171-177. doi:<https://doi.org/10.1007/s100710100109>
- Feng, L. C., Chouinard, P. A., Howell, T. J. & Bennett, P. C. (Feng2017). (2017). Why do animals differ in their susceptibility to geometrical illusions? *Psychonomic Bulletin & Review*, 24(2), 262-276. doi:10.3758/s13423-016-1133-3
- Fiset, S., Beaulieu, C. & Landry, F. (Fiset2002). (2002). Duration of dogs' (*Canis familiaris*) working memory in search for disappearing objects. *Animal Cognition*, 6(1), 1-10. doi:10.1007/s10071-002-0157-4
- Fox, M. W. (1971a). *Behavior of wolves, dogs and related canids*. London, England: The Trinity Press.
- Fox, M. W. (1971b). Integrative development of brain and behavior in the dog.
- Fox, M. W. (1978). *The dog: its domestication and behavior*: Garland Publishing Inc., 545 Madison Avenue.
- Frank, H. (Frank1980). (1980). Evolution of canine information processing under conditions of natural and artificial selection. *Z Tierpsychol*, 59.
- Frank, H. & Frank, M. G. (1982). On the effects of domestication on canine social development and behavior. *Applied Animal Ethology*, 8(6), 507-525.
- Fugazza, C. & Miklósi, Á. (2014). Should old dog trainers learn new tricks? The efficiency of the Do as I do method and shaping/clicker training method to train dogs. *Applied Animal Behaviour Science*, 153, 53-61.
- Fugazza, C. & Miklósi, Á. (2015). Social learning in dog training: The effectiveness of the Do as I do method compared to shaping/clicker training. *Applied Animal Behaviour Science*, 171, 146-151.
- Fujita, K. (1996). Linear perspective and the Ponzo illusion: a comparison between rhesus monkeys and humans. *Japanese Psychological Research*, 38(3), 136-145.
- Fujita, K. (1997). Perception of the Ponzo illusion by rhesus monkeys, chimpanzees, and humans: Similarity and difference in the three primate species. *Perception & Psychophysics*, 59(2), 284-292. doi:10.3758/BF03211896
- Fujita, K. (2004). How do nonhuman animals perceptually integrate figural fragments? *Japanese Psychological Research*, 46(3), 154-169.
- Fujita, K., Blough, D. S. & Blough, P. M. (1991). Pigeons see the Ponzo illusion. *Animal Learning & Behavior*, 19(3), 283-293. doi:10.3758/BF03197888
- Fuss, T., Bleckmann, H. & Schluessel, V. (2014). The brain creates illusions not just for us: sharks (*Chiloscyllium griseum*) can “see the magic” as well. *Frontiers in Neural Circuits*, 8, 24. doi:<https://doi.org/10.3389/fncir.2014.00024>
- Fuss, T. & Schluessel, V. (2017). The Ebbinghaus illusion in the gray bamboo shark (*Chiloscyllium griseum*) in comparison to the teleost damselfish (*Chromis chromis*). *Zoology*, 123(Supplement C), 16-29. doi:<https://doi.org/10.1016/j.zool.2017.05.006>
- Gácsi, M., Kara, E., Belényi, B., Topál, J. & Miklósi, Á. (2009a). The effect of development and individual differences in pointing comprehension of dogs. *Animal cognition*, 12(3), 471-479.

- Gácsi, M., McGreevy, P., Kara, E. & Miklósi, Á. (2009b). Effects of selection for cooperation and attention in dogs. *Behavioral and Brain Functions*, 5(1), 31.
- Gagnon, S. & Doré, F. Y. (1992). Search behavior in various breeds of adult dogs (*Canis familiaris*): Object permanence and olfactory cues. *Journal of Comparative Psychology*, 106(1), 58-68. doi:<http://dx.doi.org/10.1037/0735-7036.106.1.58>
- Gagnon, S. & Doré, F. Y. (1994). Cross-sectional study of object permanence in domestic puppies (*Canis familiaris*). *Journal of Comparative Psychology*, 108(3), 220.
- Galibert, F., Quignon, P., Hitte, C. & André, C. (2011). Toward understanding dog evolutionary and domestication history. *Comptes Rendus Biologies*, 334(3), 190-196. doi:<https://doi.org/10.1016/j.crv.2010.12.011>
- Gibson, J. J. (1966). The senses considered as perceptual systems.
- Gibson, J. J. & Gibson, E. J. (1955). Perceptual learning: Differentiation or enrichment? *Psychological review*, 62(1), 32.
- Global study: pet ownership. (2016). Retrieved 18/5/2018, from <http://www.gfk.com/insights/press-release/us-ranks-5th-in-pet-ownership-with-70-reporting-at-least-one-pet/>
- Graham, K. L., Byosiere, S.-E., Feng, L. C., Sanders, M., Bennett, P. C., Caruso, K., . . . White, A. (2018). A forced-choice preferential looking task for the assessment of vision in dogs: pilot study. 0(0). doi:doi:10.1111/jsap.12965
- Greenebaum, J. (2004). It's a Dog's Life: Elevating Status from Pet to "Fur Baby" at Yappy Hour. *Society & Animals*, 12(2), 117-135. doi:doi:<https://doi.org/10.1163/1568530041446544>
- Gregory, R. L. (1963). Distortion of visual space as inappropriate constancy scaling. *Nature*, 199(678-91), 1.
- Gregory, R. L. (1968). Visual illusions. *Scientific American*, 219(5), 66-79.
- Gregory, R. L. (1970). The intelligent eye.
- Gregory, R. L. (1997). Knowledge in perception and illusion. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 352(1358), 1121-1127.
- Gregory, R. L. (2015). *Eye and brain: The psychology of seeing*: Princeton university press.
- Haber, R. N. & Hershenson, M. (1973). *The psychology of visual perception*: Holt, Rinehart & Winston.
- Hanggi, E. B. (2003). Discrimination learning based on relative size concepts in horses (*Equus caballus*). *Applied Animal Behaviour Science*, 83(3), 201-213.
- Happé, F., Frith, U. & Briskman, J. (2001). Exploring the cognitive phenotype of autism: weak "central coherence" in parents and siblings of children with autism: I. Experimental tests. *The Journal of Child Psychology and Psychiatry and Allied Disciplines*, 42(3), 299-307.
- Happé, F. G. E. (1996). Studying Weak Central Coherence at Low Levels: Children with Autism do not Succumb to Visual Illusions. A Research Note. *Journal of Child Psychology and Psychiatry*, 37(7), 873-877. doi:doi:10.1111/j.1469-7610.1996.tb01483.x
- Hare, B., Brown, M., Williamson, C. & Tomasello, M. (Hare2002). (2002a). The domestication of cognition in dogs. *Science*, 298. doi:10.1126/science.1072702

- Hare, B., Brown, M., Williamson, C. & Tomasello, M. (2002b). The domestication of social cognition in dogs. *Science*, 298(5598), 1634-1636.
- Hare, B., Call, J. & Tomasello, M. (1998). Communication of Food Location Between Human and Dog (*Canis Familiaris*). *Evolution of Communication*, 2(1), 137-159. doi:doi:10.1075/eoc.2.1.06har
- Hare, B., Rosati, A., Kaminski, J., Bräuer, J., Call, J. & Tomasello, M. (2010). The domestication hypothesis for dogs' skills with human communication: a response to Udell et al.(2008) and Wynne et al.(2008). *Animal Behaviour*.
- Hare, B. & Tomasello, M. (1999). Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *Journal of Comparative Psychology*, 113(2), 173.
- Hare, B. & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, 9(9), 439-444. doi:<http://dx.doi.org/10.1016/j.tics.2005.07.003>
- Hart, B. L. (1995). Analysing breed and gender differences in behaviour. *The domestic dog: Its evolution, behaviour and interactions with people*, 65-77.
- Helton, W. S. & Helton, N. D. (2010). Physical size matters in the domestic dog's (*Canis lupus familiaris*) ability to use human pointing cues. *Behavioural processes*, 85(1), 77-79.
- Herron, M. E., Shofer, F. S. & Reisner, I. R. (2009). Survey of the use and outcome of confrontational and non-confrontational training methods in client-owned dogs showing undesired behaviors. *Applied Animal Behaviour Science*, 117(1), 47-54.
- Horowitz, A. (2014). Domestic Dog Cognition and Behavior. In *The Scientific Study of Canis familiaris*: Springer.
- Imura, T., Tomonaga, M. & Yagi, A. (2008). The effects of linear perspective on relative size discrimination in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). *Behavioural processes*, 77(3), 306-312.
- Ishihara, S. (1918). Tests for Color Blindness. *American Journal of Ophthalmology*, 1(5), 376.
- Itti, L. & Borji, A. (2014). Computational Models: Bottom-Up and Top-Down Aspects. In A. Nobre & S. Kastner (Eds.), *The Oxford Handbook of Attention*: Oxford University Press. doi:10.1093/oxfordhb/9780199675111.013.026
- Ittyerah, M. & Gaunet, F. (2009). The response of guide dogs and pet dogs (*Canis Familiaris*) to cues of human referential communication (pointing and gaze). *Animal Cognition*, 12(2), 257-265. doi:10.1007/s10071-008-0188-6
- Jackson, S. R. & Shaw, A. (2000). The Ponzo illusion affects grip-force but not grip-aperture scaling during prehension movements. *Journal of Experimental Psychology: Human Perception and Performance*, 26(1), 418.
- Jacobs, G. H. (1996). Primate photopigments and primate color vision. *Proceedings of the National Academy of Sciences*, 93(2), 577-581.
- Jacobs, G. H., Deegan, J. F., Crognale, M. A. & Fenwick, J. A. (1993). Photopigments of dogs and foxes and their implications for canid vision. *Visual neuroscience*, 10(01), 173-180.
- Jaeger, T. (Jaeger1978). (1978). Ebbinghaus illusions: Size contrast or contour interaction phenomena? *Perception & Psychophysics*, 24(4), 337-342. doi:10.3758/bf03204250

