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# 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*)

Audrey E. Parrish, Sarah F. Brosnan, and Michael J. Beran
Georgia State University

Studying visual illusions is critical to understanding typical visual perception. We investigated whether rhesus monkeys (*Macaca mulatta*) and capuchin monkeys (*Cebus apella*) perceived the Delboeuf illusion in a similar manner as human adults (*Homo sapiens*). To test this, in Experiment 1, we presented monkeys and humans with a relative discrimination task that required subjects to choose the larger of 2 central dots that were sometimes encircled by concentric rings. As predicted, humans demonstrated evidence of the Delboeuf illusion, overestimating central dots when small rings surrounded them and underestimating the size of central dots when large rings surrounded them. However, monkeys did not show evidence of the illusion. To rule out an alternate explanation, in Experiment 2, we presented all species with an absolute classification task that required them to classify a central dot as "small" or "large." We presented a range of ring sizes to determine whether the Delboeuf illusion would occur for any dot-to-ring ratios. Here, we found evidence of the Delboeuf illusion in all 3 species. Humans and monkeys underestimated central dot size to a progressively greater degree with progressively larger rings. The Delboeuf illusion now has been extended to include capuchin monkeys and rhesus monkeys, and through such comparative investigations we can better evaluate hypotheses regarding illusion perception among nonhuman animals.

*Keywords:* visual illusions, Delboeuf illusion, capuchin monkeys, rhesus monkeys, perceptual processing mode

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Although understanding how perceptual mechanisms rapidly and accurately process sensory information is important, it is also informative to understand when and why perception "fails." Such failures can reveal clues about how the perceptual system operates because those failures illustrate how perception interacts (correctly or incorrectly) with physical stimulation and sensory input. Studying misperception often involves studying susceptibility to illusions, and much of this work has been conducted from a comparative perspective, because in that way we can better understand the evolution of human perception. Comparative studies have revealed similarities and differences in "misperceptions" or visual illusions across primates, including the Horizontal-Vertical illusion (Dominguez, 1954), the Zöllner illusion (Agrillo, Parrish, & Beran, 2014; Benhar & Samuel, 1982), the Ponzo illusion (Bayne & Davis, 1983; Fujita, 1996, 1997, 2001), the Mueller-Lyer illusion (Suganuma, Pessoa, Monge-Fuentes, Castro, & Tavares, 2007), the Duncker illusion (Zivotofsky, Goldberg, & Powell, 2005), the rectangle illusion (Dominguez, 1954; Harris, 1968), the corridor illusion (Barbet & Fagot, 2002; Imura, Tomonaga, & Yagi, 2008), and the Delboeuf illusion (Parrish & Beran, 2014).

Despite some continuity in perceptual illusions across species, differences in the perception of other visual illusions across primates have emerged as well. A notable example is the well-known Ebbinghaus-Titchener illusion (see Figure 1), which is one of the most widely studied and robust size illusions among humans (e.g., Aglioti, DeSouza, & Goodale, 1995; Coren & Enns, 1993; Ebbinghaus, 1902; Massaro & Anderson, 1971; Weintraub, 1979). In this illusion, the sizes of two identical central dots are misperceived as a function of several surrounding circles. If small circles surround the central dot, the dot is overestimated relative to the same-sized central dot surrounded by several large circles. Of interest to the authors, baboons do not perceive this illusion as humans do (Parron & Fagot, 2007) despite positive evidence of other visual illusions in this species (e.g., Barbet & Fagot, 2002; Benhar & Samuel, 1982). When presented with the Ebbinghaus-Titchener illusion, baboons instead accurately discriminated central dot size even in the presence of the outer illusory circles,

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Audrey E. Parrish, Department of Psychology and Language Research Center, Georgia State University; Sarah F. Brosnan, Department of Psychology, Department of Philosophy, Neuroscience Institute, and Language Research Center, Georgia State University; Michael J. Beran, Department of Psychology and Language Research Center, Georgia State University.

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Correspondence concerning this article should be addressed to Audrey E. Parrish, Department of Psychology and Language Research Center, Georgia State University, P.O. Box 5010, Atlanta, GA 30302. E-mail: audrey.parrish1@gmail.com

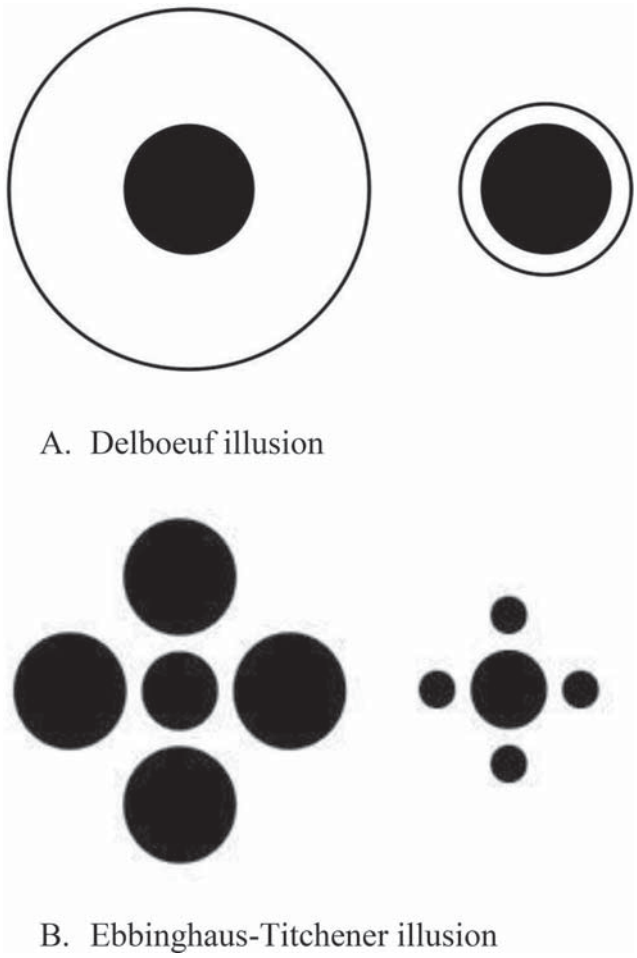



*Figure 1.* The Delboeuf (A) and Ebbinghaus-Titchener (B) illusions, both depicting identically sized central dots surrounded by differently sized inducers. The size of the central dot surrounded by a small inducer(s) (at right; ring: Delboeuf illusion or circles: Ebbinghaus-Titchener illusion) is typically overestimated relative to an identical dot surrounded by a large inducer (at left).

leading Parron and Fagot (2007) to argue that perhaps the neural substrate necessary for perceiving this illusion was lacking among Old World monkeys, instead evolving late in the primate lineage. This hypothesis was supported by a reversed Ebbinghaus-Titchener illusion documented in pigeons (*Columba livia*; Nakamura, Watanabe, & Fujita, 2008) and adult bantam chickens (*Gallus gallus domesticus*; Nakamura, Watanabe, & Fujita, 2014). However, complicating the question, various nonprimate species have since shown evidence of perceiving the Ebbinghaus-Titchener illusion as humans do, including a dolphin (*Tursiops truncatus*; Murayama, Usui, Takeda, Kato, & Maejima, 2012), domestic chicks (*Gallus gallus domesticus*; Rosa Salva, Rugani, Cavazzana, Regolin, & Vallortigara, 2013), and redtail splitfin fish (*Xenotoca eiseni*; Sovrano, Albertazzi, & Rosa Salva, 2015).

