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Object-Based Warping During Distance Discriminations by Rhesus Monkeys (*Macaca mulatta*) and Capuchin Monkeys (*Sapajus apella*)

Joseph W. McKeon[1*], Audrey E. Parrish[2], and Michael J. Beran[1*]

[1]Department of Psychology and Language Research Center, Georgia State University
[2]Department of Psychology, The Citadel

*Corresponding author (Email: emckeon1@gsu.edu, mberan1@gsu.edu)

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Abstract – Humans and nonhuman animals misperceive the world. However, they do not always share the same misperceptions. Vickery and Chun (2010) reported a visual illusion, object-based warping, wherein distances between stimuli contained within an object were perceived by adult humans as larger than distances presented against a plain background. Rhesus monkeys and capuchin monkeys were tested on their susceptibility to this illusion. After being trained to choose the pair of dots with the larger distance between them, they were tested on a variety of conditions to assess illusion susceptibility. The results showed that there were no species differences in performance, but there was an effect of how dot pairs were presented. The Congruent condition (only the pair of dots with a longer distance between them was within an object) was performed significantly better than the Baseline condition (both pairs of dots were either within objects or on the plain background) and the Incongruent condition (the pair of dots with the smaller distance between them was within an object, and the other pair was on a plain background). Performance in the Baseline condition was also significantly higher than that in the Incongruent condition. Perhaps most compelling was that on trials where the two dot pairs had equal distances between dots, but one pair was presented within an object and the other was not, all monkeys except one showed a significant bias towards the object-contained array. These results indicate that this illusion is not exclusive to humans, and that the attentional and visual processes that make humans susceptible to the illusion are present in at least some other nonhuman primate species.

Keywords – Perception, Illusions, Rhesus monkeys, Capuchin monkeys, Distance discrimination

Humans often misperceive the world. Nonhuman animals do as well (for reviews, see Agrillo et al., 2020; Feng et al., 2017; Kelley & Kelley, 2014; Parrish, 2021; Parrish & Agrillo, 2022). For nonhuman primates, who share with humans a strong reliance on visual perception to make sense of their external worlds, such misperceptions through visual illusions can impact choice behavior and possibly even fitness. For this reason, the comparative study of visual illusions is important for understanding how misperception causes cognitive and behavioral failures. From another perspective, the study of visual illusions and misperception gives us insight into the nature of visual processing and perceptual mechanisms more generally. Furthermore, better understanding visual illusions (i.e., when and why they occur) illustrates how environmental constraints such as the physical nature of stimuli that impact the sensory systems of different animals can fundamentally change how unique species and individuals experience the world.

Nonhuman animals share with humans many illusory experiences, particularly perception of geometric illusions in which a target shape is misperceived on the basis of an illusory-inducing context.

Some of these illusions occur for humans when making judgments about length or distance, such as the Ponzo and Müller-Lyer illusions. The Ponzo illusion emerges when two identical horizontal lines (target stimuli) are positioned between the apex of two converging lines in the shape of an inverted letter V (contextual stimuli). The horizontal line closer to the apex of the inverted V appears longer than the horizontal line positioned further from the apex. Sensitivity to the Ponzo illusion and the related corridor illusion, in which stimuli positioned higher are overestimated in size, suggests continuity in pictorial depth cues and size constancy across primates (e.g., Barbet & Fagot, 2002; Fujita, 1996, 1997; Hanus et al., 2022), pigeons (*Columba livia*: Fujita et al., 1991, 1993; Hataji et al., 2020), and other species tested such as horses (*Equus ferus caballus*: Timney & Keil, 1996). Similarly, a wide variety of species are sensitive to the line-length Müller-Lyer illusion, in which the length of a horizontal line is underestimated when flanked by outward-facing arrow brackets but overestimated when flanked by inverted inward-facing arrow brackets (e.g., Hanus et al., 2022; Pepperberg et al., 2008; Sakiyama & Gunji, 2013; Santacà & Agrillo, 2020; Sovrano et al., 2016; Suganuma et al., 2007; Tudusciuc & Nieder, 2010). As evidenced across a broad range of comparative studies, species- and individual-level differences in illusory perception emerge readily, highlighting important differences in perceptual mechanisms across species and underscoring the role of methodological variation in experimental procedures (Beran & Parrish, 2023; Byosiere et al., 2020). For this reason, the discovery of new illusory experiences in humans often presents the chance to see whether other species share these experiences, or whether they may be more uniquely human. A fairly new illusion reported in humans, object-based warping (Vickery & Chun, 2010), is the focus of this study.

