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Perception of shape from shading in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*)

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Abstract The perception of shape from shading was tested in two chimpanzees *(Pan troglodytes)* and five humans *(Homo sapiens)*, using visual search tasks. Subjects were required to select and touch an odd item (target) from among uniform distractors. Humans found the target faster when shading was vertical than when it was horizontal, consistent with results of previous research. Both chimpanzees showed the opposite pattern: they found the target faster when shading was horizontal. The same difference in response was found in texture segregation tasks. This difference between the species could not be explained by head rotation or head shift parallel to the surface of the monitor. Furthermore, when the shaded shape was changed from a circle to a square, or the shading type was changed from gradual to stepwise, the difference in performance between vertical and horizontal shading disappeared in chimpanzees, but persisted in humans. These results suggest that chimpanzees process shading information in a different way from humans.

Key words Shape from shading · Visual search · Texture segregation · Chimpanzees · Humans

Introduction

When we humans look at circles with gray-scale shading from top to bottom (vertical) on a gray background, as shown in the left panel of Fig. 1, we easily perceive a convex circle among concave ones. If this panel is rotated 180°, we perceive a concave circle among convex ones. In the right panel, circles are shaded from left to right (horizontal). This change of shading direction causes drastic perceptual change: it is very hard to detect an odd item among distractors. As these examples show, shading, which can be defined as variation in luminance, provides an effective source of visual information about the three-dimensional shapes of objects. The perception of three-dimensional depth or shape from shading has been frequently studied in humans ever since the 18th century (e.g., Aks and Enns 1992; Benson and Yonas 1973; Berbaum et al. 1983; Brewster 1847; von Fieandt 1938; Granrud et al. 1985b; Kleffner and Ramachandran 1992; Metzger 1936; Mingolla and Todd 1986; Ramachandran 1988a, b; Rittenhouse 1786; Todd and Mingolla 1983; Yonas et al. 1979).

Shading alone provides ambiguous information for the visual system. To extract three-dimensional shape (depth) from two-dimensional shading, two constraints or assumptions are required (Ramachandran 1988a, b; Kleffner and Ramachandran 1992). First, there must be a single source of light illuminating the whole scene. Second, and more importantly, light must be shining from “above” in relation to retinal coordinates (Brewster 1847; Kleffner and Ramachandran 1992). These two assumptions are quite appropriate considered in normal “ecological” or “ethological” contexts, but may not be universally appropriate. Imagine, for instance, animals adapted to an environment in which light shines from a source that is not necessarily above the animal (e.g., dolphins freely moving under the sea), animals living in an environment with multiple light sources (e.g., extraterrestrial organisms that have evolved on a planet with two suns), or animals reared in an artificial environment in which the light comes from “below” (e.g., Hershberger 1970; Hess 1950, 1961). Comparative or developmental studies on the perception of shape from shading are required to investigate the validity of these assumptions. Are they valid for animals other than humans? Are they a consequence of evolution? Can these constraints be modified by experience in early development or are they genetically fixed?

Developmental changes of sensitivity to shading cues have been studied in two different ways. One approach is developmental study with human children (Benson and Yonas 1973; von Fieandt 1938; Granrud et al. 1985b;

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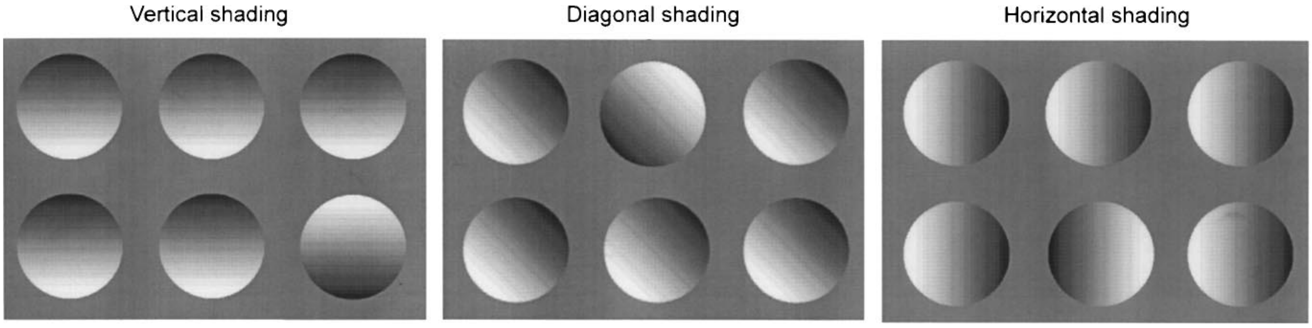

Fig. 1 Examples of shape perception from shading. Each display contains one odd item (target, *TGT*) with the apparent luminance polarity of the shading opposite to that of the other stimuli (distractors, *DST*s)

Yonas et al. 1979). For example, Granrud et al. (1985b) investigated the development of sensitivity to shading in 5- and 7-month-old human infants. Infants reach preferentially for a real convexity (Granrud et al. 1984). Using this reaching response as a dependent variable, they found that 7-month-olds preferentially reached for the apparent convexity specified by shading, while 5-month-olds showed no reaching preferences. They concluded that at least very early in life the human visual system constrains the interpretation of shading.

The second approach studies animals raised in an artificial environment. The first such study by Hess (1950, 1961) used chicks raised from birth in an environment where the light always came from below. He observed pecking responses to a photograph of grains, some with shadows above them on the background and some with shadows below them. In the first week of life, experimental chicks and normally raised control chicks showed no difference in pecking at the two types photographed grains. During development, however, their responses became different: experimental chicks preferred to peck grains with shadows above them and control chicks preferred to peck grains with shadows below them. This finding suggested that the assumed light source position might be learned through experience. However, Hershberger (1970) tried to replicate Hess's study using a discrimination task with photographs of shaded objects and the actual objects. Two groups of chickens, each raised in different light conditions, both showed positive transfer from actual to apparent convexity irrespective of their preceding experiences. Hershberger concluded that the assumption that the light comes from above is innate.

The third possible way to investigate whether the assumption that light comes from above is innate is to compare species adapted to different environments. If the position of the light source is defined by retinal coordinates but not gravitational ones, as Ramachandran (1988a, b; Kleffner and Ramachandran 1992) noted, animals moving freely in space (such as dolphins, birds, and arboreal primates) would show no, or at least reduced differences, in using shading at different angles as depth cues. Unfortunately, we have very few data from nonhuman animals on the perception of shape from shading (Hershberger 1970; Hess 1950, 1961). S.Kanazawa and K. Fujita (personal communication) conducted a study of texture segregation by Japanese macaques that had adapted to a terrestrial environment and found results similar to those of humans.