Similar to the Ebbinghaus-Titchener illusion, the Delboeuf illusion presents two identically sized central dots that are surrounded by either a small outer ring or large outer ring (rather than multiple circles; Figure 1). Dots encircled by a large ring are underestimated in terms of their size, whereas dots encircled by a small ring are overestimated. This illusion has been studied extensively in human perception (e.g., Coren & Girgus, 1978; Delboeuf, 1892; Nicolas, 1995; Van Ittersum & Wansink, 2012; Ward & Lockhead, 1970). Despite the breadth of research with human participants on these highly similar size illusions and the comparative studies investigating the Ebbinghaus-Titchener illusion in animal species, only one study has presented the Delboeuf illusion to an animal species (Parrish & Beran, 2014). In a food-choice task, chimpanzees were presented with two circular food items (to mimic central dots) from which they could choose one for consumption. Food sizes were misperceived on the basis of outer plate size (that mimicked outer rings), with chimpanzees choosing a smaller amount of food on a small plate relative to a larger amount of food on a large plate. Similar results in humans also have been reported in food choice and consumption contexts (e.g., Van Ittersum & Wansink, 2012).

The perception of the very similar Delboeuf illusion, but not the Ebbinghaus-Titchener illusion, within closely related primate species warrants additional research. Beyond documenting the perception (or not) of an additional illusion among monkey species, understanding when this illusion is most likely to occur among different primate species is essential to establishing the mechanisms that underlie size illusions of this nature. Here, we assessed the Delboeuf illusion in two additional nonhuman primate species, the rhesus macaque and the capuchin monkey. We were interested in whether monkey species also might perceive this illusion in the way great apes and humans do, or if instead they might show patterns similar to Parron and Fagot's (2007) investigation of the highly similar Ebbinghaus-Titchener illusion with a monkey species (baboons).

In Experiment 1, we presented the monkeys with a relative discrimination task in which they were trained to choose the larger of two central dots that were sometimes surrounded by the illusory-inducing Delboeuf rings. This approach matched that of Parron and Fagot's (2007) study examining the Ebbinghaus-Titchener illusion, which used a 2-choice discrimination procedure. To more fully investigate why the illusion was absent in Experiment 1, we then investigated the mechanisms underlying the Delboeuf illusion in Experiment 2. This was done by varying the ratio of the target dot diameter to concentric ring diameter to establish a range of diameter ratios at which the illusion was most likely to emerge. Here, we introduced an absolute classification task (instead of a relative discrimination) in which participants classified a central dot as "small" or "large" relative to a never presented central target size. We included rings of variable size in an effort to induce illusions of dot size perception. We presented both experiments to human participants to confirm our approach and to provide a comparison for the nonhuman primate species.

We predicted that size-judgment performance would be impacted by outer ring size for both experiments for all species. For Experiment 1, we predicted that all species would perceive the Delboeuf illusion, preferring the central dot encircled by the small ring relative to the same-sized central dot encircled by a large ring. For Experiment 2, we predicted that the larger concentric rings (target dot-to-ring ratios $< .50$) would lead participants to overclassify central dots as small as they should appear smaller in the large context. Alternatively, we predicted that the smaller concentric rings (target dot-to-ring ratios $> .50$) would lead participants

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to underclassify central dots as small as they should appear larger in the small context.

## Experiment 1

### Method

**Participants.**

***Nonhuman primates.*** The nonhuman primates included in all experiments were housed and tested at the Language Research Center (LRC) of Georgia State University (GSU) in Atlanta, GA. LRC primates are never food or water deprived for testing purposes and have 24-hr access to water, including during test sessions. They receive a daily diet of fruits, vegetables, and primate chow regardless of participation in testing, and caloric intake is kept consistent by taking into account the amount of food earned from testing when determining the diet. All testing complied with guidelines for working with nonhuman primates as established by protocols approved by the GSU Institutional Animal Care and Use Committee. GSU is accredited by the Association for Assessment and Accreditation of Laboratory Animal Care.

Seven adult rhesus macaques (all males) and 13 adult capuchin monkeys (7 females) were included in the following experiments. Rhesus monkeys are individually housed and have 24-hr access to a computerized testing apparatus within their home cage. Rhesus monkeys have constant visual and auditory access to conspecifics and receive weekly access to an indoor–outdoor enclosure with another monkey. Capuchin monkeys are group housed in indoor–outdoor enclosures, and they separate voluntarily into individual testing enclosures for computerized testing (with visual and auditory access to conspecifics). Monkeys have participated in several computerized perceptual discrimination tasks (e.g., Agrillo et al., 2014; Beran, 2006; Beran & Parrish, 2013; Beran, Smith, Coutinho, Couchman, & Boomer, 2009).

***Humans.*** Twenty-two human participants were recruited from GSU's undergraduate student body (average age: 21 years old ± 4, 12 females). Participants were required to give informed consent before participating in the experiment(s) and received course credit for their participation. Testing complied with the procedures and protocols that were approved by the Institutional Review Board.

**Apparatus.**

***Nonhuman primates.*** Nonhuman primates included in this study were joystick trained for computerized testing using the LRC's Computerized Test System, consisting of a color monitor, personal computer, digital joystick, and food pellet dispenser (Evans, Beran, Chan, Klein, & Menzel, 2008; Richardson, Washburn, Hopkins, Savage-Rumbaugh, & Rumbaugh, 1990). Primates manipulated the joystick with their hands to isomorphically control a small round cursor on the computer screen. Monkeys were not restrained during testing; thus, the viewing distance from the monitor was ~30.5 cm to 40.5 cm. Correct responses led to banana-flavored pellet rewards (45-mg pellets for capuchins and 94-mg pellets for rhesus monkeys; Bio-Serv, Frenchtown, NJ) via a pellet dispenser interfaced to the computer through a digital I/O board (PDISO8A; Keithley Instruments, Cleveland, OH). Programs were written in Visual Basic 6.0.

