DO BUDGERIGARS (*MELOPSITTACUS UNDULATUS*) PERCEIVE THE DELBOEUF ILLUSION?: A PRELIMINARY STUDY WITH A SIMULTANEOUS DISCRIMINATION TASK

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The present study investigated how budgerigars and humans perceive a version of the Delboeuf illusion. In Experiment 1, we trained 4 budgerigars to discriminate between the sizes of two square targets, one of which was embedded in a concentric square frame. The birds accurately differentiated between the sizes of the targets when the target size disparity was large; however, when this disparity was small, they tended to choose the target embedded in the frame. Experiment 2 used the same stimuli and task as Experiment 1 but the participants were humans; the results suggested that the human participants perceived a normal Delboeuf illusion. Thus, these results indicate the adequacy of our stimuli and the inadequacy of tasks with two choices in comparative studies of the Delboeuf illusion as the simultaneous presentation of the two illusory figure(s) may cause unexpected choice bias.

Key words: Delboeuf illusion, simultaneous discrimination, budgerigars

Budgerigars (*Melopsittacus undulatus*) are one of the most popular companion animals and are kept in many regions of the world. They attract humans by their colorful feathers and, when reared by them from a young age, also become attached to humans. Furthermore, they are one of the few species who can mimic human speech, prompting researchers to investigate their auditory cognition in both social (e.g., Farabaugh, Brown, & Dooling, 1992; Tu & Dooling, 2012) and non-social contexts (e.g., Hasegawa, Okanoya, Hasegawa, & Seki, 2011; Seki & Dooling, 2015; Spierings & ten Cate, 2016).

Several studies on budgerigars' visual perception have been conducted. For example, Lind and his colleagues analyzed budgerigars' achromatic and chromatic visual systems (Lind & Kelber, 2011) and brightness perception (Lind, Karlsson, & Kelber, 2013; Lind, Sunesson, Mitkus, & Kelber, 2011). Bhagavatula, Claudianos, Ibbotson, and Srinivasan (2011) found that budgerigars perceive optic flow and adjust their flying course accordingly. Haller, Lind, Steinlechner, and Kelber (2014) found that visual motion increases budgerigars' spatial contrast sensitivity. Brown & Dooling (1992, 1993) examined budgerigars' face

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perception. However, no study has as yet examined budgerigar’s basic and static figure perceptions, including length, size, angle, configuration, and perspective.

Geometric illusions powerfully illustrate how much our perceptions are distorted; they offer clues regarding how our visual system triggers such distortions. The Delboeuf illusion (Fig. 1a) is one of the best geometric illusions for analyzing the properties of our visual system because it allows us to inspect both assimilation and contrast effects, which are major concepts for systematically analyzing the phenomenon and mechanism of visual illusions. Simply put, the assimilation and contrast effects are the perceptual phenomena of underestimating and overestimating the differences between two figures, respectively (e.g., Girgus & Coren, 1982; Goto et al., 2007). In the Delboeuf illusion, which typically

Fig. 1. a) Examples of the Delboeuf illusion. The physical size of the three black disks is the same; however, for humans, the left disk looks larger than and the right one looks smaller than the one at the center. b) An example of the stimulus sets used in each trial of this study. Two filled square targets were displayed simultaneously, of which one had a concentric square frame. c) An example of placement of the two square targets in the trial. Two dashed square of 20 × 40 pixels shows the possible center position of the each target. Each position varied from trial to trial.

comprises two concentric circles, humans underestimate the difference in size between the inner stimulus (IS) and the outer stimulus (OS) if the difference is small. In other words, humans overestimate IS size and underestimate OS size. However, if the difference is quite large, humans overestimate the difference between the two sizes, thus underestimating IS size.