- Jaeger, T. & Lorden, R. (1980). Delboeuf illusions: contour or size detector interactions? *Perceptual and motor skills*, 50(2), 376-378.
- Kaminski, J. (2009). Dogs (*Canis familiaris*) are adapted to receive human communication. In *Neurobiology of "Umwelt"* (pp. 103-107): Springer.
- Kaminski, J., Schulz, L. & Tomasello, M. (2012). How dogs know when communication is intended for them. *Developmental science*, 15(2), 222-232.
- Kanizsa, G. (1955). Margini quasi-percettivi in campi con stimolazione omogenea. *Rivista di psicologia*, 49(1), 7-30.
- Kanizsa, G. (1974). Contours without gradients or cognitive contours? *Italian journal of Psychology*, 1(1), 93-112.
- Kanizsa, G., Renzi, P., Conte, S., Compostela, C. & Guerani, L. (1993). Amodal completion in mouse vision. *Perception*, 22(6), 713-721.
doi:<https://doi.org/10.1068/p220713>
- Kanizsár, O., Mongillo, P., Battaglini, L., Campana, G., Lőoke, M. & Marinelli, L. (2018). The effect of experience and of dots' density and duration on the detection of coherent motion in dogs. *Animal Cognition*. doi:10.1007/s10071-018-1200-4
- Kasparson, A. A., Badridze, J. & Maximov, V. V. (2013). Colour cues proved to be more informative for dogs than brightness. *Proceedings of the Royal Society B: Biological Sciences*, 280(1766). doi:10.1098/rspb.2013.1356
- Kelley, L. A. & Kelley, J. L. (2014). Animal visual illusion and confusion: the importance of a perceptual perspective. *Behavioral Ecology*, 25(3), 450-463.
- King, D. J., Hodgekins, J., Chouinard, P. A., Chouinard, V.-A. & Sperandio, I. (King2017). (2017). A review of abnormalities in the perception of visual illusions in schizophrenia. *Psychonomic Bulletin & Review*, 24(3), 734-751.
doi:10.3758/s13423-016-1168-5
- King, T., Marston, L. C. & Bennett, P. C. (2012). Breeding dogs for beauty and behaviour: Why scientists need to do more to develop valid and reliable behaviour assessments for dogs kept as companions. *Applied Animal Behaviour Science*, 137(1), 1-12.
- Kutsumi, A., Nagasawa, M., Ohta, M. & Ohtani, N. (2013). Importance of puppy training for future behavior of the dog. *Journal of veterinary medical science*, 75(2), 141-149.
- Lafer-Sousa, R., Hermann, K. L. & Conway, B. R. (2015). Striking individual differences in color perception uncovered by 'the dress' photograph. *Current Biology*, 25(13), R545-R546. doi:<https://doi.org/10.1016/j.cub.2015.04.053>
- Larson, G. & Bradley, D. G. (2014). How Much Is That in Dog Years? The Advent of Canine Population Genomics. *PLOS Genetics*, 10(1), e1004093.
doi:10.1371/journal.pgen.1004093
- Larson, G., Karlsson, E. K., Perri, A., Webster, M. T., Ho, S. Y. W., Peters, J., . . . Lindblad-Toh, K. (2012). Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences*, 109(23), 8878-8883. doi:10.1073/pnas.1203005109
- Lazareva, O. F. (2012). Relational learning in a context of transposition: A review. *Journal of the experimental analysis of behavior*, 97(2), 231-248.

- Lind, O., Milton, I., Andersson, E., Jensen, P. & Roth, L. S. V. (2017). High visual acuity revealed in dogs. *PLOS ONE*, 12(12), e0188557. doi:10.1371/journal.pone.0188557
- Marston, L. C., Bennett, P. C. & Coleman, G. J. (2004). What happens to shelter dogs? An analysis of data for 1 year from three Australian shelters. *Journal of Applied Animal Welfare Science*, 7(1), 27-47.
- McCready, D. (McCready1985). (1985). On size, distance, and visual angle perception. *Perception & Psychophysics*, 37(4), 323-334. doi:10.3758/bf03211355
- McGreevy, P., Grassi, T. D. & Harman, A. M. (2003). A strong correlation exists between the distribution of retinal ganglion cells and nose length in the dog. *Brain, Behavior and Evolution*, 63(1), 13-22. doi:<https://doi.org/10.1159/000073756>
- McGreevy, P., Grassi, T. D. & Harman, A. M. (McGreevy2004). (2004). A strong correlation exists between the distribution of retinal ganglion cells and nose length in the dog. *Brain Behav Evol*, 63. doi:10.1159/000073756
- McKinley, J. & Sambrook, T. D. (2000). Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*). *Animal Cognition*, 3(1), 13-22.
- Miklósi, Á. (2015). *Dog behaviour, evolution, and cognition* (2nd ed.). New York, NY: Oxford University Press.
- Miklósi, Á. & Kubinyi, E. (2016). Current Trends in Canine Problem-Solving and Cognition. *Current directions in psychological science*, 25(5), 300-306. doi:10.1177/096372141666606
- Miklósi, Á., Polgárdi, R., Topál, J. & Csányi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition*, 1(2), 113-121.
- Miklósi, Á., Topál, J. & Csányi, V. (2004). Comparative social cognition: what can dogs teach us? *Animal Behaviour*, 67(6), 995-1004. doi:<https://doi.org/10.1016/j.anbehav.2003.10.008>
- Miletto Petrazzini, M. E., Bisazza, A. & Agrillo, C. (Miletto Petrazzini2016). (2016). Do domestic dogs (*Canis lupus familiaris*) perceive the Delboeuf illusion? *Animal Cognition*, 1-8. doi:<https://doi.org/10.1007/s10071-016-1066-2>
- Miller, H. C., Gipson, C. D., Vaughan, A., Rayburn-Reeves, R. & Zentall, T. R. (2009). Object permanence in dogs: invisible displacement in a rotation task. *Psychonomic bulletin & review*, 16(1), 150-155.
- Miller, P. E. & Murphy, C. J. (1995). Vision in dogs. *Journal-American Veterinary Medical Association*, 207, 1623-1634.
- Mongillo, P., Pitteri, E., Sambugaro, P., Carnier, P. & Marinelli, L. (Mongillo2016). (2016). Global bias reliability in dogs (*Canis familiaris*). *Animal Cognition*, 1-9. doi:10.1007/s10071-016-1044-8
- Morey, D. F. (1994). The Early Evolution of the Domestic Dog. *American Scientist*, 82(4), 336-347. Retrieved from <http://www.jstor.org/stable/29775234>
- 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(4), 333.
- Nakagawa, E. (2002). Rats respond to configurations of stimuli. *The Psychological Record*, 52(4), 531.