***Humans.*** Human participants were tested at individual computer carrels with a personal computer, a digital monitor, and mouse for testing. They were not given food rewards but were given written feedback on the computer screen regarding the accuracy of their responses.

**Stimuli.** On all trials, the stimuli, including dots and (when present) concentric rings, were black, presented on a white background, to minimize enhanced attention to one of these array elements over the other. For testing, one central target size was established and was present on every trial (standard target = 3 cm in diameter; designated as Level 7). Using a psychophysical step procedure, a range of 13 possible target dots to be compared with the Level 7 dot was established. Levels 1–6 were all smaller than the Level 7 dot, and their size was generated by the following equation: $\text{Level} = 3^{*}0.98^{(7\text{-TrialLevel})}$. This made Level 1 dots the easiest to discriminate from Level 7 and Level 6 dots the hardest to discriminate. Levels 8–13 were all larger than the Level 7 dot, and their size was generated by the following equation: $\text{Level} = 3^{*}1.02^{(\text{TrialLevel-7})}$. This made Level 13 dots the easiest to discriminate from Level 7 and Level 8 dots the hardest to discriminate. When they were present, small or large concentric rings encircled the target dots. On those trials, both dots were encircled by an outer ring or both dots had no ring. There were never trials in which only one dot had a ring. A small ring was 4.5 cm in diameter for all target dots, and thus, the Level 7 dot comprised 67% of the small ring, and a large ring diameter was 9 cm in diameter and the Level 7 dot comprised 33% of the large ring.

**Design and procedure.**

***Nonhuman primates.*** On each trial, participants made a relative size judgment between two target dots of variable diameter. Each trial presented the standard target dot (Level 7) versus a randomly selected dot from the range of Level 1 to Level 13. At the outset of each trial, participants moved a small round cursor that they controlled into contact with a gray button at the top center of the computer screen. Then, that button disappeared, the cursor recentered, and two stimuli appeared as choice options. Each stimulus was comprised of a target dot. In some conditions, a ring surrounded the dot. These stimuli were simultaneously presented (left- and right-justified at center of the screen, with the larger dot size randomized for one of these two locations on each trial). Participants were required to contact one of the two stimuli within 3 s, or the trial was scored as an error. After selection of a stimulus or after 3 s of inactivity, the screen was cleared completely. Selection of the stimulus that was the larger of the two dots led to a melodic chime and a pellet reward. Selection of the smaller of the two dots led to a buzz tone and a 20-s timeout period during which the screen remained blank. The intertrial interval was 1 s. Monkeys worked on the task between 2- and 4-hr per day, completing as many trials as possible within a testing session given their motivation to engage the task.

There were six conditions. Trials in the Baseline condition presented two differently sized target dots on each trial with no concentric rings, and this established the baseline performance rate in discriminating dot sizes when concentric rings could not make any impact on the perception of the dot sizes. Trials in the Large Control condition also presented two differently sized target dots, but large rings surrounded each dot. Trials in the Small Control condition presented two differently sized target dots, but small rings surrounded each dot. These two conditions were considered control conditions because they presented an objectively larger dot to choose from in a nonillusory inducing context (i.e., identically sized rings).

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Trials in the Congruent Test condition presented the smaller of the two dots surrounded by a small ring and the larger dot surrounded by a large ring. If the Delboeuf illusion occurred, these Congruent Test trials should have led to a decrease in performance by leading participants to overestimate the small dot (because it appeared larger in the small ring) and to underestimate the large dot (because it appeared smaller in the large ring). Trials in the Incongruent Test condition presented the smaller of the two dots surrounded by a large ring and the larger dot surrounded by a small ring. If the illusion occurred, the Incongruent Test condition should have led to increased performance relative to baseline as the small dot appeared even smaller than it actually was in the large context, whereas the large dot in the small context appeared even larger than its true size.

Within the Congruent and Incongruent Test conditions, a special kind of test trial could occur that did not occur in the Baseline, Large Control, or Small Control conditions. In this trial type, called the Delboeuf Illusion trial (see Figure 1), the dots were the same size (both Level 7). However, a large concentric ring surrounded one dot and a small concentric ring surrounded the other dot. This array created the context for the standard illusion in which the target surrounded by the large ring should appear to be smaller in size than the same sized target surrounded by the small ring. There was no objectively correct choice as both targets were identical. We subdivided the monkeys into two groups, one of which received no feedback at all for the Delboeuf illusion trials and immediately began the next trial upon completion of this trial type (Gambit, Gonzo, Han, Lily, Logan, Lou, Nala, Nkima, Obi, and Wren). The other group of monkeys were randomly given either positive feedback in the form of a food pellet or immediately sent to the intertrial interval without any timeout on Delboeuf illusion trials (Chewie, Gabe, Gale, Hank, Gretel, Griffin, Liam, Mason, Murph, and Widget).

***Training.*** Monkeys completed a set of training trials to learn the rule of selecting the larger dot in the two-choice discrimination task. This was done using the three easiest absolute levels (Levels 1–3 and Levels 11–13), divided into 50% Baseline trials, 25% Large Control trials, and 25% Small Control trials. The criterion was set to 85% correct over the most recent 60 trials. After monkeys reached criterion, they immediately entered the test phase during that session.

***Testing.*** In the testing phase, we introduced the full continuum of levels (Levels 1–13). Test sessions were divided into 30% Baseline trials, 20% Large Control trials, 20% Small Control trials, 15% Congruent Test trials, and 15% Incongruent Test trials. Delboeuf illusion probe trials (Level 7) were presented only in the Congruent Test and Incongruent Test conditions, and they occurred with equal probability to the other 12 levels. Monkeys completed between 6,000–12,000 test trials depending upon their overall performance. We assessed overall accuracy after 6,000 test trials. If monkeys reached 75% accuracy across all conditions after 6,000 trials, they were finished with the experiment, and all of their data were included in the analyses. Otherwise, they continued in the experiment until they reached the 75% criterion, and we analyzed the last 6,000 test trials from those animals as we considered this mature performance on the task.