Although many studies of the Delboeuf illusion involving humans have focused on how humans perceive this illusion under various conditions (e.g., Cooper & Weintraub, 1970; Goto et al., 2007; Weintraub & Schneck, 1986), few studies regarding this illusion have been conducted with nonhumans. Chimpanzees (Parrish & Beran, 2013), rhesus monkeys, and capuchin monkeys (Parrish, Brosnan, & Beran, 2015) perceive the Delboeuf illusion as humans do; furthermore, although pigeons perceive this illusion as well, their tendency is contrary to that of humans (Hyuga, Kaneko, & Fujita, 2014). Such inconsistency is often observed in comparative studies of geometric illusions such as the Ebbinghaus and the Zöllner illusions (see Fujita, Nakamura, Watanabe, & Ushitani, *in press*). To understand the reason for such contradictory results and determine the factors that affect the perceptual tendencies of various illusory figures in animals, further studies involving other species are required.

This study aims to determine whether budgerigars perceive and display the tendency of the Delboeuf illusion. The results of this study may lead to discoveries about budgerigars' visual system; furthermore, it would also enable us to better understand the welfare of companion animals, such as the dwelling environments of the species that live with humans from birth to death, and how we engage in visual contact with them. In Experiment 1, we used two mini-size concentric squares, instead of circles, in accordance with the budgerigars' size (Fig. 1b). It was because of potential roughness of the graphics of small circles on the monitor, and their micro-configuration of graphic dots may have had any unpredictable effect on the budgerigars' performance. Weintraub and Schneck (1986) found that humans perceive a normal Delboeuf illusion when the OS is a square instead of a circle.

One of the most important points when conducting an experiment regarding the Delboeuf illusion in a nonhuman animal would be to make the animal distinguish between IS and OS. To train our subjects to do this, we used two squares in different colors. Several studies have reported that although the difference in colors and brightness influence the magnitude of illusion in humans, it does not affect the illusory tendency (Weintraub & Cooper, 1972; Weintraub & Schneck, 1986; Morinaga & Kansaku, 1961). Furthermore, by systematically analyzing the effect of color and brightness, we could isolate the effect of brightness-difference from the background as the hue itself does not have an effect (Oyama, 1962). Thus, we used two colors with RGB values of (255, 0, 0) and (0, 255, 0) in Experiment 1.

In this study, we also chose a simultaneous (and relative) discrimination task instead of a successive (and absolute) classification task (e.g., Nakamura, Fujita, Ushitani, & Miyata, 2006; Nakamura, Watanabe, & Fujita, 2008) to generate both absolute and relative clues. Thus, in the training of Experiment 1, we displayed a pair of target squares: one was always smaller and the other was always larger than 36×36 pixels. Several studies also chose the simultaneous discrimination task and succeeded in investigating the perception of geometric illusions in nonhuman animals including baboons (Benhar & Samuel, 1982), dolphins

(Murayama, Usui, Takeda, Kato, & Maejima, 2012), chicks (Rosa Salva, Rugani, Cavazzana, Regolin, & Vallortigara, 2013), and fish (Sovrano, Albertazzi, & Rosa Salva, 2015).

As stated above, we used the stimuli having atypical features for a Delboeuf illusion in Experiment 1. Therefore, in Experiment 2, we asked our human participants to perform the same task as in Experiment 1, using the same stimuli, to determine whether humans perceive the typical Delboeuf illusion and thereby confirm the validity of the stimuli and procedure used in Experiment 1.

EXPERIMENT 1

METHOD

Subjects

The subjects were four adult budgerigars (*Melopsittacus undulatus*) named Hagi (female, 2 yo.), Karatsu (female, 2 yo.), Raku (female, 3 yo.), and Shino (male, 11 mo.). All four birds had previously participated in several behavioral experiments unrelated to the present study. Their body weights were maintained at 85–100% of free-feeding weights throughout the experiment. Each budgerigar was individually housed, with water and grit freely available in each home cage. The cages were placed in a laboratory room with natural sunlight and temperature of $28 \pm 4^\circ\text{C}$. The breeding of the budgerigars and the experiments conducted on them were in accordance with the “Regulations on the implementation of animal experiments in Osaka Kyoiku University” created by Osaka Kyoiku University’s Animal Care and Use Committee, which also approved the experiment.

