Body Perception in Chimpanzees (*Pan troglodytes*): The Effect of Body Structure Changes

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Gao, J., & Tomonaga, M. (2020). Body perception in chimpanzees (*Pan troglodytes*): The effect of body structure changes. *Journal of Comparative Psychology*. Advance online publication. <https://doi.org/10.1037/com0000214>

[This is the final accepted manuscript.]

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This study was supported by the Ministry of Education, Culture, Sports, Science and
Technology of Japan (MEXT)/Japan Society for the Promotion of Science (JSPS) KAKENHI
(23220006, 24000001, 15H05709, 16H06283, and 18J21474), JSPS-LGP-U04, JSPS Core-to-
Core CCSN, National BioResource Project-Great Ape Information Network, and MEXT
Scholarship (#152121). The authors thank Drs. T. Matsuzawa, I. Adachi, M. Hayashi, Y. Hattori
and T. Takashima, and other colleagues of Language and Intelligence Section. Thanks are also
due to staff of the Center for Human Evolution Modeling Research at the Primate Research
Institute for taking care of the chimpanzees. We also thank Kumamoto Sanctuary for providing
chimpanzee photos.

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Abstract

Chimpanzees have been found to show the inversion effect to visual stimuli of intact chimpanzee bodies, suggesting that they have a specific way of body processing. In this study, we examined how changes of body structures affect the inversion effect to reveal the properties of their body processing. We focused on two aspects of body structures: the first-order relations (i.e. body part arrangements), and body proportions. The experimental conditions had stimuli of chimpanzee bodies with scrambled first-order relations in Experiment 1, and chimpanzee bodies with distorted body proportions in Experiment 2. Both experiments had a control condition consisting of stimuli of intact chimpanzee bodies. Seven chimpanzees participated in matching-to-sample tasks on touch screens. In each trial, the stimuli were chimpanzee bodies with the same kind of manipulation of body structures and were either all upright or all inverted. We compared their performances in the upright and inverted trials to examine the inversion effect. The chimpanzees did not show any inversion effect to scrambled bodies, but showed the inversion effect to distorted bodies and to intact bodies. The results suggest that chimpanzees' configural body processing relies on correct first-order relations, and distorted body proportions do not interfere with configural processing. It also implies that chimpanzees may have knowledge of the arrangement of body parts, but they may be less sensitive to body proportions. This study could facilitate the understanding of the evolution of visual processing of bodies, faces, and other objects.

Keywords: body perception, inversion effect, configural processing, body structure,

chimpanzees

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This study aims to investigate how changes of body structures influence the body perception of chimpanzees, based on the knowledge of their processing of bodies with normal structures (Gao & Tomonaga, 2018). We hope to reveal detailed mechanisms of chimpanzees' body processing by using stimuli of abnormal chimpanzee bodies, in order to understand the evolution of body processing and why bodies are processed differently from other objects. We also hope the study could shed light on chimpanzees' understanding of body structures to provide an evolutionary perspective on how objects are configured by animals.

Bodies are important social cues for animals. Chimpanzees, for example, can recognize other individuals based on bodies (Martinez & Matsuzawa 2009; Matsuzawa, Tomonaga, & Tanaka, 2006). They learn to use tools, in part, by viewing others' body actions (Matsuzawa, Humle, & Sugiyama, 2011), and use various kinds of bodily gestures for social communication (Hobaiter & Byrne, 2014). They use their own bodies for foraging, and other daily activities (Matsuzawa, Humle, & Sugiyama, 2011). Behind these behaviours, there must be certain specific perceptions and understanding in chimpanzees' minds of their bodies and how bodies are structured. The understanding of body structures might facilitate discrimination between conspecifics and other species and, potentially, special care for individuals with disabilities (Hirata, Hirai, Nogami, Morimura, & Uono, 2017; Matsumoto, Itoh, Inoue, & Nakamura, 2016), which is vital for their living. Additionally, as humans' closest living relatives, chimpanzees' understanding of their body structures could shed light on the evolutionary path of humans' perception of bodies.

In a previous study, Gao & Tomonaga (2018) found that chimpanzees show the inversion effect when visually recognizing bodies. They had better performances in recognizing chimpanzee bodies when they were upright compared to when they were inverted in a matching-to-sample task. The inversion effect suggests that chimpanzees use configural processing when recognizing bodies, that is, they use global cues of the body configuration instead of focusing on features of local parts of bodies. If they use cues of local features, the inversion would not deteriorate the performances very much. The inversion effect has been used as a robust index for configural processing (reviewed in Maurer, Le Grand, & Mondloch, 2002). Chimpanzees did not show the inversion effect to house stimuli in the previous study, suggesting a unique way to process bodies that is different from what is used for other objects.