***Humans.*** The general procedure was very similar to the monkeys' procedure described above, including the same stimuli and trial levels. Participants first were required to contact a trial-initiation stimulus and then used the computer mouse to select one of the two stimuli. Correct responses led to a flashing stimulus that said "Correct!" in the middle of the screen, whereas incorrect responses led to a flashing stimulus that said "Incorrect" in the middle of the screen. We shortened the timeout period for incorrect trials to 8 s. In accordance with the monkey procedure, Delboeuf Illusion trials were nondifferentially reinforced. Failure to respond within 3 s of stimuli presentation led to an instruction to respond more quickly to the trials. The intertrial interval was 1 s. A testing session was 60 min or until the participant completed 800 test trials. We only used data from those participants who completed at least 600 trials in the task because fewer trials than this would not have allowed for enough trials at each difficulty level for each condition. All participants met this requirement.

Minimal written instructions were provided instead of a training phase to maximize the number of test trials completed per session with each participant. Before starting the experiment, participants read the following text:

> In this experiment, you will choose between two options on the screen, one on the left and one on the right. Please choose the larger of the two black dots. Click the Start button, and then click on one of the two options. You need to make these responses fairly quickly. Correct responses move you right to the next trial. Incorrect responses lead to a short period where the task is frozen. You need to complete 800 trials, so the better you do, the faster you will finish. When you are ready, click on the START button.

## Results

For all analyses, difficulty level was the absolute value of the difference between the trial level (1–13) and Level 7. Thus, Level 6 and Level 8 stimuli, which were the objectively most difficult stimuli to discriminate from the Level 7 stimuli, were recoded as Difficulty 1 trials. Level 5 and Level 9 stimuli were recoded as Difficulty 2, and so on, so that we had a new range of levels - Difficulty 1 (hardest) to Difficulty 6 (easiest) for each condition.

**Nonhuman primates.** Throughout the remaining analyses in the current and following experiments, we removed any trials on which the monkeys timed-out because they did not respond quickly enough. These were extremely infrequent throughout all testing (ranging from 0.57% to 5.62% of trials across all monkeys).

We conducted a mixed-design analysis of variance (ANOVA) to examine the effect of condition (Baseline, Small Control, Large Control, Congruent Test, and Incongruent Test) and absolute difficulty level (1–6) on the selection of the larger central dot with species (capuchin monkeys and rhesus monkeys) as the between-subjects variable. There was a significant main effect of condition, $F(4, 72) = 8.18$, $p < .001$, $\eta_p^2 = .31$, and difficulty level, $F(5, 90) = 610.20$, $p < .001$, $\eta_p^2 = .97$. There was not a significant main effect of species, $F(1, 18) = 1.46$, $p = .24$, $\eta_p^2 = .08$. There was a significant interaction between condition and difficulty level, $F(20, 360) = 2.89$, $p < .001$, $\eta_p^2 = .14$. There was not a significant interaction between condition and species, $F(4, 72) = 0.71$, $p = .59$, $\eta_p^2 = .04$, nor between difficulty level and species, $F(5, 90) = 1.05$, $p = .39$, $\eta_p^2 = .06$, nor was there a three-way interaction, $F(20, 360) = .83$, $p = .68$, $\eta_p^2 = .04$. Figure 2 depicts group-level performance (i.e., selection of the larger central dot) as a function of condition and difficulty level for capuchin monkeys and rhesus monkeys.

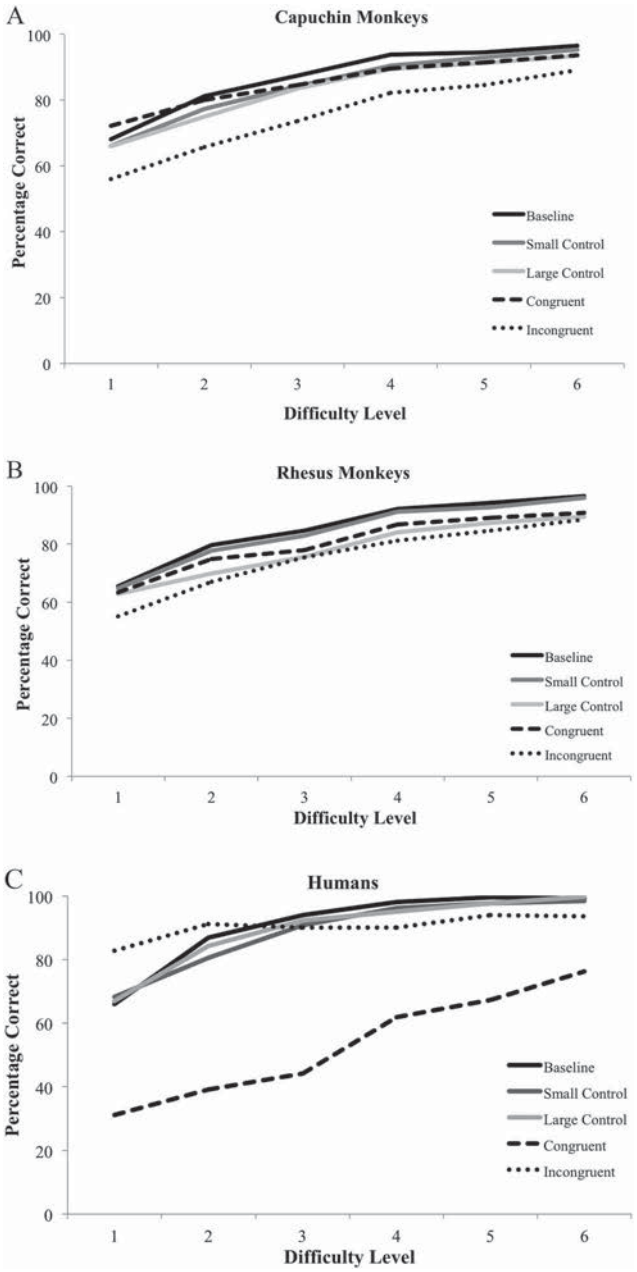



*Figure 2.* Mean percent correct (i.e., selection of the larger central dot) for capuchin monkeys (A), rhesus monkeys (B), and human participants (C) in Experiment 1, including the following conditions: Baseline, Small Control, Large Control, Congruent Test, and Incongruent Test. Absolute difficulty levels progress from 1 (hardest) to 6 (easiest).

Because there was no main effect of species and no interaction of species with either of the other variables, we combined the two species for subsequent analyses. We then used a *t* test to compare performance in selected pairs of conditions with a focus on the test conditions, collapsing across difficulty level using the average mean percentage of correct choices. A Bonferroni adjusted $\alpha$ level of .016 was used per test given the three comparisons of interest (.05/3). Performance in the Baseline condition was significantly higher than the Incongruent Test condition, $t(19) = 4.22$, $p < .001$, but did not differ significantly from the Congruent Test condition, $t(19) = 1.85$, $p = .08$. Performance in the Congruent Test condition did not differ significantly from the Incongruent Test condition, $t(19) = 2.58$, $p = .018$.

