

If I fits I sits: A citizen science investigation into illusory contour susceptibility in domestic cats (*Felis silvestris catus*)

Gabriella E. Smith^{a,b,*}, Philippe A. Chouinard^c, Sarah-Elizabeth Byosiere^{a,b}

^a Animal Behavior and Conservation Program, Department of Psychology, Hunter College, City University of New York, United States

^b Thinking Dog Center, Department of Psychology, Hunter College, City University of New York, United States

^c School of Psychology and Public Health, La Trobe University, Australia

ARTICLE INFO

Keywords:

Cat
Behavior
Vision
Cognition
Kanizsa illusion

ABSTRACT

A well-known phenomenon to cat owners is the tendency of their cats to sit in enclosed spaces such as boxes, laundry baskets, and even shape outlines taped on the floor. This investigative study asks whether domestic cats (*Felis silvestris catus*) are also susceptible to sitting in enclosures that are illusory in nature, utilizing cats' attraction to box-like spaces to assess their perception of the Kanizsa square visual illusion. Carried out during the COVID-19 pandemic, this study randomly assigned citizen science participants Booklets of six randomized, counterbalanced daily stimuli to print out, prepare, and place on the floor in pairs. Owners observed and video-recorded their cats' behavior with the stimuli and reported findings from home over the course of the six daily trials. This study ultimately reached over 500 pet cats and cat owners, and of those, 30 completed all of the study's trials. Of these, nine cat subjects selected at least one stimulus by sitting within the contours (illusory or otherwise) with all limbs for at least three seconds. This study revealed that cats selected the Kanizsa illusion just as often as the square and more often than the control, indicating that domestic cats may treat the subjective Kanizsa contours as they do real contours. Given the drawbacks of citizen science projects such as participant attrition, future research would benefit from replicating this study in controlled settings. To the best of our knowledge, this investigation is the first of its kind in three regards: a citizen science study of cat cognition; a formal examination into cats' attraction to 2D rather than 3D enclosures; and study into cats' susceptibility to illusory contours in an ecologically relevant paradigm. This study demonstrates the potential of more ecologically valid study of pet cats, and more broadly provides an interesting new perspective into cat visual perception research.

1. Introduction

In 2017, cat fans took to Twitter to document their cats' attraction to tight spaces by taping complete shape outlines on their floors and observing their cats sit inside, spurring over eighty-two-thousand retweets and trending hashtag #CatSquare (Fig. 1). Affectionately termed "if I fits I sits," the urge to inhabit enclosed spaces is well-known to cat owners and has been documented to decrease stress in laboratory cats (Carlstead et al., 1993) and shelter cats given boxes in which to hide (Hawkins, 2005; Kry and Casey, 2007; Vinke et al., 2014). In fact, cats deprived of shelter resources like boxes will attempt to manufacture their own by hiding behind or underneath box-like objects like litter pans (Gourkow and Fraser, 2006). The reason for this behavior is still

unknown but is clearly highly desirable.

Regardless of the reason for their attraction to enclosed spaces, this behavioral phenomenon proves to be an excellent tool to study the visual perception of shapes and contours in domestic cats. Neurological study of this phenomenon began in cats and found that these nonhuman animals' (hereafter animals) retinal receptive fields are sensitive to contours along a luminance gradient (Redies et al., 1986). Contour comprehension is theorized to be evolutionarily critical in the understanding of physical objects and boundary interpolation (Kellman, 2003), and the study of visuo-cognitive phenomena such as illusion susceptibility offers a fascinating perspective into the effects of environmental pressures and life experience on vision (Kelley and Kelley, 2014).

* Corresponding author at: Animal Behavior and Conservation Program, Department of Psychology, Hunter College, 695 Park Avenue, New York, NY, 10065, United States.

E-mail address: gabriella.smith28@myhunter.cuny.edu (G.E. Smith).

<https://doi.org/10.1016/j.applanim.2021.105338>

Received 1 September 2020; Received in revised form 20 April 2021; Accepted 26 April 2021

Available online 30 April 2021

0168-1591/© 2021 Elsevier B.V. All rights reserved.

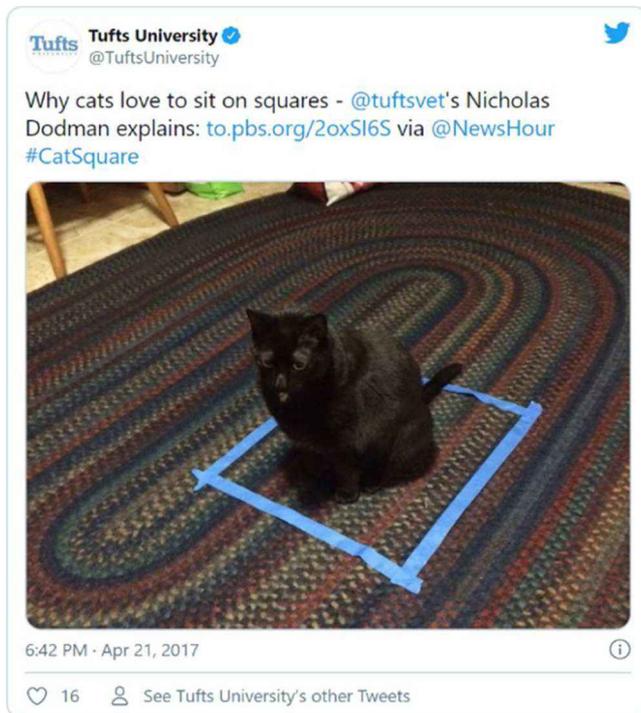


Fig. 1. Example of Trending Twitter Hashtag #CatSquare (Tufts University, 2017).

