Losing your Head: Behavioral and Electrophysiological Effects of Body Inversion

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Abstract

■ The present study aimed to further explore the mechanisms underlying the perception of human body shapes. Behavioral and electrophysiological inversion effects were studied for human bodies with and without heads and for animal bodies (cats, dogs, and birds). Recognition of human bodies (with heads) was adversely affected by stimulus inversion, and the N170 had longer latencies and higher amplitudes for inverted compared to upright human bodies. Human body shapes presented without heads yielded the opposite result pattern. The data for animal bodies did not yield consistent effects. Taken together, the present findings suggest that human bodies might be processed by specialized cortical mechanisms which are at least partly dissociable from mechanisms involved in object or face processing. ■

INTRODUCTION

Recent studies suggest that human faces and human body forms are unique stimulus classes, which are processed in specialized cortical areas (Peelen & Downing, 2007; Kanwisher & Yovel, 2006). Face processing has been linked to the "fusiform face area" (FFA) in the fusiform gyrus (Kanwisher & Yovel, 2006; Haxby, Hoffman, & Gobbini, 2000; Kanwisher, McDermott, & Chun, 1997) and the occipital face area (OFA; Gauthier et al., 2000; Haxby et al., 1999; Kanwisher et al., 1997). Perception of human body forms has also been associated with specific cortical processing units (Peelen & Downing, 2005, 2007; Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Schwarzlose, Baker, & Kanwisher, 2005; Downing, Jiang, Shuman, & Kanwisher, 2001). The extrastriate body area (EBA) is more strongly activated during perception of human bodies and body parts compared to objects or faces (Urgesi, Berlucchi, & Aglioti, 2004; Downing et al., 2001). The fusiform body area (FBA) in the posterior fusiform gyrus (Peelen, Wiggett, & Downing, 2006; Peelen & Downing, 2005; Schwarzlose et al., 2005) responds to the whole body rather than body parts (Taylor, Wiggett, & Downing, 2007). The EBA seems to be involved in the basic analysis of body features (similar to the OFA in face processing), whereas the FBA (similar to the FFA) might be implicated in processing the configuration of body parts as a whole (Taylor et al., 2007). Faces and human body forms (stimuli presented without heads/faces) appear to be processed in adjacent and overlap-

ping but distinct networks within the fusiform gyrus (Peelen & Downing, 2005, 2007; Schwarzlose et al., 2005). This assumption is further supported by behavioral studies indicating that recognition of faces is more affected by stimulus inversion than recognition of nonface stimuli (inverted face effect). There is evidence of holistic (Farah, Tanaka, & Drain, 1995; Tanaka & Farah, 1993) as well as configural processing of human faces, and both are disrupted by inversion (Maurer et al., 2007; Leder, Candrian, Huber, & Bruce, 2001; Freire, Lee, & Symons, 2000). Reed, Stone, Grubb, and McGoldrick (2006) and Reed, Stone, Bozova, and Tanaka (2003) reported slower RTs and higher error rates for decisions about inverted compared to upright human body positions. Inversion effects did not emerge for isolated body parts or scrambled bodies (Reed et al., 2006). These data offer some support to the idea that human bodies—like faces—are processed configurally.

Human faces elicit a negative event-related potential (ERP) peaking about 170 msec (termed N170) after stimulus onset, with maximum amplitudes in occipito-temporal areas (Minnebusch, Suchan, Ramon, & Daum, 2007; Eimer, 2000a, 2000b; Bentin, Deouell, & Soroker, 1999). N170 latencies are longer for inverted relative to upright faces; this effect is not observed for objects (Itier & Taylor, 2004a, 2004b; Eimer, 2000a; Rossion et al., 2000; Bentin, Allison, Puce, Perez, & McCarthy, 1996). N170 amplitudes are larger for inverted relative to upright faces (Marzi & Viggiano, 2007; Itier & Taylor, 2004a, 2004b; Rossion et al., 1999, 2000). Thierry et al. (2006) described an ERP component evoked by stimuli representing the form of the human body (N190), which

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differed significantly from the face-specific N170, with source localization identifying distinct sources for both components. Configural processing of human body shapes is supported by larger N190 amplitudes and longer latencies for inverted compared to upright human bodies (Stekelenburg & de Gelder, 2004). The latter study used photographs representing the whole body and masked the faces to minimize face processing. However, contextual cues (such as masked faces) can elicit object-specific neuronal responses (Cox, Meyers, & Sinha, 2004), and occipito-temporal activation evoked by body shapes is modulated by the presence or absence of the face (Morris, Pelphrey, & McCarthy, 2006). It is therefore possible that even masked faces might activate face-specific processing mechanisms and it is unclear whether bodies, faces, or both are critical for the reported effects.

