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Effects of element separation on perceptual grouping by humans (*Homo sapiens*) and chimpanzees (*Pan troglodytes*): perception of Kanizsa illusory figures

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Abstract The processing of Kanizsa-square illusory figures was studied in two experiments with four humans and two chimpanzees. Subjects of the two species were initially trained to select a Kanizsa-square illusory figure presented in a computerized two-alternative forced choice task. After training, adding narrow closing segments to the pacman inducers that composed the Kanizsa illusory figures lowered performance in both chimpanzees and humans, suggesting that the discrimination could be controlled by the perception of illusory forms. A second experiment assessed transfer of performance with five sets of figures in which the size of the inducers and their separation were manipulated. Only for chimpanzees was performance directly controlled by separation, suggesting that chimpanzees are more sensitive than humans to the separation between visual elements.

Keywords Chimpanzee · Illusory contour · Perceptual grouping · Kanizsa illusion

Introduction

Do chimpanzees perceive and process visual information as we (humans) do? In a recent series of experiments, Fagot and Tomonaga (1999) reported striking differences in the way humans and chimpanzees processed visual information. Fagot and Tomonaga (1999) presented chimpanzees and humans with a visual search task in which they had to detect a target stimulus among a variable number of distractors. Targets and distractors were large geometrical shapes made of small geometrical shapes, and

the difference between them could be either at a global or a local level of stimulus characteristics. Results demonstrated a speed advantage in processing the global aspects of the shapes for humans, but an advantage in processing the local aspects of the same shapes for chimpanzees.

Fagot and Tomonaga (1999; see also Fagot et al. 2001) suggested that species differences in perceptual grouping might account for the data. They proposed that chimpanzees are highly sensitive to the distance between the local elements, and therefore had difficulty in grouping these elements into a global shape. Indeed, reduction of the distance separating the local elements had little effect on the priority humans gave to the global aspects of the stimuli (Fagot and Tomonaga 1999). By contrast, the priority chimpanzees gave to the analysis of local stimulus features disappeared when the inter-element distance was reduced.

The main goal of the current study was to further test the hypothesis that chimpanzees are more sensitive to the spatial separation of visual figures than humans are. In this study, Kanizsa-type figures inducing illusory perception were chosen as natural vehicles for testing our hypothesis about spatial separation. On the one hand, there is evidence that the perception of illusory figures is produced by a unit-formation process that might be responsible for other perceptual grouping phenomena such as amodal completion (Shipley and Kellman 1992a). On the other hand, several reports indicate that the strength of illusory contours in human depends, in addition to several other perceptual (e.g., illumination level, projective size, Dumais and Bradley 1976) or cognitive factors, on the separation of the inducers.

Although several reports have suggested that animals might be sensitive to illusory contours (e.g., insects: Horridge et al. 1992; chicks: Zaforlin 1981), very little is known on the perception of illusory contours by non-human primates. von der Heydt et al. (1984; see also Peterhans and von der Heydt 1989) found that neurons in extrastriate visual area V2 (but not V1) of alert rhesus macaques (*Macaca mulatta*) respond to illusory contours. Later, Grosz et al. (1993) showed that V1 neurons also

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have the computational power to detect illusory contours. These two studies suggest that illusory contour formation is mediated by low-perceptual bottom-up mechanisms. To our knowledge, there is at this point no behavioral evidence for the perception of Kanizsa-type illusory contours in any nonhuman primate species, including the chimpanzee.

The two experiments presented below comparatively assessed the processing of Kanizsa-square illusory figures by humans and chimpanzees.

Experiment 1

This experiment used a forced-choice procedure, in which subjects were requested to select (i.e., touch) the positive stimulus in a two-stimulus display. Two types of trials were proposed. In the first type of trials, referred to as the illusory trials (I-trials), discrimination could either be made (1) on the basis of configural or featural information distinguishing S+ from S-, and/or (2) on the basis of illusory contours that could potentially be perceived in S+ but not in S-. The second type of trials, referred to as the non-illusory trials (NI-trials), served as controls for the perception of illusory contours. In NI-trials S+ and S- were identical to the I-trials, except that narrow closing line segments were added to the inducers in order to weaken perception of the illusory contours. Discrimination between S+ and S- could thus be made on the basis of configural or featural information, but presumably not on the basis of illusory information. The hypothesis was made that a direct comparison between the I- and NI-trials has the potential to reveal whether or not chimpanzees and humans perceive illusory contours in our testing condition.