Vickery and Chun (2010) reported that adult humans perceived an identical distance between two dots presented within an object as larger than an equal distance between dots presented with no surrounding object. They concluded that images with more structure surrounding the dots resulted in greater illusory space distortion than images with less structure or no structure. They suggested that object-based warping may reflect fundamental properties of visual representation separate from depth perception, which would result in the opposite effect than the object-based warping. Specifically, depth perception, which accounts for other distance and size illusions (e.g., Ponzo and corridor illusions), would lead one to perceive the stimuli placed inside the object as closer to the viewer, and therefore as having a smaller distance between them. Object-based warping may, in part, be due to enhanced attention to objects, which would lead to overestimates of the space between dots contained within, similar to enhanced contrast, size, and spatial frequency for attended objects and patterns (e.g., Anton-Erxleben et al., 2007; Carrasco et al., 2004; Gobell & Carrasco, 2005). Additionally, cortical rescaling reflects enhanced activity in the early visual cortex for stimuli in the foreground compared with background regions, and enhanced contrast sensitivity within closed contours (Kovács & Julesz, 1994; Marcus & Van Essen, 2002). These two prioritizations within visual processing may subsequently lead the visual system to devote more cortical representation to foreground or surface regions, further facilitating perception of the object's properties (see Vickery & Chun, 2010).

The goal of the current study was to examine whether object-based warping, which has been suggested to be relevant to various perceptual and attentional phenomena among humans, also arises in monkeys. If other primates also overestimate the distance of items presented as if they are within objects compared to items that are not within objects, this may illustrate a phylogenetically broad basic principle of visual representation. To assess this, we tested two primate species that are fairly phylogenetically distant within the order *Primates*, the rhesus macaque (*Macaca mulatta*), found in South, Central, and Southeast Asia, and the capuchin monkey (*Sapajus apella*), found in Central and South America. We utilized a two-choice discrimination procedure in which monkeys were first trained to choose a stimulus that presented a greater distance between dots. Having trained the monkeys on the relative discrimination task, we then presented probe trials in which some dot pairs were within surrounding ground images (rectangles) whereas others were not, and thereby conceptually replicate the main manipulation performed by Vickery and Chun (2010). We could not recreate all of the conditions that Vickery and Chun used, because in their experiment utilizing an adjustment procedure, human participants made repeated responses to physically change the distance between one pair of dots in one of two presented stimuli until they believed they had matched the distance of two other dots located elsewhere on the computer screen. Our monkeys cannot make such adjustments to stimuli in this manner, but they can be trained via the relative discrimination task, which is one of the primary behavioral methods for assessing susceptibility to visual illusions among animals and is commonly employed for testing illusions in human subjects.

Test trials included congruent, incongruent, and equal distance comparisons. Congruent test trials presented the correct stimulus (the dot pair with the greater spatial distance) within a rectangle whereas the other dot pair was on a plain background (no object). These trials were predicted to facilitate performance relative to baseline trials in which there were no rectangles for either pair of dots or both pairs were within a rectangle. Incongruent test trials presented the incorrect dot pair with smaller spatial distance between dots within a rectangle whereas the correct dot pair with the larger distance between dots was not within an object. These trials were predicted to be performed more poorly compared to baseline trials and trials in the congruent condition. As is common within human and comparative illusion studies, the equal trials were the truest test of the illusion such that they pitted dot pairs of equal distance with the illusory-inducing context (contained within a rectangle) versus without the illusory context (no rectangle). We predicted that both species would be more likely to select the dot pair contained within the rectangle on equal distance discrimination trials, which would reflect the warping effect as documented among humans by Vickery and Chun (2010).