For the Delboeuf Illusion probe trials, we conducted a one-sample *t* test to compare selection of the illusory 'larger' dot (i.e., the Level 7 dot surrounded by the small ring) to chance level. Neither species' selection of the illusory dot differed from chance (capuchins: $t(12) = -1.59$, $p = .14$; rhesus monkeys: $t(6) = 0.53$, $p = .62$). We ran individual binomial tests on these data for each monkey, which are provided in the online Appendixes (see Supplemental Materials).

**Humans.** We conducted a within-subjects repeated-measures ANOVA to examine the effect of condition (Baseline, Small Control, Large Control, Congruent Test, and Incongruent Test) and difficulty level (1–6) on the selection of the larger central dot. There was a significant main effect of condition, $F(4, 84) = 45.11$, $p < .001$, $\eta_p^2 = .68$, and difficulty level, $F(5, 105) = 231.54$, $p < .001$, $\eta_p^2 = .92$. There also was a significant interaction between condition and difficulty level, $F(20, 420) = 12.98$, $p < .001$, $\eta_p^2 = .38$. Figure 2 depicts group-level performance as a function of condition and difficulty level for human participants.

We then conducted a *t* test to compare performance in selected pairs of conditions with a focus on the test conditions, collapsing across difficulty level using the average mean percentage of correct choices. A Bonferroni adjusted $\alpha$ level of 0.016 was used per test given that three comparisons were made (.05/3). Performance in the Baseline condition was significantly higher than performance in the Congruent Test condition, $t(21) = 9.21$, $p < .001$, but did not differ significantly from the Incongruent Test condition, $t(21) = .12$, $p = .91$. Performance in the Incongruent Test condition also was significantly higher than the Congruent Test condition $t(21) = -6.07$, $p < .001$). Note that this was the expected pattern of results for illusion perception. These results differed from what was seen with monkeys, in which the Incongruent Test condition did not differ from the Congruent Test condition.

For the Delboeuf Illusion probe trials, we used a one-sample *t* test to compare selection of the illusory larger dot (i.e., the Level 7 dot surrounded by the small ring) to chance level. Human participants selected the illusory dot that was surrounded by the small ring significantly above chance levels, $t(21) = 4.71$, $p < .001$. We also ran individual binomial tests on these data for each participant, which are provided in the online Appendixes (see Supplemental Materials).

## Discussion

Human participants perceived the Delboeuf illusion in the current task, underestimating the size of central dots when large rings surrounded them and overestimating central dots when small rings surrounded them. Further, human performance was disrupted in the Congruent Test condition as expected. Participants overestimated smaller dot sizes (because they appeared larger when surrounded by the small ring) and underestimated larger dot sizes (because they appeared smaller when surrounded by the large ring). Perception of the Delboeuf illusion in the current task matches that of previous reports in the literature for human adults

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(e.g., Coren & Girgus, 1978; Delboeuf, 1892; Nicolas, 1995; Van Ittersum & Wansink, 2012).

Rhesus monkeys and capuchin monkeys successfully learned to choose the larger of two central dots in the relative discrimination task. In Delboeuf Illusion trials, some monkeys ($N = 2$) perceived the illusion in a human-like fashion, selecting the dot surrounded by a small ring as larger at significant rates. However, more monkeys ($N = 6$) appeared to perceive the illusion in a reversed manner whereas the remaining monkeys did not demonstrate a preference at all in this trial type. Further, the monkeys' performances were disrupted in the Incongruent Test trials, but in the opposite manner than was predicted and from that shown by humans (i.e., they selected the small dot encircled by the large ring).

Although these results suggest that monkeys perceived the Delboeuf illusion in a reversed direction from humans, we were concerned that these results were instead driven by a bias toward selecting the dot that was encircled by a large ring. This bias would result in the same findings that we have reported here. Nothing in our training routine had necessarily instructed the monkeys that rings were not relevant to the discrimination (i.e., dots and rings were identical in color and presented equally in training and testing); thus, we were concerned that the monkeys may have approached the task as one in which the rings and dots were to be discriminated as one stimulus. Large rings would generally be more attractive than small rings, a bias that would work against any possible Delboeuf illusion. The design of Experiment 1 may have limited our ability to interpret the resulting response patterns with regard to the Delboeuf illusion. To resolve this problem, and to better assess any possible illusion, we extended our investigation of the Delboeuf illusion to an absolute classification task with a range of ring sizes.

## Experiment 2

Here, we introduced a task in which participants classified a target dot of variable size as either small or large in comparison with a never presented central target size (Level 7). This differed from Experiment 1 in which participants made a relative judgment, selecting the larger of two black dots sometimes encircled by a ring. Now there was only ever one dot present on a given trial, reducing the reliance on a rule such as "choose the larger of two dots and/or rings." As in the former experiment, we presented a condition with no ring. We also presented a condition with a .50 dot diameter to ring diameter ratio. Previous studies have shown that a .50 ratio does not induce an illusion (e.g., Van Ittersum & Wansink, 2012), and this ratio served as an additional baseline beyond the no ring condition in the current study. Other conditions involved rings that could serve to disrupt perceptual processing of the target dot. To avoid the concerns in Experiment 1 that the monkeys might not have understood that the rings were not part of the discrimination, we introduced a continuum of ring sizes. In Experiment 1, the standard dot (Level 7–3 cm in diameter) was presented in a .67 ratio with the small ring (4.5 cm in diameter) and a .33 ratio with the large ring (9 cm in diameter). Here, we introduced eight different dot-to-ring ratios: 0 (no ring), .25, .33, .45, .50, .55, .67, and .75 that were proportional to each individual target dot. We predicted that if the Delboeuf illusion was perceived, then underestimation of dot size would be most likely to occur at lower ratios ($<.50$) as these produced larger rings relative to the target dots. Alternatively, overestimation of dot size would be most likely to occur at higher ratios ($>.50$) as these produced smaller rings relative to the target dots. This manipulation was critical to establishing whether the Delboeuf illusion emerges using a wider range of ratios within nonhumans, and how these ratios compared with the optimal ratio for demonstrating the Delboeuf illusion using this task with humans.

