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Dissociation between the behavioural and electrophysiological effects of the face and body composite illusions

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Several studies have reported similarities between perceptual processes underlying face and body perception, particularly emphasizing the importance of configural processes. Differences between the perception of faces and the perception of bodies were observed by means of a manipulation targeting a specific subtype of configural processing: the composite illusion. The composite face illusion describes the fact that two identical top halves of a face are perceived as being different if they are presented with different bottom parts. This effect disappears, if both halves are laterally shifted. Crucially, the effect of misalignment is not observed for bodies. This study aimed to further explore differences in the time course of face and body perception by using the composite effect. The present results replicated behavioural effects illustrating that misalignment affects the perception of faces but not bodies. Thus, face but not body perception relies on holistic processing. However, differences in the time course of the processing of both stimulus categories emerged at the N170 and P200. The pattern of the behavioural data seemed to be related to the P200. Thus, the present data indicate that holistic processes associated with the effect of misalignment might occur 200 ms after stimulus onset.

Recent investigations have reported similarities as well as differences regarding the neurocognitive mechanisms of face and body perception (e.g., De Gelder, 2009; Minnebusch & Daum, 2009; Righart & De Gelder, 2007; Thierry *et al.*, 2006). The current investigation aimed to explore further differences between the processing mechanisms of face and body perception by using the composite face illusion (CFI). The CFI describes the fact that two identical top halves of a face are perceived as being different if they are presented in combination with different bottom parts (aligned; for illustration, see Figure 1). The CFI disappears if the bottom part of a face is shifted (misaligned) and if the face is presented upside down (inverted; see Figure 1). The CFI illustrates that faces are perceived in terms of an integrative representation, and that it is very difficult to process some parts of the face while ignoring others. A recent study from our department (Soria Bauser, Suchan, & Daum, 2011) revealed differences in the processing of faces and bodies by means of the CFI (Young, Hellawell, & Hay, 1987). The CFI could not be observed for human body forms indicating that there are differences between the perceptual processes underlying face and body perception.

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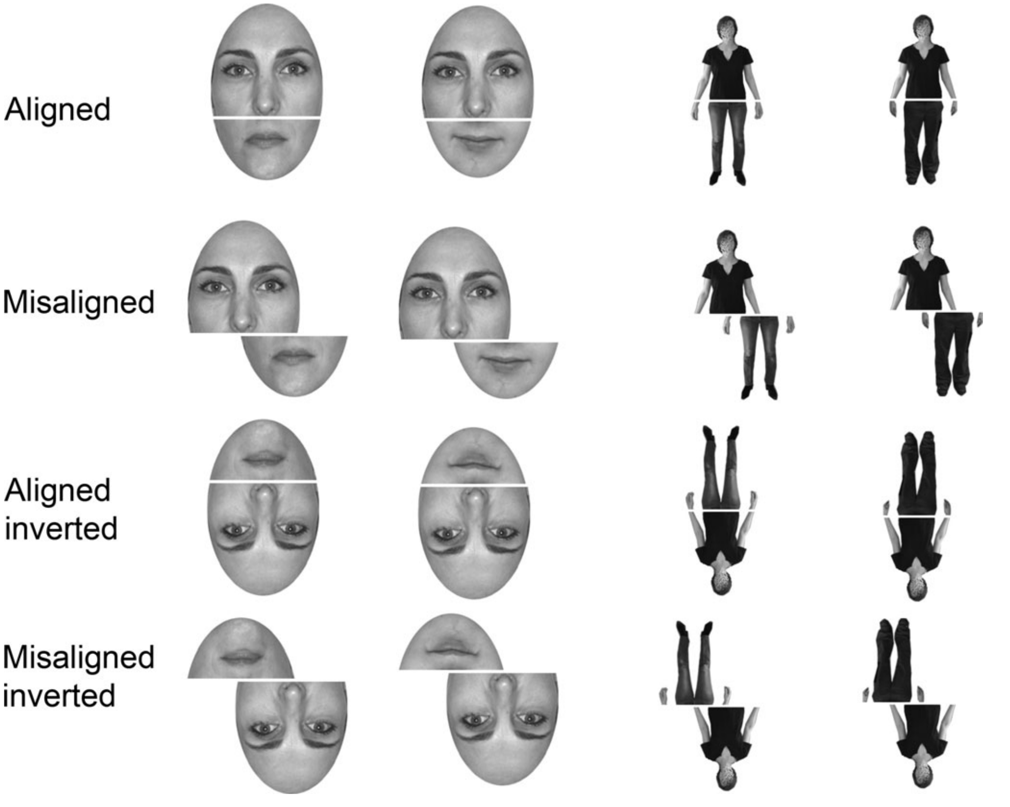

Figure 1. Illustration of the stimuli used in this study. Each top part of a face or body was paired with the bottom part of another face or body. Stimuli were presented aligned and misaligned as well as upright and inverted.