Methods

Ethics Statement

All experimental procedures were approved by the Institutional Animal Care and Use Committee of Georgia State University. Georgia State University is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care International. Some aspects of this study were preregistered with the Open Science Framework (OSF) in July 2021 under the CC-By Attribution 4.0 International License (McKeon et al., 2021). That preregistration can be found at https://doi.org/10.17605/OSF.IO/3T56V. However, we also made some changes to the experimental design at the actual time of testing that were not explicitly described in that pre-registration (e.g., using baseline trials with and without rectangles, to control for exposure to both types of stimulus presentation, something that was not included in the pre-registration description). We also had proposed analyses using response times that are not included in this article because we did not find those to be informative to the main questions of interest.

Subjects and Housing

Six adult male rhesus monkeys (*Macaca mulatta*) and 21 adult capuchin monkeys (*Sapajus apella*; 15 females, 6 males) at the Language Research Center (LRC) of Georgia State University were tested (see Table 1). All rhesus monkeys were singly housed with visual and auditory access to other monkeys, and four of these monkeys had access to a compatible partner who they shared time with each day in an outdoor enclosure (they did not complete testing during that time). All capuchin monkeys were group-housed in groups of two or more monkeys. Both species had access to indoor and outdoor enclosures with a variety of enrichment items including toys, climbing structures, and foraging puzzles. They were given a full diet of fresh fruits and vegetables daily along with monkey chow and were not food- or water-restricted in any way during this study.

Monkeys routinely participated in a variety of computerized cognitive tests throughout their day, and all were experienced with cognitive and learning tasks similar to what was done in the current study (e.g., Beran et al., 2006; Parrish et al., 2018; Smith et al., 2020).

Table 1

Demographic and Performance Data for Each Monkey

Monkey	Age (Years)	Sex	# Training Trials	# Training Sessions	% Correct Baseline Rectangles	% Correct Baseline No Rectangles	% Correct Congruent	% Correct Incongruent	% Choice Equal Array with Rectangle
Rhesus Monkeys									
Chewie	23	M	3,376	15	59.7	71.4	86.9	30.7	64.7
Han	20	M	1,509	10	54.3	75.2	68.1	61.4	62.2
Lou	29	M	1,355	9	75.7	91.2	73.5	83.0	58.7
Luke	23	M	3,000	15	54.1	80.2	63.4	61.1	56.7
Murph	29	M	1,200	4	87.7	88.1	90.9	73.7	61.7
Obi	19	M	520	2	72.4	93.9	83.2	79.4	76.7
Capuchin Monkeys									
Albert	11	M	[a]2,034	16					
Applesauce	18	F	[a]1,652	13					
Attila	10	M	1,347	6	64.7	84.4	77.4	46.4	100
Bailey	23	F	[b]1733	23					
Bias	34	F	[a]2,784	39					
Gabe	24	M	[a]1,027	14					
Gambit	26	F	[b]3,291	67					
Gonzo	16	F	1,040	3	75.4	68.4	92.0	34.3	89.5
Gretel	19	F	112	13	77.8	71.2	83.8	58.9	63.4
Ingrid	10	F	4,708	10	79.2	74.9	85.5	53.0	69.7
Irene	20	F	[a]2,550	25					
Ivory	24	F	[b]341	2					
Liam	19	M	1,342	7	76.9	78.8	84.5	72.8	100
Lily	25	F	[b]599	22					
Lychee	23	F	[a]3,514	48					
Mason	24	M	[b]704	4					
Nala	20	F	[b]1,014	15					
Nkima	15	M	[b]351	30					
Paddy	12	F	6,729	43	50.8	76.1	59.6	77.0	53.2
Widget	14	F	[b]610	8					
Wren	20	F	1,037	11	71.2	72.8	75.4	77.5	59.1

Note. Greyed cells show monkeys that did not reach the test phase. [a]Showed extreme side bias. [b]Rarely separated for testing or performed few trials when test sessions did occur.