The inversion effect has been found for body recognition in humans (e.g. Peelen & Downing, 2007; Quinn, Lee, Pascalis, & Slater, 2007; Reed, Stone, Bozowa, & Tanaka, 2003; Reed, Stone, Grubb, & McGoldrick, 2006; Yovel, Pelc, & Lubetzky, 2010) and capuchin monkeys (Matsuno & Fujita, 2018). The inversion effect and configural processing are not limited to bodies, actually. It has also been found for faces (e.g. humans: Carey, 1992; Diamond & Carey, 1986; Yin, 1969; chimpanzees: Dahl, Rasch, Tomonaga, & Adachi, 2013; Parr, Dove, & Hopkins, 1998; Tomonaga, 1999; Tomonaga & Imura, 2015), dogs, birds, and cars when the viewers were experts (Diamond & Carey, 1986; Gauthier, Skudlarski, Gore, & Anderson, 2000; Hagen & Tanaka, 2019), and a series of artificial objects called “Greebles” after the viewers were trained to be experts (Gauthier & Tarr, 1997; Gauthier, Williams, Tarr, & Tanaka, 1998). It was concluded that the objects invoking the inversion effect (and configural processing) need

to meet the following three criteria (Diamond & Carey, 1986). 1) Each class of this kind of stimuli need to share a common layout of elements. For example, all faces have two eyes above a nose, which is above a mouth; all bodies have a head on top of the torso, and arms all connect to the torso from the shoulder part. This spatial arrangement of distinguishing parts is called the first-order relations. 2) The stimuli of each class are identified by the different space between the first-order relational features. The spacing between the distinguishing features is called the second-order relations. Humans can detect at least one minute different of the angle of facial part placements (Haig, 1984), which makes it possible to distinguish faces where the eyes, noses, and mouths are in similar shapes. 3) The viewers should be able to exploit the second-order relation cues, that is, experience mediates the effect, such that dog experts showed the inversion effect to dogs but the novices did not (Diamond & Carey, 1986). The Greebles are a series of objects that share the first-order relations and differ in the second-order relations, and humans are able to develop configural processing after training to be experts (Gauthier & Tarr, 1997; Gauthier, Williams, Tarr, & Tanaka, 1998).

Bodies, apparently, also fall in one of these classes that meet the above three criteria and could invoke the inversion effect. It is necessary to dig deeper if we want to understand the underlying mechanisms of chimpanzees' configural body processing. The inversion effect suggests the use of configural processing, but if we consider only the inversion effect shown to intact bodies, this by itself cannot reveal which aspect of configural processing is used (Maurer, Le Grand, & Mondloch, 2002). Maurer and colleagues suggested that in face recognition, the configural processing has three aspects. The face inversion effect was

diminished by scrambling facial parts (e.g. Bentin, Allison, Puce, Perez, & McCarthy, 1996; Tanaka & Farah, 1993). This finding shows that the configural face processing relies on correct arrangement of facial parts, i.e. the first-order relations of faces. The variation in second-order relations are also important for invoking the configural processing. When all facial parts remained exactly the same, and only the space between them changes in each face, the inversion effect was found (Le Grand, Mondloch, Maurer, & Brent, 2001). On the contrary, when the spacing were the same and only facial features differ, there was no inversion effect and humans tend to use featural cues. The third aspect is that faces are processed holistically. Humans have better performance in naming the owner of a facial part when it is presented within the whole face, compared to when presented alone (Tanaka & Farah, 1993).

For body recognition, Reed and colleagues (2006) found that humans' configural processing relies on correct first-order relations, which is shared in face recognition (reviewed in Maurer, Le Grand, & Mondloch, 2002). They tested body recognition in a detection task. When they used human bodies with misaligned body parts, the inversion effect was gone. Similar results were reported in other studies in human adults (Gliga & Dehaene-Lambertz, 2005; Yovel, Pelc, & Lubetzky, 2010), 3-month-old human infants (Gliga & Dehaene-Lambertz, 2005), and capuchin monkeys when they recognize human bodies (Matsuno & Fujita, 2018). Studies in human infants showed that 3.5-month-old infants could discriminate between intact bodies and bodies with abnormal first-order relations, and between intact bodies and bodies with abnormal body proportions. They could make both discriminations when bodies were upright, but not when they were inverted (Zieber, Bhatt, Hayden, Kangas, Collins,

& Bada, 2010; Zieber, Kangas, Hock, & Bhatt, 2015). This finding suggests that young infants are sensitive to the first-order relations of bodies and body proportions. However, as they did not test the inversion effect directly, it is not clear how configural processing works in human infants, especially the aspect about body proportions.

In order to understand the evolution of body processing, detailed examination of body processing of chimpanzees is necessary. We investigated whether chimpanzees have similar properties in body processing with humans. At the same time, we compared the properties of face processing and body processing. There are many aspects to investigate in chimpanzees' configural body processing. We focused on two kinds of body structures in this study. Firstly, we examined the function of the first-order relations of bodies in the configural processing. We then compared the results with those in humans (Reed, Stone, Grubb, & McGoldrick, 2006) and with face processing in terms of first-order relations (Maurer, Le Grand, & Mondloch, 2002). Secondly, inspired by the studies in human infants (Zieber, Bhatt, Hayden, Kangas, Collins, & Bada, 2010; Zieber, Kangas, Hock, & Bhatt, 2015), we also studied the function of body proportions in the body processing. Although it is under debate whether body proportion is corresponding to the second-order relations of faces (Reed, Stone, Grubb, & McGoldrick, 2006; Zieber, Bhatt, Hayden, Kangas, Collins, & Bada, 2010), examining the possible effects of changing this kind of body structure on body configural processing might provide indirect information for the comparison of face and body recognition. We tested the inversion effect using stimuli of chimpanzee bodies with abnormal first-order relations and abnormal body proportions, respectively. The results might also help understand the body "prototype" in

chimpanzees.