Taken together, the available evidence suggests that human bodies, like faces, are processed in specialized cortical areas. There is, however, as yet considerable uncertainty as to whether faces and bodies are processed by the same neuronal mechanisms (domain general hypothesis) or by dissociable mechanisms (face specificity hypothesis). The domain-general hypothesis states that the mechanisms engaged by faces are not specific for a particular stimulus category, but for a particular process (configural encoding), which is more important for recognizing faces than other stimulus classes (Tarr & Cheng, 2003).

Processing of faces and bodies tends to be compared to processing of inanimate objects (Reed et al., 2003, 2006; Thierry et al., 2006; Peelen & Downing, 2005; Schwarzlose et al., 2005; Stekelenburg & de Gelder, 2004; Hole, George, & Dunsmore, 1999). Interestingly, the FFA/FBA was found to be strongly activated for animal bodies with heads (Downing et al., 2006; Chao, Martin, & Haxby, 1999; Kanwisher, Stanley, & Harris, 1999), but not for animals without heads (Kanwisher et al., 1999). The EBA yielded higher activations for pictures of mammals compared to birds, fishes, or objects (Downing et al., 2006), indicating that the EBA activations by animals with a body form is similar to that of humans. It is as yet unknown whether inversion effects are specific for human bodies or whether they are also found for animal bodies.

The aim of the present study was to further investigate whether inversion effects would support the hypothesis of configural processing of human bodies similar to the known effects for faces and whether processing of human bodies would differ from processing of animal bodies. It has previous been shown that EBA activity is modulated by the presence of a face (Morris et al., 2006). It is as yet unknown, however, whether the presence or absence of a face also modulates ERP amplitudes evoked by human body stimuli. To investigate this issue, we used human bodies with masked faces and headless human bodies as stimulus material.

METHODS

Subjects

Seventeen right-handed subjects (9 women, mean age = 23.8 years, $SD = 3.9$) participated in this study. All subjects had normal or corrected-to-normal vision. There was no history of neurological or psychiatric illness in any of the subjects. The study was performed in accordance with ethical standards laid down in the Declaration of Helsinki (Varga, 1975) and approved by the Ethics Committee of the Medical Faculty of the Ruhr-University, Bochum, Germany. Written informed consent was obtained from all subjects.

Stimuli

Gray-scaled pictures representing six different categories (human bodies, human bodies without head, birds, cats, dogs, and houses) were displayed on a white background. Pictures of houses were included to determine whether bodies generally evoked a larger early negative component than houses, similar to the face-specific N170. Each stimulus category entailed 60 items, at a size of approximately $3° \times 3°$ of visual angle per item. Photographs for the human body categories were taken from a set of photographs of whole bodies of 30 men and 30 women in natural postures, which was developed in our department. A set of photographs of animals was selected from the Internet. Stimuli were matched with respect to body postures and orientation to control for within-category similarity, and the final stimulus selection was based on extensive piloting in healthy subjects. To minimize face processing during presentation of bodies, the faces on the pictures were masked (human bodies, birds, cats, and dogs). Consistent with the procedure described by previous investigations (Taylor et al., 2007; Downing et al., 2006; Peelen & Downing, 2005), a separate category of human bodies with heads removed was added to the stimulus material. The body stimuli (human bodies, human bodies without head, birds, cats, and dogs) were presented both in upright and inverted positions.

Procedure

Subjects were seated in a sound-attenuating and electrically shielded room, facing a computer monitor at a distance of 80 cm. They were instructed to fixate the center of the screen and to avoid blinking or eye and body movements.

The task was developed in analogy to the procedure described by Yovel and Kanwisher (2005). Pairs of bodies or houses were presented sequentially either in upright (all categories) or inverted positions (all categories except houses) in random order. In each trial, the first and second pictures—belonging to the same

stimulus category—were presented in the center of the monitor for 250 msec respectively, with an ISI of 500 msec and a mean ITI of 1000 msec (see Figure 1). Each trial lasted 2000 msec. During the ITI, a black exclamation mark appeared in the center of the monitor. The subjects' task was to decide as quickly and accurately as possible whether the first and second stimuli were the same (same condition) or different (different condition). Same/different judgments were made via keypresses. Each stimulus was used once in the same and once in the different condition. Each of the 11 conditions (six categories; all categories except houses are presented upright and inverted) involved 60 trials in the "same condition" and 60 trials in the "different condition." In total, 1320 stimuli were presented in three blocks of 440 trials each.

EEG Recordings

Scalp recordings were obtained from 30 tin electrodes (10–20 standard set-up) mounted in an elastic cap. Four additional electrodes were placed above and below the left eye and on the outer canthus of each eye to record vertical and horizontal eye movements. The POz electrode served as reference. Electrode impedance was kept below 5 kΩ and digitized at a sampling rate of 250 Hz. EEG signals were filtered with a band-pass filter of 0.5–35 Hz. Trials with EOG or EEG artifacts exceeding 50 μV were omitted from further analyses.