The terms holistic and configural processing have been used synonymously in previous studies (for review, see Minnebusch & Daum, 2009). The current investigation will follow the definition by Maurer, Le Grand, and Mondloch (2002) which defined holistic processing as a subtype of configural processing. In configural processing, perception relies on the spatial relations between different stimulus features (Leder & Bruce, 2000; Maurer *et al.*, 2002). Maurer *et al.* (2002) defined three types of configural face processing: first-order relational information, second-order relational information and holistic processing. First-order relational information refers to the spatial arrangement of stimulus features which are identical for all faces (e.g., the eyes are located above the nose and the nose is located above the mouth). Second-order relational information refers to metric distance between stimulus features which differ between individual faces (e.g., the distance between the eyes). Holistic processing refers to the fact that facial features are integrated into an individual representation of the face as a whole. Thus, holistic processing and second-order relational information could be manipulated by the CFI. The observation, that misalignment did not disrupt configural body processing support the assumption, that holistic processing as well as second-order relational information manipulated by the CFI seems to be more important for the perception of faces compared to bodies (Soria Bauser *et al.*, 2011). However, until now it remains unclear, in which time window holistic face processing and non-holistic bodies processing occur. Thus, the current study aimed to further explore the time course of electrophysiological potential (P100, N170 and P200) related to face and body processing.

Faces and bodies elicit a negative event-related potential (ERP) in occipitotemporal areas about 170 ms after stimulus onset (termed N170; e.g., Bentin, Deouell, & Soroker, 1999; Eimer, 2000b; Stekelenburg & De Gelder, 2004; Eimer, 2000b; Righart & De Gelder, 2007; Stekelenburg & De Gelder, 2004; Thierry *et al.*, 2006). The N170 has been associated with configural face and body processing (Jacques & Rossion, 2007; Minnebusch, Keune, Suchan, & Daum, 2010). In addition, it has been linked to the late stages of structural encoding at which a global representation of the stimulus is created (Eimer, 2000b; Soldan, Mangels, & Cooper, 2006). The N170 is thought to reflect an integration of different processing stages (e.g., first- order relational information and holistic processing; Latinus & Taylor, 2006). In other words, it might be that the N170 mirrors processes in which first-order relational and holistic information are used to create a global face representation.

Recently, a lot of research has been dedicated to the investigation of the time course of the electrophysiological correlates (e.g., N170) which are modulated by the CFI, in order to further elucidate the nature of holistic face perception (Jacques & Rossion, 2009, 2010; Letourneau & Mitchell, 2008; Schiltz, Dricot, Goebel, & Rossion, 2010). Misaligned faces elicit a delayed and enhanced N170 compared to aligned faces. This effect disappeared if the faces were inverted (Jacques & Rossion, 2010; Letourneau & Mitchell, 2008). In addition, the CFI is reduced when a part of the face was replaced with visual noise (Jacques & Rossion, 2010). These data support the assumption that processes related to the effect of misalignment seem to appear in the time window of the N170. Furthermore, these effects might be face-specific. In contrast to the classical inversion effect with inverted faces eliciting enhanced and delayed N170 amplitudes (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000a; Itier & Taylor, 2002, 2004a; Minnebusch, Suchan, & Daum, 2009; Righart & De Gelder, 2007; Stekelenburg & De Gelder, 2004), inversion has a different effect when used in the context of the composite illusion: Inverted aligned and misaligned faces elicit comparable N170 amplitudes because both types of stimuli did not undergo configural processing. Misalignment in combination with the composite illusion seems to have a comparable impact on the N170 as the classical inversion effect. The N170 is thus associated with a global and upright face representation (Jacques & Rossion, 2010).