Gao & Tomonaga (2018) tested the inversion effect in several different conditions. There was not a condition where the body parts were misaligned in that study, but there were several where the head was missing or blurred. We found that the inversion effect was gone when the head was missing or blurred, but it was not affected when the other body parts except for the head were blurred. Therefore, we concluded that the head plays a more important role in invoking the inversion effect than the rest of the body parts. (Another important element is the body contour; see Gao & Tomonaga, 2018 for details.) The primary role of the head in body processing is also supported by other studies in humans (e.g. Ramm, Cummins, & Slaughter, 2010; Robbins & Coltheart, 2012; Yovel, Pelc, & Lubetzky, 2010). In this study, in the condition where first-order relations were manipulated, half of the stimuli had the head misplaced, and the other half did not. We additionally compared the results of the two kinds of stimuli apart from analyzing all data together in this condition, to examine whether the head contributes more than other body parts in the possible effect of body structure changes on the body processing.

Method

Participants

Seven chimpanzees participated in this study (6 chimpanzees in Experiment 1; 7 chimpanzees in Experiment 2; Table 1). They are housed at the Primate Research Institute, Kyoto University (Inuyama, Aichi, Japan). They belong to two social groups composed of 12 individuals in total. They live in a large environment that consists of an outdoor compound

(700 m²) and attached indoor areas (Matsuzawa, Tomonaga, & Tanaka, 2006). The animals were not deprived of food or water during the study. The participants had experienced various cognitive tasks with touchscreens, including acquisition of an artificial language, numerical sequence learning, short-term memory tests, tests about visual attention and visual search, and facial recognition, with sufficient experience of the matching-to-sample paradigm (e.g. Tomonaga, 1999; Tomonaga & Imura, 2015; Tomonaga, Itakura, & Matsuzawa, 1993). The method we use, touch screen tasks, prevents possible effect from doing the experiment with humans manually, and increases the accuracy and consistency of the data. Only the seven chimpanzees that we tested are familiar with touch screen and matching-to-sample tasks. The small sample size is a limitation of the study, but we hope it can provide crucial information for cognition of chimpanzees.

Table 1 General characteristics of the seven chimpanzees

Name	GAIN ID Number*	Sex	Age (when the study started)	Kinship	Participated in
Ai	0434	Female	40	Ayumu's mother	Experiments 1, 2
Ayumu	0608	Male	16	Ai's son; Pal's paternal half-sibling	Experiments 1, 2
Chloe	0441	Female	36	Cleo's mother	Experiments 1, 2
Cleo	0609	Female	16	Chloe's daughter	Experiments 1, 2
Pan	0440	Female	33	Pal's mother	Experiment 2
Pal	0611	Female	16	Pan's daughter; Ayumu's paternal	Experiments 1, 2

				half-sibling	
Pendesa	0095	Female	39	N.A.	Experiments 1, 2
203	Note: *Identification number for each chimpanzee listed in the database of the Great				
204	Ape Information Network (GAIN); https://shigen.nig.ac.jp/gain/				
205					
206	The daily care and use of the chimpanzees adhered to the Third Version of Guidelines				
207	for the Care and Use of Laboratory Primates of the Primate Research Institute, Kyoto				
208	University. The research proposal was approved by the Animal Research Committee of Kyoto				
209	University and by the Animal Welfare and Animal Care Committee of the Primate Research				
210	Institute of Kyoto University. All procedures adhered to the Japanese Act on the Welfare and				
211	Management of Animals.				
212	Apparatus				
213	The participants sat in the experimental booth and performed tasks on a touchscreen				
214	with a 15-inch LCD display (1,024 × 768 pixels, 1 pixel = 0.297 mm). During the experiments,				
215	they could move freely, but they would always sit in front of the screen about 40 cm away. The				
216	chimpanzees kept their postures natural and relaxed, and their heads were always upright. The				
217	screens were not tilted significantly in any direction (Figure 1A). When they made a correct				
218	choice, the feeder delivered a piece of apple or raisin via a tube automatically to a food tray				
219	placed at the bottom of the display with a chime sound. If they made a wrong choice, no food				
220	was provided, and an error buzzer sounded. The experiment programs were written and				
221	operated with Microsoft Visual Basic 2010 software (Microsoft Corp.; Redmond, WA, USA).				
222

Figure 1. The experiment setting (A) and the general procedure (B). A) Chimpanzee

Ai is doing the task with the stimuli of two inverted chimpanzee bodies. B) In each trial of the experiment, a start key appeared on the screen, then a sample stimulus appeared after the participants touched the start key; the sample stayed for 500 ms, and disappeared upon touching, and choice options appeared without any delay.