Data Analyses

Bebavioral Data

Correct responses and reaction times (RTs) were assessed for each subject and each condition. Efficiency scores (see Jacques & Rossion, 2007) were calculated for each subject and each condition by dividing the mean RTs by the proportion of correct responses. This procedure was adopted to obtain a single parameter for both responses. Efficiency scores were also used in order to control for possible speed–accuracy tradeoffs. A low score reflects good performance.

For efficiency scores, a $5 \times 2 \times 2$, repeated measures ANOVA with Greenhouse–Geisser corrections were performed, with factors stimulus category (human bodies, human bodies without head, birds, cats, and dogs), orientation (upright vs. inverted), and condition (same vs. different).

EEG Data

Analysis focused on the ERP response to the first picture of each pair (see Jacques & Rossion, 2007), for which both stimulus category and orientation were unpredictable, which was not the case for the second picture. All trials (correct and error trials) are included in the analysis. The raw data were segmented off-line in epochs of 550 msec, starting 200 msec prior to stimulus onset; activity 200 msec before stimulus onset served as baseline.

Figure 1. Experimental design.
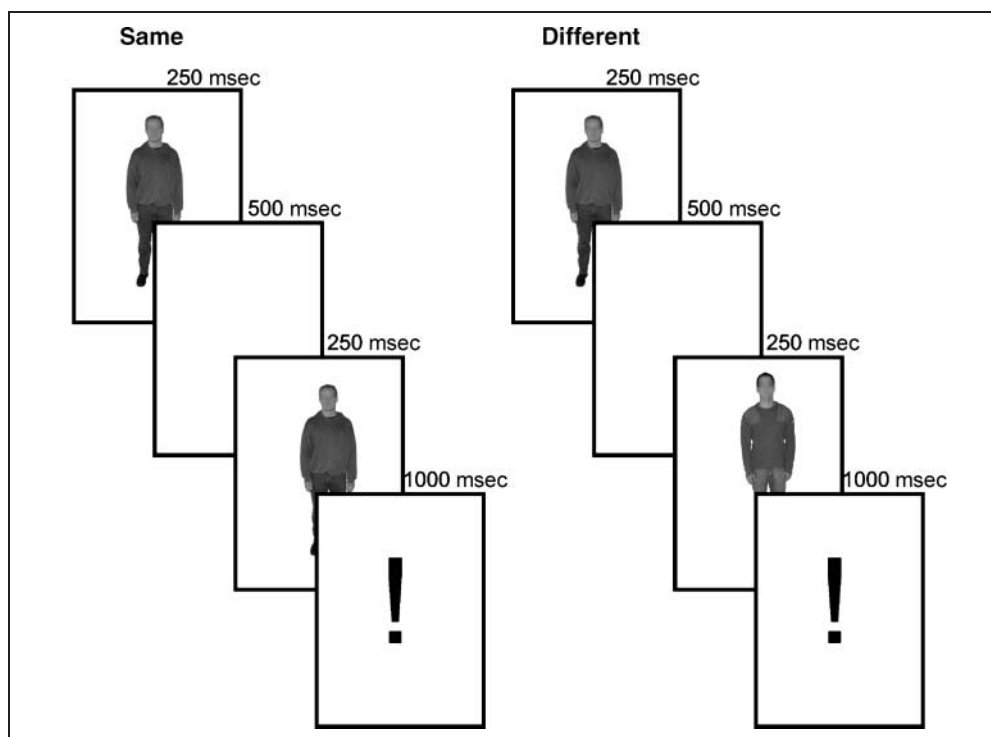
Table 1. Mean Percentage of Correct Responses and RTs (*SD* in brackets) for Each Stimulus Category and Orientation

	% Correct Responses		Median RT (msec)	
	Upright	*Inverted*	*Upright*	*Inverted*
Human body	92.4 (2.9)	90.3 (4.1)	511 (65)	519 (73)
Human body without head	92.7 (3.9)	92.4 (3.0)	519 (73)	518 (71)
Cat	93.2 (2.9)	92.9 (3.4)	510 (73)	508 (78)
Dog	93.3 (2.3)	93.2 (3.3)	504 (74)	517 (72)
Bird	92.5 (3.9)	90.3 (3.1)	509 (65)	506 (76)

ERPs were averaged separately for stimulus categories (human bodies, human bodies without head, birds, cats, dogs, and houses) and orientations (upright and inverted). The N170 peak amplitude was determined as the peak amplitude within the 140–200 msec post-stimulus latency window relative to baseline at electrode positions P7/P8. Amplitude maxima were taken to calculate N170 latencies. Visual inspection suggested that the maximal amplitudes were seen at these positions in all conditions (see Figure 3).