As well as studying the innateness of constraints on processing of shading, some researchers have investigated how shading information is processed in our visual system. For example, Kleffner and Ramachandran (1992; Ramachandran 1988a, b) and Aks and Enns (1992) investigated human perception of shape from shading using visual search and texture segregation procedures. Kleffner and Ramachandran (1992) concluded that shape information is extracted from shading preattentively. Aks and Enns (1992) further suggested that shading type (linear and gradual or black-white stepwise shading), shape of the shaded object (circle or square), and background luminance (bright, gray or dark) affect the perception of shape from shading.

In the present experiments chimpanzees were trained in visual search tasks using the shading patterns shown in Fig. 1. The main aim was to compare the processing of shading by humans and chimpanzees, which had adapted to rather different environments from each other. Previous studies in our laboratory found differences between chimpanzees and humans in visual spatial perception, such as in mental rotation (Fujita and Matsuzawa 1989) and face perception (Tomonaga et al. 1993; but see M. Tomonaga, unpublished work). Matsuzawa (1991) and Tomonaga et al. (1993) suggested that this difference might result from adaptation to different environments: chimpanzees have adapted to a more three-dimensional environment (tropical forest) than humans.The perception of shape from shading provides a way to test this hypothesis of ecological constraints on spatial perception. To check the validity of the experimental setting, human subjects were given the same tasks under the same experimental situation as chimpanzees. Furthermore, one chimpanzee was tested in the texture segregation task (M. Tomonaga, unpublished work) in order to replicate systematically the results observed in the visual search tasks.

Experiment 1A: visual search for shading directions in chimpanzees and humans

Methods

Subjects

Two adult chimpanzees *(Pan troglodytes)*, Akira (male, 17 years old) and Chloe (female, 14 years old), were the subjects of the experiments. They were experienced in various perceptual-cognitive tasks (Asano et al. 1982; Fujita and Matsuzawa 1989; Tomonaga and Matsuzawa 1992; Tomonaga et al. 1993), especially visual search tasks (Tomonaga 1993 a, b, c, 1995a, b, 1997). They live in an outdoor enclosure (624 m^2) with other chimpanzees. They had no unusual treatment throughout the experimental period. Care and use of the chimpanzees complied with the "Guide for the care and use of laboratory primates" of the Primate Research Institute, Kyoto University. Five human adults (3 male and 2 females, 23–30 years old) also participated in the experiments.

Apparatus

The experiments were conducted in an experimental compartment (2.7 × 2.1 × 1.5 m) adjacent to the outdoor enclosure. A 14-in (35-cm) color cathode-ray tube (CRT) monitor (NEC Model N5923) with an optical touch panel (Carol Touch International Model UL-94V-0) was installed on one wall about 40 cm above the floor. A touch on the screen of the CRT was defined as a response. Two steel pipes (30 cm × 1.2 cm) protected the CRT monitor and divided the screen into three rows. The chimpanzee sat about 40 cm from the CRT. A universal feeder (Davis Scientific Instruments Model UF-100) delivered a food reward to the food tray installed to the lower left of the CRT. A personal computer (NEC Model PC-98XA) controlled all experimental events and recorded data.

Stimuli

Figure 1 shows examples of search displays. Note that these are not actual arrangements. All stimuli were generated with 16-color gray-scale computer graphics using NEC N88-BASIC [4056-color mode, from &H000 (black) to &HFFF (white)]. Each circle was 1.8 cm in diameter shaded with 12 gray scale stripes 0.2 cm wide from &H444 (dark) to &HFFF (bright). Background was neutral gray (&H888). Three shape directions were prepared: vertical (0°), diagonal (45°), and horizontal (90°). Each direction had two symmetrical patterns (e.g., circle bright at the top and dark at the bottom, and vice versa).

Procedure

The visual search task was the same as in previous experiments (Tomonaga 1993b, 1995a, b). After the 3-s intertrial interval, a warning signal (white cross, 0.5 cm × 0.5 cm) appeared at the bottom center of the CRT monitor. A single touch terminated it and resulted in the presentation of the search display. Each stimulus appeared in the two upper rows, each of which had six predefined areas for stimulus presentations. The search display contained 1 target and 0 (target only), 5, or 11 distractors. Display size (i.e., the number of stimuli in the search display) varied randomly from trial to trial. Display size 1 (i.e., target only) was used to collect baseline chronometric information reflecting the processes of stimulus detection, movement preparation, and movement execution. This condition only requires detection, unlike the other display sizes which require discrimination processes. Three targets were also changed from trial to trial; top-bright (for vertical shading), upper right-bright (for diagonal shading), and right-bright (for horizontal shading). The luminance polarity of distractors was reversed in comparison to the target. Subjects were required to detect and touch the target. For chimpanzees a correct response produced a 1-s chime and food reinforcer, whereas an incorrect response produced a 0.5-s error buzzer. For humans a correct response only produced a 1-s chime.

A modified correction procedure was used in these experiments. If the subject made an error, the target alone was presented, as a correction trial. Each session consisted of 120 trials (8 target-only trials and 16 trials for display sizes 6 and 12 for each target). Training was continued for nine sessions for Akira and eight sessions for Chloe. The last six sessions were used for data analysis. Each human subject received a single 240-trial session (16 target-only trials and 32 trials for display sizes 6 and 12 for each target).

Results and discussion

Akira made 47.9% correct choices in the first session and reached 87.5% correct in the third session. Chloe made 65.5% correct in the first session and 93.8% correct in the second session. Mean percentage errors for chimpanzees and humans are shown in Table 1 and mean response times on correct trials in Fig. 2 (response times for display size 1 are not shown). Mean response times for display size 1 were 0.593 s for chimpanzees and 0.584 s for humans. Human subjects searched faster and more accurately when vertical shading was presented than when horizontal shading was presented, and their performance was as good for diagonal shading as for vertical shading. Both chimpanzeesperformed better for horizontal shading than for vertical shading, the reverse of the human pattern. No human subjects showed this pattern. A three-way ANOVA (Species × shading direction × display size) applied to the response time data showed a significant main effect of display size [$F(1,5) = 8.02$, $P < 0.05$] and a sig-

Table 1 The mean percentage of errors in experiments 1A, 2, and 3

Experiment	Shading type	Shape of contour	Shading direction	Chimpanzees[a]		Humans[b]	
				6	12	6	12
1A	Linear	Circle	Vertical	14.1	8.3	0.6	0.6
			Diagonal	3.6	2.3	3.5	0.7
			Horizontal	3.9	1.0	3.0	2.1
2	Linear	Circle	Vertical	8.3	2.6	2.5	0.6
			Horizontal	4.2	1.0	3.5	3.7
	Linear	Square	Vertical	11.5	5.7	1.5	0
			Horizontal	9.9	7.8	1.5	1.9
3	Linear	Circle	Vertical	17.8	1.0	2.2	0.7
			Horizontal	6.7	1.0	2.8	2.8
	Step	Circle	Vertical	14.6	6.3	0	0
			Horizontal	10.6	3.1	2.9	4.4