Stimuli

In Experiment 1, there were two conditions: intact body condition and scrambled body condition. In Experiment 2, there were two conditions: intact body condition and distorted body condition. In each condition of both experiments, there were 20 pairs of stimuli in the upright position, and the same 20 pairs of pictures were presented in an inverted position (after 180° rotation from the upright ones). In total, there were 80 pictures for each condition. The size of the stimuli was about 400 px × 400 px. For each pair, they showed the same individual, with whom the participants were not familiar, with the same kind of manipulations (e.g. both have their legs and arms swapped) but with different postures. Each pair had the same individual, so their heads were the same. The angles, shading and other properties of the faces were similar.

Each trial used one pair (two pictures). Randomly, one picture would serve as a sample. Each pair of pictures had the same orientation (upright or inverted), so, in each trial, all stimuli were in the same orientation. The head and torso determined the orientation. In the upright orientation, the head and torso of each stimulus were both presented upright. In the inverted orientation, the head and torso of each stimulus were both inverted. The correct stimuli and positions were counterbalanced. All stimuli were black and white and balanced in luminance.

In the intact body condition of Experiment 1, all stimuli were intact chimpanzees (Figure 2). In the scrambled body condition of Experiment 1, all stimuli were chimpanzee bodies that were scrambled in terms of first-order relations. There were ten kinds of manipulations. Two upright pairs and their inverted versions adopted each kind of manipulation. Among the ten kinds of manipulations, five included head position change: 1) head moved to one arm, 2) head moved to one leg, 3) head and one leg swapped, 4) head and one arm swapped, and 5) head moved to waist. The other five did not include head position change: 1) arms moved to legs, 2) legs moved to arms, 3) one arm moved to head, 4) one leg moved to head, and 5) legs and arms swapped.

In the intact body condition of Experiment 2, all stimuli were intact chimpanzees (Figure 2). Small blurring parts in joints in the stimuli inevitably occurred during cutting body parts and moving them in making the manipulated chimpanzee bodies using computer software. We cut and moved certain body parts to make a strange body, and after moving them, we needed to blur the joints to balance the luminance of the existing part and the newly moved part in order to make it natural. The local blurring parts might affect the results. Therefore, we

deliberately made small blurring parts in the intact body pictures for better control to rule out this possibility. We cut the body parts and blurred the joints using the blurring tool as we did when making abnormal chimpanzee bodies, although it was not necessary in making intact chimpanzee body pictures. In the distorted body condition of Experiment 2, ten upright pairs and their inverted versions had very long torso (2 times of the originals) and very short limbs (0.5 times of the originals) while the other half had very short torso (0.5 times of the originals) and very long limbs (2 times of the originals).

Figure 2. Sample Stimuli. Top three are sample stimuli for Experiment 1. Top left: a

sample for intact chimpanzee bodies. Top center: a sample for scrambled chimpanzee bodies in terms of first-order relations with the change of the head position. Top right: a sample for scrambled chimpanzee bodies without the change of the head position. Bottom three are sample stimuli for Experiment 2. Bottom left: a sample for intact chimpanzee bodies with marks of manipulating pictures in local parts. Bottom center: a sample for distorted chimpanzee bodies

with very long torso and very short limbs. Bottom right: a sample for distorted chimpanzee bodies with very short torso and very long limbs.

The pictures were manipulated using Adobe Photoshop software (Adobe Systems; San Jose, CA, USA) and Pixelmator (Pixelmator Team Ltd.; Vilnius, Lithuania). The pictures were provided by Kumamoto Sanctuary, Wildlife Research Center of Kyoto University. We evaluated the similarity of all the pictures before choosing those used in the experiment.

General procedure

We used zero-delayed matching-to-sample tasks (Figure 1B). In each trial, a circle serving as the start key initially appeared at the bottom centre of the touchscreen against a white background. After chimpanzees touched the circle, a stimulus picture appeared in the centre of the screen. This served as the sample. After 500 ms, after chimpanzees touched the sample, it would disappear, and, without any delay, two choice alternatives would appear side by side on the top of the screen. One of the two stimuli was the same as the sample, and they were a fixed pair (the other stimulus was the same individual with the same kind of manipulation yet different postures). If the participants touched the one that was the same as the sample, it was a correct choice, and they would receive a piece of apple or raisin from the feeder with a chime sound. If they chose the one that was not the same as the sample, it was a wrong choice, and a buzzer would sound without any food reward followed by a timeout of 2000 ms. The inter-trial interval was 1500 ms.

For each condition of each experiment, participants received eight sessions. Each

session had 40 trials. Twenty trials used upright stimuli (20 upright pairs), and the other half used inverted stimuli (20 inverted pairs). The upright and inverted trials were randomly mixed.