- 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(3), 375.
- Nakamura, N., Watanabe, S. & Fujita, K. (2014). A reversed Ebbinghaus-Titchener illusion in bantams (*Gallus gallus domesticus*). *Animal cognition*, 17(2), 471-481.
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive psychology*, 9(3), 353-383.
- Neitz, J., Geist, T. & Jacobs, G. H. (1989). Color vision in the dog. *Visual neuroscience*, 3(02), 119-125.
- Nicolas, S. (1995). Joseph Delboeuf on Visual Illusions: A Historical Sketch. *The American Journal of Psychology*, 108(4), 563-574. doi:10.2307/1423073
- Nieder, A. (2002). Seeing more than meets the eye: processing of illusory contours in animals. *Journal of Comparative Physiology A*, 188(4), 249-260.
- Nieder, A. & Wagner, H. (1999). Perception and neuronal coding of subjective contours in the owl. *Nature Neuroscience*, 2, 660. doi:<https://doi.org/10.1038/10217>
- Ninio, J. (1998). *La science des illusions*: Odile Jacob.
- Parrish, A. E. & Beran, M. J. (2014). When less is more: like humans, chimpanzees (*Pan troglodytes*) misperceive food amounts based on plate size. *Animal cognition*, 17(2), 427-434.
- Parrish, A. E., Brosnan, S. F. & Beran, M. J. (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(4), 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(4), 405.
- Payne, E., Bennett, P. C. & McGreevy, P. D. (2015). Current perspectives on attachment and bonding in the dog-human dyad. *Psychology Research and Behavior Management*, 8, 71-79. doi:10.2147/PRBM.S74972
- Perri, A. (2016). A wolf in dog's clothing: Initial dog domestication and Pleistocene wolf variation. *Journal of Archaeological Science*, 68, 1-4. doi:<https://doi.org/10.1016/j.jas.2016.02.003>
- Pitteri, E., Mongillo, P., Carnier, P. & Marinelli, L. (2014). Hierarchical stimulus processing by dogs (*Canis familiaris*). *Animal cognition*, 17(4), 869-877.
- Pressey, A. (1971). An extension of assimilation theory to illusions of size, area, and direction. *Perception & Psychophysics*, 9(2), 172-176.
- Pressey, A. W., Di Lollo, V. & Tait, R. W. (1977). Effects of gap size between shaft and fins and of angle of fins on the Müller-Lyer illusion. *Perception*, 6(4), 435-439.
- Pressey, A. W. & Epp, D. (1992). Spatial attention in Ponzo-like patterns. *Perception & Psychophysics*, 52(2), 211-221. doi:10.3758/BF03206774
- Prinzmetal, W. & Beck, D. M. (2001). The tilt-consistency theory of visual illusions. *Journal of Experimental Psychology: Human Perception and Performance*, 27(1), 206.
- Pylyshyn, Z. (1999). Is vision continuous with cognition?: The case for cognitive impenetrability of visual perception. *Behavioral and brain sciences*, 22(03), 341-365.

- Range, F., Aust, U., Steurer, M. & Huber, L. (Range2008). (2008). Visual categorization of natural stimuli by domestic dogs (*Canis familiaris*). *Anim Cogn*, 11. doi:10.1007/s10071-007-0123-2
- Range, F., Hentrup, M. & Virányi, Z. (2011). Dogs are able to solve a means-end task. *Animal cognition*, 14(4), 575-583.
- Riedel, J., Schumann, K., Kaminski, J., Call, J. & Tomasello, M. (2008). The early ontogeny of human–dog communication. *Animal Behaviour*, 75(3), 1003-1014.
- Roberts, T., McGreevy, P. & Valenzuela, M. (2010). Human induced rotation and reorganization of the brain of domestic dogs. *PLoS One*, 5(7), e11946.
- Rosengren, A. (1969). *Experiments in colour discrimination in dogs*: Societas pro fauna et flora Fennica.
- Salman, M. D., Hutchison, J., Ruch-Gallie, R., Kogan, L., New Jr, J. C., Kass, P. H. & Scarlett, J. M. (2000). Behavioral reasons for relinquishment of dogs and cats to 12 shelters. *Journal of Applied Animal Welfare Science*, 3(2), 93-106.
- Salva, O. R., 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(6), 895-906.
- Santacà, M., Regaiolli, B., Miletto Petrazzini, M., Spiezio, C. & Agrillo, C. (2017). Preliminary study to investigate the Delboeuf illusion in ring-tailed lemurs (*Lemur catta*): Methodological challenges. *Animal Behavior and Cognition*, 4(3), 365-377.
- Schumann, F. (1900). Beiträge zur Analyse der Gesichtswahrnehmungen. Erste Abhandlung. Einige Beobachtungen über die Zusammenfassung von Gesichtseindruecken zu Einheiten. *Zeitschrift für Psychologie und Physiologie der Sinnesorgan*, (23), 1–32.
- Segurson, S. A., Serpell, J. A. & Hart, B. L. (2005). Evaluation of a behavioral assessment questionnaire for use in the characterization of behavioral problems of dogs relinquished to animal shelters. *Journal of the American Veterinary Medical Association*, 227(11), 1755-1761.
- Sherman, J. A. & Chouinard, P. A. (2016). Attractive Contours of the Ebbinghaus Illusion. *Perceptual & Motor Skills*, 122(1), 88-95. Retrieved from <http://ez.library.latrobe.edu.au/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=s3h&AN=113369700&site=ehost-live&scope=site>
- Shettleworth, S. J. (2010). *Cognition, evolution, and behavior* (pp. 215–232): Oxford University Press.
- Siniscalchi, M., Ingeo, S., Fornelli, S. & Quaranta, A. (2017). Are dogs red–green colour blind? *Royal Society Open Science*, 4(11). Retrieved from <http://rsos.royalsocietypublishing.org/content/4/11/170869.abstract>
- Soproni, K., Miklósi, A., Topál, J. & Csányi, V. (2002). Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *Journal of Comparative Psychology*, 116(1), 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(2), 122.
- Sovrano, V. A., Albertazzi, L. & Salva, O. R. (2014). The Ebbinghaus illusion in a fish (*Xenotoca eiseni*). *Animal cognition*, 18(2), 533-542.

- Sovrano, V. A. & Bisazza, A. (2009). Perception of Subjective Contours in Fish. *Perception*, 38(4), 579-590. doi:<https://doi.org/10.1068/p6121>
- Sperandio, I. & Chouinard, P. A. (2015). The Mechanisms of Size Constancy. *Multisensory Research*, 28(3-4), 253-283.
- Spinozzi, G., De Lillo, C. & Truppa, V. (2003). Global and local processing of hierarchical visual stimuli in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 117(1), 15.
- Staats, S., Wallace, H. & Anderson, T. (2008). Reasons for Companion Animal Guardianship (Pet Ownership) from Two Populations. *Society & Animals*, 16(3), 279-291. doi:<https://doi.org/10.1163/156853008X323411>
- Stevens, M. & Merilaita, S. (2009). Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1516), 423-427.
- Stevens, M. & Merilaita, S. (2011). *Animal camouflage: mechanisms and function*: Cambridge University Press.
- Tanaka, T., Watanabe, T., Eguchi, Y. & Yoshimoto, T. (2000). Color Discrimination in Dogs. *Nihon Chikusan Gakkaiho*, 71(3), 300-304. doi:10.2508/chikusan.71.300
- Tapp, P. D., Siwak, C. T., Head, E., Cotman, C. W., Murphey, H., Muggenburg, B. A., . . . Milgram, N. W. (2004). Concept abstraction in the aging dog: development of a protocol using successive discrimination and size concept tasks. *Behavioural Brain Research*, 153(1), 199-210. doi:<http://dx.doi.org/10.1016/j.bbr.2003.12.003>
- Tauzin, T., Csík, A., Kis, A. & Topál, J. (2015). What or where? The meaning of referential human pointing for dogs (*Canis familiaris*). *Journal of Comparative Psychology*, 129(4), 334.
- Thayer, G. H. (1909). *Concealing-coloration in the animal kingdom: an exposition of the laws of disguise through color and pattern: being a summary of Abbott H. Thayer's discoveries*: Macmillan Company.
- Timney, B. & Keil, K. (1996). Horses are sensitive to pictorial depth cues. *Perception*, 25(9), 1121-1128.
- Titchener, E. B. (1901). *Experimental psychology: A manual of laboratory practice, Vol 1: Qualitative experiments: Part II. Instructor's manual*. New York, NY, US: MacMillan Co.
- Topál, J., Miklósi, Á. & Csányi, V. (1997). Dog-Human Relationship Affects Problem Solving Behavior in the Dog. *Anthrozoös*, 10(4), 214-224. doi:10.2752/089279397787000987
- Udell, M. A., Dorey, N. R. & Wynne, C. D. (2008). Wolves outperform dogs in following human social cues. *Animal Behaviour*, 76(6), 1767-1773.
- Udell, M. A., Dorey, N. R. & Wynne, C. D. (2010). What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological reviews*, 85(2), 327-345.
- Udell, M. A. & Wynne, C. D. (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(2), 247-261.

