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A ground-like surface facilitates visual search in chimpanzees (*Pan troglodytes*)

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Ground surfaces play an important role in terrestrial species' locomotion and ability to manipulate objects. In humans, ground surfaces have been found to offer significant advantages in distance perception and visual-search tasks ("ground dominance"). The present study used a comparative perspective to investigate the ground-dominance effect in chimpanzees, a species that spends time both on the ground and in trees. During the experiments chimpanzees and humans engaged in a search for a cube on a computer screen; the target cube was darker than other cubes. The search items were arranged on a ground-like or ceiling-like surface, which was defined by texture gradients and shading. The findings indicate that a ground-like, but not a ceiling-like, surface facilitated the search for a difference in luminance among both chimpanzees and humans. Our findings suggest the operation of a ground-dominance effect on visual search in both species.

How do human and nonhuman species efficiently search for objects in the real world? Previous studies have shown that the visual system selects the characteristics that are necessary or desired from the large amount of visual information available to recognise objects. For example, some evidence has demonstrated that visual attention is automatically distributed along three-dimensional surfaces[1–4] He and Nakayama (1995) reported that humans engaging in visual-search tasks easily found an odd-coloured target among various numbers of search items even if same-coloured items were presented on steroscopically different surfaces. Morita and Kumada (2003) showed that searches were facilitated when they occurred on a surface defined not only by binocular disparity but also by pictorial depth cues such as perspective and compression.

Furthermore, the importance of the particular kind of "ground" surface has been reported in various kinds of tasks[5–9] McCarley and He (2000, 2001) showed that the detection of an odd-coloured target on a three-dimensional ground-like display was more rapid than that on a three-dimensional ceiling-like display. Their findings suggest that a ground-like surface, which has ecological and behavioural relevance, facilitates texture segregation and perceptual organisation. Bian, Braunstein, and Andersen (2005, 2006) clearly demonstrated the superiority of ground surfaces over ceiling surfaces in the perception of the relative distance of objects. Participants in their experiments relied more on information in contact with the ground surface than to the ground surface for judgments of the relative distance between two cylinders. They referred to this phenomenon as the "ground-dominance effect".

Given that the objects most frequently encountered and manipulated are situated on ground surfaces, such as floors, tables, and so on[10,11], the privileging of attention devoted to ground surfaces among terrestrial species such as humans seems to make ecological sense. However, the way in which arboreal species process the three-dimensional information from different types of surfaces remains unclear. In the present study, we examined how chimpanzees, members of the species that is most closely related to humans but that has different locomotion and spends time both on the ground and in the trees[12], search on three-dimensional surfaces defined by pictorial depth cues.

Previous comparative studies have produced evidence that nonhuman primates perceive depth based on binocular disparity and pictorial depth cues (chimpanzees[13–15]; rhesus macaques[16–18]) in a way that is similar to the process in humans (but please see[19,20]).

In this study, texture gradients and shading cues were used to define surfaces and the target items located on these surfaces to investigate the advantages offered by a ground-like surface to chimpanzees engaged in searching. Following Morita and Kumada's (2003) study, various numbers of identically shaded cubes were arranged on an imaginary ground-like surface or on an imaginary ceiling-like surface. In the present experiment, the depth of surfaces was defined by texture gradients, and the size of each cube became smaller when presented at a higher (more distant) position. During the experiment, both chimpanzees and humans were asked to find the cube with the odd brightness among all the cubes presented on a computer screen. The experiment consisted of two conditions with the ground-like surface and two with the ceiling-like surface. Under the "in-surface" condition, the top face or the bottom face of the target cube was darker than those of other cubes. Under the "not-in-surface" condition, one side of the target cube was darker than that of other cubes.

When a search along a ground-like surface is efficient, targets can be detected more rapidly under the in-surface than under the not in-surface condition. When a search along a ceiling-like surface is inefficient, the conditions should not differ with respect to search times. Based on these hypotheses, if chimpanzees, like humans, demonstrated the ground-dominance effect in visual-search tasks, we would expect to find efficient searches in both species only under conditions including the ground-like surface.

Results

The experiment investigated the effect of ground-like and ceiling-like surfaces, defined by texture gradients and shading cues, on the search for a cube with different degrees of brightness that was or was not located on the surface.