Method

Participants

Two adult female chimpanzees (*Pan troglodytes*), Pendesa (21 years old) and Chloe (17 years old), and four humans (3 men and 1 women, mean age=30 years, SD=7) served as subjects. The two chimpanzees were highly familiar with the set-up, because of their involvement in a variety of previous experiments on cognitive or perceptual processes (e.g., Fagot and Tomonaga 1999). These animals had however never specifically been trained or tested for illusory line perception. Chimpanzees lived in a social group of 11 individuals maintained at the Primate Research Institute, Inuyama, Japan. They were raised in indoor and outdoor enclosures (770 m²) connected to the experimental room by a tunnel. Humans were paid for participation. They were naïve with respect to the purpose of the current research.

Apparatus

Training and test sessions were conducted inside an experimental (1.8×2.15×1.75 m) booth for chimpanzees. A 21-inch (53 cm) color cathode-ray monitor (CRT; NEC Model PC-KH2021) with a touch-screen device (Micro-touch Model SM-T2) was installed 15 cm from the floor on one side of the experimental booth. The screen was protected from deterioration by a transparent Plexiglas panel, fitted with a 10×47 cm armhole, which allowed hand contact with the CRT. Below the CRT was a food tray that was baited by a universal feeder (Biomedica Model BUF-310) delivering pieces of apple or raisins whenever a correct response was given. The equipment was connected to a personal computer (NEC Model PC-9821 Xn) controlling stimulus display, the detection of the touches on the CRT, reward delivery and data collection.

Stimuli

Figure 1 illustrates the stimulus pairs used in the I- and NI-trials. Stimuli used in the I-trials (upper part of Fig. 1) were composed of four white inducing pacman-shaped elements (luminance=57.2 cd m⁻²) arranged to form a potentially illusory square. Central and perpendicular to each side of the squares were four 3-pixels-wide line segments (i.e., 1.7 mm wide) of two possible lengths: short (24 pixels, 13.4 mm) or long (36 pixels, 20.5 mm). The internal endpoints of the short lines were located on the exact border of the potentially illusory square. The long line segments crossed the border of the potentially illusory square. These lines were either expected to enhance (short lines) or weaken (long lines) the strength of the illusory contours. Stimuli used in the NI-trials (bottom of Fig. 1) were identical to those of the I-trials, except that narrow closing lines had been added to the missing segments of the pacman shapes (Fig. 1). Use of such closing lines has been shown to block the response of the neurons located in the brain area V2 that are sensitive to illusory

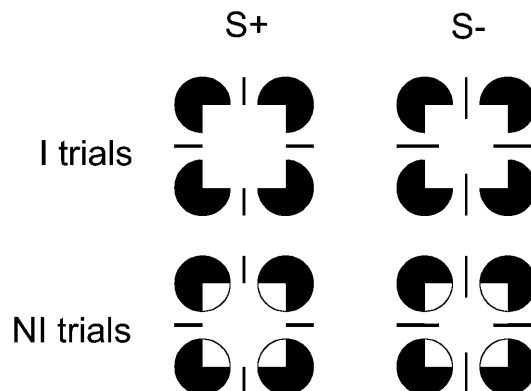


Fig. 1 Stimulus set used during training and testing (Experiment 1) (*I-trials* illusory trials, with illusory figure, *NI-trials* non-illusory trials, with line added to reduce the illusion)

contours to fire (e.g., von der Heydt et al. 1984). Inducers had a radius of 24 pixels (13.4 mm) for all stimuli, and were separated by 280 pixels (155 mm). All stimuli were displayed on a uniformly black background (luminance = 1.4 cd m^{-2}). They were created using Quick-Basic version 4.5 for PC.