Data analyses

We analysed accuracy and response-time data. We compared the accuracy and response time between the upright and inverted trials. If either the error rate (100% - accuracy) or response time was significantly higher in the inverted trials than in the upright trials, it showed the inversion effect. We used the method of generalized linear mixed modelling (GLMM) in R 3.4.3 (R Core Team; Vienna, Austria) using the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015). We calculated the accuracy of the 20 upright and 20 inverted trials on a session-by-session basis. The distribution of the accuracy was binomial. We did the analyses for each experiment separately. The model included as fixed effects condition (intact and scrambled/distorted) and orientation (upright and inverted), and the interaction of condition and orientation. The interaction was analyzed in order to examine whether the magnitude of the inversion effect differs between the two conditions. The random effects were participant ID and session number. To examine the potential effect of the manipulation of head in the scrambled body condition of Experiment 1, we did another analysis using data from the scrambled body condition only. We separated the data from the trials where the head position was changed and the trials where the head position remained the same while only the positions of other body parts were changed and marked them with the tag of 'sub-condition'. In these analyses the model included sub-condition (with or without head position change) and orientation (upright or inverted) as fixed effects, and the interaction between condition and

orientation. The interaction could reveal a difference in the magnitude of the inversion effect. The random effects were participant ID and session number. Response time refers to the duration of time from the chimpanzee touching the sample to when s/he chose any of the alternatives. Only the response times from correct trials were included in the analyses. We calculated the average response time of all correct upright trials and all correct inverted trials on a session-by-session basis. During the experiment, there would sometimes be unexpected sounds from outside the experimental booths, and the chimpanzees were interrupted; therefore, we initially discarded response times that were longer than the mean value plus 3 SDs. We then calculated the average of the remaining data points and used them for further analyses. The distribution of response time data was best fit with a gamma distribution. The analyses were the same as for accuracy data except that the dependent variable was changed to response time, and the distribution was changed to gamma distribution.

Experiment 1

Results

1. The intact body condition and the scrambled body condition

Accuracy

There was an inversion effect in the intact body condition ($p < .001$) but not in the scrambled body condition ($p = .14$). A significant interaction was found between condition and orientation ($p < .001$).

In the intact body condition, the mean accuracy in the upright trials was $80.8 \pm 1.6\%$, 95% CI [60.8, 92.3], and the mean accuracy in the inverted trials was $72.1 \pm 1.4\%$, 95% CI

[48.5, 88.1] (Figure 3). In the scrambled body condition, the mean accuracy in the upright trials was $64.7 \pm 1.6\%$, 95% CI [53.2, 89.7], and the mean accuracy in the inverted trials was $67.1 \pm 1.4\%$, 95% CI [56.7, 91.2] (Figure 3).

The GLMM analyses showed that the accuracy was significantly higher in the upright than in the inverted trials in the intact condition (estimate of the fixed effect orientation: 0.50, standard error: 0.11, z value = 4.52, $p < .001$; estimate of the fixed effect condition: 0.34; estimate of the intercept: 0.97). The GLMM analyses showed no difference in accuracy between the upright and inverted in the scrambled condition (estimate of the fixed effect orientation: -0.16 , standard error: 0.11, z value = -1.47 , $p = .14$; estimate of the fixed effect condition: -0.34 ; estimate of the intercept: 1.31).

Figure 3. Chimpanzees' performances in Experiment 1. The conditions were intact bodies (control) and scrambled bodies (with abnormal body part arrangements). Error bar: SEM; n.s.: not significant; *** $p < .001$.

352

353 *Response time*

354 There was no inversion effect in the intact ($p = .81$) or scrambled body condition (p
355 $= .18$). No interaction was found between condition and orientation ($p = .26$).

356 In the intact body condition, the mean response time in the upright trials was 961 ± 25
357 ms, 95% CI [749, 1298], and the mean response time in the inverted trials was 968 ± 27 ms,
358 95% CI [754, 1306]. In the scrambled body condition, the mean response time in the upright
359 trials was 952 ± 24 ms, 95% CI [745, 1275], and the mean response time in the inverted trials
360 was 915 ± 24 ms, 95% CI [723, 1209].

361 The GLMM analyses did not show significant differences between the upright and
362 inverted trials in the intact condition (estimate of the fixed effect orientation: < 0.001 , standard
363 error: < 0.001 , t value = -0.24 , $p = .81$; estimate of the fixed effect condition: < 0.001 ; estimate
364 of the intercept: < 0.001) or the scrambled condition (estimate of the fixed effect orientation:
365 < 0.001 , standard error: < 0.001 , t value = 1.34 , $p = .18$; estimate of the fixed effect condition:
366 < 0.001 ; estimate of the intercept: < 0.001).

2. The effect of head position change in the scrambled body condition

Figure 4. Chimpanzees' performances in the two sub-conditions in the scrambled body condition (the one with head position changes and the one without head position changes). Error bar: SEM; n.s.: not significant.

Accuracy

There was no inversion effect in the sub-conditions with ($p = .23$) or without head position changes ($p = .39$). No difference was found in accuracy between the two sub-conditions for the upright ($p = .13$) or inverted trials ($p = .24$). No interaction between sub-condition and orientation was found ($p = .85$).

In the sub-condition with head position changes, the mean accuracy in the upright trials was $73.3 \pm 2.1\%$, 95% CI [42.6, 91.2], and the mean accuracy in the inverted trials was $76.7 \pm 2.0\%$, 95% CI [47.6, 92.4] (Figure 4). In the sub-condition without head position changes, the

mean accuracy in the upright trials was $77.5 \pm 1.9\%$, 95% CI [48.9, 92.7], and the mean accuracy in the inverted trials was $79.8 \pm 1.8\%$, 95% CI [52.8, 93.5] (Figure 4).