In the first analysis, N170 amplitudes for upright conditions were submitted to a 6×2 repeated measures ANOVA with factors stimulus category (human bodies, human bodies without head, birds, cats, dogs, and houses) and hemisphere (left vs. right) to investigate whether body categories evoked a significantly higher N170 than houses. N170 amplitudes and latencies were then submitted to repeated measures ANOVA with factors category (human bodies, human bodies without head, birds, cats, and dogs), orientation (upright vs. inverted), and hemisphere (left vs. right). Greenhouse–Geisser corrections were used where appropriate.

RESULTS

Behavioral Results

Correct responses and RTs are presented in Table 1. Efficiency scores for each condition are presented in Table 2. ANOVA yielded main effects of stimulus category [$F(1, 17) = 4.4, p = .01$], orientation [$F(1, 17) = 6.9, p = .02$], and condition [$F(1, 17) = 16.2, p = .001$], with better performance in the same compared to the different condition as well as an interaction between category and orientation [$F(1, 17) = 4.4, p = .009$; Figure 2].

Subsequent paired comparisons revealed a better performance for upright compared to inverted human bodies [$F(1, 17) = 8.6, p = .01$] and upright compared to inverted dogs [$F(1, 17) = 6.3, p = .02$; Figure 2]. Human bodies without heads showed the opposite pattern with better performance for inverted compared to upright bodies [$F(1, 17) = 5.5, p = .03$; Figure 2]. None of the other effects reached significance.

Electrophysiological Results
Amplitude

Grand averages elicited by upright human bodies, upright human bodies without head, upright birds, upright cats, upright dogs, and upright houses at left and right parietal electrodes (P7/P8) are presented in Figure 3. ANOVA yielded a main effect of category [$F(1, 17) = 18.1, p < .001$], with significantly smaller N170 amplitudes for houses compared to each of the five body categories (see Figure 3).

A further ANOVA based on the body categories only (human bodies, human bodies without head, birds, cats, and dogs), and including the upright/inverted condition, yielded a main effect of category [$F(1, 17) = 6.6, p = .001$] and an interaction between category and orientation [$F(1, 17) = 5.5, p = .006$], as well as an Orientation $\times$ Hemisphere interaction [$F(1, 17) = 11.9, p = .003$], the latter being due to higher amplitudes for upright bodies compared to inverted bodies [$F(1, 17) = 7.6, p = .02$] in the left hemisphere. However, inverted human bodies evoked a larger N170 compared to upright human bodies [$F(1, 17) = 6.3, p = .02$]. Human bodies without heads [$F(1, 17) = 5.3, p = .04$] and cats [$F(1, 17) = 5.8, p = .03$] showed the

Table 2. Efficiency Scores (*SD* in brackets) for Each Stimulus Category, Orientation, and Condition

Category	*Orientation*	*Same*	*Different*
Human body	upright	531 (80.6)	577 (79.1)
	inverted	540 (94.7)	614 (72.2)
Human body without head	upright	554 (104.6)	602 (76.0)
	inverted	546 (91.4)	576 (70.0)
Bird	upright	527 (88.6)	574 (65.5)
	inverted	532 (82.7)	593 (80.9)
Dog	upright	518 (83.8)	564 (81.6)
	inverted	541 (95.6)	571 (71.8)
Cat	upright	520 (92.1)	573 (88.8)
	inverted	529 (95.8)	574 (88.7)