Test procedure

A common two-alternative forced choice procedure was adopted with humans and chimpanzees. Each trial began by the presentation of a warning stimulus (a 1-cm-diameter blue dot) that appeared in the central bottom portion of the screen, and an accompanying 0.5-s beep sound. A hand touch on the warning stimulus induced presentation of two discriminative stimuli. One of them was the positive stimulus (S+), i.e., is the stimulus that had to be touched for food reinforcement. The other one was the negative stimulus (S-). Stimuli remained on the screen until a hand touch on either S+ or S- had been detected by the computer, or a 5-s delay had elapsed. Correct responses triggered the delivery of a food reward and a 1-s high-pitched tone for the chimpanzees. For humans, only the tone was presented after correct trials. Whenever the humans or chimpanzees had touched S- (i.e., error trial), the identical display was again presented in a first and if necessary in a second correction trial. This correction procedure was introduced because chimpanzees may stop working when the rate of non-reinforced trials is too high.

Prior to the test, chimpanzees received baseline training sessions of I-trials using the two stimuli shown at the top of Fig. 1. Training sessions consisted of series of 72 trials during which S+ was randomly located on the left (half of the trials) or right (half of the trials) of the screen. Sessions were repeated until subjects achieved 90% correct or more. Chloe and Pendesa needed three and ten sessions, respectively, to achieve training criterion. Because humans quickly understood the task, they received only one session of 72 training trials in which the positions of S+ and S- stimuli were counterbalanced.

The test consisted of two sessions of 144 trials per subject. Two types of testing trials were proposed: the I- and NI-trials. I-trials were similar to the baseline training trials, and therefore consisted of the simultaneous presentation of the two stimuli shown at the top of Fig. 1. NI-trials consisted in the simultaneous presentation of the two stimuli shown at the bottom of Fig. 1. Each testing session contained 72 I-trials and 72 NI-trials; the order was randomly determined prior to the session. For those two types of trials, location of the S+ and S- stimuli was counterbalanced. No physical restriction was imposed during training or test trials. The apes however invariably adopted a fixed sitting position corresponding to an estimated eye-screen distance of 50 cm (verified by video recording). To keep the viewing distance constant across species, humans sat on a pad in front of the screen, and were requested to maintain a viewing distance of 50 cm.

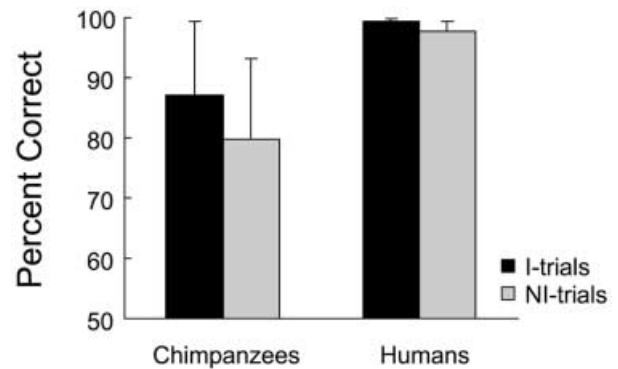


Fig. 2 Average performance of chimpanzees and humans in the I- and NI-trials (Experiment 1)

Results

Performance scores were computed for each subject and condition, and then submitted to an analysis of variance (ANOVA) with species (human, chimpanzee) as the unique between-subject factor, and test session (session 1, session 2) and test condition (I, NI) as within-subject factors. The main effect of test condition was significant: performance was better on average in the I-trials (93.3% correct) than in the NI-trials (mean=88.8%; $F_{1,4}=41.9$, $P=0.003$). Also significant was the species by test condition interaction ($F_{1,4}=15.9$, $P=0.016$). That interaction is shown in Fig. 2. Post hoc analyses (Tukey HSD, $P<0.05$) revealed that only for chimpanzees was performance for I-trials significantly better than for NI-trials.

Median response times for correct trials were analyzed following the same procedure as for scores. The only significant effect emerging from this analysis was an effect of test condition, $F_{1,4}=36.8$, $P=0.004$: For both humans and chimpanzees, response times were significantly faster in the I- than in the NI-trials (Fig. 3).

Discussion

This first experiment demonstrates that adding closing lines to the pacman inducers (NI condition) lowered dis-

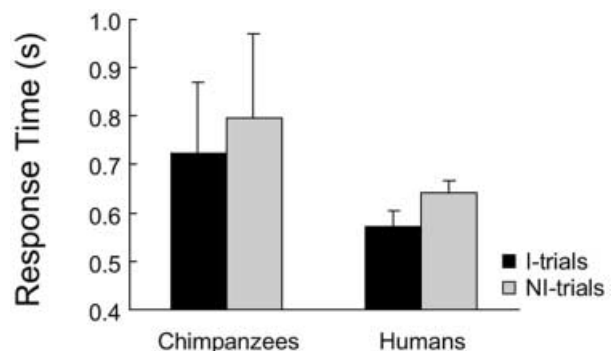


Fig. 3 Median correct response times of chimpanzees and humans in the I- and NI-trials (Experiment 1)

crimination performance in chimpanzees. For those animals, response times were longer, and the scores lower in the NI than in the I condition. Results consistent with those of chimpanzees were obtained in humans, as demonstrated in Fig. 3.