We first examined the inversion effect in the two sub-conditions, and then compared the performances in upright and inverted trials between the two sub-conditions, respectively.

The GLMM analyses showed no difference between the upright and inverted trials when the sub-condition was the one with head position changes (estimate of the fixed effect orientation: -0.18 , standard error: 0.15 , z value $= -1.20$, $p = .23$; estimate of the intercept: 1.20) or when the sub-condition was the one without head position changes (estimate of the fixed effect orientation: -0.14 , standard error: 0.16 , z value $= -0.87$, $p = .39$; estimate of the intercept: 1.38).

There was no difference in the performances between the two sub-conditions in the upright trials (when the reference of ‘sub-condition’ was set to the one with head position changes, estimate of the fixed effect sub-condition: 0.23 , standard error: 0.15 , z value $= 1.50$, $p = .13$) or the inverted trials (estimate of the fixed effect sub-condition: 0.18 , standard error: 0.16 , z value $= 1.18$, $p = .24$).

Response time

There was no inversion effect from response-time data in the sub-conditions with ($p = .20$) or without head position changes ($p = .34$). No difference in accuracy between the two sub-conditions was found for the upright ($p = .14$) or inverted trials ($p = .07$). No interaction between sub-condition and orientation was found ($p = .77$).

In the sub-condition with head position changes, the mean response time in the upright

trials was 945 ± 24 ms, 95% CI [718, 1345], and that in the inverted trials was 903 ± 24 ms, 95% CI [696, 1256]. In the sub-condition without head position changes, the mean response time in the upright trials was 996 ± 35 ms, 95% CI [743, 1463], and that in the inverted trials was 963 ± 30 ms, 95% CI [728, 1386].

We first examined the inversion effect in the two sub-conditions, and then compared the performances in upright and inverted trials between the two sub-conditions, respectively.

The GLMM analyses did not show significant differences between the upright and inverted trials when the sub-condition was the one with head position changes (estimate of the fixed effect orientation: < 0.001 , standard error: < 0.001 , t value = -1.30 , $p = .20$; estimate of the intercept: < 0.001) or when the sub-condition was the one without head position changes (estimate of the fixed effect orientation: < 0.001 , standard error: < 0.001 , t value = -0.95 , $p = .34$; estimate of the intercept: 0.001).

There was no difference in the performances between the two sub-conditions in the upright trials (when the reference of ‘sub-condition’ was set to the one with head position changes: estimate of the fixed effect sub-condition: < 0.001 , standard error: < 0.001 , t value = -1.48 , $p = .14$) or the inverted trials (estimate of the fixed effect sub-condition: < 0.001 , standard error: < 0.001 , t value = 1.83 , $p = .07$).

Discussion

No inversion effect was shown to scrambled chimpanzee bodies, suggesting that the configural body processing in chimpanzees relies on correct first-order relations. This is consistent with previous studies about body recognition in human adults (Gliga & Dehaene-

Lambertz, 2005; Reed, Stone, Grubb, & McGoldrick, 2006; Yovel, Pelc, & Lubetzky, 2010), in 3-month-old infants (Gliga & Dehaene-Lambertz, 2005), and in capuchin monkeys (to human bodies; Matsuno & Fujita, 2018). It is also the same as humans' face processing, where correct first-order relations are necessary to invoke the inversion effect (e.g. Bentin, Allison, Puce, Perez, & McCarthy, 1996; Tanaka & Farah, 1993). The results also indicate that chimpanzees recognize correct first-order relations in building their body configuration.

No difference was found in the performances between the sub-conditions with or without head position changes. This contradicts the predictions based on the findings in humans (e.g. Ramm, Cummins, & Slaughter, 2010; Robbins & Coltheart, 2012; Yovel, Pelc, & Lubetzky, 2010) and chimpanzees (Gao & Tomonaga, 2018). However, it might indicate that the overall strange arrangement of body parts caught more attention in the chimpanzees.

In our previous study (Gao & Tomonaga, 2018), we used individual discrimination to test the inversion effect, that is, in each trial, the choice options were different individuals. It could be possible that the body inversion effect we found was actually from the face inversion effect, if there was no control condition to rule it out. We had a control condition consisting of only chimpanzee faces, and the faces were in the same size as that of the faces in the bodies we used (i.e. relatively small). There was no inversion effect, so actually the chimpanzees could not use cues from only faces in recognizing bodies. However, a more direct evidence would be more persuasive. In this study, we used posture discrimination, that is, both choice options in one trial were the same individual (with the same head of course). The inversion effect shown here directly supported that the inversion effects we found were not from the face inversion

effect.

In order to understand further the properties of the configural body processing in chimpanzees, in Experiment 2 we tested the effect of changes in another aspect of body structures, body proportions, on the inversion effect.

Experiment 2

Results

Accuracy

There was an inversion effect in the intact ($p < .001$) and distorted body conditions ($p = .03$). No significant interaction between condition and orientation was found ($p = .11$).