Figure 1 shows the mean correct RTs for the search on the ground-like and ceiling-like surfaces as a function of the number of items under each condition. We used the median for each subject for calculation of the mean RTs to increase the statistical power. Among chimpanzees, the search time on the ground-like surface was faster under the in-surface condition than under the not-in-surface condition, whereas we found only minimal differences in the RTs between the in-surface and the not-in-surface conditions on the ceiling-like surface. Overall, the search times decreased as the number of items increased. A three-way repeated-measures ANOVA with surface (2) × condition (2) × display size (3) for chimpanzees revealed significant main effects of display size [$F(2, 10) = 47.14, p < 0.001$] and a significant interaction between surface and condition [$F(1, 5) = 45.51, p < 0.01$]. *Post hoc* analysis further revealed a simple main effect of condition when the ground-like

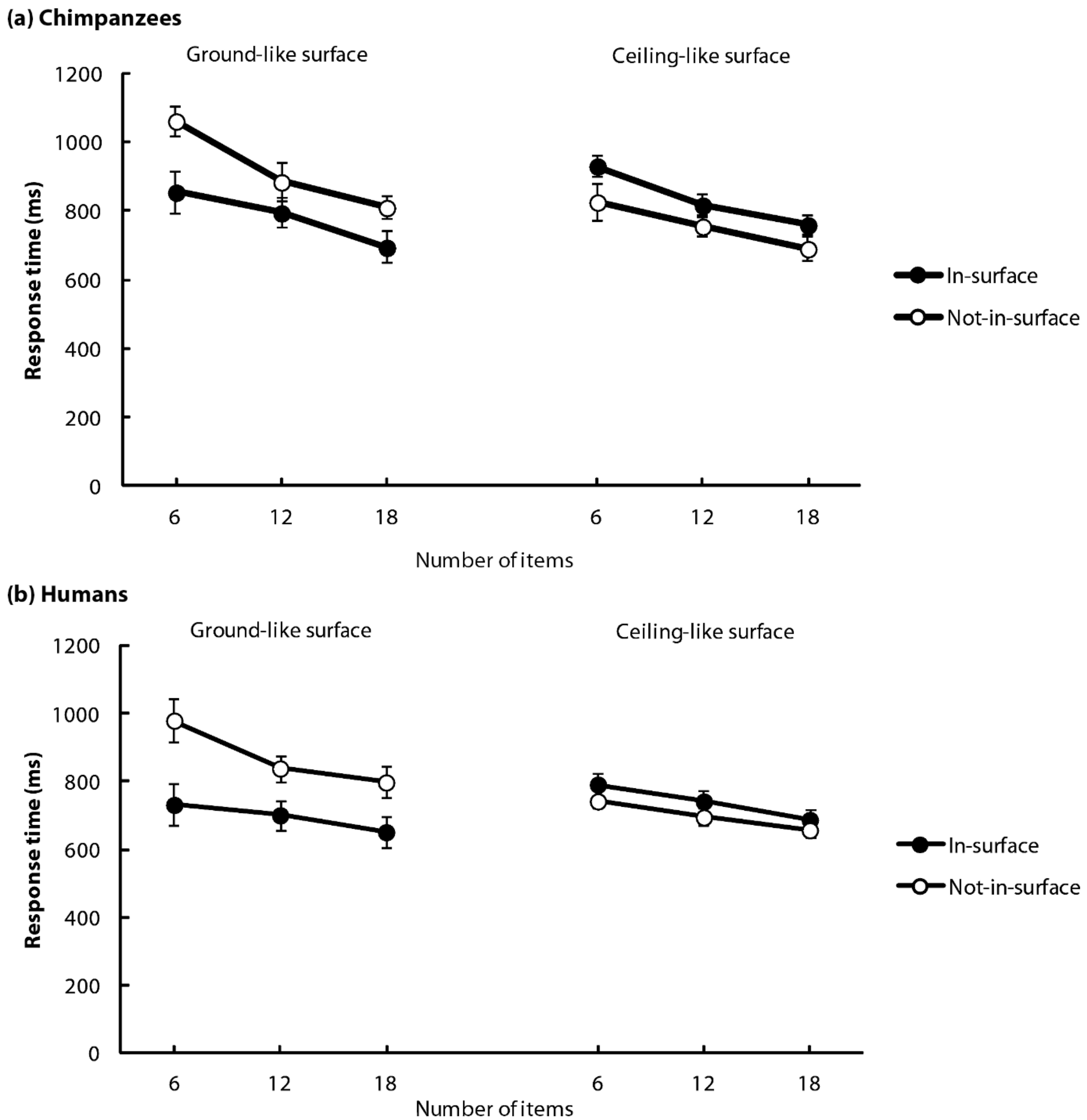

Figure 1 | Mean correct response times as a function of the number of items under each condition with each surface ((a) chimpanzees; (b) humans). Error bars show standard errors of the mean.