Inspection of Fig. 1 suggests that it was possible for chimpanzees and humans to use four types of cues for recognizing the S+ stimuli. Possible cues were (1) the saliency of the perpendicular segments, which were longer for S- than for S+ (featural cue), (2) the distance between the internal endpoints of the bars (configural cue), which was greater for S+ than for S-, (3) the alignment (for S+) or misalignment (for S-) of the internal endpoints of the lines relative to the borders of the edges of the two adjacent pacmen (configural cue), and/or (4) the phenomenal perception of illusory squares or contours. It should be noted that the featural and configural cues listed above (i.e., cues 1-3) could have all been used for recognizing S+ in both the NI- and I-trials. By contrast, the perception of an illusory square was likely to contribute to discrimination in the I-trials only, because the use of closing lines has been shown to weaken the strength of illusory contours (e.g., von der Heydt et al. 1984). Because performance was better in the I than in the NI condition, results are in accordance with the hypothesis that the chimpanzees experienced the phenomenal perception of illusory contours or squares in that task. Caution is advised, however, because other explanations cannot be ruled out at this point. For instance, due to the initial discrimination training, chimpanzees were more familiar with I-trials, presented during both training and testing, than with NI-trials, presented during the test sessions only. The lower performance obtained in NI-trials compared to I-trials might therefore also be accounted for by a novelty effect or a generalization decrement, rather than by a lack of illusory cues in NI displays.

Experiment 2

Experiment 1 provided baseline comparative information on the possible perception of illusory contours by chimpanzees and humans. The aim of Experiment 2 was to more directly test the hypothesis, proposed by Fagot and Tomonaga (1999; see also Fagot et al. 2001), that chimpanzees are more sensitive to element separation than humans are.

Methods

Subjects and apparatus

Subjects and apparatus were identical to those of Experiment 1.

Stimuli

Five sets of stimuli were used during testing (Fig. 4). These sets, referred to as sets A-E, were constructed from

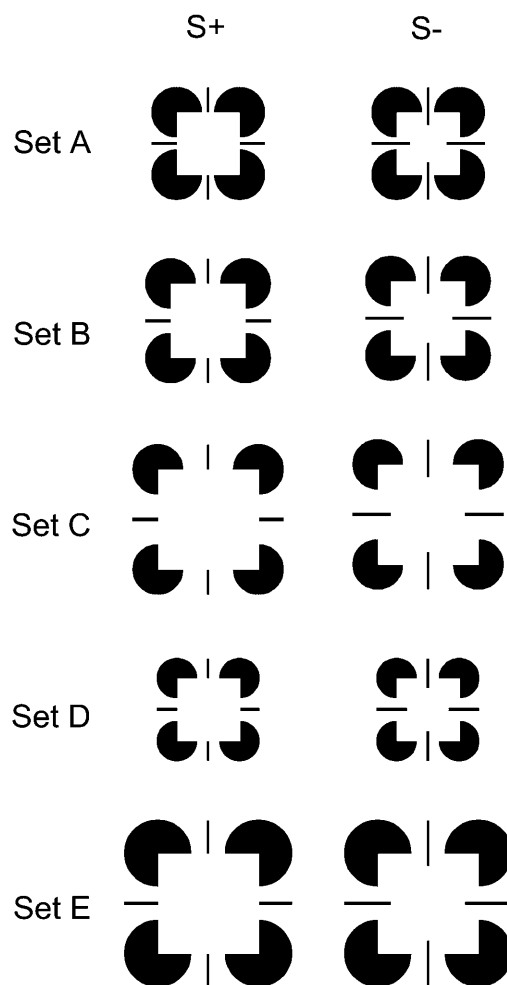


Fig. 4 Stimuli used in Experiment 2. S+ stimuli are shown on the left, and S- stimuli are shown on the right of the figure