Apparatus

The monkeys were tested using the LRC's Computerized Test System, which is comprised of a personal computer, digital joystick, 17-inch color monitor, and pellet dispenser (Evans et al., 2008; Richardson et al., 1990). They manipulated the joystick with their hands to produce isomorphic movements of a small cursor on the computer. Correct responses to the computer program led to a positive auditory tone and the delivery of a food reward (a 45-mg banana-flavored chow pellet; Bio-Serv, Frenchtown, NJ) via a pellet dispenser at the end of each trial, whereas incorrect responses lead to a negative auditory tone and a 5-second timeout period for each incorrect answer at the end of each trial. Rhesus monkeys were not restrained during testing and viewed the monitor from approximately 30 to 40 cm, while capuchin monkeys freely entered a testing box for a food reward and were released at the end of the testing period after receiving a jackpot fruit reward, three to four hours after entering the box. They also were not restrained during testing and viewed the monitor from the same approximate distance as the rhesus monkeys. The computer program was written in Visual Basic 6.0.

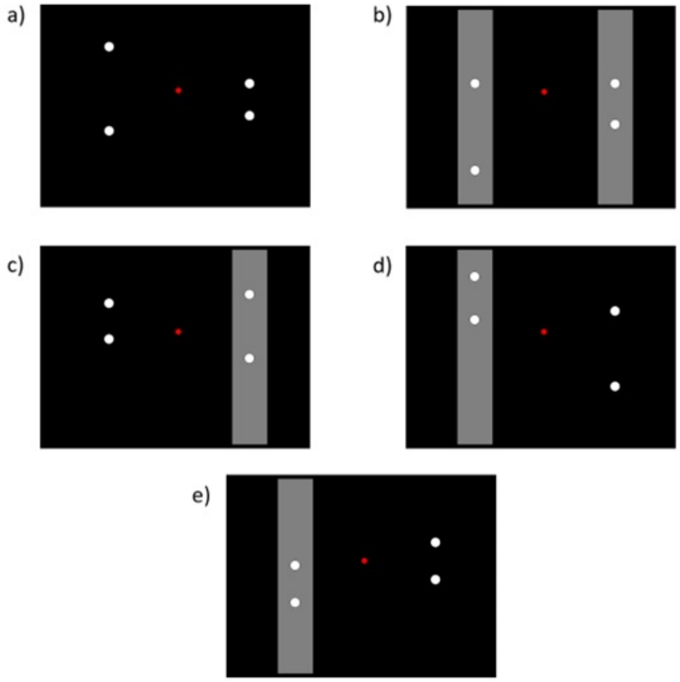
Procedure

Training Phase

Monkeys completed a two-item discrimination task by manipulating a red circular cursor onscreen through their joystick manipulations (Figure 1). In the training phase of the task, they were presented with trials in which two vertically aligned sets of white dots (8 mm in diameter) appeared on the left and right side of the screen after monkeys selected a "Start Trial" icon presented against a black screen with their cursor (4.5 mm in diameter; see Figure 1). The dot arrays were non-centered vertically on the screen to prevent monkeys from judging the difference in distance by comparing the relative height of the left and right dots. The higher dot in each array was presented 20 to 70 mm from the top edge of the screen (randomly determined). The left pair of dots was 50 mm from the left edge of the screen, and the right pair of dots was 110 mm from the left pair of dots (towards the right edge of the screen). The vertical distance between the centers of the two dots in each array was chosen randomly from a range of 20 to 80 mm. One array always had a larger distance between dots than the other. The array with the larger vertical distance between dots always had a distance that was 30 to 41 mm greater than the distance between dots in the other array (randomly selected across trials). The dot pairs were both presented on a plain background (no rectangles), or they were presented within grey rectangles presented onscreen, randomly determined on each trial in this condition. The grey rectangles were 153 mm tall and 28 mm wide and were presented in RGB (0, 128, 128) coloration.

