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# Differences between chimpanzees and humans in visual temporal integration

## SUBJECT AREAS:

EVOLUTIONARY  
DEVELOPMENTAL  
BIOLOGY

DEVELOPMENTAL BIOLOGY

PSYCHOLOGY

ANIMAL BEHAVIOUR

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30 April 2013Accepted  
25 September 2013Published  
19 November 2013Correspondence and  
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**Humans have a superior ability to integrate spatially separate visual information into an entire image. In contrast, comparative cognitive studies have demonstrated that nonhuman primates and avian species are superior in processing relatively local features; however, animals in these studies were required to ignore local shape when they perceived the global configuration, and no studies have directly examined the ability to integrate temporally separate events. In this study, we compared the spatio-temporal visual integration of chimpanzees and humans by exploring dynamic shape perception under a slit-viewing condition. The findings suggest that humans exhibit greater temporal integration accuracy than do chimpanzees. The results show that the ability to integrate local visual information into a global whole is among the unique characteristics of humans.**

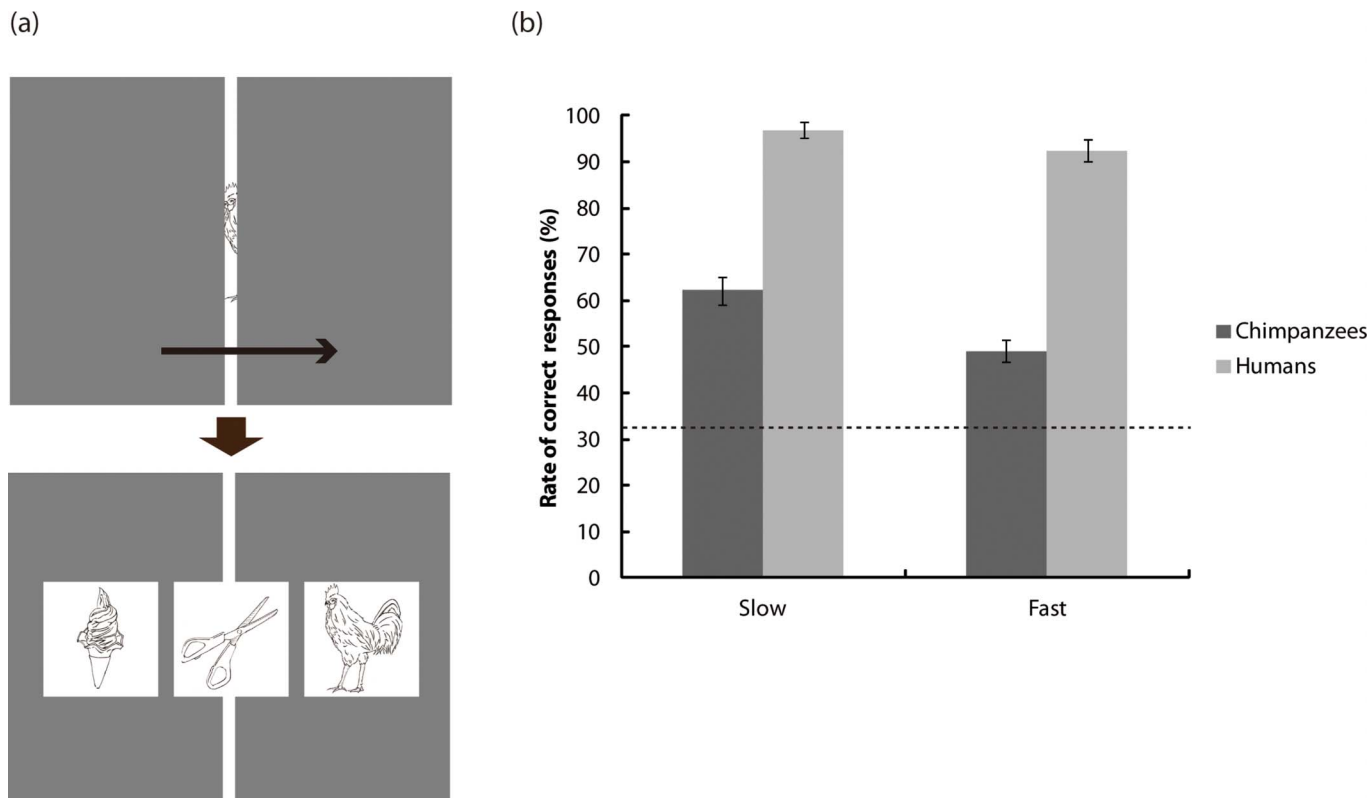
Comparative cognitive studies have clarified that the processing of global configuration is a unique characteristic of human vision<sup>1</sup>. For example, in response to a hierarchical stimulus consisting of a larger figure comprised of arrangements of smaller component shapes, humans tend to prioritise global over local information<sup>2</sup>, whereas non-human animals, such as birds and primates, tend to prioritise the local features of such stimuli (pigeons<sup>3</sup>; monkeys<sup>4-6</sup>; chimpanzees<sup>5,7,8</sup>). Studies using other types of stimuli have also found differences between humans and avian species in perceptual organisation<sup>9</sup>. In support of local processing, birds perceive reversed visual illusions (Ebbinghaus-Titchener illusion<sup>10</sup>; Zollner illusion<sup>11</sup>) and do not complete partly occluded objects<sup>12,13</sup>. Studies of primates closely related to humans have also reported large individual variations and different results depending on experimental procedures, such as stimulus size and distances between elements<sup>14,15</sup>. In contrast, developmental studies in humans have suggested that 3- and 4-month-old infants are more sensitive to the global level of visual stimuli<sup>16,17</sup>, although individual variations have been found depending on the amount of time that infants tend to fixate on stimuli<sup>18</sup>.