Apparatus

An operant chamber (24.5 cm $\times$ 14 cm $\times$ 11.5 cm, inside dimension) was used, with its front side (24.5 cm $\times$ 14 cm) open; an LCD color monitor (Iiyama, PL2001) with an infrared-beam camera system touch screen (EIT Co. Ltd, custom-made) was placed in front of this side. A millet-ball magazine dispenser (Okubo Instruments, custom-made) located outside the chamber delivered millet-balls through a tube into a food cup, located at the left rear corner. A food light was placed above the food cup, and a ceiling house light illuminated the operant chamber. The chamber was controlled by a personal computer (CPU: Intel, Core i3-2120 3.30GHz) and the program was written in Microsoft Visual Studio 2012.

Stimuli

The graphic resolution of the monitors was 1600 $\times$ 900 pixels (44.4 $\times$ 25.1 cm), but as the chamber size (24.5 $\times$ 14 cm) was smaller than the monitor, the actual display size was 887 $\times$ 506 pixels. We used three types of stimuli in each trial: red target squares, a green inducing frame, and a blue self-start key on a black background. A frame was 1 pixel thick (measured approximately 0.28 mm on the display) and concentrically surrounded a target. The self-start key was a blue dot with a diameter of 44 pixels (approximately 12.2 mm on the display), but its actual response area was a concentric square of 50 $\times$ 50 pixels (approximately 13.9 mm $\times$ 13.9 mm). In this study, the RGB values for these colors were (255, 0, 0) for red, (0, 255, 0) for green, (0, 0, 255) for blue, and (0, 0, 0) for black.

We defined the Center Point as the point at the approximate center of the display as seen from the chamber and which was easy for our birds to peck. The position of the self-start key was fixed to the Center Point. In each trial, a pair of target squares was displayed to the right and left of the Center Point. To prevent subjects from using any unexpected cue when performing our task, we randomized both horizontal and vertical positions of each target square. The left and right target squares were positioned randomly within a distance of 170–190 pixels to the left and right of the Center Point, making the distance between the two target squares a range of 340–380 pixels, center-to-center (Fig. 1c). We also randomized the vertical position of each stimulus within -20 to $+20$ pixels of the Center Point. Furthermore, as the inducer frame was always concentric to the target, the frame position was also randomized. The birds’ pecks on the targets were detected using two invisible response areas, both of which were also concentric to the target. Although the target and frame size varied from trial to trial, the response area was fixed to a square of 50 $\times$ 50 pixels.

Procedure

The task was to peck at one of the two targets according to the target size. We assigned Hagi and Karatsu to the Small group (the smaller target being the correct one) and Raku and Shino to the Large group (the larger target being the correct one). We quasi-randomly determined whether the left or the right target was larger. Three pecks at the correct target resulted in a millet-ball of a defined proportion being fed (described later) and the feeder light being illuminated. Three pecks at the wrong target were followed by a time-out of 8 s. Pecking at other areas produced no programmed outcome. Intertrial intervals were 2 s. To increase the number of trials per session, we adopted partial reinforcement schedules; correct responses not followed by food were conditionally reinforced by a brief illumination (2 s) of the feeder light. We conducted one training or test session daily, with 5–7 sessions a week.

Phase 1: Preliminary training First, we displayed an 8×8 pixel-sized target square for the Small group and a 28×28 pixel-sized square for the Large group. At first, hand-shaping procedure was used to train the birds to peck at the target; a single peck was continuously reinforced. For each subsequent session, the number of pecks was increased from one to three as required. This phase had no wrong target.

Phase 2: Training without frame This phase comprised four sub phases. First, we displayed a pair of the target squares (8×8 and 28×28 pixels ([8 VS 28] and [28 VS 8]). For this training, 80–100 trials were conducted per session. All four birds' rate of accurate target selection was nearly 100% from the beginning, thus eliminating the need to set any achievement standards. Next, the primary reinforcement (food) probability was gradually lowered from 100% to 40%, and the number of trials per session was increased from 80 to 200. An error on our part led to Hagi proceeding to Phase 3, but for the other three birds, we displayed four target pair patterns: [8 VS 28], [12 VS 24], [24 VS 12], and [28 VS 8]. We then displayed four patterns: [12 VS 24], [16 VS 20], [20 VS 16], and [24 VS 12]. Finally, we displayed six patterns: [12 VS 24], [16 VS 20], [17 VS 19], [19 VS 17], [20 VS 16], and [24 VS 12]. As all three birds showed an accuracy rate of more than 80% at the first session of each step, they proceeded to Phase 3. The accuracy rate of all four birds for [12 VS 24] was more than 95% in this phase.