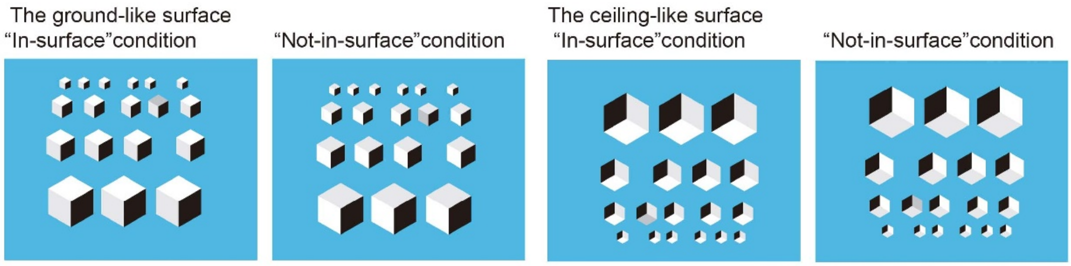

Figure 2 | A sample of the search displays. The search displays in each experiment consisted of in-surface and not-in-surface conditions using a ground-like and a ceiling-like surface. Each display includes 18 search items.

surface was used [$F(1, 10) = 37.01, p < 0.001$] and when the ceiling-like surface was used [$F(1, 10) = 11.97, p < 0.01$]. Additionally, *post hoc* analysis revealed a simple main effect of surface under the not-in-surface condition [$F(1, 10) = 7.86, p < 0.05$].

Among humans, the search time under the in-surface condition on the ground-like surface was faster than that under the not-in-surface condition, whereas we found only minimal differences in the RTs between the in-surface and the not-in-surface conditions on the ceiling-like surface. The search times for both surfaces decreased depending on the number of items. A three-way repeated-measures ANOVA with surface (2) × condition (2) × display size (3) for humans revealed significant main effects of surface [$F(1, 9) = 5.47$, $p < 0.05$], condition [$F(2, 18) = 10.76, p < 0.05$] and display size [$F(2, 18) = 24.28, p < 0.001$], and a significant interaction between surface and condition [$F(2, 18) = 23.91, p < 0.01$]. *Post hoc* analysis revealed a simple main effect of condition on the ground-like surface [$F(1, 18) = 33.87, p < 0.001$]. Additionally, *post hoc* analysis revealed a simple main effect of surface under the not-in-surface [$F(1, 18) = 24.05, p < 0.001$] conditions.

Discussion

The current study investigated whether chimpanzees would demonstrate the ground-dominance effect when the ground-like surface was defined by shading and texture gradients. The findings demonstrated that the ground-like surface facilitated search performance among chimpanzees as well as humans; however, the ceiling surface did not affect the search results. These findings are consistent with the previous studies showing that the ground surface bears more ecological importance than the ceiling surface[5,6].

These results suggest that the optical contact that identifies apparent contact between an object and the background in a two-dimensional image[10] may facilitate the perception of an imaginary surface and the efficient detection of a discrepancy in the degree of luminance of the objects on such a surface. These findings show that chimpanzees, a species whose locomotor system differs from that of humans, show the ground-dominance effect when performing a visual-search task, implying that chimpanzees and humans experience similar attentional processes when searching in a three-dimensional space.

Previous comparative studies have investigated the sensitivity to various kinds of depth cues, such as binocular disparity, motion information, and pictorial depth cues[13–18]. However, the way in which nonhuman animals search for objects in three-dimensional space has been unclear. The findings of the present study using a visual-search task suggest that both chimpanzees and humans distribute attention along a ground-like surface defined by shading and texture gradients. These findings imply that the ground surface is important for both human and nonhuman species when searching for objects. To further confirm the general importance of ground surface in nonhuman animals, we should also examine the ground-dominance effects in different tasks, such as perceptions of relative distance.

The current study demonstrates that the dominance of ground-like surfaces in a visual search is shared by chimpanzees and humans. This finding implies that the ground surface is highly important even in species that spend much time in trees. However, the relationship between locomotion and the extent of the ground-dominance effect remains unclear. To address this issue, it will be necessary to investigate how ground dominance develops. Interestingly, developmental studies of human infants have reported that the ability to perceive three-dimensional depth from pictorial cues, such as texture gradients and shading, develops by 6 months after birth[21,22], which is earlier than the maturation of locomotion. Future research should investigate whether the extent of the ground-dominance effect changes before or after development of the ability to move. Recent studies show that wild chimpanzees spend a time at least a third of their time on the ground[23]. In captivity, they might spend more time on the ground[24]. It will be also required to compare the extent of the ground-dominance effect using mostly arboreal species (e.g., gibbons). Further developmental and comparative research will contribute to understanding the characteristics and the evolutionary value of human visual processing.

Methods

Participants. *Humans*. Ten humans (two males and eight females) between the ages of 18 and 27 years participated in this experiment. All participants had normal or corrected-to-normal vision. Informed consent was obtained from all human participants.