Figure 1

Examples of Each Trial Type in the Experimental Phase



Note. The red circle at center is the cursor which is used to make responses through movement to the left or right onscreen. The trial types are displayed as follows: a) baseline – no rectangles, b) baseline – rectangles, c) congruent, d) incongruent, and e) equal.

Monkeys were trained that the array with a larger distance between the dots in that array was the correct choice. When they selected that array, they received a food reward, and the next trial was presented immediately. When they selected the incorrect array, with the smaller vertical distance between dots, the screen was cleared and a timeout period of 5 seconds occurred before the next trials was presented. After meeting a criterion of 50 of the last 60 trials completed correctly (83.3%), they moved to the testing phase.

Testing Phase

For all trials in this phase, the vertical distances between the two dots in each array again was 20 to 80 mm. However, the relative difference between the two arrays was much closer (from a 2 mm difference to a 41 mm difference, randomly selected across trials). Thus, the task was more difficult than in training. In this phase, on each trial there was a 50% chance of a baseline trial like that in the training phase, and a 50% chance of an experimental trial which could take one of three forms not seen in the training phase. These new trial types always involved one pair of dots being presented on the plain black background (no rectangle present), but the other pair presented within a grey rectangle (see Figure 1). On these trials, the location of the rectangle (left or right) was randomized.

These new trial types consisted of congruent, incongruent, and equal vertical distance comparisons. Congruent test trials were those in which the distance between dots contained within a grey rectangle was greater than the distance between dots presented against the plain black background (thus, congruent with the illusion as demonstrated in humans such that the dots were truly further apart and within an object that should facilitate correct responding; Vickery & Chun, 2010). Incongruent trials were those in which the distance between dots contained within the grey rectangle was shorter than the distance between dots presented against the plain black background. Equal trials were those in which there was no difference in vertical distance for the two pairs of dots, and so only the background differed (black background/no rectangle present versus grey rectangle).

For trial types with a real difference in distances between dots, monkeys again were rewarded with one food pellet when choosing the array with the greater distance between dots. For trials in which the distance was equal for both arrays, non-differential reinforcement was provided (i.e., there was a 50% chance of reward and a 50% chance of simply moving to the next trial regardless of which array was chosen). Monkeys completed 1,200 trials in the testing phase.

On each trial in the training and testing phase, the program recorded the monkey's name, the date, the time, the trial number, the phase (Train or Test), the condition (baseline, congruent, incongruent, equal), the distance between dot stimuli on the left, the distance between dot stimuli on the right, the difference in the distances between the left and right stimuli, the side of the screen that the correct stimulus appeared on (in the case of equal trials, this was the side of the screen the object-contained dot array appeared on), the side of the screen the chosen stimulus was on, the reaction time from selecting the "Start Trial" icon to selecting the stimulus, and the outcome (correct/incorrect for trials with real differences in vertical distance, box/not box for trials in the Equal condition).

The data for analyses consisted of the percentage of trials choosing the correct pair of dots with the greater distance between them (or, in the case of equal trials, the percentage of trials choosing the pair of dots contained within the rectangle), and those data were normally distributed as determined using a Kolmogorov-Smirnova test and a Shapiro-Wilk test, so parametric analyses were used. We combined the two types of baseline trials so that we could compare performance when background could not affect one dot pair more than the other to the congruent and incongruent conditions where that could happen, and so that we could assess our three hypotheses.