- Van Ittersum, K. & Wansink, B. (2012). Plate Size and Color Suggestibility: The Delboeuf Illusion's Bias on Serving and Eating Behavior. *Journal of Consumer Research*, 39(2), 215-228. doi:10.1086/662615
- Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D. & Miklósi, Á. (2008). Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal cognition*, 11(3), 373-387.
- Wayne, R. K. (1986a). Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution*, 243-261.
- Wayne, R. K. (1986b). Limb morphology of domestic and wild canids: the influence of development on morphologic change. *Journal of morphology*, 187(3), 301-319.
- Westheimer, G. (2008). Illusions in the spatial sense of the eye: Geometrical-optical illusions and the neural representation of space. *Vision Research*, 48(20), 2128-2142. doi:<https://doi.org/10.1016/j.visres.2008.05.016>
- Whitwell, R. L., Buckingham, G., Enns, J. T., Chouinard, P. A. & Goodale, M. A. (Whitwell2016). (2016). Rapid decrement in the effects of the Ponzo display dissociates action and perception. *Psychonomic Bulletin & Review*, 23(4), 1157-1163. doi:10.3758/s13423-015-0975-4
- Witkin, H. A. (1967). A COGNITIVE-STYLE APPROACH TO CROSS-CULTURAL RESEARCH1. *International Journal of Psychology*, 2(4), 233-250. doi:doi:10.1080/00207596708247220
- Wobber, V. & Hare, B. (2009). Testing the social dog hypothesis: are dogs also more skilled than chimpanzees in non-communicative social tasks? *Behavioural Processes*, 81(3), 423-428.
- Wynne, C. D., Udell, M. A. & Lord, K. A. (2008). Ontogeny's impacts on human-dog communication. *Animal Behaviour*, 76(4), e1-e4.
- Wyzisk, K. & Neumeyer, C. (2007). Perception of illusory surfaces and contours in goldfish. *Visual Neuroscience*, 24(3), 291-298. doi:<https://doi.org/10.1017/S095252380707023X>
- Zigler, E. (1960). Size estimates of circles as a function of size of adjacent circles. *Perceptual and Motor Skills*, 11(1), 47-53.
- Zigler, E. & Phillips, L. (1960). Social effectiveness and symptomatic behaviors. *The Journal of Abnormal and Social Psychology*, 61(2), 231.
- Zimmermann, R. R. (1962). Form generalization in the infant monkey. *Journal of Comparative and Physiological Psychology*, 55(6), 918-923. doi:<https://doi.org/10.1037/h0042446>

References

- Agrillo, C., Parrish, A. E. & Beran, M. J. (2014). Do primates see the solitaire illusion differently? A comparative assessment of humans (*Homo sapiens*), chimpanzees (*Pan troglodytes*), rhesus monkeys (*Macaca mulatta*), and capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 128(4), 402-413. doi:10.1037/a0037499
- Alexander, M. (2003). *Generalization*. Retrieved from <http://www.clickersolutions.com/articles/2003/generalization.htm>
- Arden, R., Bensky, M. K. & Adams, M. J. (2016). A Review of Cognitive Abilities in Dogs, 1911 Through 2016: More Individual Differences, Please! *Current Directions in Psychological Science*, 25(5), 307-312.
- Awh, E., Belopolsky, A. V. & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: a failed theoretical dichotomy. *Trends in cognitive sciences*, 16(8), 437-443. doi:10.1016/j.tics.2012.06.010
- Axelrod, V., Schwarzkopf, D. S., Gilaie-Dotan, S. & Rees, G. (2017). Perceptual similarity and the neural correlates of geometrical illusions in human brain structure. *Scientific Reports*, 7, 39968. doi:10.1038/srep39968
- Barbet, I. & Fagot, J. (2002). Perception of the corridor illusion by baboons (*Papio papio*). *Behavioural brain research*, 132(1), 111-115.
- Bayne, K. A. L. & Davis, R. T. (1983). Susceptibility of rhesus monkeys (*Macaca mulatta*) to the Ponzo illusion. *Bulletin of the Psychonomic Society*, 21(6), 476-478. doi:10.3758/BF03330013
- Bell, M. A. & Fox, N. A. (1997). Individual differences in object permanence performance at 8 months: Locomotor experience and brain electrical activity. *Developmental Psychobiology*, 31(4), 287-297.
- Bennett, P. C. & Rohlf, V. I. (2007). Owner-companion dog interactions: Relationships between demographic variables, potentially problematic behaviours, training engagement and shared activities. *Applied Animal Behaviour Science*, 102(1), 65-84. doi:<https://doi.org/10.1016/j.applanim.2006.03.009>
- Bensky, M. K., Gosling, S. D. & Sinn, D. L. (2013). The world from a dog's point of view: a review and synthesis of dog cognition research. *Advances in the Study of Behaviour*, 45, 209-406. doi:<https://doi.org/10.1016/B978-0-12-407186-5.00005-7>
- Beran, M. J., Menzel, C. R., Parrish, A. E., Perdue, B. M., Sayers, K., Smith, J. D. & Washburn, D. A. (2016). Primate cognition: attention, episodic memory, prospective memory, self-control, and metacognition as examples of cognitive control in nonhuman primates. *Wiley Interdisciplinary Reviews: Cognitive Science*, n/a-n/a. doi:10.1002/wcs.1397
- Berry, J. W. (1968). Ecology, Perceptual Development and the Müller-Lyer Illusion. *British Journal of Psychology*, 59(3), 205-210. doi:10.1111/j.2044-8295.1968.tb01134.x
- Berry, J. W. (1971). Müller-Lyer Susceptibility: Culture, Ecology or Race? *International Journal of Psychology*, 6(3), 193-197. doi:10.1080/00207597108246682
- Blackwell, E. J., Twells, C., Seawright, A. & Casey, R. A. (2008). The relationship between training methods and the occurrence of behavior problems, as reported

- by owners, in a population of domestic dogs. *Journal of Veterinary Behavior: Clinical Applications and Research*, 3(5), 207-217.
- Blouin, D. D. (2013). Are Dogs Children, Companions, or Just Animals? Understanding Variations in People's Orientations toward Animals. *Anthrozoös*, 26(2), 279-294. doi:10.2752/175303713X13636846944402
- Bouton, M. E. (2007). *Learning and behavior: A contemporary synthesis*: Sinauer Associates.
- Bradley, D. R. & Dumais, S. T. (1975). Ambiguous cognitive contours. *Nature*, 257, 582. doi:10.1038/257582a0
- Bräuer, J., Kaminski, J., Riedel, J., Call, J. & Tomasello, M. (2006). Making inferences about the location of hidden food: social dog, causal ape. *Journal of Comparative Psychology*, 120(1), 38.
- Bravo, M., Blake, R. & Morrison, S. (1988). Cats see subjective contours. *Vision Research*, (28), 861-865. doi:[https://doi.org/10.1016/0042-6989\(88\)90095-8](https://doi.org/10.1016/0042-6989(88)90095-8)
- Byosiére, S.-E., Chouinard, P. A., Howell, T. J. & Bennett, P. C. (Byosiére2017). (2017). What do dogs (*Canis familiaris*) see? A review of vision in dogs and implications for cognition research. *Psychonomic Bulletin & Review*. doi:10.3758/s13423-017-1404-7
- Byosiére, S.-E., Feng, L. C., Woodhead, J. K., Rutter, N. J., Chouinard, P. A., Howell, T. J. & Bennett, P. C. (Byosiére2016). (2016). Visual perception in domestic dogs: susceptibility to the Ebbinghaus–Titchener and Delboeuf illusions. *Animal Cognition*, 1-14. doi:<https://doi.org/10.1007/s10071-016-1067-1>
- Carbon, C.-C. (2014). Understanding human perception by human-made illusions. *Frontiers in Human Neuroscience*, 8, 566. doi:10.3389/fnhum.2014.00566
- Cattet, J. (2013). Generalization in dogs and humans – the difference is in the brain. Retrieved from <http://blog.smartanimaltraining.com/2013/12/03/generalization-in-dogs-and-humans-the-difference-is-in-the-brain/>
- Chalmers, D. J. (1996). *The conscious mind: In search of a fundamental theory*: Oxford university press.
- Chouinard, P. A., Noulty, W. A., 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(2), 219-231. doi:<https://doi.org/10.1007/s00221-013-3646-6>
- Chouinard, P. A., Unwin, K. L., 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(6), 2224-2239. doi:<https://doi.org/10.1007/s10803-016-2753-1>
- Clark, G. I. & Boyer, W. N. (1993). The effects of dog obedience training and behavioural counselling upon the human-canine relationship. *Applied Animal Behaviour Science*, 37(2), 147-159.
- Clutton-Brock, J. (1995). Origins of the dog: domestication and early history. In J. Serpell (Ed.), *The domestic dog: Its evolution, behaviour and interactions with people* (1st ed., pp. 7-20).