[a] $n = 2$ (except for experiment 2, $n = 1$)
[b] $n = 5$

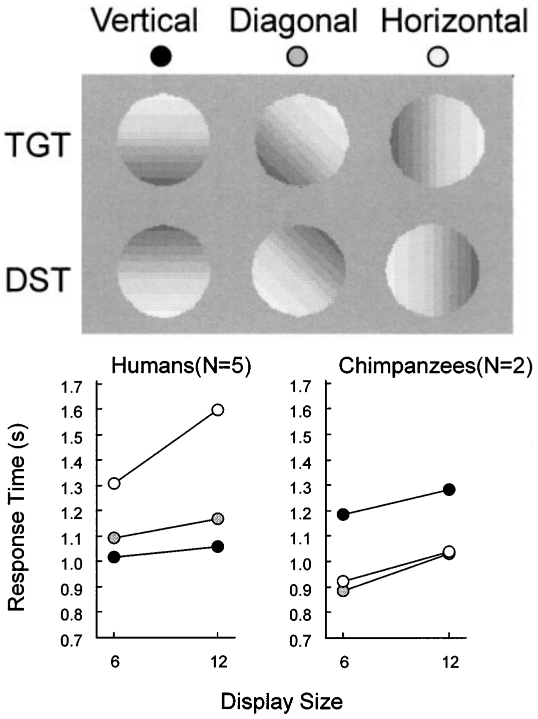

Fig. 2 Mean response times as a function of display size for humans and chimpanzees in experiment 1A. The data from display size 1 are not shown in this figure

nificant interaction between species and shading direction [$F(2,10) = 10.19$, $P < 0.01$].

The percentage of errors was negatively correlated with the display size in any conditions for both species, especially for chimpanzees, as shown in the upper part of Table 1. This has frequently been observed in animals searching a display containing a pop-out target (Blough 1989; Tomonaga 1993b, 1995a). A similar decrease in percentage of errors in visual search for vertical shading patterns was also observed by Aks and Enns (1992) for the target-present trials. This might be due to a grouping effect (e.g., Humphreys et al. 1989), and suggests that searching for shading direction does not require attentional processing. It is still unclear why chimpanzees showed stronger grouping effects than humans. One reason might be that the chimpanzees had long and extensive experience of discrimination tasks, unlike the human subjects.

Another interesting finding is the difference in the slopes of the response time functions between humans and chimpanzees. The slope of the response time function was steeper for horizontal than vertical or diagonal shading in humans (for all subjects), while chimpanzees had similar flat slopes for all shading directions. (The patterns for both individual chimps were similar to the averaged ones shown in Fig. 2.) Such patterns of results, with the same slopes but different intercepts, are frequently observed in animal visual search experiments (Deruelle and Fagot, in press; Tomonaga 1993b).

It is not possible to explain the difference between humans and chimpanzees as due to the present experimental setting, because human subjects showed similar patterns to those found in previous studies (Aks and Enns 1992; Kleffner and Ramachandran 1992). One possible explanation is the effect of search asymmetry. Kleffner and Ramachandran (1992) reported that humans showed search asymmetry for shading. Searching was faster and search functions flatter when the target was “concave” (bottom-bright shading) than when it was “convex”. In the present experiment the shape with top-bright shading was the target. How much search asymmetry affects the subjects’ performance is unclear. Chimpanzees did show search asymmetries for various types of simple stimuli such as geometric forms (Tomonaga 1993b) and line orientations (M. Tomonaga, unpublished work). The effects of search asymmetries on visual search for shading need to be tested. This problem will be further investigated in the texture segregation task in experiment 4.

Another possible factor is the viewing position. Kleffner and Ramachandran (1992) found that the perception of shape from shading was based on retinal coordinates, not on gravitational ones. In the present experiment, the chimpanzees never tilted their heads as much as 90°, so that the retinal coordinates for a given image should not differ too much from the gravitational ones. Furthermore, if the chimpanzees tilted their heads about 45°, both vertical and horizontal (with respect to gravity) shading patterns would be equivalent to diagonal shading with respect to the retina. There would then have been no difference in response times among conditions. The different patterns of response times in humans and chimpanzees cannot therefore be explained by head rotation by the chimpanzees.

In addition to head rotation, however, head shift parallel to the surface of the monitor could affect the perception of shape from shading. All human subjects sat in front of the CRT monitor, while the chimpanzee subjects sometimes viewed the CRT monitor from the left or right side because they could move freely in the experimental compartment. For a shaded circle viewed from left or right rather than straight on, horizontal shading would produce a more strongly modulated retinal image than vertical shading, as illustrated in Fig. 3. To test this possibility, I conducted an additional experiment with humans as subjects. If humans show similar patterns of results to chimpanzees when the angle of view is changed, the viewing position could explain the difference in results.

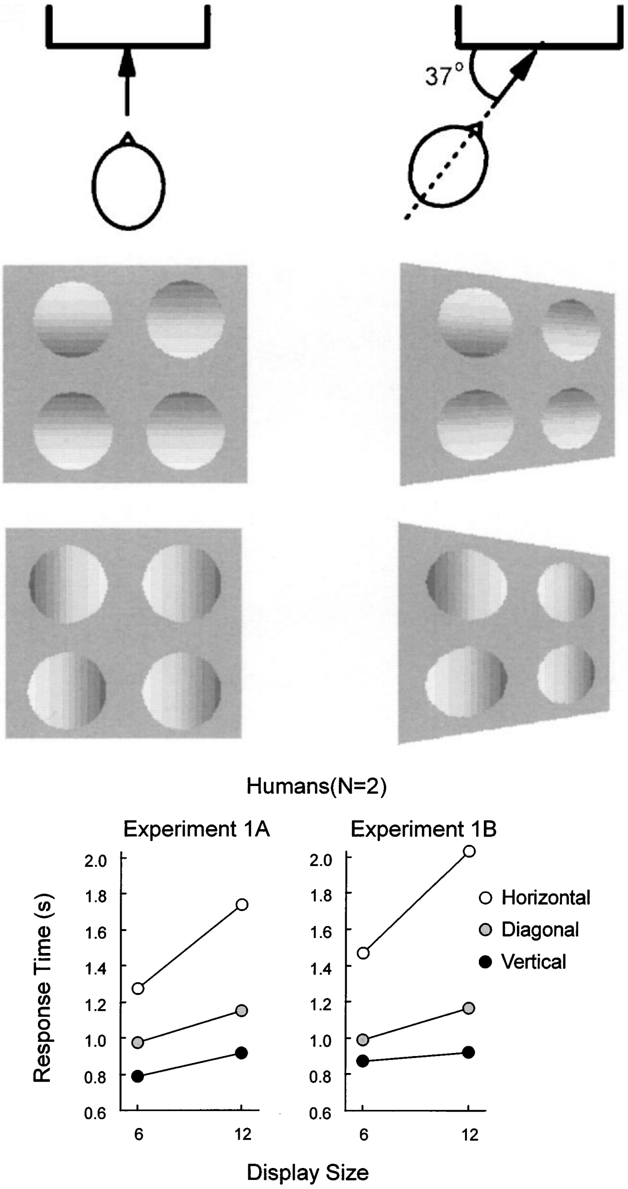

Fig. 3 Effects of the viewing position on visual search for shading directions in humans. The viewing position and the response time in experiments 1A and 1B are shown. The data for experiment 1A come from the same two subjects as in experiment 1B