However, these previous studies using hierarchical stimuli required both humans and animals to ignore local shape when they perceived the global configuration. As studies of human infants and children have reported<sup>19,20</sup>, it is difficult to identify whether such species differences are due to the allocation of visual attention or to the ability to integrate local features into a global image.

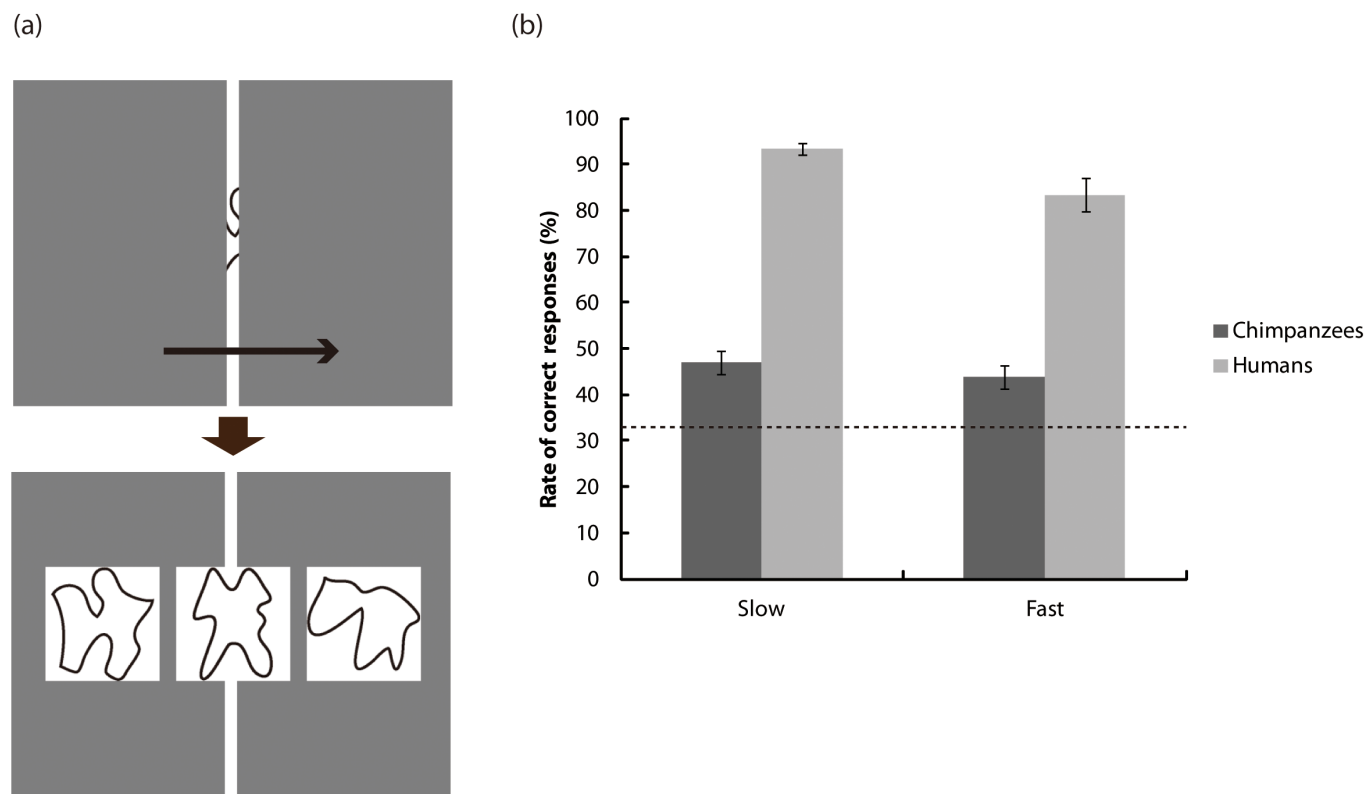
In the present study, we used a “slit-viewing (anorthoscopic-viewing) task”. Anorthoscopic perception occurs when an object is moving behind the slit<sup>21-23</sup>. Under the slit-viewing condition, the observer can not only see a part of an object at a time, however, it is possible to report the whole shape of an object by integrating the fragmented visual information. In recent studies, it has been used as a paradigm for measuring the ability of spatio-temporal integration in humans<sup>24-26</sup>. Chimpanzees and humans have engaged in a “slit-viewing task” to compare their abilities to integrate visual information into an entire image. In this task, a line drawing of a daily object or nonsense figure is moved behind a narrow slit, and this is followed by three line drawings presented on a monitor screen (Figs. 1a and 2a). In the present study, participants were required to choose the same drawing among three alternatives.