- 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>
- Collier-Baker, E., Davis, J. M. & Suddendorf, T. (2004). Do dogs (*Canis familiaris*) understand invisible displacement? *Journal of Comparative Psychology*, 118(4), 421.
- Coren, S. & Enns, J. T. (1993). Size contrast as a function of conceptual similarity between test and inducers. *Perception & Psychophysics*, 54(5), 579-588.
- Coren, S. & Girgus, J. S. (1978). *Seeing is deceiving: The psychology of visual illusions*. Oxford, England: Lawrence Erlbaum.
- Coren, S. & Porac, C. (1987). Individual differences in visual-geometric illusions: Predictions from measures of spatial cognitive abilities. *Perception & Psychophysics*, 41(3), 211-219.
- Cott, H. B. (1940). *Adaptive coloration in animals*: Methuen; London.
- Dakin, S. & Frith, U. (2005). Vagaries of Visual Perception in Autism. *Neuron*, 48(3), 497-507. doi:<https://doi.org/10.1016/j.neuron.2005.10.018>
- Dawson, J. L. (1967). Traditional versus Western attitudes in West Africa: The construction, validation, and application of a measuring device. *British Journal of Social and Clinical Psychology*, 6(2), 81-96.
- 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(3), 738.
- Delboeuf, F. J. (1865). Note sur certaines illusions d'optique: Essai d'une théorie psychophysique de la manière dont l'oeil apprécie les distances et les angles. *Bulletins de l'Académie Royale des Sciences, Lettres et Beaux-arts de Belgique*, 19, 195-216.
- Deldalle, S. & Gaunet, F. (2014). Effects of 2 training methods on stress-related behaviors of the dog (*Canis familiaris*) and on the dog-owner relationship. *Journal of Veterinary Behavior: Clinical Applications and Research*, 9(2), 58-65.
- Deruelle, C. & Fagot, J. (Deruelle 1998). (1998). Visual search for global/local stimulus features in humans and baboons. *Psychonomic Bulletin & Review*, 5(3), 476-481. doi:10.3758/bf03208825
- Doherty, M. J., Campbell, N. M., Tsuji, H. & Phillips, W. A. (2010). The Ebbinghaus illusion deceives adults but not young children. *Developmental Science*, 13(5), 714-721. doi:doi:10.1111/j.1467-7687.2009.00931.x
- Dorey, N. R., Udell, M. A. & Wynne, C. D. (2010). When do domestic dogs, *Canis familiaris*, start to understand human pointing? The role of ontogeny in the development of interspecies communication. *Animal Behaviour*, 79(1), 37-41.
- Ehrenstein, W. (1987). Modifications of the Brightness Phenomenon of L. Hermann. In S. Petry & G. E. Meyer (Eds.), *The Perception of Illusory Contours* (pp. 35-39). New York, NY: Springer New York. doi:https://doi.org/10.1007/978-1-4612-4760-9_3
- Fagot, J. & Deruelle, C. (1997). Processing of global and local visual information and hemispheric specialization in humans (*Homo sapiens*) and baboons (*Papio papio*).

- Journal of Experimental Psychology: Human Perception and Performance*, 23(2), 429.
- Fagot, J. & Tomonaga, M. (Fagot2001). (2001). Effects of element separation on perceptual grouping by humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*): perception of Kanizsa illusory figures. *Animal Cognition*, 4(3), 171-177. doi:<https://doi.org/10.1007/s100710100109>
- Feng, L. C., Chouinard, P. A., Howell, T. J. & Bennett, P. C. (Feng2017). (2017). Why do animals differ in their susceptibility to geometrical illusions? *Psychonomic Bulletin & Review*, 24(2), 262-276. doi:10.3758/s13423-016-1133-3
- Fiset, S., Beaulieu, C. & Landry, F. (Fiset2002). (2002). Duration of dogs' (*Canis familiaris*) working memory in search for disappearing objects. *Animal Cognition*, 6(1), 1-10. doi:10.1007/s10071-002-0157-4
- Fox, M. W. (1971a). *Behavior of wolves, dogs and related canids*. London, England: The Trinity Press.
- Fox, M. W. (1971b). Integrative development of brain and behavior in the dog.
- Fox, M. W. (1978). *The dog: its domestication and behavior*: Garland Publishing Inc., 545 Madison Avenue.
- Frank, H. (Frank1980). (1980). Evolution of canine information processing under conditions of natural and artificial selection. *Z Tierpsychol*, 59.
- Frank, H. & Frank, M. G. (1982). On the effects of domestication on canine social development and behavior. *Applied Animal Ethology*, 8(6), 507-525.
- Fugazza, C. & Miklósi, Á. (2014). Should old dog trainers learn new tricks? The efficiency of the Do as I do method and shaping/clicker training method to train dogs. *Applied Animal Behaviour Science*, 153, 53-61.
- Fugazza, C. & Miklósi, Á. (2015). Social learning in dog training: The effectiveness of the Do as I do method compared to shaping/clicker training. *Applied Animal Behaviour Science*, 171, 146-151.
- Fujita, K. (1996). Linear perspective and the Ponzo illusion: a comparison between rhesus monkeys and humans. *Japanese Psychological Research*, 38(3), 136-145.
- Fujita, K. (1997). Perception of the Ponzo illusion by rhesus monkeys, chimpanzees, and humans: Similarity and difference in the three primate species. *Perception & Psychophysics*, 59(2), 284-292. doi:10.3758/BF03211896
- Fujita, K. (2004). How do nonhuman animals perceptually integrate figural fragments? *Japanese Psychological Research*, 46(3), 154-169.
- Fujita, K., Blough, D. S. & Blough, P. M. (1991). Pigeons see the Ponzo illusion. *Animal Learning & Behavior*, 19(3), 283-293. doi:10.3758/BF03197888
- Fuss, T., Bleckmann, H. & Schluessel, V. (2014). The brain creates illusions not just for us: sharks (*Chiloscyllium griseum*) can “see the magic” as well. *Frontiers in Neural Circuits*, 8, 24. doi:<https://doi.org/10.3389/fncir.2014.00024>
- Fuss, T. & Schluessel, V. (2017). The Ebbinghaus illusion in the gray bamboo shark (*Chiloscyllium griseum*) in comparison to the teleost damselfish (*Chromis chromis*). *Zoology*, 123(Supplement C), 16-29. doi:<https://doi.org/10.1016/j.zool.2017.05.006>
- Gácsi, M., Kara, E., Belényi, B., Topál, J. & Miklósi, Á. (2009a). The effect of development and individual differences in pointing comprehension of dogs. *Animal cognition*, 12(3), 471-479.