Experiment 1B: effect of viewing position on visual search for shading directions in humans

Methods

Two human adults, who were also subjects in experiment 1A, participated in this experiment. Experimental procedure was the same as in experiment 1B except for the viewing position of the subject, who sat to the left of the CRT monitor. The distance from the center of the screen to the subject was 50 cm, so the angle between the surface and head was about 37° (Fig. 3). Each subject had a single session of 240 trials.

Results and discussion

Both subjects had more than 95% correct responses. Figure 3 depicts the response times on correct trials for experiments 1A and 1B averaged across subjects. Mean response times on display size 1 were 0.563 s for experiment 1A and 0.643 s for 1B. Response time functions were almost the same in both experiments. A three-way ANOVA (viewing condition × shading direction × display size) applied to response time data showed significant main effects of shading direction [$F(2,4) = 84.64$, $P < 0.001$] and display size [$F(1,2) = 376.97$, $P < 0.01$]. It is evident that a shift in viewing position parallel to the display did not affect the perception of shape from shading in humans, unlike head rotation. These results suggest that difference in viewing position is not sufficient to explain the difference between chimpanzees and humans observed in experiment 1A. Cutting (1987) also reported that human perception preserves shape constancy of images projected onto a screen or television monitor irrespective of viewing direction. Although this needs further investigation, chimpanzees may have the same mechanism as humans.

The difference between humans and chimpanzees observed in experiment 1A was qualitatively similar to that found in other studies on visual spatial perception (Fujita and Matsuzawa 1989; Tomonaga et al. 1993). The same bias established as a result of adaptation to the species-specific environment might affect mental rotation, face perception (but see M. Tomonaga, unpublished work), and perception of shape from shading. Chimpanzees show residual anatomical adaptations for brachiation, a locomotion pattern adapted to forest conditions. They use the arboreal environment for their locomotion as much as the terrestrial one. The use of the arboreal environment might affect their reference coordinates for perception. On the other hand, humans, adapted to open land such as the savanna, might be likely to rely on gravitational coordinates much more than chimpanzees.

The next two experiments investigate the effects on visual perception of shading direction of two other factors, shape of contour and type of shading, both of which are known to have an effect (Aks and Enns 1992; Kleffner and Ramachandran 1992).

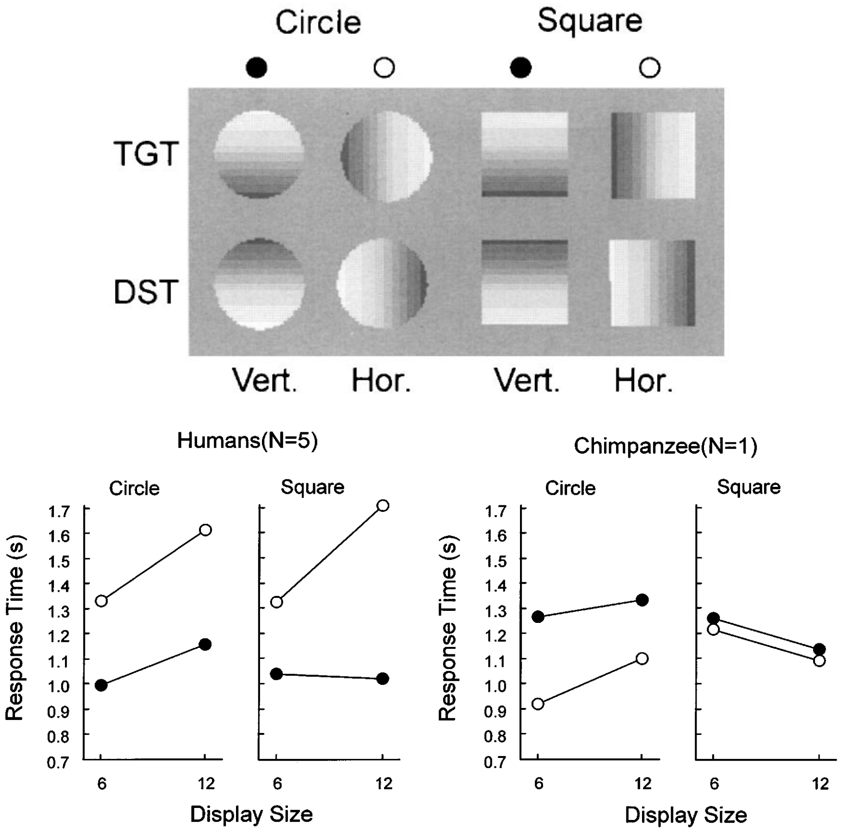

Fig. 4 Mean response times for the five humans and the single chimpanzee in experiment 2

Experiment 2: effects of shape of contour on visual perception of shading directions

Methods

There was only one chimpanzee subject, Akira. Human subjects were the same as in experiment 1A. In addition to gradually shaded circles, shaded rectangles (1.8 cm × 1.8 cm) were used. Shading directions were vertical and horizontal. Akira received nine 128-trial sessions in which four types of targets appeared, with the display size 6 or 12. The last six sessions were used for data analysis. For humans, eight target-only trials were added for each target. Human subjects received a single 288-trial session.

In the present experiment, I tested only one chimpanzee in a single-subject factorial design. The data obtained cannot be analyzed by standard ANOVA. All statistical analyses, of both human and chimpanzee data to maintain consistency, used randomization test techniques (Edgington 1987; Manly 1991; May et al. 1989). The null hypothesis is that “the measurement (or set of measurements) associated with each experimental unit is independent of the assignment of units to treatments” (Edgington 1987, p.39). The upgraded version of NPSTAT (May et al. 1989), and NPFACT for factorial designs, were used. NPFACT calculates *F* values for each permutated data set and calculates a probability for the given data. Permutation was randomly repeated 10,000 times to calculate *P* values. The results of statistical analyses are presented giving *F* values from standard factorial ANOVA on the data and *P* values calculated from random permutations (Edgington 1987).