The ability to perceive visual illusions is remarkable. One's susceptibility to an illusion derives from the visual system processing an image's features as the most likely physical reality based on learnt probabilities, a top-down incorporation of one's preconceptions and past experience—even if it is not a true representation of reality (Gregory, 1997; Haber and Hershenson, 1973). In the real world, this processing is usually veridical or close to veridical (Palmer, 1999). Graphically rendered illusions are special cases where the same processing will result in a perception that deviates considerably from what is physically real.

The type of visual illusion considered here is subjective illusory contours, in which one mentally perceives fictitious contours connecting a shape's inducers (modal completion) due to luminance contrast (Kanizsa, 1955). Study of the effects of age on susceptibility to the Kanizsa contour illusion in humans finds that illusory-contour perception may develop around 3–4 months and strengthens with age (Otsuka et al., 2004). Susceptibility to illusory contours has also been studied in a wide range of animal species in almost exclusively train-and-transfer testing paradigms comprising dogs (Byosiere et al., 2017), chimpanzees (Fagot and Tomonaga, 2001), bamboo sharks (Fuss et al., 2014), honeybees (Horridge et al., 1992), mice (Kanizsa et al., 1993), barn owls (Nieder and Wagner, 1999), redbtail splitfin fish (Sovrano and Bisazza, 2009), and goldfish (Wyzisk and Neumeyer, 2007) (for a full reviews, see Byosiere et al., 2020; Feng et al., 2017; Kelley and Kelley, 2014; Nieder, 2002).

Previous research reveals that cats are, indeed, susceptible to certain visual illusions. De Weerd et al. (1990) found that domestic cats could discriminate illusory contour orientation via contour-inducing semi-circles. In 2019, Szenczi et al. revealed that cats are susceptible to the size distorting Delboeuf illusion. Further, two studies found that both lions (*Panthera leo*) (Regaiolli et al., 2019) and domestic cats (Bååth et al., 2014) are susceptible to the Rotating Snake illusion, comprising a “moving” image caused by peripheral drift eliciting hunting-related behavior.

Perhaps most relevant, a study by Bravo et al. (1988) examined domestic cats' susceptibility to subjective contours via operant response

to the Kanizsa square illusion. Two young, female cats were trained to indicate where they viewed a subjective contour on an array of sectorized disks in various orientations. The researchers controlled for other potential cues like luminance, temporal changes, and local patterns by introducing and modifying variables like motion and duration of stimuli exposure. They found that the cats demonstrated susceptibility to the Kanizsa illusion, indicating that cats likely perceive subjective contours as humans do (see Table 1 for a summary for illusion studies in cat species).

The present study supplements the results of Bravo et al.'s (1988) experiment with the addition of an increased sample size and a more inclusive sex and age range, in pet, rather than laboratory, cats. Moreover, rather than using standard operant conditioning procedures, the current study utilizes a more ecologically valid, real-world setting in which to evaluate spontaneous behavior. As cats transferred to novel environments can exhibit stress-related behaviors and thus not behave naturally (Amat et al., 2015), this study also offers an at-home environment to explore domestic cats' susceptibility to Kanizsa square contours in a natural setting. Specifically, we evaluate whether cats will sit or stand within the contours of an illusory Kanizsa square more often than a control stimulus in a spontaneous choice task. Importantly, to date, cats' attraction to enclosed spaces has been limited to 3D spaces (Carlstead et al., 1993; Gourkow and Fraser, 2006; Hawkins, 2005; Kry and Casey, 2007; Vinke et al., 2014), and thus this study also aims to formally examine the extension of this behavior to 2D shapes (such as that which was seen in the #CatSquare challenge). This study was conducted entirely remotely through citizen science engagement during the COVID-19 pandemic, and to the best of our knowledge, is the first published citizen science experiment to examine cat cognition.

2. Methods

2.1. Rationale and approval

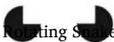
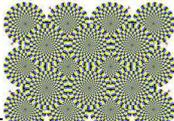
The Kanizsa square illusion, rather than the classic Kanizsa triangle (Kanizsa, 1955, 1974), was chosen for consistency with the Bravo et al. (1988) study. In order to avoid priming subjects to the experimental square stimuli (for effects of exposure to visual tasks on visual perception in cats, see Hua et al., 2010; Sasaki et al., 2010), as well as the evidence for cats' high motivation to sit in enclosed spaces (Gourkow and Fraser, 2006; Hawkins, 2005; Kry and Casey, 2007; Vinke et al., 2014), this study chose not to include a phase of initial baseline trials as control for the cats' general attraction to square stimuli.

This two-month study was conducted from June to August 2020 and was designed as a citizen science project and not a laboratory study for a variety of reasons: 1) the known effects of novel environments causing stress behaviors in cats (Amat et al., 2015); 2) the paradigm's success in studying companion animals including cats (Bååth et al., 2014; Roetman et al., 2018; Stewart et al., 2015); 3) as well as the COVID-19 pandemic requiring owners to stay at home. This study was approved by CUNY Hunter College Institutional Animal Care and Use Committee (DR-Cats-15/23) and an IRB review was not required by CUNY Hunter College Human Research Protection Program (HRPP) as no identifiable information from the pet owner was collected for research purposes.

2.2. Subjects and housing

Cats were volunteered and enrolled by their owners via completion of a preliminary Qualtrics survey made accessible on social media (e.g., researchers' public Twitter and Instagram accounts) and the project's website <https://catillusions2020.wixsite.com/iffitsitsits>. The 30 subjects studied were pets in the homes of the owners, and trials were incorporated into the average day of the cat and owner (for demographic data, see Table 2). Owners were not aware of the study's investigative purpose at any point before or during the experiment.

Table 1
Summary of Illusion Susceptibility in Cat Species.