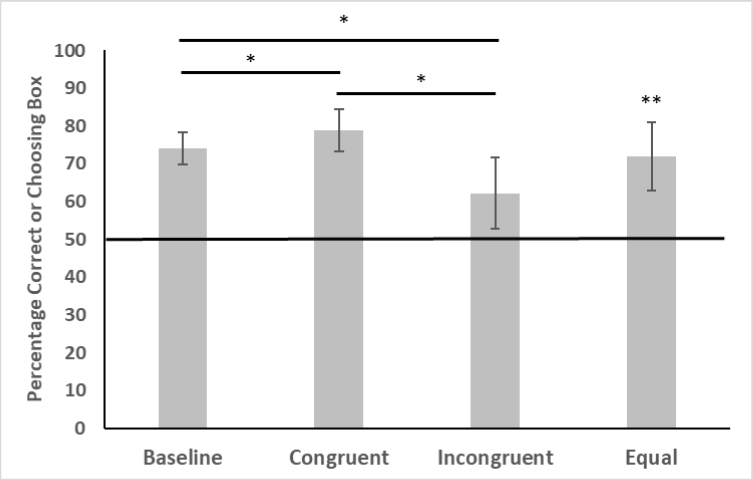
Results

We found that some capuchin monkeys showed substantial deficits in motivation to work on the task or in the learning the task demands, to the extent that 14 of the 21 capuchin monkeys did not advance to the testing phase (see Table 1). Three monkeys did not willingly separate often enough from their social group to make progress during the six-month duration of data collection for the study. Four monkeys did not engage the task enough, even when separating for testing, and the remaining seven monkeys developed very strong side biases during training that prevented them from passing the criterion even after a large number of trials (see Table 1). All rhesus monkeys progressed to the test phase.

Capuchin monkeys (N = 7) that met criterion during training took an average of 2,490 trials (SD = 2,284) and rhesus monkeys that met criterion took on average 1,827 trials (SD = 1,114) to reach the training criterion. This species difference was not statistically significant, $t_{11} = 0.64$, $p = .53$.

Figure 2

Average Performance in Each Condition for All Monkeys



Note. For the Equal condition, the bar represents the mean percentage of trials in which the dots within the rectangle were chosen. For all other conditions, the bars represent the mean percentage correct. *indicates a significant difference between two compared conditions. **indicates a significant difference from a chance level of 50%. Error bars reflect the 95% confidence intervals of the means.

The results are shown in Figure 2. For the three conditions in which there was a difference in the distance between dots in each array (baseline, congruent, incongruent), a 2 (species) by 3 (condition) mixed ANOVA with proportion of correct responses as the dependent variable was conducted. There was not a main effect of species, $F(1, 11) = 0.16$, $p = .70$, $\eta p^2 = .01$. There was an effect of condition, $F(2, 11)$, 5.99, $p = .008$, $\eta p^2 = .35$. The interaction between the two factors was not significant, $F(3, 11)$, 0.26, $p = .77$, $\eta p^2 = .02$. We conducted post hoc directional (one-tailed) paired *t*-tests to assess each of the hypotheses. We modified the alpha level to accommodate repeated use of the dependent variable using Holm's Sequential Bonferroni Correction (Holm, 1979). First, we assessed whether performance on the baseline condition exceeded performance on the incongruent test condition, and it did, $t(12) = 2.74$, $p = .009$. Next we assessed whether performance on congruent trials exceeded that of incongruent trials, and it did, $t(12) = 2.58$ $p = .012$. Finally, we assessed whether performance on congruent trials exceeded that of baseline trials, and it did, $t(12) = 1.92$, $p = .04$. It is important to note, however, that use of two-tailed tests, without directional hypotheses, and with the Bonferroni correction, would have indicated that not all of these comparisons reached conventional levels of statistical significance. Additionally, a paired t-test on the difference in performance between the two baseline trial types (rectangle and no rectangle) revealed that monkeys performed better on trials without rectangles than on trials with rectangles, $t(12) = -2.82$, $p = .016$.