## Results

**Line drawings of the objects.** The mean rates of correct responses were lower among chimpanzees than among humans under both speed conditions (Fig. 1b). A two-way analysis of variance (ANOVA) with species (2) × speed (2) revealed significant main effects of species [ $F(1, 10) = 231.00, p < 0.001$ ] and speed [ $F(1, 10) = 13.48, p < 0.001$ ]. However, the line drawings of objects used in this experiment were so familiar to humans that the performance of chimpanzees may have been underestimated. To exclude this possibility, we examined nonsense figures, which were novel to both species.



**Figure 1** | (a) An example of the stimulus displays used in a slit-viewing task. A black line drawing is moving behind the slit from left to right, followed by three items presented on a monitor screen. (b) Performance of chimpanzees and humans under the slow and fast conditions.



**Figure 2** | (a) An example of the nonsense figures and stimulus displays used in a slit-viewing task. (b) Performance of chimpanzees and humans under the slow and fast conditions.



**Nonsense figures.** The mean rates of correct responses were lower among chimpanzees than among humans (Fig. 2b). A two-way ANOVA with species (2)  $\times$  speed (2) revealed significant main effects of species [ $F(1, 10) = 212.06, p < 0.001$ ] and speed [ $F(1, 10) = 5.03, p < 0.05$ ]. These findings suggest that the humans were better able to integrate local visual information into a whole global image than were chimpanzees. In a sequential presentation task, we examined whether the chimpanzees' inferior performance was due to preferential processing of local features.

## Discussion

In this study, we compared the spatio-temporal visual integration of chimpanzees and humans by exploring dynamic shape perception under a slit-viewing condition. We found that both chimpanzees and humans integrated spatio-temporal visual information but that the extent of the integration differed between species. The findings with nonsense figures demonstrated that semantic processing couldn't account for the species differences. These findings are consistent with those of previous studies of spatial integration in nonhuman primates. Our results show that the ability to integrate motion and shape information may be more prominent in humans than chimpanzees.

Although the fundamental mechanism of motion perception in chimpanzees has not been studied well, some studies have found species differences in terms of motion integration processing<sup>27–29</sup>. For example, humans have a great advantage when detecting a stationary dot among consistently moving rather than randomly moving dots; however, chimpanzees have not shown any differences in performance based on motion coherence<sup>27</sup>. These findings suggest that humans are superior to chimpanzees with respect to organising coherently moving objects. As another example, humans observing the “stream-bounce display”, which consists of two identical disks approaching each other, overlapping, and separating, tend to interpret this display as streaming rather than as bouncing, even though it can be interpreted in terms of both streaming and bouncing. In contrast, chimpanzees do not show a bias toward a “streaming” perception. This species difference can be explained in terms of abilities related to spatio-temporal integration<sup>28</sup>. The findings of dynamic shape perception under the slit-viewing condition extend the evidence for relative local biases in spatial and temporal processing by chimpanzees.

In humans, functional magnetic resonance imaging (fMRI) studies have shown that such spatio-temporal integration under a slit-viewing condition evokes responses in the ventral occipital complex and motion complex<sup>26</sup>. These cortical networks are implicated in the other type of motion-defined grouping task in which the fragmented line drawings are integrated into one object<sup>30</sup>. Although the neurophysiological processes of nonhuman primates during slit viewing remain unclear, recent fMRI studies using the same paradigms and stimuli in humans and monkeys have shown pronounced differences in the middle part of the intra-parietal sulcus, which has been implicated in three-dimensional motion perception, including visuomotor control of actions<sup>31–33</sup>. Species differences between chimpanzees and humans reported in behavioural studies may carry further implications for neurophysiological research.