Illusion	Reference	Sample	Task Type	Susceptible?
Contour-Inducing Semicircles ¹				
	De Weerd et al. (1990)	Two domestic cats (Felis silvestris catus)	Two-choice discrimination task	Yes
				
Kanizsa Square ¹	Szenczi et al. (2019)	18 domestic cats (Felis silvestris catus)	Two-choice spontaneous task	Susceptibility at the group level despite incongruity between control and experimental stimuli at the individual-level
	Bravo et al. (1988)	Two domestic cats (Felis silvestris catus)	Two-choice discrimination task	Yes
				
Rotating Squares ³	Bååth et al. (2014)	69 domestic cats (Felis silvestris catus)	Single stimulus presentation conducted as community-science and evaluated through survey report	Yes
				
	Bååth et al. (2014)	11 domestic cats (Felis silvestris catus)	Two-choice preferential looking task	Yes
	Regaioli et al. (2019)	Three lions (Panthera leo)	Three triplet spontaneous choice task	2/3 subjects demonstrated susceptibility

Note. ¹ Created by author GES. ² From *File:Delboeuf.jpg* [Image], by Famousdog (talk), 2009, Wikimedia Commons (<https://commons.wikimedia.org/w/index.php?curid=36039989>). CC BY 3.0. ³ From *Rotating Snake Illusion* [Image], by Jim's Photo World, 2011, Flickr (<https://www.flickr.com/photos/42546226@N08/5796170241>). CC BY-SA 2.0.

Table 2
Demographics of Participant Subjects and Chosen Stimuli.

Name	Sex	Age	Breed	Booklet	Counts of stimuli selected		
							
Ash	Male	Between 5 and 10 years old	Russian Blue	B	2	0	2
Bloshka	Female	Between 1 and 5 years old	unknown	B	0	0	1
Danae	Female	More than 10 years old	American shorthair	A	1	0	1
Eleanor	Female	Between 1 and 5 years old	Siberian	A	3	0	0
Fuleco	Male	Between 5 and 10 years old	unknown	C	1	0	0
Misha	Male	More than 10 years old	Ragdoll	C	0	0	1
Olly	Male	Between 1 and 5 years old	Domestic shorthair	B	0	0	2
Stinky Valium	Male	Between 1 and 5 years old	unknown	C	0	0	1
Totoro	Female	Less than 1 year old	unknown	A	0	1	0

2.3. Materials

To participate, cat-owning citizen scientists created the daily stimuli and therefore needed access to the following: a printer with black ink and printer paper; scissors; tape; and a ruler. To record their cats, owners needed a camera or smartphone, and to avoid possible visual attention cueing, dark sunglasses were to be worn.

2.3.1. Stimuli

Stimuli included the Kanizsa square illusion, a square outline, and a Kanizsa control. The dimensions of the real and illusory squares were equal at 20.32cm × 20.32cm each. Both the Kanizsa and Kanizsa control were made up of four “Pac-Mans” (circles into which a right-angle corner is cut, forming a ¾ circle), the corners facing inwards in the

Kanizsa and outwards in the control (Fig. 2). To satisfy the support ratio (r/h , r = radius of Pac-Man; h = half the length of illusory square side, based on research by Shipley and Kellman, 1992; Yankelovich and Spitzer, 2019) of “seeing” the Kanizsa square illusion as humans do (between 0.5 and 1), the support ratio for the Kanizsa square here was 0.5 ($r = 5.08$ cm, $h = 10.16$ cm). Dimensions within and between stimuli were determined to ensure that: a cat could comfortably sit or stand inside with all limbs and not be able to sprawl between and contact both at once. To avoid potential confound effects of area size, the total area of each stimulus was ensured to be nearly equal at 232.26 cm² each.

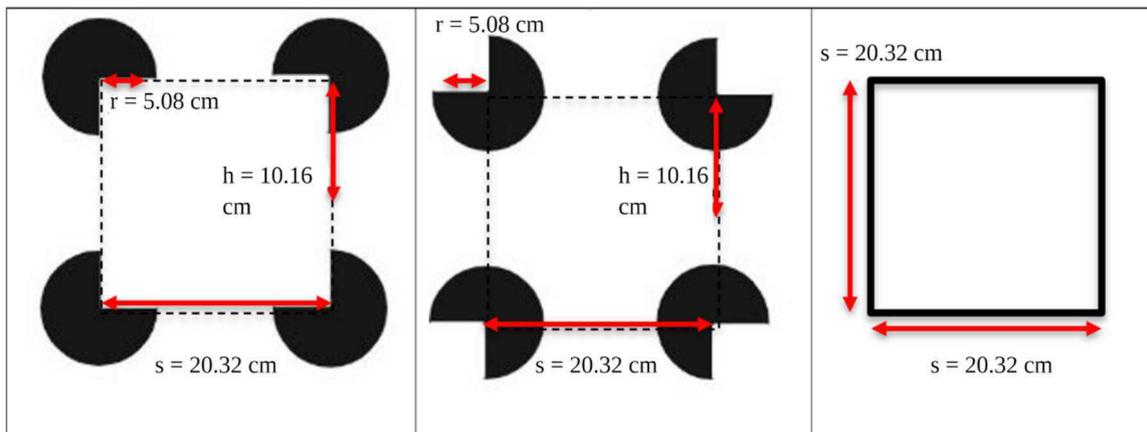


Fig. 2. Dimensions of Kanizsa, Kanizsa Control, and Square Stimuli.

Note. Label “r” refers to radius; label “h” refers to height; label “s” refers to side. Stimuli created by GES with BioRender.com.