Figure 2. (A) Efficiency scores and standard errors for upright and inverted human bodies and human bodies without heads. (B) Efficiency scores and standard errors for upright and inverted cats, dogs, and birds.
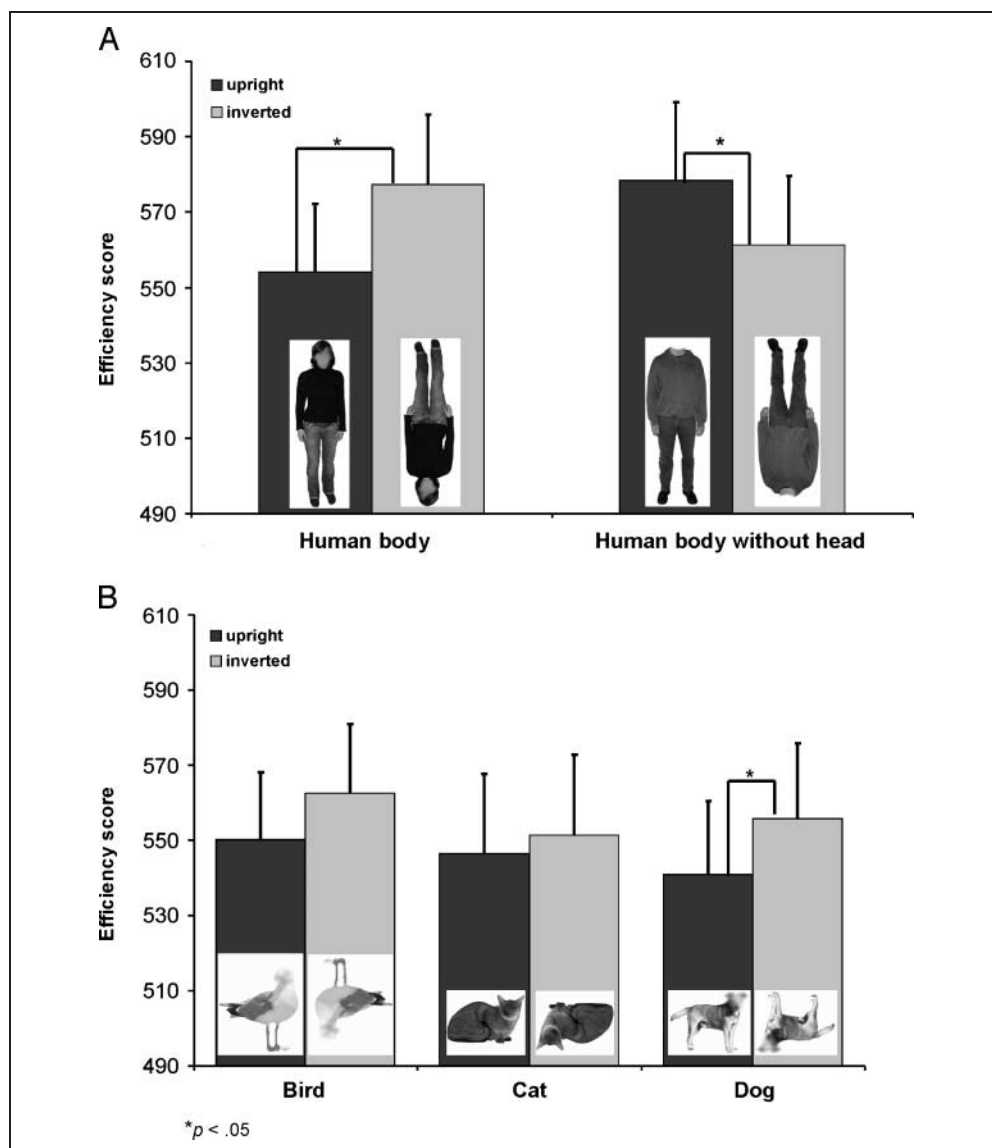
opposite pattern, with larger N170 for upright compared to inverted bodies (Figures 4 and 5).