### Method

**Participants.**

***Nonhuman primates.*** The same seven rhesus monkeys were tested. Eleven of the 13 capuchin monkeys from Experiment 1 (excluding Gabe and Widget, who were assigned to other unrelated experimental tasks) participated in the current study.

***Humans.*** Twenty-four new human participants were recruited from GSU's undergraduate student body (average age: 19.41 years old $\pm$ 2.24, 22 females). Participants were tested using the computerized system described in Experiment 1. Again, all participants were required to give informed consent before participating in the experiment and received course credit for their participation. Testing complied with procedures and protocols approved by the GSU Institutional Review Board (IRB).

**Design and procedure.**

***Nonhuman primates.*** Each trial proceeded as described in Experiment 1 (i.e., trial initiation, reinforcement, and intertrial interval) with one major difference. Now, a single target stimulus (a central dot that was sometimes surrounded by a concentric ring) was presented at the top middle of the screen, and participants were required to classify the central dot as small (by moving the cursor to the bottom left of the screen to a blue rectangle) or large (by moving the cursor to the bottom right of the screen to a green rectangle). Testing stimuli included the same 13 levels of dots that were used in Experiment 1. A concentric ring sometimes surrounded the central dot at the top of the screen, and these rings could generate the following target dot to ring ratios: .25, .33, .45, .50, .55, .67, and .75. The baseline conditions were the 0 (no ring) ratio and the .50 ratio. These were used to establish classification performance without the effects of any inducing stimuli (0) or with a nonillusory ring size (.50). All other ring sizes were presented randomly with each of the target dot sizes (Levels 1–13, excluding Level 7). We oversampled the more difficult levels to increase the number of critical test trials presented (44% of test trials presented a randomly selected Level 4 to Level 10 trial whereas the remaining trials randomly sampled from the full range of levels).

***Training.*** Monkeys completed a set of training trials to learn the rule of selecting the appropriate classification icon (small or large) using the three easiest difficulty levels. These were presented in half of the trials in the 0 (no ring) ratio condition and in half of the trials in the .50 ratio. The criterion for passing the training phase was set to 85% correct over the most recent 60 trials, at which point testing immediately began. One capuchin monkey (Gambit) failed to reach training criterion after 6,000 trials, and she was removed from the study.

***Testing.*** Each monkey completed 12,000 testing trials including the following ratios presented in equal proportions: 0, .25, .33, .45, .50, .55, .67, and .75 ratios. Again, we analyzed the last 6,000 test trials as we considered this mature performance on the task.

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***Humans.*** Human participants were tested using the same apparatus as was used in Experiment 1. The same general procedures were presented to humans as were used with the monkeys, including the same absolute judgment task, classifying a central dot as small or large. Participants were presented with as many as 800 trials, and we used data from those participants who completed at least 600 trials in the task. Seven participants failed to complete at least 600 trials, and the data from those participants were not included in the following analyses.

Minimal written instructions were provided instead of a training phase to maximize the number of test trials completed per session with each participant. Before starting the experiment, participants read the following text:

> In this experiment, you will see a black dot at the top center of the screen. Then, you must assign that dot as being either "Small" or "Large" by clicking on one of those two words on the screen. Click the Start button, and then click on one of the two options. You need to make these responses fairly quickly. Correct responses move you right to the next trial. Incorrect responses lead to a short period where the task is frozen. You need to complete 800 trials, so the better you do, the faster you will finish. When you are ready, click on the START button.

## Results

For all analyses, we reduced the number of levels from 13 levels to 6 levels. The new Levels 1–3 included all small dots (Level 1 combined former Levels 1 and 2, Level 2 combined former Levels 3 and 4, Level 3 combined Levels 5 and 6). The new Levels 4–6 included all large dots (Level 4 combined former Levels 8 and 9, Level 5 combined former Levels 10 and 11, Level 6 combined Levels 12 and 13). Thus, Levels 1–6 ranged from the smallest central dots to the largest central dots, with Level 1 (smallest) to Level 6 (largest).

**Nonhuman primates.** Again, we removed any trials on which the monkeys timed-out of a trial because they did not respond quickly enough. These were extremely infrequent throughout all testing in the current experiment (ranging from 0.49% to 4.14% of trials across all monkeys).

We used a mixed-design ANOVA to examine the effect of ratio (0, .25, .33, .45, .50, .55, .67, and .75) and absolute difficulty level (1–6) on the proportion of trials where the participants made a dot classification of small with species (capuchin monkeys and rhesus monkeys) as the between-subjects variable. There was a significant main effect of ratio, $F(7, 105) = 2.71$, $p = .01$, $\eta_p^2 = .15$, difficulty level, $F(5, 75) = 106.63$, $p < .001$, $\eta_p^2 = .88$, and of species, $F(1, 15) = 6.89$, $p = .02$, $\eta_p^2 = .32$. There was a significant interaction between ratio and difficulty level, $F(35, 525) = 4.17$, $p < .001$, $\eta_p^2 = .22$, and between difficulty level and species, $F(5, 75) = 5.62$, $p < .001$, $\eta_p^2 = .27$. There was not a significant interaction between ratio and species $F(7, 105) = .54$, $p = .80$, $\eta_p^2 = .04$. There was a three-way interaction between ratio, level, and species, $F(35, 525) = 1.94$, $p = .001$, $\eta_p^2 = .11$. Figure 3 depicts group-level performance (i.e., selection of the larger central dot) as a function of target dot to ring ratio and difficulty level for capuchin monkeys and rhesus monkeys.

Given the three-way interaction, we conducted separate within-subjects repeated-measures ANOVAs for each species with ratio and difficulty level as within-subjects variables. For capuchin monkeys, there was a significant main effect of ratio, $F(7, 63) = 7.67$, $p < .001$, $\eta_p^2 = .46$ and of difficulty level, $F(5, 45) = 291.93$, $p < .001$, $\eta_p^2 = .97$, and a significant interaction between ratio and difficulty level, $F(35, 315) = 4.12$, $p < .001$, $\eta_p^2 = .31$. For rhesus monkeys, the repeated-measures ANOVA revealed a significant main effect of difficulty level, $F(5, 30) = 13.48$, $p < .001$, $\eta_p^2 = 0.69$, but not of ratio, $F(35, 210) = 2.13$, $p = .75$, $\eta_p^2 = .09$. There was a significant interaction between ratio and difficulty level, $F(35, 210) = 2.13$, $p = .001$, $\eta_p^2 = .26$.