Results

Mean percentage errors are shown in Table 1 and response times in Fig. 4. Akira showed the same pattern of results for the shaded circle as in experiment 1A. However, when a shaded square was presented,there was a decrease in response time as a function of display size, and responses did not differ for different shading directions. Response time data for Akira were analyzed by three-way ANOVA (contour × shading direction × display size) plus random permutation, using sessions as repeated measures. The main effect of shading direction was significant [$F(1,5) = 36.29$, $P = 0.0023$]. Furthermore, interactions between contour and shading direction [$F(1,5) = 11.39$, $P = 0.0184$] and display size [$F(1,5) = 21.87$, $P = 0.0056$] were also significant. For humans, when the shaded square was presented, the interaction between shading direction and display size was greater than for the circle. Three-way ANOVA plus random permutation showed that the main effects of shading direction [$F(1,4) = 25.36$, $P = 0.0076$], display size [$F(1,4) = 17.36$, $P = 0.0123$], and their interaction [$F(1,4) = 22.89$, $P = 0.0099$], were significant. Furthermore, as shown in Fig. 4, the interaction between contour and shading direction [$F(1,4) = 8.99$, $P = 0.0399$] and the triple interaction [$F(1,4) = 7.98$, $P = 0.0442$] were also significant.

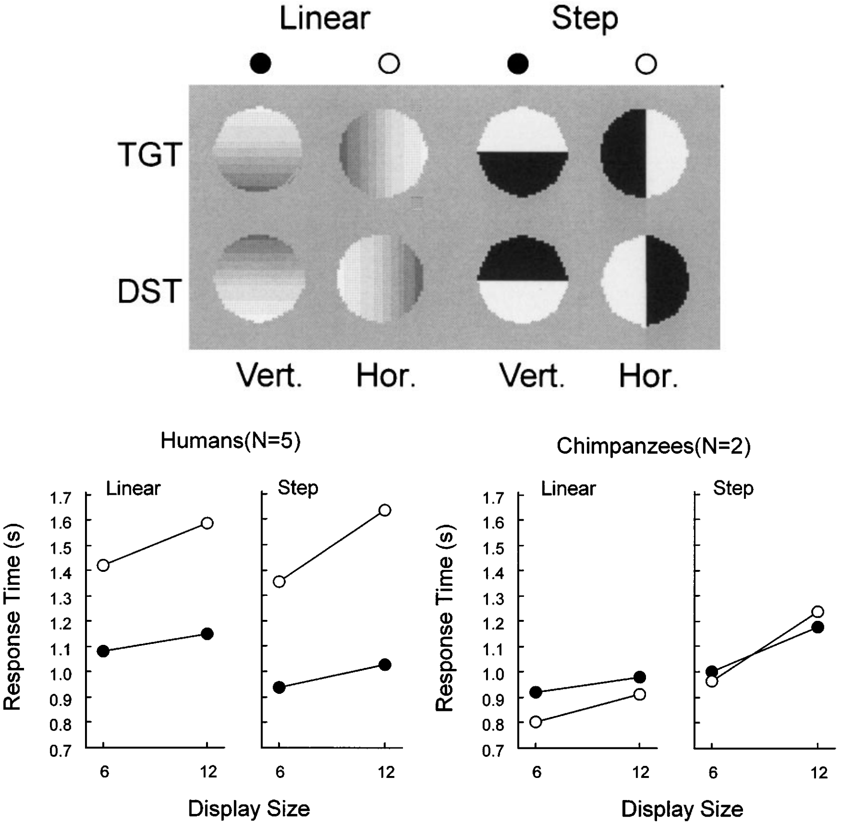

Fig. 5 Mean response times for humans and chimpanzees in experiment 3

Experiment 3: effects of type of shading on visual search for shading directions

Methods

The subjects in experiment 3 were both chimpanzees and the same human subjects as in experiment. Circles with two directions (vertical and horizontal) and two types (gradual and stepwise) of shading were employed (Fig. 5). Circles with stepwise shading had only two luminance values, black and white.

Each chimpanzee received eight 128-trial sessions. Four types of target (2 shading directions × 2 shading types) appeared at random. The target was bright at the top (vertical shading) or at the right (horizontal shading). Display size varied between 6 and 12. The last six sessions were used for data analysis. Each human subject received a single 288-trial session. For humans, eight target-only trials were added for each target.

Results

The mean percentage of errors for each species is shown in Table 1 and mean response times on correct trials in Fig. 5. The difference in the chimpanzees' responses to different shading directions for gradually shaded targets was lower than in the previous experiments, although the response times were longer for horizontal shading than vertical. Closer inspection of the data showed that one chimpanzee showed no difference in response times between horizontal and vertical shading, while the other did show this difference. This discrepancy may have been due to a training or perceptual learning effect (Sireteanu and Rettenbach 1995). A more important finding is that, the difference in response time between shading directions disappeared for both chimpanzees for targets with stepwise shading. In humans, unlike chimpanzees, no difference in response times to different shading types was found: the difference in response times between shading directions remained the same for both shading types. Separate parametric three-way ANOVAs (shading type × shading direction × display size) were applied to response time data for each species. For chimpanzees, none of the main effects or interactions were significant. For humans, on the other hand, the main effects of shading direction $[F(1,4) = 18.58, P < 0.05]$, display size $[F(1,4) = 12.75, P < 0.05]$, and their interaction $[F(1,4) = 20.92, P < 0.05]$ were significant.

Discussion

In experiments 2 and 3, when the shaded shape or shading type were changed from a circle or gradual shading, respectively, the difference in performance between shading directions disappeared in chimpanzees. The results for humans are also inconsistent with those in the study of Aks and Enns (1992). They found clear effects of shading type

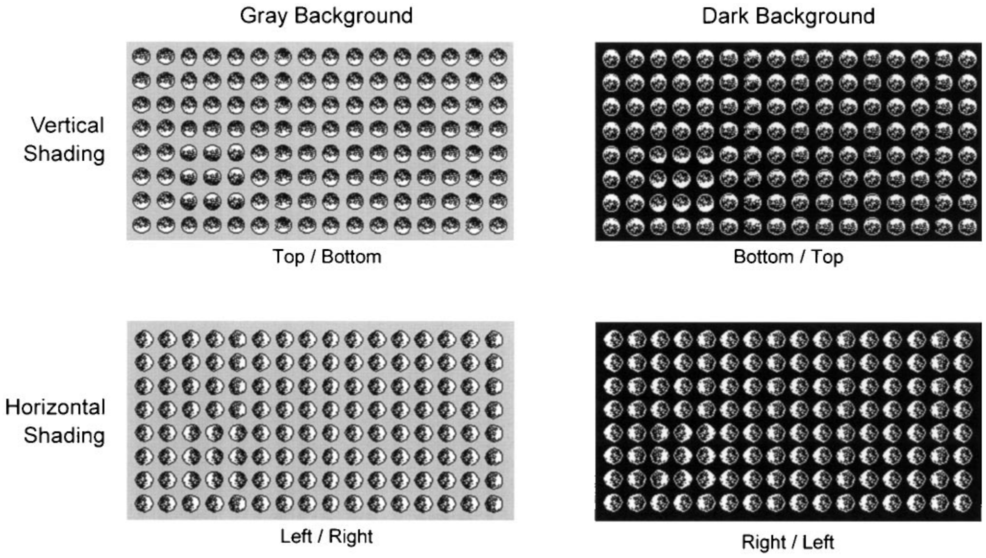

Fig. 6 Examples of texture displays used in experiment 4. All displays have the target area at *bottom left*