Latency

A 5 × 2 × 2 ANOVA revealed a trend toward a significant interaction between category, orientation, and hemisphere [$F(4, 17) = 2.6, p = .06$]. Subsequent exploratory pairwise comparisons yielded longer N170 latencies for inverted ($M = 174$ msec, $SD = 20$) compared to upright human bodies ($M = 168$ msec, $SD = 21$) in the left hemisphere. None of the other effects reached significance.
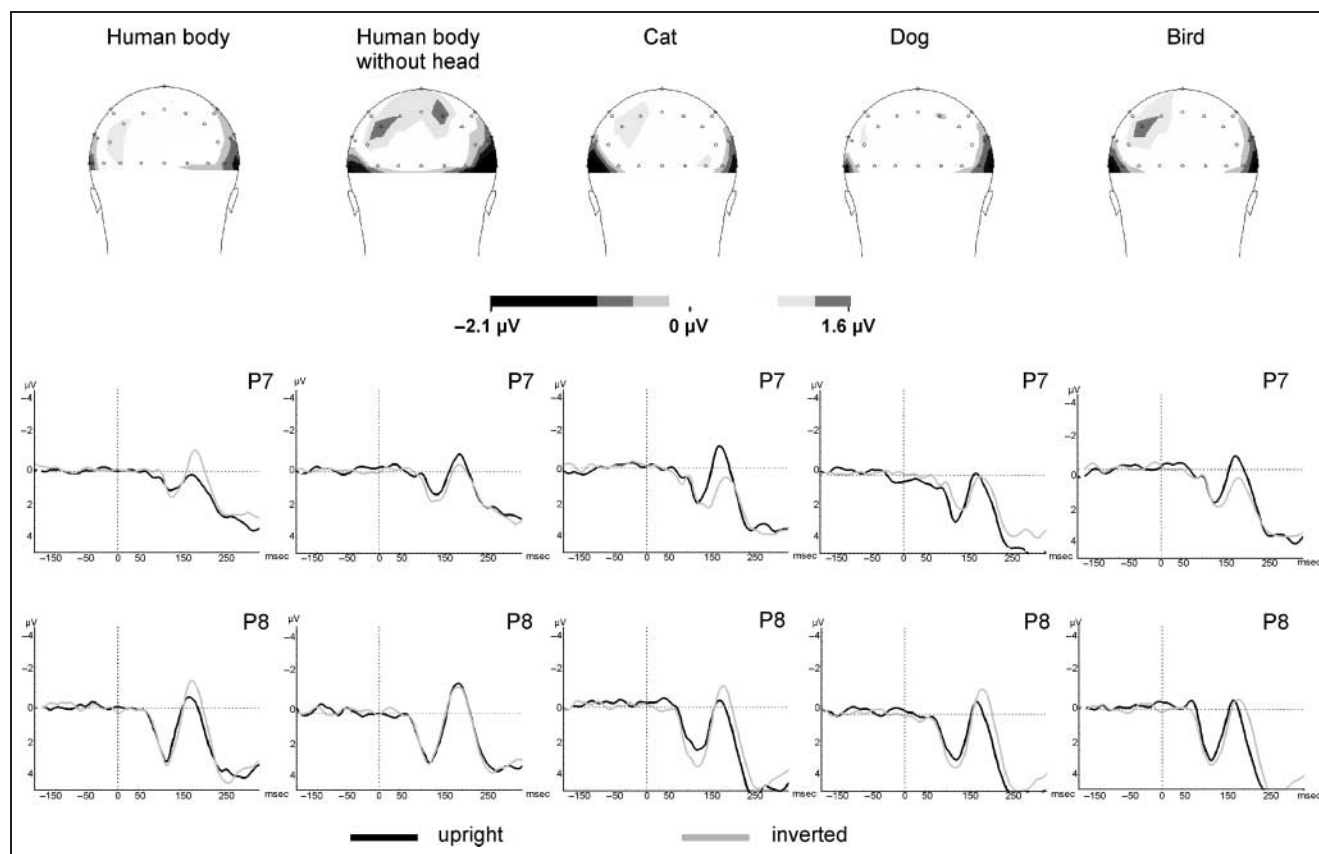
DISCUSSION

The aim of the present study was to further investigate the neurocognitive mechanisms underlying human

body perception by assessing the behavioral and electrophysiological effects of inversion of body stimuli. By including body forms without heads as a stimulus category, the findings should help to clarify whether human body forms, faces, or both are responsible for previously reported stimulus inversion effects on behavioral information processing and an early ERP component (N170). A further issue of interest was the specificity of these effects for human bodies relative to animal body forms.

Consistent with previous findings (Reed et al., 2003, 2006; Stekelenburg & de Gelder, 2004), recognition of human bodies (whole shapes with heads) was significantly affected by inversion. The N170 amplitudes were higher and latencies were prolonged for inverted compared to upright human bodies. These results clearly suggest similarities to the well-known effects of inversion on processing of human faces, which has been linked to the perceptual encoding stage (Jacques &

Human body

P7

μV
-4
-2
0
2
4
-150   -50   0 50   150   250   msec

P8

μV
-4
-2
0
2
4
-150   -50   0 50   150   250   msec

Human body
without head

P7

μV
-4
-2
0
2
4
-150   -50   0 50   150   250   msec

P8

μV
-4
-2
0
2
4
-150   -50   0 50   150   250   msec

Cat

P7

μV
-4
-2
0
2
4
-150   -50   0 50   150   250   msec

P8

μV
-4
-2
0
2
4
-150   -50   0 50   150   250   msec

Dog

P7

μV
-4
-2
0
2
4
-150   -50   0 50   150   250   msec

P8

μV
-4
-2
0
2
4
-150   -50   0 50   150   250   msec

Bird

P7

μV
-4
-2
0
2
4
-150   -50   0 50   150   250   msec

P8

μV
-4
-2
0
2
4
-150   -50   0 50   150   250   msec

Upright houses

Figure 4. Grand mean maps for upright body categories (top). Grand-average ERPs elicited by upright and inverted body categories recorded at P7 (left side) and P8 (right side, bottom).

Rossion, 2007). As discussed by Rossion et al. (2000), a possible explanation for the enhanced and delayed N170 for inverted compared to upright faces implies that the effect reflects a mechanism specific for face perception. Processing of inverted faces recruits both face- and object-related regions in the brain. In addition, inverted faces are more difficult to process compared to upright faces and, therefore, recruit more processing resources.