- Gácsi, M., McGreevy, P., Kara, E. & Miklósi, Á. (2009b). Effects of selection for cooperation and attention in dogs. *Behavioral and Brain Functions*, 5(1), 31.
- Gagnon, S. & Doré, F. Y. (1992). Search behavior in various breeds of adult dogs (*Canis familiaris*): Object permanence and olfactory cues. *Journal of Comparative Psychology*, 106(1), 58-68. doi:<http://dx.doi.org/10.1037/0735-7036.106.1.58>
- Gagnon, S. & Doré, F. Y. (1994). Cross-sectional study of object permanence in domestic puppies (*Canis familiaris*). *Journal of Comparative Psychology*, 108(3), 220.
- Galibert, F., Quignon, P., Hitte, C. & André, C. (2011). Toward understanding dog evolutionary and domestication history. *Comptes Rendus Biologies*, 334(3), 190-196. doi:<https://doi.org/10.1016/j.crv.2010.12.011>
- Gibson, J. J. (1966). The senses considered as perceptual systems.
- Gibson, J. J. & Gibson, E. J. (1955). Perceptual learning: Differentiation or enrichment? *Psychological review*, 62(1), 32.
- Global study: pet ownership. (2016). Retrieved 18/5/2018, from <http://www.gfk.com/insights/press-release/us-ranks-5th-in-pet-ownership-with-70-reporting-at-least-one-pet/>
- Graham, K. L., Byosiére, S.-E., Feng, L. C., Sanders, M., Bennett, P. C., Caruso, K., . . . White, A. (2018). A forced-choice preferential looking task for the assessment of vision in dogs: pilot study. 0(0). doi:doi:10.1111/jsap.12965
- Greenebaum, J. (2004). It's a Dog's Life: Elevating Status from Pet to "Fur Baby" at Yappy Hour. *Society & Animals*, 12(2), 117-135. doi:doi:<https://doi.org/10.1163/1568530041446544>
- Gregory, R. L. (1963). Distortion of visual space as inappropriate constancy scaling. *Nature*, 199(678-91), 1.
- Gregory, R. L. (1968). Visual illusions. *Scientific American*, 219(5), 66-79.
- Gregory, R. L. (1970). The intelligent eye.
- Gregory, R. L. (1997). Knowledge in perception and illusion. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 352(1358), 1121-1127.
- Gregory, R. L. (2015). *Eye and brain: The psychology of seeing*: Princeton university press.
- Haber, R. N. & Hershenson, M. (1973). *The psychology of visual perception*: Holt, Rinehart & Winston.
- Hanggi, E. B. (2003). Discrimination learning based on relative size concepts in horses (*Equus caballus*). *Applied Animal Behaviour Science*, 83(3), 201-213.
- Happé, F., Frith, U. & Briskman, J. (2001). Exploring the cognitive phenotype of autism: weak "central coherence" in parents and siblings of children with autism: I. Experimental tests. *The Journal of Child Psychology and Psychiatry and Allied Disciplines*, 42(3), 299-307.
- Happé, F. G. E. (1996). Studying Weak Central Coherence at Low Levels: Children with Autism do not Succumb to Visual Illusions. A Research Note. *Journal of Child Psychology and Psychiatry*, 37(7), 873-877. doi:doi:10.1111/j.1469-7610.1996.tb01483.x
- Hare, B., Brown, M., Williamson, C. & Tomasello, M. (Hare2002). (2002a). The domestication of cognition in dogs. *Science*, 298. doi:10.1126/science.1072702

- Hare, B., Brown, M., Williamson, C. & Tomasello, M. (2002b). The domestication of social cognition in dogs. *Science*, 298(5598), 1634-1636.
- Hare, B., Call, J. & Tomasello, M. (1998). Communication of Food Location Between Human and Dog (*Canis Familiaris*). *Evolution of Communication*, 2(1), 137-159. doi:doi:10.1075/eoc.2.1.06har
- Hare, B., Rosati, A., Kaminski, J., Bräuer, J., Call, J. & Tomasello, M. (2010). The domestication hypothesis for dogs' skills with human communication: a response to Udell et al.(2008) and Wynne et al.(2008). *Animal Behaviour*.
- Hare, B. & Tomasello, M. (1999). Domestic dogs (*Canis familiaris*) use human and conspecific social cues to locate hidden food. *Journal of Comparative Psychology*, 113(2), 173.
- Hare, B. & Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, 9(9), 439-444. doi:<http://dx.doi.org/10.1016/j.tics.2005.07.003>
- Hart, B. L. (1995). Analysing breed and gender differences in behaviour. *The domestic dog: Its evolution, behaviour and interactions with people*, 65-77.
- Helton, W. S. & Helton, N. D. (2010). Physical size matters in the domestic dog's (*Canis lupus familiaris*) ability to use human pointing cues. *Behavioural processes*, 85(1), 77-79.
- Herron, M. E., Shofer, F. S. & Reisner, I. R. (2009). Survey of the use and outcome of confrontational and non-confrontational training methods in client-owned dogs showing undesired behaviors. *Applied Animal Behaviour Science*, 117(1), 47-54.
- Horowitz, A. (2014). Domestic Dog Cognition and Behavior. In *The Scientific Study of Canis familiaris*: Springer.
- Imura, T., Tomonaga, M. & Yagi, A. (2008). The effects of linear perspective on relative size discrimination in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). *Behavioural processes*, 77(3), 306-312.
- Ishihara, S. (1918). Tests for Color Blindness. *American Journal of Ophthalmology*, 1(5), 376.
- Itti, L. & Borji, A. (2014). Computational Models: Bottom-Up and Top-Down Aspects. In A. Nobre & S. Kastner (Eds.), *The Oxford Handbook of Attention*: Oxford University Press. doi:10.1093/oxfordhb/9780199675111.013.026
- Ittyerah, M. & Gaunet, F. (2009). The response of guide dogs and pet dogs (*Canis Familiaris*) to cues of human referential communication (pointing and gaze). *Animal Cognition*, 12(2), 257-265. doi:10.1007/s10071-008-0188-6
- Jackson, S. R. & Shaw, A. (2000). The Ponzo illusion affects grip-force but not grip-aperture scaling during prehension movements. *Journal of Experimental Psychology: Human Perception and Performance*, 26(1), 418.
- Jacobs, G. H. (1996). Primate photopigments and primate color vision. *Proceedings of the National Academy of Sciences*, 93(2), 577-581.
- Jacobs, G. H., Deegan, J. F., Crognale, M. A. & Fenwick, J. A. (1993). Photopigments of dogs and foxes and their implications for canid vision. *Visual neuroscience*, 10(01), 173-180.
- Jaeger, T. (Jaeger1978). (1978). Ebbinghaus illusions: Size contrast or contour interaction phenomena? *Perception & Psychophysics*, 24(4), 337-342. doi:10.3758/bf03204250

- Jaeger, T. & Lorden, R. (1980). Delboeuf illusions: contour or size detector interactions? *Perceptual and motor skills*, 50(2), 376-378.
- Kaminski, J. (2009). Dogs (*Canis familiaris*) are adapted to receive human communication. In *Neurobiology of "Umwelt"* (pp. 103-107): Springer.
- Kaminski, J., Schulz, L. & Tomasello, M. (2012). How dogs know when communication is intended for them. *Developmental science*, 15(2), 222-232.
- Kanizsa, G. (1955). Margini quasi-percettivi in campi con stimolazione omogenea. *Rivista di psicologia*, 49(1), 7-30.
- Kanizsa, G. (1974). Contours without gradients or cognitive contours? *Italian journal of Psychology*, 1(1), 93-112.
- Kanizsa, G., Renzi, P., Conte, S., Compostela, C. & Guerani, L. (1993). Amodal completion in mouse vision. *Perception*, 22(6), 713-721.
doi:<https://doi.org/10.1068/p220713>
- Kanizsár, O., Mongillo, P., Battaglini, L., Campana, G., Lőoke, M. & Marinelli, L. (2018). The effect of experience and of dots' density and duration on the detection of coherent motion in dogs. *Animal Cognition*. doi:10.1007/s10071-018-1200-4
- Kasparson, A. A., Badridze, J. & Maximov, V. V. (2013). Colour cues proved to be more informative for dogs than brightness. *Proceedings of the Royal Society B: Biological Sciences*, 280(1766). doi:10.1098/rspb.2013.1356
- Kelley, L. A. & Kelley, J. L. (2014). Animal visual illusion and confusion: the importance of a perceptual perspective. *Behavioral Ecology*, 25(3), 450-463.
- King, D. J., Hodgekins, J., Chouinard, P. A., Chouinard, V.-A. & Sperandio, I. (King2017). (2017). A review of abnormalities in the perception of visual illusions in schizophrenia. *Psychonomic Bulletin & Review*, 24(3), 734-751.
doi:10.3758/s13423-016-1168-5
- King, T., Marston, L. C. & Bennett, P. C. (2012). Breeding dogs for beauty and behaviour: Why scientists need to do more to develop valid and reliable behaviour assessments for dogs kept as companions. *Applied Animal Behaviour Science*, 137(1), 1-12.
- Kutsumi, A., Nagasawa, M., Ohta, M. & Ohtani, N. (2013). Importance of puppy training for future behavior of the dog. *Journal of veterinary medical science*, 75(2), 141-149.
- Lafer-Sousa, R., Hermann, K. L. & Conway, B. R. (2015). Striking individual differences in color perception uncovered by 'the dress' photograph. *Current Biology*, 25(13), R545-R546. doi:<https://doi.org/10.1016/j.cub.2015.04.053>
- Larson, G. & Bradley, D. G. (2014). How Much Is That in Dog Years? The Advent of Canine Population Genomics. *PLOS Genetics*, 10(1), e1004093.
doi:10.1371/journal.pgen.1004093
- Larson, G., Karlsson, E. K., Perri, A., Webster, M. T., Ho, S. Y. W., Peters, J., . . . Lindblad-Toh, K. (2012). Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences*, 109(23), 8878-8883. doi:10.1073/pnas.1203005109
- Lazareva, O. F. (2012). Relational learning in a context of transposition: A review. *Journal of the experimental analysis of behavior*, 97(2), 231-248.