and shape (steeper response time functions for stepwise shading and square contour), whereas I found steeper response time functions only for squares with gradual horizontal shading, but no other effect of shading types. My results are more similar to those of Kleffner and Ramachandran (1992) in which they also found flat response time functions for vertical step shading. Various factors may contribute to the inconsistency of results among researchers, such as shading method (dot density gradients or gray-scale gradients), and procedures (difference in response types and experimental designs). In the present experiments, I tested subjects in a mixed design, while Aks and Enns (1992) used a blocked design. A blocked design might encourage subjects to use a constant search strategy during a session, in contrast to a mixed design in which all conditions appear randomly from trial to trial.

To sum up, comparison of the results from chimpanzees and humans suggests that there may be an underlying qualitative differences in processing of shading between the two species, although exactly what this might be is unclear from the experiments described so far.

Experiment 4: texture segregation with shading by the chimpanzee

Kleffner and Ramachandran (1992) also examined the perception of shape from shading using a texture segregation procedure. They found similar results to those from visual search tasks. In experiment 4, I explored the chimpanzee's ability to segregate textures composed of circles with shading for comparison with the results of the visual search experiments. Additionally I tested one other factor that might affect the perception of shape from shading, background luminance (Aks and Enns 1992; Kleffner and Ramachandran 1992). One chimpanzee, was initially trained on texture displays with neutral gray backgrounds (condition 1) and then shifted to sessions in which either gray or dark background appeared randomly (condition 2).

Methods

Subject and apparatus

The subject was one of the chimpanzees, Akira, who had been trained on a texture segregation task immediately before the experiments (M. Tomonaga, unpublished work). The same apparatus was used as in experiments 1–3.

Stimuli

Shading with a dot-density gradient instead of a gray-scale gradient was used (Aks and Enns 1992). Each circle was 1.0 cm in diameter and had a white-line border. The density of white pixels changed gradually from 100% (bright side) to 0% (dark side). The texture display consisted of 16 × 8 circles and the target area of 3 × 3 elements. Figure 6 illustrates some examples of the eight types of texture displays with two different background luminances used.

Procedure

The texture segregation task was identical to that used in the previous experiments (M. Tomonaga, unpublished work). Each trial proceeded as follows. After the 3-s intertrial interval, a white cross (warning signal, 0.5 cm × 0.5 cm) was presented at the center of the bottom row. A single touch on the warning signal resulted in its termination, followed by the presentation of the texture display. If the subject touched a target area, the texture display disappeared, and a 1-s chime and food reinforcer was given to the subject. If the subject touched the background area, the texture display disappeared, but only the 0.5-s error buzzer was was heard. If the subject made an error, the same trial (correction trial) was repeated. After two successive errors, however, only the target area was presented (i.e., the background texture was blank but only colored in gray or black) on the third correction trial.

Akira was tested in two conditions successively. In condition 1, four types of target areas (top-bright, bottom-bright, left-bright, and right-bright) with four different background textures (bottom-bright, top-bright, right-bright, and left-bright, respectively) were displayed with gray background luminance. Four sessions of blocked-trial training in which the same target repeatedly appeared in a trial block were followed by six sessions of mixed-target training in which four targets appeared randomly from trial to trial. After completing condition 1, Akira was immediately shifted to condition 2, in which gray and dark background luminance levels were used. Akira was tested in eight mixed-target sessions. Each session consisted of 64 trials for all conditions. For each condition, mixed-target sessions were used for data analyses. As in experiment 2, experiment 4 involved single-subject designs, and permutation-based factorial ANOVAs were used to analyze the results, as well as correlated *t*-tests with systematic permutations (Edgington 1987).

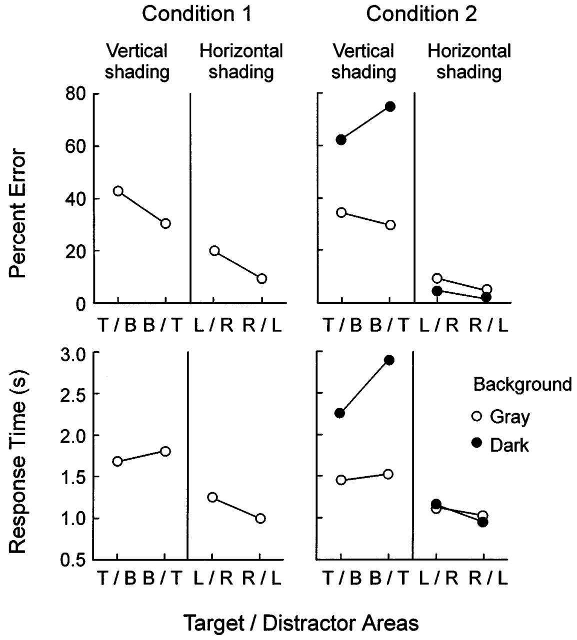

Fig. 7 Results of experiment 4, for condition 1 (gray background, *left*) and condition 2 (gray or dark background, *right*). The mean percentage of errors (*above*) and the mean response times (*below*) are shown (*T* top bright, *B* bottom bright, *L* left bright, *R* right bright)