2.4. Procedure

2.4.1. Preliminary survey

Permissions (i.e., owner age above 18 years-old) and consent to participate by the owner, use of owners’ names and e-mail addresses for research-related correspondence, and data such as pet cats’ demographic information (i.e., age, breed, sex) were collected via a preliminary Qualtrics survey (see Appendix A). Booklets—documents containing daily stimuli randomized by trial order and side orientation name to account for any trial order effects—were distributed based on each owner’s last name: Booklet A (last name starting with letter A–F); Booklet B (last name starting with letter G–N); and Booklet C (last name starting with letter O–Z) (see Appendix B).

2.4.2. Experimental trial surveys

Upon completion of the preliminary survey, owners received Trial 1 stimuli, a link to the first trial’s respective survey to report that day’s results (see Appendix C for general daily survey), and an instructions document (see Appendix D). Each experimental period lasted approximately 30 min consisting of stimuli preparation, a 5-minute daily trial, and electronic submission. Upon completion of every trial, owners followed a simple routine of clicking the link in that day’s stimuli Booklet to report their name, their cat’s name, that day’s trial number, Booklet assignment, that day’s trial results, and instructions to upload a video of

the trial. Each trial survey completion triggered an e-mail with the next trial’s stimuli until the sixth and final trial, in which they received a certificate of participation. Owners received no monetary or gift compensation for their participation.

2.4.3. Conducting trials 1–6

At the start of the experiment, per the instructions, owners were asked to place their cat out of the room while preparing and taping the assigned trial stimuli on the floor. The stimuli were placed 60.96 cm apart from the inner corners (Fig. 3). Measuring from the inner corners, each Pac-Man of the Kanizsa was taped on the floor 20.32 cm apart from each other, the corners either facing inwards or outwards from the center as presented in the Booklet. The owners were then asked to put on sunglasses, bring the cat into the room, not interact with the cat to avoid cueing to either stimulus, and begin videotaping the cat’s interaction with the two stimuli. On the occasions that individual owners made mistakes presenting stimuli (e.g., swapping left/right stimuli or inward/outward Pac-Man orientation) and alerted the researchers of the mistake soon after, owners were instructed how to treat future trials to ensure that all were completed. Those that did not alert the researchers in time were removed from the dataset.

If the cat sat/stood with all legs within the contours of a stimulus within the first five minutes, owners were asked to end the trial by stopping the video and making note of the chosen shape. If the cat did

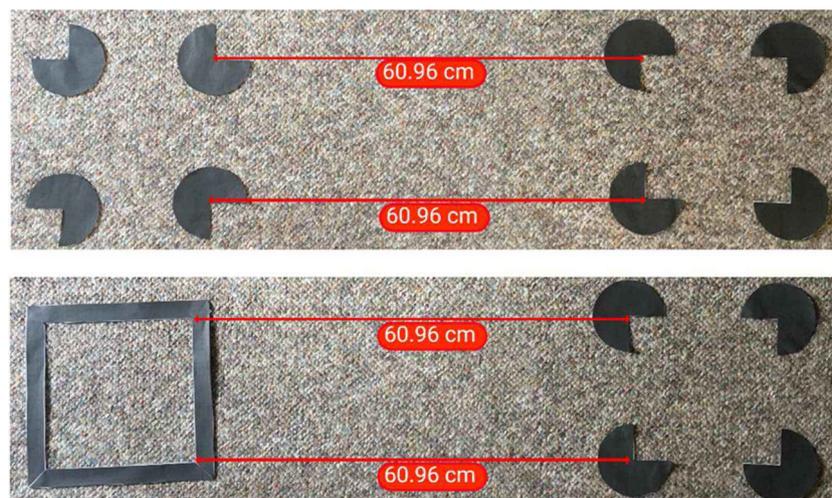


Fig. 3. Example Placement of Stimuli Pairs.

Note. Top: Kanizsa control on left and Kanizsa illusion on right; Bottom: Square on left and Kanizsa illusion on right.

not sit/stand in either shape within the first five minutes, owners were asked to end the trial. In either case, once the trial was over, owners completed that day's survey, uploaded that day's video, and removed the stimuli from the floor and disposed of them as they were not used again.

2.4.4. Statistical tests

Researchers GES and S-EB reviewed each video trial (regardless of citizen scientists' reports to the daily survey) using video-viewing software (e.g., Windows Media Player), indicating at what timestamp the participating cat sat on/in or near a stimulus over the course of the trial. Cats were considered "participant" if they sat or stood within the contours of a stimulus with all limbs for at least three seconds. The data of participant cats were compiled into Excel spreadsheets. Inter-observer reliability tests were performed for integrity and consistency of data, and GES and S-EB collaborated to agree upon participant versus non-participant cats. Chi square tests were performed to calculate differences in right/left selections, trial order between Booklets, and overall individual stimuli selections. Two-tailed Fisher's exact tests were performed to calculate the cats' relative preferences to sit in the square, the illusion, or the control (see Table 3), as well as the control versus the combined selections of the two square contour shapes, the Kanizsa (illusory) and square (non-illusory).

3. Results

3.1. Descriptive data

The preliminary survey received 561 enrollments. Over the course of the experiment, 121 cat-owner pairs completed Trial 1 (~22% of total); 53 completed Trial 2 (~9% of total); 43 completed Trial 3 (~8% of total); 38 completed Trial 4 (~7% of total); 34 completed Trial 5 (~6% of total); and 30 completed Trial 6 (5% of total). Of the 30 that completed the experiment, the nine subjects that made at least one stimulus selection came to 16 total stimulus selections: the square was chosen on eight occasions; the Kanizsa was chosen on seven occasions; and the Kanizsa control was chosen on one occasion (Table 2).