the orthogonal manipulation of the radius of the Pac-Man elements and their separation in the Kanizsa figure. Sets A-E were defined as follows: set A: radius (R)=24 pixels (13.4 mm), separation (S)=12 pixels (6.7 mm); set B: R =24 pixels, S =24 pixels; set C: R =24 pixels, S =48 pixels (26.8 mm); set D: R =20 pixels (11.2 mm), S =20 pixels; set E: R =32 pixels (17.9 mm), S =32 pixels. Note that the stimuli of sets A, B, and C differed in terms of separation only, because R remained constant for those stimuli (i.e., 24 pixels). By contrast, stimuli of sets B, D and E differed in visual size only, because the R/S ratio was equal to 1 in these three sets. Whatever the stimulus set, the endpoint of the bar was always adjacent to the border of the potentially illusory square for S+, whereas the bars entered the squares for S-.

Testing procedure

The general testing procedure was identical to that of Experiment 1. Each human and chimpanzee received five test sessions of 120 trials each. Test sessions contained

24 trials per set in which the location of S+, either on the left or right of the display, was counterbalanced. The experiment was run without any preliminary training because all subjects were already familiar with the task. All the other aspects of the test, for instance in terms of reinforcement contingencies or stimulus brightness were identical to those of Experiment 1.

Results and discussion

Inspection of Fig. 4 suggests that three factors might affect the perception of the illusory figure, and might consequently control discrimination between the S+ (illusory) stimulus and the S- (non-illusory) stimulus. These factors are: (1) the absolute radius length of the pacman figures, (2) the absolute size of the potentially illusory square, and (3) the absolute distance between the inducers. As demonstrated by Gillam (1981), there is also the possibility that factors of size and distance may interact, and affect in

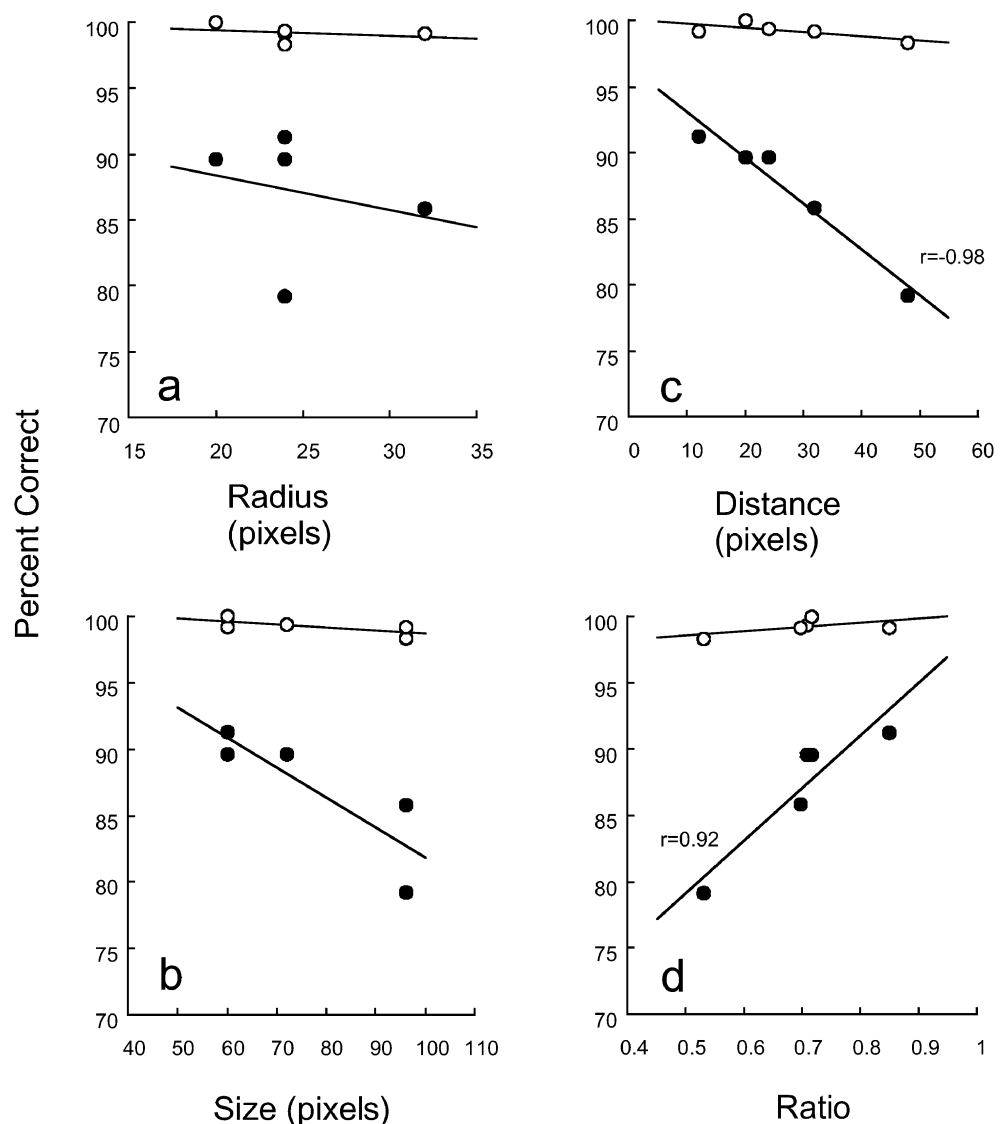
concert the saliency of the illusory perception. In order to assess this possibility, a fourth variable was computed that combines the effects of size and distance. That variable will be referred to as the ratio of specified to total edge length. In line with Shipley and Kellman (1992b), it was computed as follows:

$$V=(2R+W)/(D+2R)$$

where R is the radius of the pacman shape, W is the width of the perpendicular bars, and D is the absolute distance between the inducing elements.

In order to evaluate in which extent these four factors affected discrimination, performance was firstly plotted separately for each species as a function of radius length (Fig. 5a), size of the potentially illusory square (Fig. 5b), distance between the inducers (Fig. 5c), and ratio of the specified to total edge length (Fig. 5d). Then, linear regressions were computed in order to assess the relative contribution of these four factors on discrimination performance.

Fig. 5 **a** Performance of humans and chimpanzees plotted as a function of the absolute radius length. **b** Performance of humans and chimpanzees plotted as a function of the absolute size of the potentially illusory square. **c** Performance of humans and chimpanzees plotted as a function of the absolute distance between the inducers. **d** Performance of humans and chimpanzees plotted as a function of the radius of the specified to total potentially illusory figure edge length



Regression analyses revealed that none of the four factors defined above significantly affected performance of humans (radius length: $F_{1,3}=0.38$, $P=0.58$; square size: $F_{1,3}=3.1$, $P=0.177$; distance: $F_{1,3}=3.5$, $P=0.157$; ratio: $F_{1,3}=1.5$, $P=0.308$). Humans indeed exhibited almost perfect scores in all test conditions (mean correct=92.2%; Fig. 5a–d).

Interestingly, different results emerged from the analysis of chimpanzees' performance. For those subjects, the radius length did not control discrimination (Fig. 5a), $F_{1,3}=0.17$, $P=0.703$. Regarding square size, performance tended to decrease with large sizes (see Fig. 5b), but that effect did not reach significance level, $F_{1,3}=7.8$, $P=0.068$. There was however a significant relation between performance and distance $F_{1,3}=70.9$, $P=0.0035$, performance being inversely related to distance (Fig. 5c). Similarly, performance was under the control of the ratio of the specified to total edge length, $F_{1,3}=16.9$, $P=0.026$, (Fig. 5d).

Did the ratio exert a stronger control on performance than distance? The data provide a negative answer to that question. There was a higher correlation between performance and distance ($r=0.98$) than between performance and ratio ($r=0.92$). Note that distance and ratio were highly correlated ($r=0.96$, $P=0.01$); this correlation is accounted for by the fact that distance is a component of the equation used to compute ratio.

Considering median response times, humans responded faster on average (mean=566 ms, $SD=60$) than chimpanzees (mean=799 ms, $SD=59$), $F_{1,4}=20.4$, $P=0.011$. Regression analyses revealed that neither the radius, the size of the potentially illusory square, the distance between the inducer elements, nor the ratio of the specified to total edge length controlled response speed of either species (all $P>0.1$). In brief, Experiment 2 confirmed that chimpanzees are much more sensitive than humans to element separation.