An independent samples t-test was conducted to see whether capuchins (M = 76.4, SD = 19.7) or rhesus monkeys (M = 66.8, SD = 11.3) were more likely to select the array within the grey rectangle on equal distance trials. There was no species difference, $t(11) = 1.03$, $p = .31$. We then combined the two species to conduct a one sample *t*-test to examine whether performance on the equal trials showed a significant bias above 50% toward the array within the rectangle. The monkeys showed a significant bias to choose the array that was within the grey rectangle, $t(12) = 4.80$, $p < .001$, an outcome that matched the reported direction of the illusion in humans. Every monkey except Paddy (a capuchin monkey) showed a significant bias to choose the array within the rectangle, binomial test, all $p < .05$. Paddy showed no significant bias to choose either stimulus type, $p = .40$.

Discussion

The results support object-based warping among rhesus and capuchin monkeys using a two-choice discrimination task. In non-equal distance trials, monkeys performed better at selecting the set with a greater distance between the dots when the correct choice was congruent with the illusion (the array with the larger distance was the object-contained one) than in any other condition. Monkeys also showed poorer performance on incongruent trials (the array with the larger distance was the one presented against a plain background) compared to all other conditions. Furthermore, every monkey except one showed a significant bias towards the object-contained array when there was no true difference in distance between the two stimuli (equal trials). These results provide support for the idea that this illusion is based on an emphasis on objecthood in visual representation, leading to an over-estimation of the distance between the dots presented within a rectangle – or, as it may be perceived, against the rectangle's surface.

The results map onto those of Vickery and Chun's (2010) human adults who significantly over-adjusted the spatial distance between dots presented against the ground stimuli when allowed to change the distance between two dots to match an object-contained sample. This finding has implications for our understanding of primate perception, human or otherwise. Specifically, Vickery and Chun's assertion was that warping may reflect attentional and/or perceptual processes that create a strong focus on objects or stimuli that belong to a figure's foreground or that occupy some sort of closed figural region. Our data indicate that these may be fundamental perceptual processes across primates that evolved earlier than the evolutionary split roughly 35 million years ago between the species tested in this study (Schrago & Russo, 2003). Similarities in processing of the warping-based illusion further support continuity in critical Gestalt principles of organization, particularly those relevant to figure-ground organization. Accordingly, the weakest evidence of the warping effect among adults in the Vickery and Chun (2010) article came from trials with arguably the lowest grouping, reflecting the importance of structure and objecthood.

It is possible that preference for the contained stimuli (those in the rectangles) supports just that – a preference for these stimuli rather than a true overestimation; however, the enhanced discrimination performance in the congruent trials relative to baseline by the monkeys suggests a true overestimation in distance, akin to human performance. Additionally, performance on incongruent trials also shows that monkeys still chose pairs of dots without an inducer on the majority of trials when that was the correct choice, even if this overall performance level was lower than in the other conditions. Lastly, monkeys' reinforcement history on baseline trials (wherein they performed better when there were no rectangles on screen) would suggest that monkeys would prefer non-contained stimuli, but we did not find that to be the case. That said, it remains to be determined whether the presence of inducers alone in this type of task leads to biases that may not specifically manifest in the illusory experience of smaller distances between items in an array. A future replication of our study could address this question by introducing two training conditions, one wherein the correct response is the dot array with the greater distance between them, and another wherein the correct response is the dot array with the smaller distance, and then assessing performance as we did here. If all subjects show a bias towards and perform better on trials where the correct answer is the array with a larger distance, then object-based warping is the likely cause. If the patterns of performance seen here were a product of the training process artificially increasing the salience of the dot array with the greater distance, than animals trained to select the array with the smaller distance would show the opposite patterns.

We also could not give the monkeys a method of adjustment procedure as Vickery and Chun (2010) did, and so this is a noteworthy difference in methodological approaches across the studies. Despite the fact that the monkeys' testing systems did not allow them to control and adjust the distance between dots via continuous adjustment, there could be potential ways to test the other conditions that Vickery and Chun (2010) used such as presenting an object occluder, an illusory-object condition, and a same/different object condition. Testing systems that allow touch-and-drag manipulation, such as touchscreen computers, may be a way to provide these tests to nonhuman participants. Built into these, or into the control/probe paradigm of our study, could be manipulations of the strength of both the background (e.g., containing distractor stimuli or a repeating visual pattern) and objects (e.g., changing their opacity or introducing a clear visual border).