3.2. Interobserver reliability test

Cohen's κ of interobserver reliability test was performed on whether or not participant cats reached the metric of stimulus selection. There was almost perfect agreement (as deemed by Landis & Koch, 1977) between the two raters' judgements, $\kappa = .833$ (91.67% CI, 0.612–1.000).

3.3. Between booklets

Between Booklets, a stimulus was chosen on six occasions in Booklet A, seven occasions in Booklet B, and three occasions in Booklet C. A chi square of independence reveals no significant difference in stimulus selection between Booklets and therefore between trial order: $\chi^2(1, N = 16) = 1.625, p = .44$. Also between Booklets, a chi square of independence reveals the cats' combined right and left choices did not differ significantly from chance: $\chi^2(1, N = 16) = 2.250, p = .134$. Given the small sample size and the number of instances a cat selected a stimulus,

Table 3
Stimuli Selections.

	Total Number of Stimuli Selections	Number of Square Selections	Number of Kanizsa Selections	Number of Control Selections	Significance at $p = .05$
Kanizsa vs. Control	5	–	5	0	$p < .05^*$
Control vs. Square	4	3	–	1	$p = .40$
Kanizsa vs. Square	7	5	2	–	$p = .29$

Note. Summed across the nine cats, each stimuli pair was presented 18 times. Asterisk (*) indicates significance at the $p = .05$ level.

it is not possible to evaluate stimulus selection or side preference in individual cats.

3.4. Stimuli selection

Considering the nine total subjects, each unique pair (e.g., Kanizsa and square; Kanizsa control and square; Kanizsa and Kanizsa control; etc.) was presented a total of 18 times, and each individual stimulus presented a total of 36 times (for examples of the cats' selections, see Fig. 4). A chi square of independence reveals a significant difference in overall stimuli choices: $\chi^2(1, N = 108) = 6.310, p < .05$. See Table 3 and Fig. 5 for direct comparisons between stimuli.

3.4.1. Control vs. Kanizsa & square

This test combines the square and Kanizsa selections to compare square-like contour selection versus the non-square control. Of the total 36 combined occasions in which there was equal opportunity to choose Kanizsa or square versus the control across the nine subjects, a stimulus was chosen nine times. Of these, the Kanizsa or square was chosen eight times, and the control was chosen once. A Fisher's exact test reveals a significant preference for the Kanizsa or square stimuli over the control ($p < .05$).

4. Discussion

The cats in this study stood or sat in the Kanizsa and square stimuli more often than the Kanizsa control, revealing susceptibility to illusory contours and supporting our hypothesis that cats treat an illusory square as they do a real square. These findings confirm preexisting research of cats' susceptibility to illusory contours (De Weerd et al., 1990), and to the Kanizsa square illusion specifically (Bravo et al., 1988). To the best of our knowledge, this study is the first of its kind in three regards: 1) the first published citizen science study of cat cognition; 2) a formal examination into cats' attraction to 2D rather than 3D enclosures; 3) and an investigation into cats' susceptibility to illusory contours in an ecologically relevant paradigm (Table 1). As cats are known to exhibit stress-related behaviors such as territoriality and aggression in novel environments (e.g., laboratories) and thus not behave naturally (Amat et al., 2015), more ecologically valid experiments could hold an important place in future cat cognition research. This study supplements preliminary evidence of compelling efficacy in cat cognition experimental paradigms of this kind (Bååth et al., 2014; Dumas, 1992; Vitale Shreve and Udell, 2015).

Although this study had more diverse group of subjects in terms of age and sex than the Bravo et al.'s study, a weakness of this study was still the small dataset. The most likely cause of this was significant owner participation attrition, which likely occurred due to the study's lengthy design. The rate of attrition could have been avoided by requiring only one day of owner participants' time of study rather than six days. Another possible explanation for the study's small dataset could be due to cats' varying personalities (Feaver et al., 1986). It is possible that this, as well as individual differences in global or local processing and experience could have affected illusion susceptibility and therefore response to the stimuli (Hua et al., 2010; Sasaki et al., 2010; for global vs. local processing of illusions in humans, see Berry, 1968; Dakin and

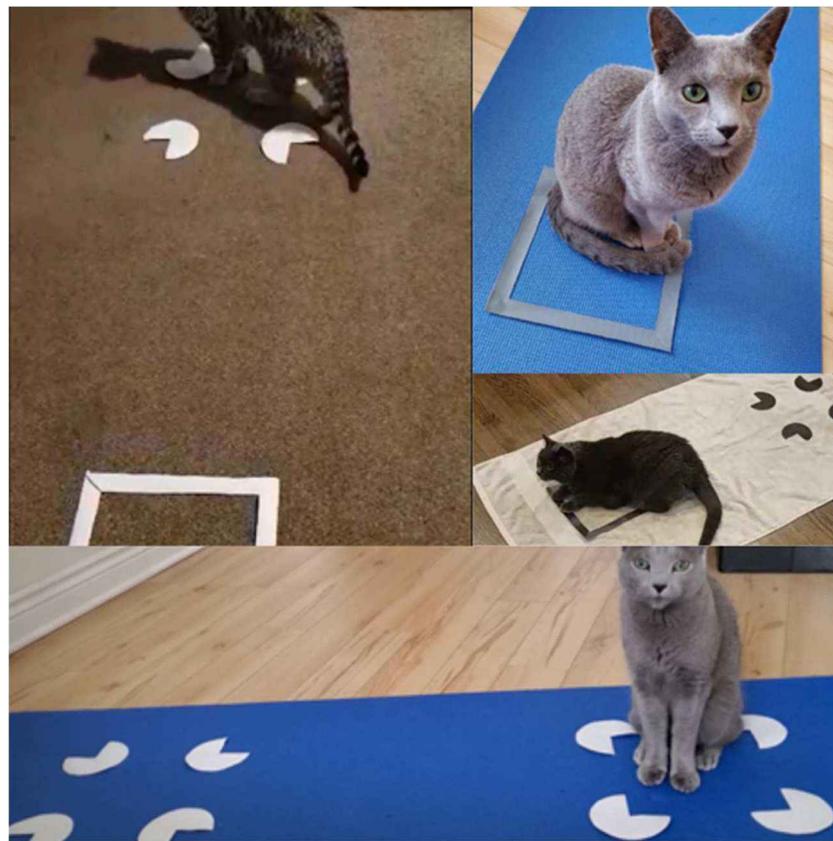


Fig. 4. Video Screenshots of Participant Cats' Stimuli Selections.