Phase 3: Training with frame This phase aimed to habituate the birds to the stimulus-set of a target square and its frame and make them perform exactly the same task as before (i.e., choose the smaller/larger square, irrespective of the frame size). In this phase, we displayed two target size patterns: [12 VS 24] and [24 VS 12]. We used frames whose sizes were 1.5, 2, 4, 8, or 10 times the size of the square (Fig. 2). For example, if the left square was 24×24 pixels and had a frame attached to it, the frame was 36, 48, 96, 192, or 240 pixels on a side. For each subsequent session, the frame gradually faded in from black (background color) to green. The primary reinforcement probability was 40%, and each bird conducted 200 trials per session. All birds maintained an accuracy rate of 95% or higher during this phase.

Phase 4: Test We conducted 20 consecutive test sessions involving 196 trials, which randomly appeared as baseline (168 trials) and test (28 trials). The 168 baseline trials were further divided into 84 trials in which a frame was attached to one of the targets ("On-Frame baseline") and 84 trials without a frame ("Off-Frame baseline"). In the On-Frame baseline trials, we displayed two target size patterns ([12 VS 24] and [24 VS 12]) as in Phase 3 and used a frame whose size was 1.5, 4, or 10 times the target square. In the Off-Frame baseline trials, we displayed six target size patterns ([12 VS 24], [16 VS 20], [17 VS 19], [19 VS 17], [20 VS 16], and [24 VS 12]) as in the final of Phase 2. In all sessions, all four birds maintained an accuracy rate of 85% or higher in the baseline trials.

Given that our stimulus presentation was on an LCD monitor, we had to use target squares whose sizes were in multiples of 4 on a side (otherwise a 1-pixel misalignment would occur from the pure concentricity of a target and its frame). Therefore, in the test trials, the target size was either [16 VS 20], [16 VS 16], [20 VS 20], or [16 VS 20], and the frame size was either 0 (no frame), 1.5, 4, or 10 times the size of its encircling square (i.e., there were seven frame patterns: None, L1.5, L4, L10, R1.5, R4, and R10). All 28 patterns (4 target patterns $\times$ 7 frame patterns) were displayed once in each session. In the test trials, the subjects were rewarded (or conditionally rewarded) regardless of the target they pecked.

RESULTS AND DISCUSSION

The two groups showed considerable differences in response tendency. We plotted

Fig. 2. Frames used in Phase 3 of Experiment 1. The filled squares denote the target squares, and the surrounding squares denote the frames. In this experiment, only one of the frames was displayed on each trial, either on the left or right target, and its size was either 1.5, 2, 4, 8, or 10 times its surrounding square. The areas enclosed by the dashed line denote Response Areas. In the experiment, the dashed lines were invisible, and both the right and left targets had Response Areas.

the proportion of responses suggesting that the right target was “larger” as a function of the difference calculated by the size of the left square as compared with the right (Fig. 3). The upper and lower two graphs show the data for Hagi and Karatsu (Small group) and for Shino and Raku (Large group), respectively. The Small group judged the right target as “larger” more frequently when the left square was embedded in a frame than when the right one was. In contrast, the Large group judged the right square as “larger” more frequently when the frame was attached on the right.