- Lind, O., Milton, I., Andersson, E., Jensen, P. & Roth, L. S. V. (2017). High visual acuity revealed in dogs. *PLOS ONE*, 12(12), e0188557. doi:10.1371/journal.pone.0188557
- Marston, L. C., Bennett, P. C. & Coleman, G. J. (2004). What happens to shelter dogs? An analysis of data for 1 year from three Australian shelters. *Journal of Applied Animal Welfare Science*, 7(1), 27-47.
- McCready, D. (McCready1985). (1985). On size, distance, and visual angle perception. *Perception & Psychophysics*, 37(4), 323-334. doi:10.3758/bf03211355
- McGreevy, P., Grassi, T. D. & Harman, A. M. (2003). A strong correlation exists between the distribution of retinal ganglion cells and nose length in the dog. *Brain, Behavior and Evolution*, 63(1), 13-22. doi:<https://doi.org/10.1159/000073756>
- McGreevy, P., Grassi, T. D. & Harman, A. M. (McGreevy2004). (2004). A strong correlation exists between the distribution of retinal ganglion cells and nose length in the dog. *Brain Behav Evol*, 63. doi:10.1159/000073756
- McKinley, J. & Sambrook, T. D. (2000). Use of human-given cues by domestic dogs (*Canis familiaris*) and horses (*Equus caballus*). *Animal Cognition*, 3(1), 13-22.
- Miklósi, Á. (2015). *Dog behaviour, evolution, and cognition* (2nd ed.). New York, NY: Oxford University Press.
- Miklósi, Á. & Kubinyi, E. (2016). Current Trends in Canine Problem-Solving and Cognition. *Current directions in psychological science*, 25(5), 300-306. doi:10.1177/096372141666606
- Miklösi, Á., Polgárdi, R., Topál, J. & Csányi, V. (1998). Use of experimenter-given cues in dogs. *Animal Cognition*, 1(2), 113-121.
- Miklósi, Á., Topál, J. & Csányi, V. (2004). Comparative social cognition: what can dogs teach us? *Animal Behaviour*, 67(6), 995-1004. doi:<https://doi.org/10.1016/j.anbehav.2003.10.008>
- Miletto Petrazzini, M. E., Bisazza, A. & Agrillo, C. (Miletto Petrazzini2016). (2016). Do domestic dogs (*Canis lupus familiaris*) perceive the Delboeuf illusion? *Animal Cognition*, 1-8. doi:<https://doi.org/10.1007/s10071-016-1066-2>
- Miller, H. C., Gipson, C. D., Vaughan, A., Rayburn-Reeves, R. & Zentall, T. R. (2009). Object permanence in dogs: invisible displacement in a rotation task. *Psychonomic bulletin & review*, 16(1), 150-155.
- Miller, P. E. & Murphy, C. J. (1995). Vision in dogs. *Journal-American Veterinary Medical Association*, 207, 1623-1634.
- Mongillo, P., Pitteri, E., Sambugaro, P., Carnier, P. & Marinelli, L. (Mongillo2016). (2016). Global bias reliability in dogs (*Canis familiaris*). *Animal Cognition*, 1-9. doi:10.1007/s10071-016-1044-8
- Morey, D. F. (1994). The Early Evolution of the Domestic Dog. *American Scientist*, 82(4), 336-347. Retrieved from <http://www.jstor.org/stable/29775234>
- 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(4), 333.
- Nakagawa, E. (2002). Rats respond to configurations of stimuli. *The Psychological Record*, 52(4), 531.

- 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(3), 375.
- Nakamura, N., Watanabe, S. & Fujita, K. (2014). A reversed Ebbinghaus-Titchener illusion in bantams (*Gallus gallus domesticus*). *Animal cognition*, 17(2), 471-481.
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive psychology*, 9(3), 353-383.
- Neitz, J., Geist, T. & Jacobs, G. H. (1989). Color vision in the dog. *Visual neuroscience*, 3(02), 119-125.
- Nicolas, S. (1995). Joseph Delboeuf on Visual Illusions: A Historical Sketch. *The American Journal of Psychology*, 108(4), 563-574. doi:10.2307/1423073
- Nieder, A. (2002). Seeing more than meets the eye: processing of illusory contours in animals. *Journal of Comparative Physiology A*, 188(4), 249-260.
- Nieder, A. & Wagner, H. (1999). Perception and neuronal coding of subjective contours in the owl. *Nature Neuroscience*, 2, 660. doi:<https://doi.org/10.1038/10217>
- Ninio, J. (1998). *La science des illusions*: Odile Jacob.
- Parrish, A. E. & Beran, M. J. (2014). When less is more: like humans, chimpanzees (*Pan troglodytes*) misperceive food amounts based on plate size. *Animal cognition*, 17(2), 427-434.
- Parrish, A. E., Brosnan, S. F. & Beran, M. J. (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(4), 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(4), 405.
- Payne, E., Bennett, P. C. & McGreevy, P. D. (2015). Current perspectives on attachment and bonding in the dog-human dyad. *Psychology Research and Behavior Management*, 8, 71-79. doi:10.2147/PRBM.S74972
- Perri, A. (2016). A wolf in dog's clothing: Initial dog domestication and Pleistocene wolf variation. *Journal of Archaeological Science*, 68, 1-4. doi:<https://doi.org/10.1016/j.jas.2016.02.003>
- Pitteri, E., Mongillo, P., Carnier, P. & Marinelli, L. (2014). Hierarchical stimulus processing by dogs (*Canis familiaris*). *Animal cognition*, 17(4), 869-877.
- Pressey, A. (1971). An extension of assimilation theory to illusions of size, area, and direction. *Perception & Psychophysics*, 9(2), 172-176.
- Pressey, A. W., Di Lollo, V. & Tait, R. W. (1977). Effects of gap size between shaft and fins and of angle of fins on the Müller-Lyer illusion. *Perception*, 6(4), 435-439.
- Pressey, A. W. & Epp, D. (1992). Spatial attention in Ponzo-like patterns. *Perception & Psychophysics*, 52(2), 211-221. doi:10.3758/BF03206774
- Prinzmetal, W. & Beck, D. M. (2001). The tilt-consistency theory of visual illusions. *Journal of Experimental Psychology: Human Perception and Performance*, 27(1), 206.
- Pylyshyn, Z. (1999). Is vision continuous with cognition?: The case for cognitive impenetrability of visual perception. *Behavioral and brain sciences*, 22(03), 341-365.