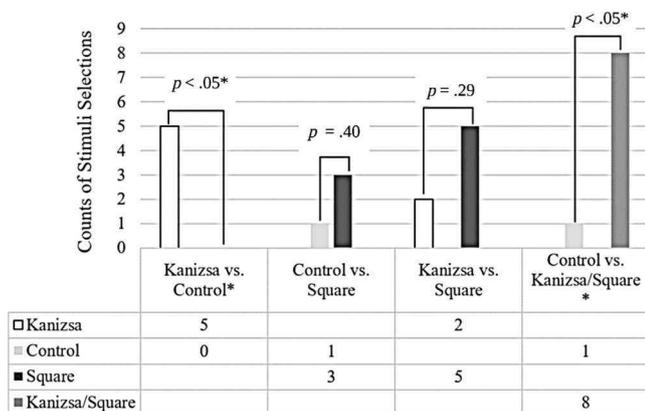


Fig. 5. Stimuli Selections in Pair Presentations.

Note. Asterisk (*) indicates significance (p) at the .05 level in stimuli selections within pairs.

Frith, 2005; de Fockert et al., 2007; Happé et al., 2003; Jahoda and Stacey, 1970; Ropar and Mitchell, 1999; Wagner, 2007).

Contrary to expectations, there was no significant difference in sitting in the square versus the Kanizsa control. We justify that, although this study is the first to formally investigate cats' attraction to 2D shapes, further experimental validity is needed to directly compare the stimuli. Furthermore, the Kanizsa control was likely an unsuitable comparison for contour treatment to the square. If performed again, a second control/fourth stimulus could be developed to better compare behavior towards the Kanizsa versus the square. Furthermore, to better understand cats elusive attraction to enclosures, future controls could introduce three-dimensional sides to the Kanizsa, square, and control.

Since illusion susceptibility may vary across species (Feng et al.,

2017), in conjunction with the known effects of domestication pressures on physiological abilities (Trut et al., 2009), future research should aim to explore the evolution of vision in domestic cats via the study of illusion susceptibility in non-domestic feline species like lions and tigers. Any difference in illusory contour susceptibility between domestic and big cats could point to the effects of domestication on cat vision, indicating a parallel in vision evolution in humans and their domesticates (for life experience effects on cat vision and behavior, see Blake and Hirsch, 1975; Blakemore and Cooper, 1970; Żernicki, 1993). Another important feature of illusion perception is luminance (Byosiere et al., 2019; Gove et al., 1995; Watanabe and Sato, 1989). To ensure that all stimuli are presented in equal conditions between cat subjects, luminance could be controlled for in the future to ensure stimulus treatment based strictly on contour perception.

In conclusion, cat cognition research is certainly lacking in comparison to domestic dogs, and although the reason for this is unclear, the use of citizen science as a precursor to in-lab investigations of cat cognition could greatly help bridge this divide.

Data statement

All data and materials are accessible within this manuscript. All data and materials will also be made available by contacting the corresponding author.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgments

We wish to extend our gratitude to the cats, the citizen scientists, and the reviewers/editors for their instrumental feedback in helping to

improve the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.applanim.2021.105338>.