At baseline, all birds performed at high accuracy levels, ranging from 90.8% to 94.3%. In four out of eighteen baseline stimulus sets, one target square size was larger than

Fig. 3. The mean percentages of the budgerigars' responses reporting that the right target was larger than the left one. The horizontal axis represents the disparity in size between the two squares ("right" minus "left"). In these graphs, symbols depicted at -4 , 0 , and 4 of the horizontal axis represent the data on test trials and those depicted at -12 and 12 represent the data on the baseline trials. The solid or open symbols and continuous vs. dashed lines represent the square and the surrounding frame (left or right). Circles, triangles, and squares denote the relative size of the surrounding frames: 1.5, 4, or 10 times the surrounded target. The isolated cross marks represent the square without a frame.

the other but smaller than the frame size encircling the other square. For example, the left target of 24 pixels was larger than the right target of 12 pixels but smaller than the R4 frame (48 pixels) and R10 frame (120 pixels) attached to the right target. All the budgerigars continuously chose accurate targets, with an accuracy rate ranging from 96.4% to 100%. Such high accuracy was also maintained in test trials. Their accuracy rate ranged from 97.4% to 99.5% in easy trials (in which the size difference between the two squares was 12) and from 78.9% to 87.5% in difficult trials (in which the difference was 4). Binomial tests indicated that all four birds chose the "accurate" answer even in the difficult test trials despite the fact that they received reinforcements regardless of the target they chose ($ps < .001$). These results strongly suggest that all the birds learned to judge the target square size successfully; however, they did not learn to judge the other stimuli, such as the frame size or relational target size to the frame, and this behavior was maintained throughout

the test sessions.

In the test trials, the birds displayed strong individual differences in their judgment tendency. We conducted a two-way repeated-measures analysis of variance (ANOVA) on the difference between the size of the left square and that of the right ($-4, 0$, or 4) $\times$ the frame condition (None, L1.5, L4, L10, R1.5, R4, and R10) for each subject. Five consecutive sessions were organized into one block; we analyzed four blocks (20 sessions) and entered the percentage of “the right is larger” responses in each condition of each block of the analysis. The main effect of square size differences was highly significant for all subjects (minimum $F(2, 6) = 86.64, p < .001$, for Hagi). The main effect of frame condition (minimum $F(6, 18) = 8.30, p < .001$, for Kara) was also significant for all subjects. However, interaction of the square size difference and frame condition was not significant for Raku ($F(12, 36) = 1.14, p = .36$), although it was significant for the other three (minimum $F(12, 36) = 2.41, p < .05$, for Shino). These results suggest that the frame condition strongly affected the subjects’ response tendencies in the test trials, although the two groups demonstrated opposite tendencies (see Fig. 3).

The results also suggest that the Small group (Hagi and Karatsu) underestimated Delboeuf squares while the Large group (Raku and Shino) overestimated them. The Small group tended to judge that “the right square is larger” more frequently when a frame was attached on the left square than when a frame was attached on the right. However, it is quite unlikely that only the training group critically affected the geometric illusion tendency, in spite of the constancy of the species, the apparatus, the stimulus-set, and the training procedures.

A more reasonable explanation is that the frame that surrounded a target square induced all the subjects to peck it. Based on Fig. 3, it would be difficult to examine the data and determine which target they chose because the Small group showed a high percentage of choosing the left target while the Large group showed a high percentage of choosing the one on the right. Fig. 4 represents the mean ratio of pecking the right target among the four budgerigars. As we conducted an equal number of trials with a larger right or left target, it is reasonable to assume that the ratio of the baseline trials (± 12) converges to 50%. An important point is the choice bias, indicated by the 0 on the horizontal axis: the subjects showed a consistent tendency of choosing the target that was surrounded by a frame. One-way repeated-measures ANOVA found a significant main effect of the frame condition ($F(6, 18) = 14.90, p < .001$). Post hoc paired comparisons with Shaffer’s correction among the seven frames revealed that the ratio for L4 ($p = .004$) and L10 ($p = .016$) was significantly lower than that for R1.5.

Thus, these results suggest that the smaller the size difference between the right and left target, the more the subjects tended to choose the framed square in the test trials. As shown in Fig. 2, the frame was larger and nearer to the center of the display than the targets; therefore, the birds were probably attracted to it. Of course, as the birds had learned to peck the larger/smaller target, irrespective of a frame, they successfully chose the correct target in most of the test trials. However, where the two targets were identical, a frame appearing on either the right or left may have attracted the birds.