In the intact body condition, the mean accuracy in the upright trials was $80.1 \pm 1.5\%$, 95% CI [62.7, 91.0], and the mean accuracy in the inverted trials was $72.3 \pm 1.5\%$, 95% CI [50.9, 87.2] (Figure 5). In the distorted body condition, the mean accuracy in the upright trials was $76.3 \pm 1.4\%$, 95% CI [56.6, 89.3], and the mean accuracy in the inverted trials was $72.4 \pm 1.6\%$, 95% CI [51.4, 87.1] (Figure 5).

The GLMM analyses showed that accuracy was significantly higher in the upright trials than in the inverted trials in the intact condition (estimate of the fixed effect orientation: 0.44, standard error: 0.10, z value = 4.33, $p < .001$; estimate of the fixed effect condition: 0.01; estimate of the intercept: 0.98) and also in the distorted condition (estimate of the fixed effect orientation: 0.21, standard error: 0.10, z value = 2.14, $p = .03$; estimate of the fixed effect condition: -0.01 ; estimate of the intercept: 0.98).

Figure 5. Chimpanzees' performances in Experiment 2. The conditions were intact

bodies (control) and distorted bodies (with abnormal body part proportions). Error bar: SEM;

* $p < .05$; *** $p < .001$.

Response time

No inversion effect was shown in the response-time data in the intact ($p = .33$) or distorted body condition ($p = .47$). No interaction was found between condition and orientation ($p = .23$).

In the intact body condition, the mean response time in the upright trials was 922 ± 19 ms, 95% CI [776, 1099], and the mean response time in the inverted trials was 939 ± 22 ms, 95% CI [788, 1123]. In the distorted body condition, the mean response time in the upright trials was 949 ± 21 ms, 95% CI [795, 1138], and the mean response time in the inverted trials was 936 ± 21 ms, 95% CI [785, 1119].

The GLMM analyses did not show significant difference between the upright and inverted trials in the intact condition (estimate of the fixed effect orientation: < 0.001 , standard error: < 0.001 , t value = 0.97, $p = .33$; estimate of the fixed effect condition: < 0.001 ; estimate of the intercept: 0.001) or the distorted condition (estimate of the fixed effect orientation: < 0.001 , standard error: < 0.001 , t value = -0.73 , $p = .47$; estimate of the fixed effect condition: < 0.001 ; estimate of the intercept: 0.001).

Discussion

Chimpanzees showed the inversion effect in both distorted and intact body conditions. The violation of body proportions did not make the inversion effect disappear. This finding reveals that the body configural processing in chimpanzees does not rely on normal body proportions. It also suggests that body proportions might not matter as much to chimpanzees as the first-order relations in the body configuration prototype.

In the control condition of intact bodies, we included blurring parts that inevitably occurred in abnormal bodies when making the stimuli, although the structure and proportion formed normal bodies. The inversion effect remained, suggesting that chimpanzees do not pay attention to the strange small local parts when they process bodies, and that the results for the manipulated bodies are not affected by the local marks that appear in making the stimuli.

General discussion

In this study, we investigated how changes in body structures influence the body configural processing of chimpanzees. We tested the inversion effect in matching-to-sample tasks. In Experiment 1, we used chimpanzee bodies with abnormal first-order relations, i.e.

body part arrangements. The chimpanzee participants did not show the inversion effect in this condition, suggesting that their configural body processing relies on correct first-order relations. In Experiment 2, where we used chimpanzee bodies with abnormal body proportions, they also showed the inversion effect. These findings suggest that the violation of body proportions does not interfere with the configural processing of bodies. In both experiments, the control conditions were normal chimpanzee bodies, to which they showed the inversion effect. The results also implied that the first-order relations are probably important for the body configuration prototype in chimpanzees' mind, while body proportions may not be.

The changes of first-order relations interfering with configural processing is the same as what happens in humans (Gliga & Dehaene-Lambertz, 2005; Reed, Stone, Grubb, & McGoldrick, 2006; Yovel, Pelc, Tubetzky, 2010) and capuchin monkeys when they recognize human bodies (Matsuno & Fujita, 2018). At least this aspect of body processing is conservative in evolution. Chimpanzees, humans and capuchin monkeys rely on correct body part arrangements to process bodies configurally. This finding provides implications on how configural processing is shaped by experience and evolution. From the ontogenetic perspective, the experience of seeing bodies with normal structures may facilitate the specific processing, and a violation of normal structures would diminish the configural processing. However, this specific body processing and its property regarding first-order relations must have been developed during the process of evolution. From the phylogenetic perspective, the common ancestors of these species may already have developed this special processing for biologically important objects, bodies, and the processing may be based on correct structures.