References

- Amat, M., Camps, T., Manteca, X., 2015. Stress in owned cats: behavioural changes and welfare implications. *J. Feline Med. Surg.* 18 (8), 577–586. <https://doi.org/10.1177/1098612X15590867>.
- Bååth, R., Seno, T., Kitaoka, A., 2014. Cats and illusory motion. *Psychology* 5 (9), 1131–1134. <https://doi.org/10.4236/psych.2014.59125>.
- Berry, J.W., 1968. Ecology, perceptual development and the Müller-Lyer illusion. *Br. J. Psychol.* 59 (3), 205–210. <https://doi.org/10.1111/j.2044-8295.1968.tb01134.x>.
- Blake, R., Hirsch, H.V., 1975. Deficits in binocular depth perception in cats after alternating monocular deprivation. *Science* 190 (4219), 1114–1116. <https://doi.org/10.1126/science.1188391>.
- Blakemore, C., Cooper, G.F., 1970. Development of the brain depends on the visual environment. *Nature* 228 (5270), 477–478. <https://doi.org/10.1038/228477a0>.
- Bravo, M., Blake, R., Morrison, S., 1988. Cats see subjective contours. *Vision Res.* 28 (8), 861–865. [https://doi.org/10.1016/0042-6989\(88\)90095-8](https://doi.org/10.1016/0042-6989(88)90095-8).
- 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. *Anim. Cogn.* 20, 435–448. <https://doi.org/10.1007/s10071-016-1067-1>.
- 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. *Appl. Anim. Behav. Sci.* 212, 58–65. <https://doi.org/10.1016/j.applanim.2019.01.004>.
- Byosiere, S.E., Chouinard, P.A., Howell, T.J., Bennett, P.C., 2020. Illusion susceptibility in domestic dogs. *Ethology* 00, 1–17. <https://doi.org/10.1111/eth.13083>.
- Carlstead, K., Brown, J.L., Strawn, W., 1993. Behavioral and physiological correlates of stress in laboratory cats. *Appl. Anim. Behav. Sci.* 38 (2), 143–158. [https://doi.org/10.1016/0168-1591\(93\)90062-T](https://doi.org/10.1016/0168-1591(93)90062-T).
- Dakin, S., Frith, U., 2005. Vagaries of visual perception in autism. *Neuron* 48 (3), 497–507. <https://doi.org/10.1016/j.neuron.2005.10.018>.
- 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. *J. Exp. Psychol. Hum. Percept. Perform.* 33 (3), 738–742. <https://doi.org/10.1037/0096-1523.33.3.738>.
- De Weerd, P., Vandenbussche, E., De Bruyn, B., Orban, G.A., 1990. Illusory contour orientation discrimination in the cat. *Behav. Brain Res.* 39 (1), 1–17. [https://doi.org/10.1016/0166-4328\(90\)90117-W](https://doi.org/10.1016/0166-4328(90)90117-W).
- Dumas, C., 1992. Object permanence in cats (*Felis catus*)—an ecological approach to the study of invisible displacements. *J. Comp. Psychol.* 106, 404–410. <https://doi.org/10.1037/0735-7036.106.4.404>.
- Fagot, J., Tomonaga, M., 2001. Effects of element separation on perceptual grouping by humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*): perception of Kanizsa illusory figures. *Anim. Cogn.* 4, 171–177. <https://doi.org/10.1007/s100710100109>.
- Famousdog (talk), 2009. File:Delboeuf.jpg [Image]. Wikimedia Commons. <https://commons.wikimedia.org/w/index.php?curid=36039989>.
- Feaver, J., Mendl, M., Bateson, P., 1986. A method for rating the individual distinctiveness of domestic cats. *Anim. Behav.* 34 (4), 1016–1025. [https://doi.org/10.1016/S0003-3472\(86\)80160-9](https://doi.org/10.1016/S0003-3472(86)80160-9).
- Feng, L.C., Chouinard, P.A., Howell, T.J., Bennett, P.C., 2017. Why do animals differ in their susceptibility to geometrical illusions? *Psychon. Bull. Rev.* 24, 262–276. <https://doi.org/10.3758/s13423-016-1133-3>.
- Fuss, T., Bleckmann, H., Schluessel, V., 2014. The brain creates illusions not just for us: sharks (*Chiloscyllium griseum*) can “see the magic” as well. *Front. Neural Circuits* 8 (24), 1–17. <https://doi.org/10.3389/fncir.2014.00024>.
- Gourkow, N., Fraser, D., 2006. The effect of housing and handling practices on the welfare, behaviour and selection of domestic cats (*Felis sylvestris catus*) by adopters in an animal shelter. *Anim. Welf.* 15, 371–377.
- Gove, A., Grossberg, S., Mignolla, E., 1995. Brightness perception, illusory contours, and corticogeniculate feedback. *Vis. Neurosci.* 12 (6), 1027–1052. <https://doi.org/10.1017/S0952523800006702>.
- Gregory, R.L., 1997. *Eye and Brain: The Psychology of Seeing*, 5th ed. Princeton Science Library.
- Haber, R.N., Hershenson, M., 1973. *The Psychology of Visual Perception*. Rinehart & Winston, Holt.
- Happé, F., Briskman, J., Frith, U., 2003. Exploring the cognitive phenotype of autism: weak “central coherence” in parents and siblings of children with autism: I. Experimental tests. *J. Child Psychol. Psychiatry* 42 (3), 299–307. <https://doi.org/10.1111/1469-7610.00723>.
- Hawkins, K.R., 2005. *Stress, Enrichment and Welfare of Domestic Cats in Rescue Shelters*. Doctoral dissertation. University of Bristol.
- Horridge, G.A., Zhang, S.-W., O’Carroll, D., 1992. Insect perception of illusory contours. *Philos. Trans. Biol. Sci.* 337 (1279), 59–64. <https://doi.org/10.1098/rstb.1992.0083>.
- Hua, T., Bao, P., Huang, C.-B., Wang, Z., Xu, J., Zhou, Y., Lu, Z.-L., 2010. Perceptual learning improves contrast sensitivity of V1 neurons in cats. *Curr. Biol.* 20 (10), 887–894. <https://doi.org/10.1016/j.cub.2010.03.066>.
- Jahoda, G., Stacey, B., 1970. Susceptibility to geometrical illusions according to culture and professional training. *Percept. Psychophys.* 7, 179–184. <https://doi.org/10.3758/BF03208653>.
- Jim’s Photo World, 2011. Rotating Snake Illusion [Image]. Flickr. <https://www.flickr.com/photos/42546226@N08/5796170241>.
- 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? *Giornale Italiano di Psicologia* 1 (1), 93–113.