Based on a visual inspection of Figure 3, the clearest examples of deviation from baseline were the .75 and .25 ring ratios. Here,

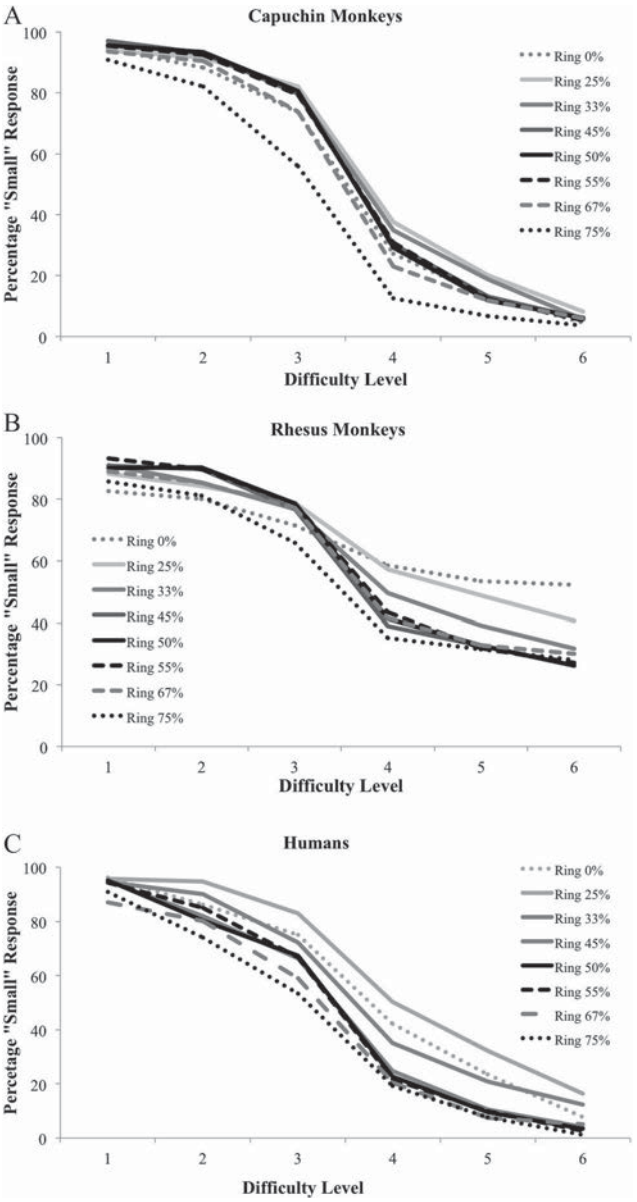



*Figure 3.* Mean percentage of "small" responses for capuchin monkeys (A), rhesus monkeys (B), and human participants (C) in Experiment 2, including the following ratios: 0, .25, .33, .45, .50, .55, .67, and .75. Difficulty levels progress from 1 (smallest dot) to 6 (largest dot).

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and for the human participants, we used the .50 ratio as the baseline to compare against our critical test trials (.25 and .75 ratios) instead of the 0 (no ring) ratio as monkeys and human participants often overclassified the 0 (no ring) ratio as small. Thus, the .50 ring ratio appeared to be a truer reflection of baseline performance given the full distribution of data across all ring ratios. A Bonferroni adjusted α level of .016 was used per test (.05/3). For capuchin monkeys, central dots were classified as small significantly less often in the .75 ratio than in the .50 ratio, $t(9) = 7.18$, $p < .001$ or in the .25 ratio, $t(9) = 3.72$, $p = .005$, but there was not a significant difference between the .25 ratio and .50 ratio, $t(9) = 1.02$, $p = .33$. For rhesus monkeys, performance did not differ significantly for the .50 and .25 ratios, $t(6) = .86$, $p = .42$), for the .50 and .75 ratios, $t(6) = .72$, $p = .50$), nor for the .25 and .75 ratios, $t(6) = 1.06$, $p = .33$). Thus, capuchin monkeys overclassified dots as small when surrounded by large rings as would be expected in a human-like perception of this illusion, but rhesus did not as a group. We also explored individual differences by comparing each animal's performance (percent correct) in the critical test trials (.25 vs. .75 ratios). Individual data are provided in the online Appendixes (see Supplemental Materials).

**Humans.** We conducted a within-subjects ANOVA to examine the effect of target dot to ring ratio (0, .25, .33, .45, .50, .55, .67, and .75) and absolute difficulty level (1–6) on the proportion of trials where the participants made a dot classification of small. There was a significant main effect of ring ratio, $F(7, 112) = 9.19$, $p < .001$, $\eta_p^2 = .37$, and difficulty level, $F(5, 80) = 351.07$, $p < .001$, $\eta_p^2 = .97$. There was a significant interaction between ring ratio and difficulty level, $F(35, 560) = 2.26$, $p < .001$, $\eta_p^2 = .12$. Figure 3 depicts group-level performance as a function of condition and difficulty level for human participants.

Collapsing across levels using the average mean percentage of small choices, we used a paired-samples *t* test to compare the .50 ratio to the .25 ratio and .75 ratio. We also compared the .25 ratio to the .75 ratio. Finally, we compared the .75 and .67 ratios and the .25 and .33 ratios to establish whether there was an 'optimal' ratio at which under- or overestimation occurred as has been reported in the previous literature (e.g., Nicolas, 1995; Ogasawara, 1952; Piaget et al., 1942; Van Ittersum & Wansink, 2012). A Bonferroni adjusted α level of .01 was used per test (.05/5). Central dots were classified as small significantly more in the .25 ratio than in the .33 ratio, $t(16) = 4.66$, $p < .001$, and in the .50 ratio, $t(16) = 5.35$, $p < .001$, and in the .75 ratio, $t(16) = 5.02$, $p < .001$. Performance did not differ significantly for the .50 and .75 ratios, $t(16) = -1.73$, $p = .10$, nor for the .67 and .75 ratios, $t(16) = -1.14$, $p = .27$. Data for individual participants are provided in the online Appendixes (see Supplemental Materials).

## Discussion

As expected, the presence of smaller rings led to overestimation of dot size and larger rings led to underestimation of dot size for human participants. Ultimately, the .25 ratio led to the highest cases of underestimation in the present experiment, and did so significantly more often than the .33 ratio. Although previous studies reported that a ratio close to .33 led to maximal underestimation and a ratio close to .67 led to maximal overestimation of the central dot (e.g., Nicolas, 1995; Ogasawara, 1952; Piaget et al., 1942; Van Ittersum & Wansink, 2012), we did not find evidence of these as optimal ratios in the current experiment. Rather, the even more extreme ratios produced even greater evidence of the illusion.