General discussion

This research had two main goals: (1) assessing the possibility that chimpanzees do perceive Kanizsa illusions and (2) verifying whether chimpanzees are more sensitive to element separation than humans are. These two aspects of the research will be discussed sequentially.

Do chimpanzees perceive the Kanizsa illusion?

Two important results emerged from Experiments 1 and 2. First, discrimination performance in Experiment 1 was reduced when closing lines were added to pacman inducers. Second, performance in Experiment 2 improved when the distance between the inducers was reduced. Complementarily, performance deteriorated when the distance increased. Performance was also to a lesser extent under the control of the ratio of the illusory to specified edge length. Interestingly, use of closing lines was reported to block the response of V2 neurons to illusory contours (e.g., von

der Heydt et al. 1984). Moreover, the inter-element distance and the ratio of the illusory to specified edge length were both reported to affect the strength of illusory perception by humans, this strength being enhanced with lower distances and higher ratios (e.g., Shipley and Kellman 1992b). The hypothesis can therefore be made that, in chimpanzees, the use of closing lines (in Experiment 1) and the changes introduced in the distance or ratio (in Experiment 2) weakened the strength of the illusory perception (for long distance) and, in turn, made it more difficult to use illusory cues for S+ versus S- discrimination. This hypothesis can explain why chimpanzees showed their best performance when the distance between the inducers was minimal.

Although the results of Experiments 1 and 2 are in accordance with the hypothesis that the chimpanzees did perceive the Kanizsa illusion, caution is advised in the conclusion. As already mentioned, behavioral differences between the I- and NI-trials in Experiment 1 might be explained by a novelty effect, instead of by reference to illusory phenomena. In the same vein, effects of element separation have been reported in both humans and non-human primates in experiments on grouping processes involving non-illusory stimuli (humans: e.g., Martin 1979; chimpanzees: e.g., Fagot and Tomonaga 1999; baboons: e.g., Fagot and Deruelle 1997). Further experiments will thus be needed to evaluate the reliability of the findings, and to ascertain the hypothesis that the chimpanzees are sensitive to Kanizsa illusions.

Are chimpanzees more sensitive than humans to element separation?

Experiment 2 demonstrated that chimpanzees are not as proficient as humans in overcoming spatial separations between the elemental features of the stimuli. Thus, chimpanzees' performance was affected by an increment of the inter-element distance, whereas humans' performance remained unchanged across separations. The decreased efficiency of the chimpanzees with maximal distances may reflect a diminished capacity to group the four pacman inducers into a single and coherent unit, which might impede the comparison between S+ and S-. Interestingly, a reduced capacity for grouping by proximity, in comparison to humans, has previously been reported in non-illusory tasks involving chimpanzees (Fagot and Tomonaga 1999; see also Fagot et al. 2001), baboons (Deruelle and Fagot 1998) and rats (Kurylo et al. 1997). It might be proposed that a reduced capacity for perceptual grouping has the potential to hamper the general efficiency of object recognition processes. However, as pointed out by Kurylo et al. (1997) grouping might be achieved from a variety of stimulus characteristics, such element similarity, alignment or common fate (e.g., Koffka 1935). It may be that proximity cues are less important for chimpanzees than for humans, and that the process of unit formation in chimpanzees relies more strongly on the analysis of other grouping cues, such as motion or texture, than on proxim-

ity cues. This explanation calls for further comparative experiments in which processes of unit formation will be more directly studied in animals, including chimpanzees, using parametric manipulations of the various factors that might affect grouping.

The question remains of whether or not physiological explanations can account for the differences between species in the ability to overcome spatial separations. Unfortunately, very little is known on the functional sensitivity of the visual system of chimpanzees (Fobes and King 1982). The available evidence suggests, however, that chimpanzees have a visual acuity similar to that of humans (Matsuzawa 1990), and do not differ from humans in terms of spectral sensitivity (Dulai et al. 1994; Jacobs et al. 1996). Moreover, the visual systems of primate species even more remotely related to humans than chimpanzees (e.g., macaques) share numerous properties with that of humans, for instance in terms of contrast sensitivity or temporal fusion frequency (see Fobes and King 1982). Although it is impossible to completely rule out the possibility that more subtle perceptual differences exist between species and might account for the findings, these consistencies across primates suggest that the effect of separation has post-perceptual rather than purely perceptual origins.

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