Previous reports of behavioral and electrophysiological body form inversion effects, using bodies with heads as stimuli (Reed et al., 2003, 2006; Stekelenburg & de Gelder, 2004), concluded that both configural and holistic processing might be important for the recognition of both human faces and bodies. However, in the present study, human bodies shown without heads yielded the opposite pattern to the face inversion effects, with better performance and a reduced N170 amplitude for inverted compared to upright human bodies. Comparable ERP inversion effects have also been reported for point-light walker stimuli, which provide information about human body shape but not the face (Jokisch, Daum, Suchan, & Troje, 2005). There are two possible explanations for the observed effect. The results might suggest that configural processing may be important for the recognition of human bodies with heads, representing a realistic silhouette, but not for bodies without heads. The latter stimulus class elicited longer N170 latencies compared to human bodies with heads. This implies that even masked faces (used as stimuli by Stekelenburg & de Gelder, 2004) might activate face-specific processing mechanisms to some degree, which in turn might be responsible for the reported behavioral and electrophysiological inversion effects in this study. Alternatively, if the N170 is a marker for configural processing that is elicited in response to both upright faces and upright human bodies with faces, the reversed inversion effect for human bodies without heads might be related to a lack of configural processing of these stimuli (comparable to inverted faces). Upright human bodies without heads may partly, but not closely, match the generalized template for human body shape and therefore provide a confusing stimulus input. Inverted human body shapes without heads, on the other hand, clearly do not match the typical representation. The present findings need to be interpreted with caution, and further investigations of face

Figure 3. Grand-average ERPs elicited by upright body categories (black lines) and upright houses recorded at P7 (left side) and P8 (right side).

Figure 5. (A) Grand-average amplitudes and standard errors at electrode positions P7 and P8 for upright and inverted human bodies and human bodies without heads. (B) Grand-average amplitudes and standard errors at electrode positions P7 and P8 for upright and inverted cats, dogs, and birds.
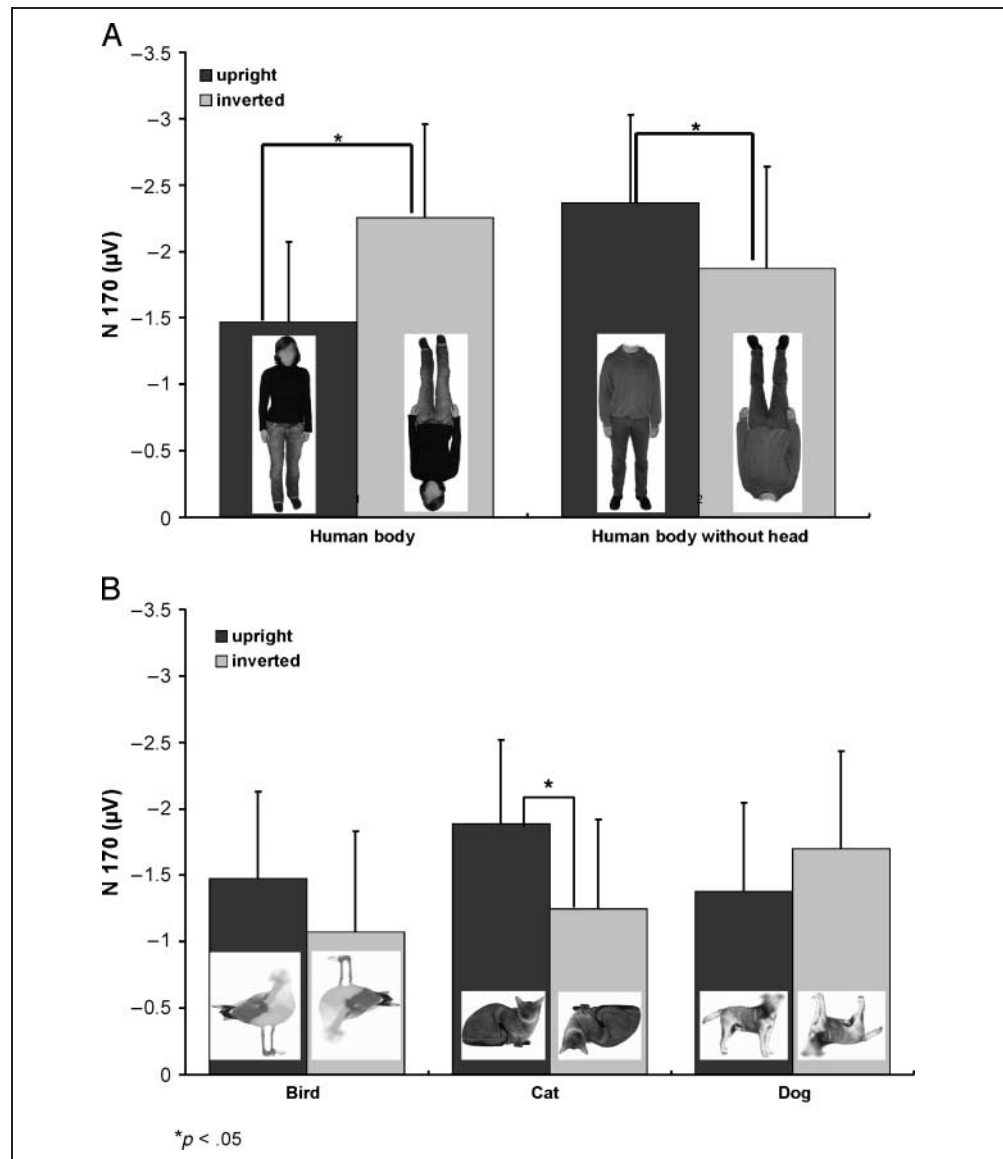
and body inversion effects and their implications for configural processing are needed. Because inversion disrupts configural processing, the reported inversion effect for human bodies with heads might suggest disruption of configural processing. However, it is not known which other processes are also disrupted by inversion and alternative explanations must remain open. A further explanation of the reversed effect for human bodies without heads would imply that the most distinctive feature of human bodies without heads is the position or shape of their feet, which are probably more prominent for inverted bodies without head.