Capuchin monkeys and some rhesus monkeys showed very similar performance patterns to the human participants, overestimating dots encircled by a small ring (.75 ratio) and underestimating dots encircled by a large ring (.25 ratio). The ratios of .25 and .75 appeared to be most effective for monkeys and humans, although there may be other ratios leading to a stronger illusion if the range were extended beyond the ratios presented here. An increased number of individual monkeys (14 of 17) perceived the illusion in Experiment 2 compared with Experiment 1 (2 of 19; see Supplemental Materials). We did find evidence of a reversed illusion among three monkeys, but this was much less common than in Experiment 1 (where 6 monkeys showed evidence of the reversed illusion). This difference in results between Experiment 1 and Experiment 2 suggested that the classification task assisted in isolating the central dot, reducing the possible reliance that the monkeys had on using the outer ring to help guide choice behavior in the first experiment. The results from Experiment 2 suggest that two nonhuman primate species other than chimpanzees (Parrish & Beran, 2014) perceive the Delboeuf illusion in a human-like fashion when tested using an absolute classification task.

## General Discussion

Humans and both species of monkeys were proficient in the current set of size-judgment experiments, successfully choosing the larger of two central dots in the relative discrimination task (Experiment 1) and the absolute classification task (Experiment 2). The introduction of Delboeuf rings impacted perception of central dot size to varying degrees. In Experiment 1, humans demonstrated evidence of the illusion, choosing the dot surrounded by the small ring as larger than the same-sized dot in the larger ring. The monkeys did not show the same evidence of this illusion in Experiment 1. Rather, several of the monkeys revealed a pattern indicative of a potential reversed illusion (i.e., they preferred a dot in a *large* ring relative to an identical dot in a small ring).

Following Experiment 1, we were concerned that the monkeys may have had a bias to choose the larger of two stimuli when incorporating both dot size *and* ring size into the discrimination when differently sized rings were presented. This bias would conflict with the task demand to select only on the basis of target dot size. This large-ring bias could account for the current pattern of results, leading to a potential misidentification of a reversed Delboeuf illusion among monkey species. In Experiment 1, we presented stimuli (central dots and concentric rings) that were identical in their presentation (black on a white background). Further, we used a training procedure that presented dots and rings at equal rates to minimize enhanced attention toward either of these elements within the illusory array. This approach differed from similar illusion studies with animals using the Ebbinghaus-Titchener illusion that presented target and inducer features with different colors, or purposefully trained the animals to ignore the illusory-inducing stimuli (e.g., Nakamura et al., 2008, 2014; Parron & Fagot, 2007).

We chose our approach in Experiment 1 because there was sufficient evidence that differential attention to various elements within an array leads to differences in the perception and magni-

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tude of many geometric illusions within humans, even leading to their complete elimination or reversal (e.g., Coren & Girgus, 1972; Ebert & Pollack, 1972, 1973; Girgus et al., 1972; Martin, 1979; Massaro & Anderson, 1971; Weintraub & Cooper, 1972; Yamazaki, Otsuka, Kanazawa, & Yamaguchi, 2010). Further, positive comparative evidence for the Ebbinghaus-Titchener illusion has been cited in tasks that do not isolate the different features of the visual array during training or testing (e.g., Murayama et al., 2012; Rosa Salva et al., 2013; Sovrano et al., 2015). Thus, we deliberately did not enhance attention toward the central dot to avoid inadvertently reducing the natural emergence of the Delboeuf illusion. However, our training paradigm and the results of Experiment 1 suggested that the monkeys may have inappropriately incorporated rings into their size judgments of central dots because we did not visually differentiate the feature of interest (dot or ring). This could have led to a reversed illusion.

In Experiment 2, we used an absolute classification task to eliminate this concern. In the classification task, the monkeys no longer could choose on the basis of a stimulus with a relatively larger ring, but instead had to learn to classify dot sizes surrounded by a continuum of outer ring sizes when only the target dot mattered to determining the correct classification. Human participants overestimated dot sizes surrounded by smaller rings and underestimated dot sizes surrounded by larger rings—this is the traditional illusion. We also found positive evidence of the illusion in capuchin monkeys at the group level and at the individual level for most capuchin and rhesus monkeys. These positive results matched evidence of the Delboeuf illusion in chimpanzees (Parrish & Beran, 2014) and of other geometric illusions among capuchin monkeys and rhesus monkeys (e.g., Agrillo, Parrish, & Beran, 2014; Bayne & Davis, 1983; Fujita, 1996; Suganuma et al., 2007; Zivotofsky et al., 2005).

Illusions rely on the simultaneous processing of multiple parts of a visual array. Humans with an increased global or holistic perceptual mode of processing demonstrate greater degrees of perceiving illusions (e.g., Berry, 1968, 1971; Dawson, 1967; Witkin, 1967), whereas humans who are more locally oriented failed to perceive illusions as readily (e.g., Dakin & Frith, 2005; de Fockert, Davidoff, Fagot, Parron, & Goldstein, 2007; Happé, 1996; Happé, Briskman, & Frith, 2001). Of interest to the current study, comparative evidence supports a more locally oriented processing style for capuchin monkeys (De Lillo, Spinozzi, Truppa, & Naylor, 2005; Spinozzi, De Lillo, & Salvi, 2006; Spinozzi, De Lillo, & Truppa, 2003) and rhesus monkeys (Hopkins & Washburn, 2002, but see Tanaka & Fujita, 2000; Tanaka, Onoe, Tsukada, & Fujita, 2001). Processing style plays a large role in the emergence of geometric illusions, but the methodology used to elicit these illusions can favor one style of processing over the other. Critically, using procedures that do not isolate or enhance attention to different elements may be an important feature for illusion emergence, especially among species that are more locally oriented (see Rosa Salva et al., 2013, for more discussion). Of course, therein lies the challenge of instructing nonverbal species to attend to one specific element of interest in a complex multielement array, especially if that one element is not visually differentiated from the other(s). This can inadvertently lead to a different, but equally challenging problem that we encountered in the first experiment, in which monkeys might have incorporated the inducer into their size judgment. The absolute classification task that we used in Experiment 2 allowed us to overcome these concerns, but this cannot eliminate these concerns completely.

Studies presenting the Delboeuf illusion (and other size illusions) to additional nonhuman species will be needed for establishing when, why, and for whom these illusions emerge and the mechanisms that lead to their emergence. Through the current and related investigations, we can begin to disentangle competing hypotheses of illusion perception among nonhuman animals, and the complementary roles that methodology and perceptual processing mode play.

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