Critics may point out the possibility that the stimuli used in Experiment 1 were

Fig. 4. The mean percentages of the budgerigars' choosing the target on the right. The horizontal axis represents the disparity in size between the two squares ("right" minus "left"). Symbols depicted at -4, 0, and 4 of the horizontal axis represent the data on test trials and those depicted at -12 and 12 represent the data on the baseline trials. The solid or open symbols and continuous vs. dashed lines represent the square and the surrounding frame (left or right). Circles, triangles, and squares denote the relative size of the surrounding frames: 1.5, 4, or 10 times the surrounded target. The isolated cross marks represent the square without a frame.

inadequate to analyze the Delboeuf illusion. As described above, our stimuli were unlike the typical Delboeuf-illusion figures: both the targets and encircling frames were square-shaped, instead of circle-shaped, and the color of the frame differed from that of the targets. These unconventional stimuli may not lead animals to perceive a normal Delboeuf illusion. Therefore, in Experiment 2, we replicated Experiment 1 with human participants to confirm the validity of the stimuli used in Experiment 1.

EXPERIMENT 2

METHOD

Participants

Participants in this experiment were seven students (three female and four males) at the Osaka Kyoiku University aged between 19 and 22 years with normal or corrected-to-normal visual acuity. They were unfamiliar with visual illusions and unaware of the experiment's purpose. This experiment was implemented with the approval of Osaka Kyoiku University's Ethical Committee.

Apparatus and Stimuli

The participants placed their heads on a hand-built chin rest in front of an HD+ (1600 × 900 pixels) LCD color monitor (Iiyama, ProLite E2008HDD); one hundred pixels measured about 27.6 mm. A computer keyboard with a numeric keypad was used as a pointing device to replace the touch panel. Tasks were controlled using a personal computer (CPU: Intel, Core i3-2120 3.30GHz) and the program was written in Microsoft Visual Studio 2012.

To match the stimulus sizes for humans approximately with those used for the budgerigars in visual angle, we doubled the sizes and spatial intervals of all the stimuli used in Experiment 1 and set the viewing distance to 20 cm. As in Experiment 1, we used three types of stimuli: red target squares, a green inducing frame, and a blue self-start key on a black background. A frame was 2 pixels thick (measured approximately 0.55 mm on the display) and concentric with a target. A self-start key was a blue dot with a diameter of 44 pixels (approximately 12.1 mm on the display). In this experiment, the RGB values for these colors were (255, 0, 0) for red, (0, 255, 0) for green, (0, 0, 255) for blue, and (0, 0, 0) for black.

We defined the Center Point as the center of the display and the position of the self-start key was fixed to the Center Point. In each trial, a pair of target squares was displayed to the right and left of the Center Point. In conformity with Experiment 1, we randomized both horizontal and vertical positions of target squares. The positions of the left and right target squares were randomized within 340–380 pixels left and right of the Center Point, respectively. Thus, the distance between the two target squares was randomized within 640–740 pixels (approximately 17.7–20.4 cm), center-to-center. Furthermore, we also randomized the vertical position of the stimulus pairs within –40 to +40 pixels of the Center Point.

Procedure

We quasi-randomly determined whether the left or right target was larger. All the responses were entered from the numeric keypad. Each trial began with the self-start key; pressing “5” resulted in the self-start key being replaced with two target squares (and one frame, in some cases). We randomly assigned the seven participants to the Small group ($N = 3$) and the Large group ($N = 4$), as in Experiment 1, and requested the Small group to choose the smaller target and the Large group to choose the larger one. In each trial, the participants chose the left or right target by pressing the “4” or “6” key. No feedback was provided for the choices. Intertrial intervals were 0.5 s. Each participant joined in one session, which comprised 420 trials.

We displayed six target size patterns: [16 VS 56], [32 VS 40], [36 VS 36], [40 VS 40], [40 VS 32], and [56 VS 16]. One of the targets was embedded in a frame whose size was either 0 (no frame), 1.5, 4, or 10 times the size of the target square. In each session, we gave 42 (6 target $\times$ 7 frame) stimulus patterns 10 times in random order (totally 420 trials). We termed the stimulus set in which the right and left target size were equal the “Test set,” and the others were termed the “Baseline set.”