Results and discussion

Akira made 50% correct responses in the first session and 76.6% on average in the next three blocked-trial sessions. Figure 7 shows the mean percentage of errors and response times for mixed-target sessions for each condition. For condition 1, Akira had difficulty in texture segregation with vertical shading, as in the visual search experiments, in spite of the differences in the task and shading method. Correlated *t*-tests based on systematic permutations showed a significant difference between vertical and horizontal shading [percentage error, $t(5) = 5.653$, $P = 0.0313$; response time, $t(5) = 6.638$, $P = 0.0313$]. When the target and background area were reversed, there was a significant difference in percentage of errors for vertical shading [$t(5) = 2.928$, $P = 0.0313$], but not for horizontal shading [$t(5) = 1.686$, $P = 0.25$], and a significant difference in response times for horizontal shading [$t(5) = 5.515$, $P = 0.0313$] but not for vertical shading [$t(5) = 1.385$, $P = 0.0938$]. For condition 2, when the background luminance was darkened, texture segregation was much worse, especially for vertical shading textures. Two-way ANOVAs with random permutation [background × shading direction (average across two targets for each condition)], with sessions as repeated measures, were used to analyze percentage error and response time data. For percentage error, both the main effects [background, $F(1,7) = 9.56$, $P = 0.019$; shading direction, $F(1,7) = 420.5$, $P = 0.0001$] and their interaction [$F(1,7) = 39.43$, $P = 0.0005$] were significant. For response time also, both main effects and their interaction were significant [background, $F(1,7) = 23.16$, $P = 0.0023$; shading direction, $F(1,7) = 82.78$, $P = 0.0001$; interaction, $F(1,7) = 23.23$, $P = 0.0014$]. Separate correlated *t*-tests based on systematic permutations were used to analyze the effect of the targets. Only the difference in response time between horizontal-shading targets with dark backgrounds was significant [$t(7) = 7.599$, $P = 0.0078$], in spite of the apparently large differences shown in Fig. 7, because of the high variance among sessions.

Akira showed the same pattern of results as found in the visual search experiments of Kleffner and Ramachandran (1992), although the difficulty of the tasks for the chimpanzee was the opposite of that found in humans. Furthermore, the results were consistent with those of Kleffner and Ramachandran (1992) and Aks and Enns (1992), who reported that visual search performance was better for the neutral background than for the dark background. For Akira, this effect was much stronger for vertical than horizontal shading.

As discussed in experiment 1, Kleffner and Ramachandran (1992) also reported search asymmetry. In their visual search experiments, humans detected the concave target faster than convex one. In the present experiment, Akira showed asymmetries in both accuracy and speed. However, the patterns of asymmetry were quite inconsistent, possibly because of effects of transfer from previous visual search experiments. Human infants preferentially reach for an actual or apparent convex target rather than a concave one (Granrud et al. 1985a), which is also inconsistent with the results of Kleffner and Rramachandran (1992). Asymmetry in the perception of shape from shading needs further investigation.

To sum up, the experiment on texture segregation clearly demonstrated that the different patterns of perception of shading direction in chimpanzees and humans found in visual search experiments are replicated in this context. Further, the perception of shape from shading was influenced by the background luminance in the chimpanzee as well as in humans. Chimpanzees and humans have both similarities and differences in the perception of shape from shading. Background luminance might not be critical in perceptual adaptations to the different environments.

General discussion

In the present series of experiments, two chimpanzees were trained in visual search and texture segregation tasks using shaded patterns. Surprisingly, both chimpanzees showed different patterns of performance from humans participating in the experiments under identical conditions. For humans, search was quite fast irrespective of the display size when the shading was vertical, but slower as the display size increased when the shading was horizontal. For chimpanzees, however, search rate was almost the same irrespective of shading directions, and slower for vertical than horizontal shading. The same patterns of results were obtained by the chimpanzee in a texture segregation task. Experiment 1B indicated that these results could not be explained by head rotation or shift of viewpoint parallel to the surface of the monitor. Further tests showed that when the shaded shape not round but square, or the shading type was not gradual but stepwise, the difference in performance between shading directions disappeared in chimpanzees. These results can be interpreted in several ways. These experiments have shown a change in sensitivity to shading directions under some conditions. From our previous studies (Fujita and Matsuzawa 1989; Tomonaga et al. 1993, but see M. Tomonaga, unpublished work), this difference between the species is closely related to their processing of spatial information. The results from experiments on the perception of shape from shading imply that there are important underlying differences between the two species. Tomonaga et al. (1993) and Matsuzawa (1991) proposed that residual adaptations to the three-dimensionally rich arboreal environments had resulted in the difference in sensitivity to orientation. To address this hypothesis we need further experimental investigations (M. Tomonaga, unpublished work) using more elaborate tasks and comparing different species. As noted in the Introduction, K. Fujita and S. Kanazawa (personal communication) found that Japanese macaques (*Macaca fuscata)* showed similar response patterns to humans in texture segregation tasks. Japanese macaques are considered to be terrestrial primates. It is plausible that the environments to which the animals have adapted might affect the perception of shape from shading.

Kleffner and Ramachandran (1992) suggest that the extraction of three-dimensional shape from shading is processed preattentively. The results for humans tested in these experiments are consistent with this view. In contrast, chimpanzees showed "parallel" search for all shading direction conditions. The difference among directions could only be detected in the mean response time averaged across display sizes. One possible interpretation is that the chimpanzees' response time functions were modified by the speed-accuracy trade-off. In fact, the mean percentage of errors for chimpanzees was apparently negatively correlated with display size (see Table 1). As noted in the discussion of experiment 1A, however, this pattern was frequently observed in our chimpanzees, and was interpreted as the sign of a pop-out or grouping effect (Tomonaga 1995; also see Blough 1989).

Another possibility is that the chimpanzees did *not* use depth cues derived from shading. In our experimental setting, neither chimpanzees nor humans need to extract apparent depth to detect an odd target or target area among distractors. If it costs more to extract the depth cues from shading information than to use other cues, the chimpanzees' strategy would rapidly shift to easier cues. This speculation would be supported by the results of experiments 2 and 3 in which the chimpanzees showed quite different patterns of results from humans when additional factors were manipulated. Even if it is true, however, it is still unclear what the easier cues for chimpanzees might be. It is also unlikely that use of alternative cues can explain why the chimpanzees showed the opposite pattern to humans. Furthermore, in the same experimental setting, why did humans use shading information while chimpanzees did not? The chimpanzee visual system might not rely as much on shading information as that of humans. Where could this difference come from? I prefer to interpret this by a hypothesis of ecological constraints on spatial cognition.

A different experimental design is needed to evaluate whether the chimpanzees actually use shading information to extract three-dimensional shape. One candidate is the discrimination and transfer task employed by Hershberger (1970). He first trained chickens to discriminate actual (three-dimensional) convex from concave objects with ambiguous lighting (discrimination based on binocular depth cues), and then tested the transfer of discrimination to photographs of convex and concave objects with shading produced by a single light source coming from "above".

In addition, developmental studies of chimpanzees could also yield important information on the development of the perception of shape from shading. Shading cues are one of the cues of pictorial depth. The development of the perception of pictorial depth has been extensively explored in human infants using cues such as the trapezoidal window illusion (Yonas et al. 1978), familiar size (Granrud et al. 1985a), relative size (Yonas et al. 1985), and also shading (Granrud et al. 1985b). They all reported that 7-month-old infants respond to pictorial cues of depth but 5-month-old infants do not. Granrud et al. (1985b) suggest that infants might become sensitive to all pictorial depth cues simultaneously. For nonhuman primates, on the other hand, we have very little data on the development of the perception of pictorial depth, although there is much more literature about binocular depth cues such as the visual cliff (e.g., Walk and Gibson 1961).