An additional limitation to acknowledge in this study is that many capuchin monkeys did not reach the formal test phase. The cause of this for roughly half of these subjects was a refusal to participate in testing, and for the other half the issue was an extreme bias to choose either the left or right stimulus on all trials. This suggests that the discrimination of the distance between dots may not be an easy one to learn potentially resulting in a lack of motivation for testing, though the reverse relationship could also be true, that the lack of motivation for the task caused difficulty for learning. Of course, other factors may affect how productive these monkeys are, as they are not restrained for testing, are fed full daily diets whether they perform tasks or not, and thus can control which tasks they choose to perform and how well they attend to those tasks. Additionally, the larger social groups that the capuchin monkeys live in sometimes result in social pressure to either separate for testing to get away from dominant animals, or to avoid separation because of social instability or intimidation. A necessary consequence of this is that some tasks may not be considered sufficiently motivating for the monkeys to engage.

Lastly, future studies may extend this illusion to other animal species in addition to primates and to assess the developmental emergence of warping in our species as well. The monkeys in the current study and the human participants in Vickery and Chun's study were adults. Research has shown that children sometimes perceive the same visual illusions as adults (e.g., Innes-Brown et al., 2011; McKeon et al., 2022; Over, 1967; Piaget et al., 1960), but they sometimes do not (e.g., Coren & Porac, 1978; Doherty et al., 2010; Káldy & Kovács, 2016; Leibowitz & Gwozdecki, 1967). With regards to development of Gestalt principles relevant to object-based warping, several phenomena appear to emerge early in infanthood, such as a global-to-local precedence, configural superiority, and subjective contours (Ghim, 1990; Ghim & Elmas, 1988; Quinn & Eimas, 1986), whereas others critical to configural perception develop across childhood (e.g., Quinn et al., 2002; Spelke et al., 1993). Recent work on the Solitaire illusion supports age-related differences in the development of Gestalt mechanisms that may be relevant to the current investigation (Parrish et al., 2016). The Solitaire illusion is a numerosity illusion in which clustered items within a multi-item set are perceived as more numerous than an equal number of items dispersed on the periphery. Older children more consistently perceived the Solitaire illusion as compared to younger children, suggesting that susceptibility to grouping cues, such as the laws of proximity, continuity, and good form, increase across childhood (Parrish et al., 2016). Akin to young children, rhesus monkeys and capuchin monkeys showed evidence of illusory susceptibility but demonstrated individual differences in the perception and strength of the Solitaire illusion and how consistently it emerged (Agrillo et al., 2014; Parrish et al., 2016). An examination of how children perceive object-based warping could grant us even more insight into just how our perceptual processes develop, and how they affect our adult perception of the world.

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Conflict of Interest Statement: We have no known conflicts of interest to disclose.

Transparency and Openness Statement: Some aspects of this study were preregistered with the Open Science Framework (OSF) in July 2021 under the CC-By Attribution 4.0 International License (McKeon et al., 2021). That preregistration can be found at https://doi.org/10.17605/OSF.IO/3T56V. See Methods section for additional details. We report how we determined our sample size, all data exclusions (if any), all manipulations, and all measures in the study.

Data Availability: Raw data from this study are here: https://doi.org/10.17605/OSF.IO/3T56V

Author Contributions: Conceptualization – JWM, AEP, MJB; Methodology – MJB; Software – MJB; Formal analysis – JWM, AEP, MJB; Investigation – JWM, MJB; Resources – MJB; Data Curation – JWM, MJB; Writing – Original Draft – AEP, JWM; Writing – Review & Editing – AEP, MJB; Visualization – JWM, MJB; Supervision – MJB; Project administration – MJB; Funding acquisition – MJB

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