Comparing body and face processing could help shed light on why they are processed differently than other objects, and provide information about object processing in general. In the three aspects (sensitivity to first-order relations, second-order relations, and holistic processing) of face configural processing reviewed by Maurer and colleagues (2002), we did not focus on holistic processing of bodies in this study. The changes of first-order relations in the body interfering with configural processing is consistent with the findings in studies of face recognition, where the inversion effect was diminished by scrambling facial parts (e.g. Bentin, Allison, Puce, Perez, & McCarthy, 1996; Tanaka & Farah, 1993). Body proportions, once regarded as potentially corresponding with the second-order relation, are actually different from it (Reed, Stone, Grubb, & McGoldrick, 2006; Zieber, Bhatt, Hayden, Kangas, Collins, & Bada, 2010; Zieber, Kangas, Hock, & Bhatt, 2015). The second-order relations in faces refers to the space between the first-order relational features, i.e. facial parts. However, bodies and faces are different, although they share many common properties. Faces all have the same contour, while the shape of body contours changes with different postures. On faces, the distinguishing parts are separated from each other, but body parts are connected. Therefore, it is difficult to transfer the content of the second-order relations of faces directly to bodies and to compare the properties in terms of processing the second-order relation in faces and bodies directly. In Experiment 2, we used intact bodies with local blurring in the control condition, and chimpanzees showed the inversion effect regardless of it. This finding implies that the local features do not influence configural processing. This is the same in face processing (e.g. Donnelly, Humphreys, & Sawyer, 1994). Researchers replaced the facial parts with objects,

and still found an inversion-effect like effect.

Previous studies about the inversion effect have suggested that faces and bodies share configural processing, but at the same time, the detailed mechanisms might be different (Reed, Stone, Grubb, & McGoldrick, 2006; Slaughter, Stone, & Reed, 2004; Yovel, Pelc, Lubetzky, 2010). This proposal is supported by fMRI studies finding distinct brain areas activated by body and face processing, although in certain conditions they are adjacent and partially overlapping (Peelen & Downing, 2005, 2007; Popivanov, Jastorff, Vanduffel, & Vogels, 2012; Premereur, Taubert, Janssen, Vogels, & Vanduffel, 2016). Also, as discussed previously, the properties of shapes are actually different between faces and bodies. However, the above findings were all from human participants. It is not clear how these processes differ in other species. In answering how different the processing of bodies and faces are, this study provided evidence in humans' closest relatives, chimpanzees. Future studies could include more species and adopt more diverse paradigms to examine other aspects of configural processing, for example, the holistic processing or more unique processing of bodies. The fact that humans and nonhuman animals can be trained to use configural processing (Diamond & Carey, 1986; Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier & Tarr, 1997; Gauthier, Williams, Tarr, & Tanaka, 1998; Hagen & Tanaka, 2019) suggests that this mode of processing may support quick detection of things that need expertise to deal with, including bodies and faces. Research from different perspectives in various species could determine if and how different factors tune object processing in different ways.

The results also imply how chimpanzees might build the body prototype. Chimpanzees

show the inversion effect to intact chimpanzee bodies, and not to other objects. It is reasonable to infer that if they do not show the inversion effect to certain stimuli, they might not see those stimuli as the same as intact bodies. Therefore, the inversion effect might be an index of their understanding of body structures in recognizing bodies with abnormal structures. However, the testing paradigm used in this study cannot directly evaluate discrimination between intact and abnormal bodies, so this inference is premature. Still, if we follow this logic, the conclusion would be that chimpanzees are sensitive to first-order relations but not to body proportions. The body prototype in their mind must have correct body part arrangements, but not necessarily normal proportions. From the ecological perspective, a serious violation in the first-order relations may indicate a major injury: loss of a body part or a twisted joint causing weird or impossible postures. Chimpanzees have been shown to be sensitive to certain injuries (Sato, Hirata, & Kano, 2019). For body proportions, individuals actually vary in their body proportions; therefore, chimpanzees would use the same strategy to process the distorted bodies in Experiment 2 as they use for normal bodies, although their proportions deviated from the normal level to some extent.

Previous studies have found that 3.5-month-old human infants could discriminate between intact and abnormal bodies, both in terms of first-order relations and body proportions. The insensitivity of chimpanzees to body proportions in our experiments could reflect different experimental design from those used with human infants, or a true difference between humans and chimpanzees in this perceptual domain. The difference could arise from differences in ability to summarize body samples and to build an average body figure with structures in the

normal range. However, chimpanzees showed comparable performances as humans in a task to choose the average sizes of objects (Imura, Kawakami, Shirai, & Tomonaga, 2017), suggesting that they are able to make summaries and averages. The groups in our study were composed of 12 or 13 individuals. Perhaps their limited experience of conspecifics was not enough for the chimpanzees to build pictures of a normal range of body proportions, although it was apparently enough for them to have a clear understanding of body part arrangements. The latter is fixed, but the former can vary across individuals. For future directions, more direct paradigms could be adopted to test chimpanzees' understanding of body structures, including discrimination tasks that were used in infants (Zieber, Bhatt, Hayden, Kangas, Collins, & Bada, 2010; Zieber, Kangas, Hock, & Bhatt, 2015). Other techniques, for example, eye tracking, could be used to examine their attention to (abnormal) body structures in a more direct and probably more detailed way (Kano & Tomonaga, 2009).

In summary, this study shows that chimpanzees' configural processing for bodies relies on correct first-order relations, but the body proportion does not matter. The results also imply that chimpanzees may be more sensitive to first-order relations than body proportions in their understanding of body structures.

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710

711 Supplementary Materials

712 Data file S1 Accuracy and response-time data in each condition