Chimpanzees. Six chimpanzees (*Pan troglodytes*) (Ai, 29-year-old female; Ayumu, 6-year-old male; Chloe, 25-year-old female; Cleo, 6-year-old female; Pendesa, 29-year-old female; and Pal, 6-year-old female) participated in the experiment. All chimpanzees lived at the Primate Research Institute of Kyoto University with other group members in an enriched outdoor enclosure. They were not food-deprived and were fed fruits, vegetables, and monkey chow three times each day during the period of experimentation. The chimpanzees had previously engaged in various kinds of computer-controlled perceptual and cognitive tasks, including visual-search tasks[19,20,25–28]. The present study of humans and chimpanzees was approved by the Animal Welfare and Animal Care Committee of the Primate Research Institute of Kyoto University, and the chimpanzees were tested and cared for according to "The Guide for the Care and Use of Laboratory Primates, 2nd edition" issued by the ethics committee of the Primate Research Institute of Kyoto University (2002).

Apparatus. The experiments with chimpanzees and humans were conducted in an experimental booth (1.8 × 2.15 × 1.75 m) adjacent to the chimpanzee facility. Stimuli were presented on a 17-in colour LCD monitor with touch-screen device (I-O DATA, LCD-AD-171F-T) located 40 cm above the floor. The resolution of the monitor was 1,280 × 1,024 pixels, and the viewing distance was approximately 40 cm. The monitor was protected by a transparent Plexiglas panel, and subjects could touch the monitor through an armhole (38.5 × 12 cm). A food dispenser (Biomedica BUF-310) delivered rewards to the chimpanzees following each correct trial via the food trays attached below the monitor. All experimental events and responses were controlled by a computer (Hewlett-Packard Compaq, PM215AV) located outside the experimental booth.

Materials. Figure 2 shows examples of stimuli used in this study. We prepared search displays in which four, six, 12, or 18 cubes were arranged on the imaginary ground or ceiling surfaces. The cubes consisted of three diamond shapes, and each face had different luminance (black: 0.04 cd/m^2; light grey: 74.68 cd/m^2; white: 112 cd/m^2). These cubes were presented on a light blue background (37.36 cd/m^2). Placed among the identical cubes was one cube (target) with a dark-grey (37.36 cd/m^2) instead of a light-grey face at the top, bottom, or side. The size of the cube was changed according to the depth of the three-dimensional surfaces. Four cube sizes were prepared (3.1 × 3.5 deg, 4.7 × 4.8 deg, 6.6 × 7.4 deg, 9.6 × 11.0 deg).

Methods. *General method*. Each trial began with the presentation of a grey square at the bottom centre of the computer screen. As soon as a chimpanzee or human touched the square, a search display appeared. The search display consisted of one target and different numbers of distractors. Each stimulus was presented at 18 predetermined positions. The configuration of the stimuli was randomly changed from trial to trial. If a chimpanzee or a human touched the target, the search display disappeared, followed by the presentation of a chime. A food reward (a small piece of apple) was provided for the chimpanzees only. If participants touched one of the distractors, the search display disappeared, but a buzzer sound was presented as error feedback. Response time (RT) was defined as the time from the onset of the search display to the touch of the stimulus. Following an error trial, the target was presented alone (correction trials). The correction trials were inserted to maintain chimpanzees' motivation to complete the task. The intertrial interval was 2 sec.

Training. Before participating in the testing with cubes, each chimpanzee received three training sessions. In the first training, only one face of a cube was presented on a light blue background. Each chimpanzee was trained to touch a dark grey diamond shape (target) among four white diamond shapes (distractors). Next, two faces of a cube were used. A target was composed of a combination of a dark grey diamond shape and a black diamond shape, and distractors were composed of a combination of a white diamond shape and a black diamond shape. Finally, a cube created by adding a light grey face was used. Each chimpanzee was trained to choose a cube with a dark grey face from among four cubes with a light grey face. Each training session consisted of 36 trials. Each training phase was continued until the rate of correct responses exceeded 90% in two consecutive sessions. All chimpanzees satisfied the performance criterion within 26 training sessions. Humans participated in two training sessions using cubes (corresponded to last training phase in chimpanzees) before testing.

Test. During test sessions, six, 12, or 18 cubes were presented on a light blue background. The sessions consisted of two conditions. Under the in-surface condition, a unique face appeared along the imaginary surface, whereas under the not-in-surface condition, no unique face appeared along the imaginary surface. The effect of a three-dimensional surface on the search performance was examined by comparing the reaction times (RTs) for detecting a target under these two conditions. Each session consisted of 108 trials: 2 conditions $\times$ 3 display sizes $\times$ 18 target positions. Each chimpanzee participated in six sessions with the ground-like surface and six with the ceiling-like surface, and each human participated in one session with the ground-like surface and one with the ceiling-like surface.

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Author contributions

T.I. and M.T. conceived the experiments. T.I. performed the experiments, and analysed the data. Both authors co-wrote the paper, and discussed the results and commented on the manuscript.

Additional information

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