RESULTS AND DISCUSSION

All participants showed high performance for the Baseline set (98.4% on average), thus suggesting that all of them accurately understood and performed the task. For the Test set, considerable differences were observed for the response tendency between the seven frame conditions. Again, we plotted the proportion of responses suggesting that the right target was “larger” as a function of the difference calculated by the size of the left square as compared with the right one (Fig. 5a). A one-way repeated-measures ANOVA for the effect of the frame revealed a main effect of the frame, $F(6, 36) = 11.17, p < .001$. Fig. 5b depicts the simplified data of Fig. 5a and indicates the average ratio of choosing a frame-embedded target. Again, high performance can be seen for the Baseline set. For the Test set, human participants showed a strong bias for judging the target surrounded by the 1.5-fold frame as larger and a bias for judging the target surrounded by the 10-fold frame as smaller, thus indicating overestimation and underestimation of the frame-embedded targets. A repeated-measures ANOVA for the effect of the frame revealed a main effect of the frame, $F(2, 12) = 28.43, p < .001$, and post-hoc paired comparisons with Shaffer’s correction among the three frames revealed the significant differences between all of the pairs ($ps < .01$). These statistical analyses consistently support the interpretation that the humans

Fig. 5. Results of the human participants. a) The mean percentages of responses in which the right target was judged as larger than the left one. The horizontal axis represents the disparity in size between the two squares ("right" minus "left"). The solid or open symbols and continuous vs. dashed lines represent the square and the surrounding frame (left or right). Circles, triangles, and squares denote the relative size of the surrounding frames: 1.5, 4, or 10 times the surrounded target. The isolated cross marks represent the square without a frame. b) The mean percentages of responses indicating that the target surrounded by a frame was judged to be larger than the one without a frame. The horizontal axis represents the disparity in size between the two squares ("with frame" minus "without frame"). Circles, triangles, and squares denote the relative size of the surrounding frames: 1.5, 4, or 10 times the surrounded target.

who participated in our study perceived the normal Delboeuf illusion for the stimuli we had used for birds. Furthermore, it also leads to the conclusion that, as indicated in previous studies (e.g., Oyama, 1962; Morinaga & Kansaku, 1961), the stimuli used in Experiment 1 are suitable for analyzing the perception of the Delboeuf illusion in nonhuman animals.

GENERAL DISCUSSION

This study mainly aimed to examine whether and how budgerigars perceive a version of Delboeuf illusion. Data obtained from Experiment 2 suggest that humans perceive normal Delboeuf illusion in spite of stimuli differing in shapes and colors than standard figures of this illusion. Data obtained from Experiment 1 suggest that the outer frame (OS) attracted the budgerigars' choice, thus suggesting the inadequacy of the forced choice task, which simultaneously displays two stimulus sets for experiments regarding Delboeuf illusion in nonhuman animals. In both experiments, two red square targets and a concentric green square frame on one of the targets were displayed simultaneously. Both the budgerigars and humans were divided into Large and Small groups, where the former had to choose the larger target and the latter the smaller one. In test trials, although the humans showed the tendency of normal Delboeuf illusion, the two groups of budgerigars showed the different tendency of reporting that "the right target is larger as compared to the left."

However, this different tendency of *reporting* may not reflect the different tendency of *perception* between the two groups. In fact, all the subjects showed sufficiently high performance levels in the baseline trials of the test sessions. Even in the test stimulus sets, their performance was in accordance with the tasks' difficulty levels, denying the possibility that the budgerigars performed the task systematically differently only in the test trials. Thus, both budgerigars and humans performed the test trial tasks by following the same rules as those applied during training. All our avian subjects showed the tendency of choosing the frame-surrounded target in the test trials. It seems plausible that in the test trials, especially in conditions of equal sized targets, a frame attracted the birds' attention and influenced their choice behaviors.

The results of Experiment 2 strongly suggest that humans perceive normal Delboeuf illusion with the stimuli used in the two experiments. The results also suggest that a black background does not influence the perception of the Delboeuf illusion.