- Kanizsa, G., Renzi, P., Conte, S., Compostela, C., Guerani, L., 1993. Amodal completion in mouse vision. *Perception* 22 (6), 713–721. <https://doi.org/10.1068/p220713>.
- Kelley, L.A., Kelley, J.L., 2014. Animal visual illusion and confusion: the importance of a perceptual perspective. *Behav. Ecol.* 25 (3), 450–463. <https://doi.org/10.1093/beheco/art118>.
- Kellman, P.J., 2003. Interpolation processes in the visual perception of objects. *Neural Netw.* 16, 915–923. [https://doi.org/10.1016/S0893-6080\(03\)00101-1](https://doi.org/10.1016/S0893-6080(03)00101-1).
- Kry, K., Casey, R.A., 2007. The effect of hiding enrichment on stress levels and behaviour of domestic cats (*Felis sylvestris catus*) in a shelter setting and the implications for adoption potential. *Anim. Welf.* 16, 375–383.
- Nieder, A., 2002. Seeing more than meets the eye: processing of illusory contours in animals. *J. Comp. Physiol. A* 188, 249–260. <https://doi.org/10.1007/s00359-002-0306-x>.
- Nieder, A., Wagner, H., 1999. Perception and neuronal coding of subjective contours in the owl. *Nat. Neurosci.* 2, 660–663. <https://doi.org/10.1038/10217>.
- Otsuka, Y., Kanazawa, S., Yamaguchi, M.K., 2004. The effect of support ratio on infants’ perception of illusory contours. *Perception* 33 (7), 807–816. <https://doi.org/10.1068/p5129>.
- Palmer, S.E., 1999. *Vision Science: Photons to Phenomenology*. MIT Press.
- Redies, C., Crook, J.M., Creutzfeldt, O.D., 1986. Neuronal responses to borders with and without luminance gradients in cat visual cortex and dorsal lateral geniculate nucleus. *Exp. Brain Res.* 61, 469–481. <https://doi.org/10.1007/BF00237572>.
- Regaioli, B., Rizzo, A., Ottolini, G., Petrazzini, M.E., Spiezio, C., Agrillo, C., 2019. Motion illusions as environmental enrichment for zoo animals: a preliminary investigation on lions (*Panthera leo*). *Front. Psychol.* 10 (2220) <https://doi.org/10.3389/fpsyg.2019.02220>.
- Roetman, P., Tindle, H., Litchfield, C., 2018. Management of pet cats: the impact of the cat tracker citizen science project in south Australia. *Animals* 8 (11), 190. <https://doi.org/10.3390/ani8110190>.
- Ropar, D., Mitchell, P., 1999. Are individuals with autism and Asperger’s syndrome susceptible to visual illusions? *J. Child Psychol. Psychiatry Allied Discip.* 40 (8), 1283–1293. <https://doi.org/10.1111/1469-7610.00544>.
- Sasaki, Y., Gold, J., Watanabe, T., 2010. Perceptual learning: cortical changes when cats learn a new trick. *Curr. Biol.* 20 (13), R557–R558. <https://doi.org/10.1016/j.cub.2010.05.004>.
- Shipley, T.F., Kellman, P.J., 1992. Strength of visual interpolation depends on the ratio of physically specified to total edge length. *Percept. Psychophys.* 52, 97–106. <https://doi.org/10.3758/BF03206762>.
- Sovrano, V.A., Bisazza, A., 2009. Perception of subjective contours in fish. *Perception* 38 (4), 579–590. <https://doi.org/10.1068/p6121>.
- Stewart, L., MacLean, E.L., Ivy, D., Woods, V., Cohen, E., Rodriguez, K., McIntyre, M., Mukherjee, S., Call, J., Kaminski, J., Miklósi, Á., Wrangham, R.W., Hare, B., 2015. Citizen science as a new tool in dog cognition research. *PLoS One* 10 (9), e0135176. <https://doi.org/10.1371/journal.pone.0135176>.
- Szenci, P., Velázquez-López, Z.I., Urrutia, A., Hudson, R., Bánszegi, O., 2019. Perception of the Delboeuf illusion by the adult domestic cat (*Felis sylvestris catus*) in comparison with other mammals. *J. Comp. Psychol.* 133 (2), 223–232. <https://doi.org/10.1037/com0000152>.
- Trut, L., Oskina, I., Khramlova, A., 2009. Animal evolution during domestication: the domesticated fox as a model. *Bioessays* 31 (3), 349–360. <https://doi.org/10.1002/bies.200800070>.
- Tufts University. [@TuftsUniversity], 2017. Why Cats Love to Sit on Squares - @tuftsvet’s Nicholas Dodman Explains. [http://to.pbs.org/20xSI6Svia@NewsHour#CatSquare \[Image and link attached\] \[Tweet\]. Twitter April 21. https://twitter.com/TuftsUniversity/status/85555225506017280?s=20](http://to.pbs.org/20xSI6Svia@NewsHour#CatSquare [Image and link attached] [Tweet]. Twitter April 21. https://twitter.com/TuftsUniversity/status/85555225506017280?s=20).
- Vinke, C.M., Godijn, L.M., van der Leij, W.J.R., 2014. Will a hiding box provide stress reduction for shelter cats? *Appl. Anim. Behav. Sci.* 160, 86–93. <https://doi.org/10.1016/j.applanim.2014.09.002>.
- Vitale Shreve, K.R., Udell, M.A., 2015. What’s inside your cat’s head? A review of cat (*Felis sylvestris catus*) cognition research past, present and future. *Anim. Cogn.* 18 (6), 1195–1206. <https://doi.org/10.1007/s10071-015-0897-6>.
- Wagner, D.A., 2007. Ontogeny of the Ponzo illusion: effects of age, schooling, and environment. *Int. J. Psychol.* 12 (3), 161–176. <https://doi.org/10.1080/00207597708247386>.
- Watanabe, T., Sato, T., 1989. Effects of luminance contrast on color spreading and illusory contour in the neon color spreading effect. *Percept. Psychophys.* 45, 427–430. <https://doi.org/10.3758/BF03210716>.
- Wyzisk, K., Neumeier, C., 2007. Perception of illusory surfaces and contours in goldfish. *Vis. Neurosci.* 24 (3), 291–298. <https://doi.org/10.1017/S095252380707023X>.
- Yankelovich, A., Spitzer, H., 2019. Predicting illusory contours without extracting special image features. *Front. Comput. Neurosci.* 12 (106) <https://doi.org/10.3389/fncom.2018.00106>.
- Žemicki, B., 1993. Learning deficits in lab-reared cats. *Acta Neurobiol. Exp.* 53 (1), 231–236.