Gunderson et al. (1993) reported that 3- or 4-week-old infants of pigtailed macaques (*Macaca nemestrina*) showed sensitivity to pictorial depth cues of linear perspective and relative size. Hayashibe et al. (1983) reported that 3- or 4-month-old Japanese macaque infants responded to pictorial depth cues of texture gradient using the same procedure as for the visual pitfall test. Unfortunately, we have no information about responses to shading cues or developmental relations among various types of pictorial depth cues. Developmental studies on the perception of pictorial depth in chimpanzees are also lacking. The development of perception of shape from shading, as well as other pictorial depth cues, should be investigated in a range of species adapted to different spatial and visual environments in order to clarify the developmental course of emergence of species differences.

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References

Aks DJ, Enns JT (1992) Visual search for direction of shape is influenced by apparent depth. Percept Psychophys 52:63–74

Asano T, Kojima T, Matsuzawa T, Kubota K, Murofushi K (1982) Object and color naming in chimpanzees (*Pan troglodytes*). Proc Jpn Acad 58B:118–122

Benson KA, Yonas A (1973) Development of sensitivity to static pictorial depth information. Percept Psychophys 13:361–366

Berbaum K, Bever T, Chung C (1983) Light source position in the perception of object shape. Perception 12:411–415

Blough DS (1989) Odd-item search in pigeons: display size and transfer effects. J Exp Psychol Anim Behav Proc 15:14–22

Brewster D (1847) On the conversion of relief by inverted vision. Edinburgh Philos Trans 15:657

Deruelle C, Fagot J (in press) Access to the global and local properties of compound stimuli in a visual search task: effects of perceptual grouping in humans and baboons. Psychonom Bull Rev

Edgington ES (1987) Randomization tests, 2nd edn. Dekker, New York

Fieandt K von (1938) Über Sehen von Tiefengebilden bei Wechselender Beleuchtungsrichtung. Psychological Institute of the University of Helsinki, Helsinki, Finland

Fujita K, Matsuzawa T (1989) Comparison of representational abilities of chimpanzees and humans: short-term memory reproduction and mental rotation (in Japanese with English abstract). Primate Res 5:58–74

Granrud CE, Yonas A, Pattersen L (1984) A comparison of monocular and binocular depth perception in five- and seven-month-old infants. J Exp Child Psychol 38:19–32

Granrud CE, Haake RJ, Yonas A (1985a) Infants' sensitivity to familiar size: The effect of memory on spatial perception. Percept Psychophys 37:459–466

Granrud CE, Yonas A, Opland EA (1985b) Infants' sensitivity to the depth cue of shading. Percept Psychophys 37:415–419

Gunderson VM, Yonas A, Sargent PL, Grant-Webster KS (1993) Infant macaque monkeys respond to pictorial depth. Psychol Sci 4:93–98

Hayashibe K, Tsuji K, Hara M (1983) Analyses of depth perception in infant monkeys and humans (Research report of Grant-in-Aid for scientific research) (in Japanese). Ministry of Education, Tokyo

Hershberger W (1970) Attached-shadow orientation perceived as depth by chickens reared in an environment illuminated from below. J Comp Physiol Psychol 73:407–411

Hess EH (1950) Development of chick's responses to light and shade cues of depth. J Comp Physiol Psychol 43:112–122

Hess EH (1961) Shadows and depth perception. Sci Am 204:138–148

Humphreys GW, Quinlan PT, Riddoch MJ (1989) Grouping processes in visual search: effects with single- and combined-feature targets. J Exp Psychol Gen 118:258–279

Kleffner DA, Ramachandran VS (1992) On the perception of shape from shading. Percept Psychophys 52:18–36

Manly BFJ (1991) Randomization and Monte Carlo methods in biology. Chapman and Hall, London

Matsuzawa T (1991) The visual world of a chimpanzee (in Japanese). University of Tokyo Press, Tokyo

May RB, Masson ME, Hunter MA (1989) Randomization tests: Viable alternatives to normal curve tests. Behav Res Methods Instr Comput 21: 482–483

Metzger W (1936) Gesetze des Sehens. Kramer, Frankfurt

Mingolla E, Todd JT (1986) Perception of solid shape from shading. Biol Cybern 53:137–151

Ramachandran VS (1988a) Perceiving shape from shading. Sci Am 269:76–83

Ramachandran VS (1988b) Perception of shape from shading. Nature 331:163–166

Rittenhouse D (1786) Explanation of an optical deception. Trans Am Philos Soc 2:37–42

Sireteanu R, Rettenbach R (1995) Perceptual learning in visual search: fast, enduring, but non-specific. Vision Res 35:2037–2043

Todd JT, Mingolla E (1983) Perception of surface curvature and direction of illumination from patterns of shading. J Exp Psychol Hum Percept Perform 9:583–595

Tomonaga M (1993a) Use of multiple-alternative matching-to-sample in the study of visual search in a chimpanzee (*Pan troglodytes*). J Comp Psychol 107:75–83

Tomonaga M (1993b) A search for search asymmetry in chimpanzees (*Pan troglodytes*). Percept Mot Skills 76:1287–1295

Tomonaga M (1993c) Facilitatory and inhibitory effects of blocked-trial fixation of the target location on a chimpanzee's (*Pan troglodytes*) visual search performance. Primates 34:161–168

Tomonaga M (1995a) Transfer of odd-item search performance in a chimpanzee (*Pan troglodytes*). Percept Mot Skills 80:35–42

Tomonaga M (1995b) Visual search by chimpanzees (*Pan*): assessment of controlling relations. J Exp Anal Behav 63:175–186

Tomonaga M (1997) Precuing the target location in visual searching by a chimpanzee (*Pan troglodytes*): effects of precue validity. Jpn Psychol Res 39:200–211

Tomonaga M, Matsuzawa T (1992) Perception of complex geometric figures in chimpanzees (*Pan troglodytes*) and humans (*Homo saPiens*): analyses of visual similarity on the basis of choice reaction time. J Comp Psychol 106:43–52

Tomonaga M, Itakura S, Matsuzawa T (1993) Superiority of conspecific faces and reduced inversion effect in face perception by a chimpanzee. Folia Primatol 61:110–114

Walk RD, Gibson EJ (1961) A comparative and analytical study of visual depth perception. Psychol Monogr 75:1–44

Yonas A, Cleaves W, Pettersen L (1978) Development of sensitivity to pictorial depth. Science 200:77–79

Yonas A, Kuskowski M, Sternfels S (1979) The role of frames of reference in the development of responsiveness to shading information. Child Dev 50:495–500

Yonas A, Granrud CE, and Pettersen L (1985) Infants' sensitivity to relative size information for distance. Dev Psychol 21:161–167