A previous study (Thierry et al., 2006) reported a body-sensitive ERP component peaking about 190 msec (N190) after stimulus onset. This observation was not replicated in the present study. Both human bodies with masked faces and bodies presented without heads elicited ERP components peaking about 170 msec after

stimulus onset, which are comparable to the well-known face-specific N170.

Despite the fact that human bodies without heads yielded inversion effects (better recognition and reduced amplitude for inverted compared to upright human bodies), which are opposite to previously reported effects, processing of human bodies appears to be clearly dissociable from object processing. Recognition performance tends to be similar for upright and inverted objects (Reed et al., 2003, 2006) as are N170 amplitudes and latencies (Eimer, 2000a; Bentin et al., 1999; Tanaka & Farah, 1993).

The present results are inconsistent with previously reported face and object perception data (Hole et al., 1999; Lewis & Johnston, 1997; Johnston, Hill, & Carman, 1992), which indicated that human bodies might not be processed configurally like faces or analytically like objects. There is evidence for clear differences between

the neuronal and functional systems involved in body and face processing (Peelen & Downing, 2005, 2007; Downing et al., 2001, 2006; Morris et al., 2006; Schwarzlose et al., 2005). Similarities in processing mechanisms of faces and human bodies have, however, also been reported (Reed et al., 2003, 2006; Stekelenburg & de Gelder, 2004). The present data indicate that human bodies, like faces, may represent a unique stimulus class with specialized processing mechanisms, which differ from face and object processing.

All human and animal body categories elicited an ERP component peaking 170 msec after stimulus onset, which was larger for bodies than for houses. This component did not differ between human and animal bodies, supporting the assumption that the N170 is evoked by body forms in general. It should be noted that animal bodies were presented with heads in the present study. Recent imaging studies reported body-sensitive FBA activation for animal bodies with but not without heads (Downing et al., 2006; Chao et al., 1999; Kanwisher et al., 1999). It remains to be determined whether animal bodies without heads would activate an ERP component comparable to the N170 evoked by human bodies without heads. The N170 elicited by bodies is similar to the face-specific N170, indicating that faces and bodies might be processed by distinct but adjacent neuronal networks.

For the animal categories, the behavioral and electrophysiological data show a heterogeneous pattern. The behavioral data indicate an inversion effect for dogs but not for cats and birds. Thus, inversion seems to influence the recognition of dogs more than the recognition of birds and cats, although there is as yet no convincing explanation for this finding. The electrophysiological data showed an enhanced N170 for upright cats compared to inverted cats but not for dogs and birds. These results are similar to those of human bodies without heads, tentatively suggesting that cats and human bodies without heads might share some processing mechanisms. There is as yet no explanation for this puzzling and unexpected pattern of results. The underlying mechanisms remain to be explored in further studies, which should include human faces as well as animal bodies with and without heads to compare directly the well-known face inversion effect with inversion effects for other stimuli.

In summary, there is no clear evidence for an exclusively configural or analytical processing mechanism involved in human body form perception. A surprising finding is the better recognition of inverted compared to upright body shapes without heads, which might be related to a lack of configural processing of these stimuli. In everyday life, human body shapes are always perceived with heads. Pictures of human bodies without heads might be disturbing stimuli with negative connotations, which lead to higher error rates and slower processing. In summary, human bodies seem to be a special

stimulus class, which are processed by specialized neuronal areas which are at least partly dissociable from areas responsible for face or object processing.

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