## Methods

**Participants.** Eight humans (mean age, 21.4 years) participated in a slit-viewing task. All participants had normal or corrected-to-normal vision. Four chimpanzees (*Pan troglodytes*) (Ai, 33-year-old female; Ayumu, 9-year-old male; Cleo, 9-year-old female, and Pal, 9-year-old female) participated in a slit-viewing task. All chimpanzees lived in an enriched outdoor enclosure at the Primate Research Institute of Kyoto University with other group members. They were fed fruits, and vegetables three times daily during the experimental period. These chimpanzees have previously engaged in various kinds of computer-controlled perceptual and cognitive tasks<sup>27,29,34–36</sup>. The experimental protocol 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). The human participants were undergraduate students, who participated in the experiment voluntarily. Informed consent was obtained from all human participants.

**Apparatus.** The experiments with chimpanzees and humans were conducted in an experimental booth (1.8  $\times$  2.15  $\times$  1.75 m) adjacent to the chimpanzee facility. Stimuli were presented on an 18.1-inch colour LCD monitor with a touch-screen device (Iiyama, A4146D) located 40 cm above the floor. The resolution of the monitor was 1,280  $\times$  1,024 pixels with a refresh rate of 60 Hz, and the viewing distance was approximately 40 cm. The monitor was protected by a transparent Plexiglas panel, and participants could touch the monitor through an armhole (38.5  $\times$  12 cm). A food dispenser (Biomedica BUF-310) delivered rewards to the chimpanzees following each correct trial via 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.** The stimuli were black-and-white line drawings or nonsense figures containing the images shown in Figures 1a and 2a. The lines of figures were black (0.04 cd/m<sup>2</sup>) and the background was white (112 cd/m<sup>2</sup>). We used 40 types of objects and nonsense figures subtended approximately 6–7° of visual angle<sup>25,26</sup> (the original images were constructed by Snodgrass and Vanderwart<sup>37</sup>, and Endo et al.<sup>38</sup>). A grey surface (74.68 cd/m<sup>2</sup>) with a slit in the centre was used to partially occlude the image. The widths of the slit were 6 pixels (0.31°), 18 pixels (0.93°), and 30 pixels (0.55°). The image was translated at 14.3°/sec under the fast condition and at 7.15°/sec under the slow condition. The item always moved from left to right once per trial.

**Procedure.** A line drawing of an object or nonsense figure moved behind a slit at either a slow or fast speed, followed by three items presented on a monitor screen. One of the three items was identical to a drawing that previously moved behind the slit. The task was to select this same drawing from among the three alternatives. Before testing, the chimpanzees were trained to choose the correct item under a condition in which whole images were presented in front of the slit. Each block consisted of 120 trials (40 items  $\times$  3 slit widths) under each speed condition. It took the chimpanzees 2–7 blocks to meet the criterion of a >90% correct response rate during consecutive sessions.

Data from the trials with the narrowest slit were used for analyses. The remaining slit width conditions were provided for chimpanzees to keep the motivation for the task. However, it might be wide enough for humans to use a local cue. The trials with other conditions were excluded from the analysis. Data from 10 test blocks in total from all chimpanzees and one test block in total from all humans were used for analyses.

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## Acknowledgments

This study was financially supported by the JSPS-MEXT Grants in Aid for Scientific Research (196211, 21830053, 23135516, and 23700312 to T.I., 20002001, and 23220006 to M.T.), Global COE Programs (A06, D07), and the Benesse Corporation. We thank T. Kaneko, I. Adachi, M. Hayashi, and T. Matsuzawa for their helpful support and suggestions. We also thank the members of the Center for Human Evolution Modeling Research and the Language and Intelligence Section of the Primate Research Institute for technical advice and support and for their care of the chimpanzees. We appreciate T. Hasegawa for preparing figure 1.

## Author contributions

T.I. and M.T. were involved in study design; T.I. collected and analysed data; T.I. and M.T. discussed the results and wrote main manuscript text.

## Additional information

**Competing financial interests:** The authors declare no competing financial interests.

**How to cite this article:** Imura, T. & Tomonaga, M. Differences between chimpanzees and humans in visual temporal integration. *Sci. Rep.* **3**, 3256; DOI:10.1038/srep03256 (2013).



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