The results of our study offer two major methodological suggestions for conducting comparative studies of visual illusions. The first is the importance of counterbalancing the subjects. If we had required all our budgerigars to choose the larger or smaller target instead of dividing them into the Large and Small groups, we would have erroneously reached either the conclusion that budgerigars consistently underestimate (top of Fig. 3) IS, irrespective of OS size, or they overestimate it (bottom of Fig. 3).

The second is that the simultaneous discrimination task may be inadequate for examining perceptions of the Delboeuf illusion in nonhuman animals. The results of Experiment 1, obtained by simultaneously displaying two targets, suggest that all four birds were biased toward choosing the target that was surrounded by a concentric frame. Such a frame bias is unavoidable in procedures that present multiple targets simultaneously. Although the bias cannot be considered very strong, as our birds chose the correct target in most of the trials, it was strong enough for them to choose the framed target in cases where there was little or no difference between the sizes of the two targets.

Several previous studies of Delboeuf illusion in nonhuman animals offered further corroboration of the second suggestion. Experiment 1 of Parrish et al. (2015) failed to reveal the tendency of the Delboeuf illusion in capuchin monkeys and rhesus monkeys due to the monkeys' bias toward choosing the target that was surrounded by a larger frame. On the other hand, Experiment 2 of Parrish et al. (2015) and Hyuga et al. (2014) in pigeons used absolute classification tasks in which only one IS (and OS, in some cases) was displayed in each trial and subjects were required to judge the absolute size of the IS, instead of the relative size. The results successfully demonstrated the illusory tendency of monkeys and pigeons.

The study of Parrish and Beran (2013), using the simultaneous discrimination task, also appeared to demonstrate the illusory tendency of chimpanzees: they simultaneously showed their chimpanzees a circular-shaped food (IS) on a larger circular dish (OS) and on a smaller circular dish. The chimpanzees tended to choose the latter more frequently, thus suggesting that chimpanzees perceive a version of the Delboeuf illusion like humans. However, it is near-impossible to rule out the possibility of a small-frame bias in the chimpanzees of their simultaneous discrimination task: the chimpanzees maybe consistently

cued by the smaller dish, the edge of which was nearer to the food than that of the larger dish and maybe more attractive to them. It is possible that chimpanzees perceived the Delboeuf illusion, but ruling out potential non-illusory explanations is indispensable in nonhuman studies. In fact, several studies have reported an opposite tendency of illusionary perception in birds for various illusory figures (Hyuga et al., 2014; Nakamura, et al., 2008; Watanabe, Nakamura, & Fujita, 2011, 2013).

Previous research highlighted the possibility that experimental designs affect the tendency and/or magnitude of geometric illusions in humans (e.g., Guirao, 1991; Goto et al., 2007). Hamada, Nishimura, Paramei, and Ehrenstein (2002) measured the Delboeuf illusion magnitude in humans using the magnitude-estimation method, which also required subjects to judge the absolute size of IS, and reported that not only the ratio between IS and OS but also the absolute size of both influence the perception of the Delboeuf illusion in humans. The same authors argued that the results qualitatively differ from those of previous human studies in which both the Delboeuf figure and control circle (or dot) were displayed simultaneously, and that displaying plural stimulus sets triggers a particular kind of interaction between the sets and does not purely measure the Delboeuf illusion.

In summary, this study demonstrated that square IS and OS, discrepancy of colors between IS and OS, and black background do not affect the perception of the normal Delboeuf illusion in humans. Thus, it appears reasonable to use such stimulus sets in experiments with nonhuman animals. This study has also provided empirical support for the idea that displaying two stimulus sets possibly entails a risk of unexpected problems such as behavioral bias (Parrish et al., 2015) and perceptual interaction between the sets (Hamada et al., 2002). Testing that involves an absolute classification task and the stimulus sets used in this study may enable us to reveal the tendency of the Delboeuf illusion in budgerigars and other animals. Although this study examined the perception of IS, humans are found to underestimate OS when it is close to IS (e.g., Robinson, 1972; Weintraub & Cooper, 1972). The absolute classification task with the stimuli used in this study may help in revealing nonhuman animals' perceptual tendency of OS.

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