- Range, F., Aust, U., Steurer, M. & Huber, L. (Range2008). (2008). Visual categorization of natural stimuli by domestic dogs (*Canis familiaris*). *Anim Cogn*, 11. doi:10.1007/s10071-007-0123-2
- Range, F., Hentrup, M. & Virányi, Z. (2011). Dogs are able to solve a means-end task. *Animal cognition*, 14(4), 575-583.
- Riedel, J., Schumann, K., Kaminski, J., Call, J. & Tomasello, M. (2008). The early ontogeny of human–dog communication. *Animal Behaviour*, 75(3), 1003-1014.
- Roberts, T., McGreevy, P. & Valenzuela, M. (2010). Human induced rotation and reorganization of the brain of domestic dogs. *PLoS One*, 5(7), e11946.
- Rosengren, A. (1969). *Experiments in colour discrimination in dogs*: Societas pro fauna et flora Fennica.
- Salman, M. D., Hutchison, J., Ruch-Gallie, R., Kogan, L., New Jr, J. C., Kass, P. H. & Scarlett, J. M. (2000). Behavioral reasons for relinquishment of dogs and cats to 12 shelters. *Journal of Applied Animal Welfare Science*, 3(2), 93-106.
- Salva, O. R., 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(6), 895-906.
- Santacà, M., Regaiolli, B., Miletto Petrazzini, M., Spiezio, C. & Agrillo, C. (2017). Preliminary study to investigate the Delboeuf illusion in ring-tailed lemurs (*Lemur catta*): Methodological challenges. *Animal Behavior and Cognition*, 4(3), 365-377.
- Schumann, F. (1900). Beiträge zur Analyse der Gesichtswahrnehmungen. Erste Abhandlung. Einige Beobachtungen über die Zusammenfassung von Gesichtseindruecken zu Einheiten. *Zeitschrift für Psychologie und Physiologie der Sinnesorgan*, (23), 1–32.
- Segurson, S. A., Serpell, J. A. & Hart, B. L. (2005). Evaluation of a behavioral assessment questionnaire for use in the characterization of behavioral problems of dogs relinquished to animal shelters. *Journal of the American Veterinary Medical Association*, 227(11), 1755-1761.
- Sherman, J. A. & Chouinard, P. A. (2016). Attractive Contours of the Ebbinghaus Illusion. *Perceptual & Motor Skills*, 122(1), 88-95. Retrieved from <http://ez.library.latrobe.edu.au/login?url=http://search.ebscohost.com/login.aspx?direct=true&db=s3h&AN=113369700&site=ehost-live&scope=site>
- Shettleworth, S. J. (2010). *Cognition, evolution, and behavior* (pp. 215–232): Oxford University Press.
- Siniscalchi, M., Ingeo, S., Fornelli, S. & Quaranta, A. (2017). Are dogs red–green colour blind? *Royal Society Open Science*, 4(11). Retrieved from <http://rsos.royalsocietypublishing.org/content/4/11/170869.abstract>
- Soproni, K., Miklósi, A., Topál, J. & Csányi, V. (2002). Dogs' (*Canis familiaris*) responsiveness to human pointing gestures. *Journal of Comparative Psychology*, 116(1), 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(2), 122.
- Sovrano, V. A., Albertazzi, L. & Salva, O. R. (2014). The Ebbinghaus illusion in a fish (*Xenotoca eiseni*). *Animal cognition*, 18(2), 533-542.

- Sovrano, V. A. & Bisazza, A. (2009). Perception of Subjective Contours in Fish. *Perception*, 38(4), 579-590. doi:<https://doi.org/10.1068/p6121>
- Sperandio, I. & Chouinard, P. A. (2015). The Mechanisms of Size Constancy. *Multisensory Research*, 28(3-4), 253-283.
- Spinozzi, G., De Lillo, C. & Truppa, V. (2003). Global and local processing of hierarchical visual stimuli in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 117(1), 15.
- Staats, S., Wallace, H. & Anderson, T. (2008). Reasons for Companion Animal Guardianship (Pet Ownership) from Two Populations. *Society & Animals*, 16(3), 279-291. doi:<https://doi.org/10.1163/156853008X323411>
- Stevens, M. & Merilaita, S. (2009). Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1516), 423-427.
- Stevens, M. & Merilaita, S. (2011). *Animal camouflage: mechanisms and function*: Cambridge University Press.
- Tanaka, T., Watanabe, T., Eguchi, Y. & Yoshimoto, T. (2000). Color Discrimination in Dogs. *Nihon Chikusan Gakkaiho*, 71(3), 300-304. doi:10.2508/chikusan.71.300
- Tapp, P. D., Siwak, C. T., Head, E., Cotman, C. W., Murphey, H., Muggenburg, B. A., . . . Milgram, N. W. (2004). Concept abstraction in the aging dog: development of a protocol using successive discrimination and size concept tasks. *Behavioural Brain Research*, 153(1), 199-210. doi:<http://dx.doi.org/10.1016/j.bbr.2003.12.003>
- Tauzin, T., Csík, A., Kis, A. & Topál, J. (2015). What or where? The meaning of referential human pointing for dogs (*Canis familiaris*). *Journal of Comparative Psychology*, 129(4), 334.
- Thayer, G. H. (1909). *Concealing-coloration in the animal kingdom: an exposition of the laws of disguise through color and pattern: being a summary of Abbott H. Thayer's discoveries*: Macmillan Company.
- Timney, B. & Keil, K. (1996). Horses are sensitive to pictorial depth cues. *Perception*, 25(9), 1121-1128.
- Titchener, E. B. (1901). *Experimental psychology: A manual of laboratory practice, Vol 1: Qualitative experiments: Part II. Instructor's manual*. New York, NY, US: MacMillan Co.
- Topál, J., Miklósi, Á. & Csányi, V. (1997). Dog-Human Relationship Affects Problem Solving Behavior in the Dog. *Anthrozoös*, 10(4), 214-224. doi:10.2752/089279397787000987
- Udell, M. A., Dorey, N. R. & Wynne, C. D. (2008). Wolves outperform dogs in following human social cues. *Animal Behaviour*, 76(6), 1767-1773.
- Udell, M. A., Dorey, N. R. & Wynne, C. D. (2010). What did domestication do to dogs? A new account of dogs' sensitivity to human actions. *Biological reviews*, 85(2), 327-345.
- Udell, M. A. & Wynne, C. D. (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(2), 247-261.

- Van Ittersum, K. & Wansink, B. (2012). Plate Size and Color Suggestibility: The Delboeuf Illusion's Bias on Serving and Eating Behavior. *Journal of Consumer Research*, 39(2), 215-228. doi:10.1086/662615
- Virányi, Z., Gácsi, M., Kubinyi, E., Topál, J., Belényi, B., Ujfalussy, D. & Miklósi, Á. (2008). Comprehension of human pointing gestures in young human-reared wolves (*Canis lupus*) and dogs (*Canis familiaris*). *Animal cognition*, 11(3), 373-387.
- Wayne, R. K. (1986a). Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution*, 243-261.
- Wayne, R. K. (1986b). Limb morphology of domestic and wild canids: the influence of development on morphologic change. *Journal of morphology*, 187(3), 301-319.
- Westheimer, G. (2008). Illusions in the spatial sense of the eye: Geometrical-optical illusions and the neural representation of space. *Vision Research*, 48(20), 2128-2142. doi:<https://doi.org/10.1016/j.visres.2008.05.016>
- Whitwell, R. L., Buckingham, G., Enns, J. T., Chouinard, P. A. & Goodale, M. A. (Whitwell2016). (2016). Rapid decrement in the effects of the Ponzo display dissociates action and perception. *Psychonomic Bulletin & Review*, 23(4), 1157-1163. doi:10.3758/s13423-015-0975-4
- Witkin, H. A. (1967). A COGNITIVE-STYLE APPROACH TO CROSS-CULTURAL RESEARCH1. *International Journal of Psychology*, 2(4), 233-250. doi:doi:10.1080/00207596708247220
- Wobber, V. & Hare, B. (2009). Testing the social dog hypothesis: are dogs also more skilled than chimpanzees in non-communicative social tasks? *Behavioural Processes*, 81(3), 423-428.
- Wynne, C. D., Udell, M. A. & Lord, K. A. (2008). Ontogeny's impacts on human-dog communication. *Animal Behaviour*, 76(4), e1-e4.
- Wyzisk, K. & Neumeyer, C. (2007). Perception of illusory surfaces and contours in goldfish. *Visual Neuroscience*, 24(3), 291-298. doi:<https://doi.org/10.1017/S095252380707023X>
- Zigler, E. (1960). Size estimates of circles as a function of size of adjacent circles. *Perceptual and Motor Skills*, 11(1), 47-53.
- Zigler, E. & Phillips, L. (1960). Social effectiveness and symptomatic behaviors. *The Journal of Abnormal and Social Psychology*, 61(2), 231.
- Zimmermann, R. R. (1962). Form generalization in the infant monkey. *Journal of Comparative and Physiological Psychology*, 55(6), 918-923. doi:<https://doi.org/10.1037/h0042446>