Another face and body sensitive ERP is the P100, a positive component with an occipitotemporal distribution peaking about 100 ms after stimulus onset (Itier & Taylor, 2004b; Minnebusch *et al.*, 2010; Righart & De Gelder, 2007; Rossion *et al.*, 1999, 2000; Thierry, Martin, Downing, & Pegna, 2007; Thierry *et al.*, 2006). It is a matter of debate, wheater the P100 is associated with stimulus classification (Herrmann, Ehlis, Muehlberger, & Fallgatter, 2005; Itier & Taylor, 2004b), stimulus categorization (Liu, Harris, & Kanwisher, 2002) or visual properties (Latinus & Taylor, 2006; Rossion & Caharel, 2011). Some researchers assume that the P100 mirrors the classification of a stimulus as a face/body as the P100 seemed to be enhanced for faces and bodies compared to other stimulus classes (Herrmann *et al.*, 2005; Itier & Taylor, 2004b). However, some studies reported greater P100 amplitudes for faces compared to other categories, whereas other investigations failed to observe these differences (see Rossiojn & Jacques, 2008). Moreover, the P100 appears to be associated with the successful categorization of a face (Liu *et al.*, 2002) and is sensitive to the low-level visual properties of stimuli (Latinus & Taylor, 2006 Rossion & Caharel, 2011). To sum up, the N170 seems to be a more reliable face-specific ERP component compared to the P100 (Ganis, Smith, & Schedan, 2012; Liu *et al.*, 2002; Rossiojn & Jacques, 2008). In accordance to previous studies (Jacques & Rossion, 2010; Kuefner, Jacques, Prieto, & Rossion, 2010; Letourneau & Mitchell, 2008), we decided to investigate whether alignment modulate the P100 to replicate the observation, that the CFI did not modulate the P100.

Processing differences for faces relative to other categories as well as within the class of different face stimuli (e.g., for familiar faces vs. unfamiliar faces) are also observed for ERP components occurring later than the N170, for example, the P200 (Boehm, Dering, & Thierry, 2011; Caharel *et al.*, 2002). The P200 is thought to reflect processing stages associated with second-order relations between facial features (Latinus & Taylor, 2006). In addition, it has been argued that the P200 mirrors a reactivation of the ventral visual pathway (Latinus & Taylor, 2006). However, previous investigations have predominantly focused on the N170 and sometimes on the P100 while ignoring possible differences between faces and other categories as well as manipulations affecting configural processing (e.g., inversion, CFI) in later time windows. Jacques and Rossion (2007) used multiple face orientations to investigate the relationship between the behavioural inversion effect and the electrophysiological responses. They reported three time windows which seemed to be linked to the behavioural performance (110–145, 155–220 and 320–600 ms). Other investigations exploring the effect of stimulus repetition have also reported effects in later time windows (Itier & Taylor, 2004a,b; Schweinberger, Pfütze, & Sommer, 1995; Schweinberger, Pickering, Burton, & Kaufman, 2002a; Schweinberger, Pickering, Jentzsh, Burton, & Kaufman, 2002b). Two recent investigations explored electrophysiological correlates of the CFI which occur later than the N170 (Kuefner *et al.*, 2010; Wiese, Kachel, & Schweinberger, 2013). Kuefner *et al.* (2010) analysed the decisional P3b as well as the lateralized readiness potential to distinguish between perceptual and decisional processes of holistic face processing. In addition, Wiese *et al.* (2013) used a repetition priming task and focussed on the N250r to explore holistic face processing in young and older subjects. The N250r is typically enhanced for repeated relative to non-repeated faces (see, Schweinberger *et al.*, 1995, 2002a,b).

Taken together, several studies have reported similarities as well as differences in the neural mechanisms underlying face and body perception (for review see Minnebusch & Daum, 2009). Faces and bodies are processed configurally as an inversion effect could be observed for both stimuli. In addition, faces and bodies evoke comparable ERP components (P100, N170) and seem to be processes in comparable but not identical brain areas. Previous investigations have focused mainly on the P100 and N170 while ignoring later ERP components. This study therefore aimed to investigate differences between the processing mechanisms of face and body perception by analysing the P100, N170 and P200. Additionally, we aimed to determine whether inversion affects body sensitive ERPs for aligned and misaligned bodies in a similar manner. If this is the case, the present data support the assumption that holistic processing is not necessary for successful body perception. An inversion effect for aligned and misaligned bodies would seem to provide evidence that body perception relies on first-order relational information. In addition, this would imply that different types of configural processing are necessary to perceive faces and bodies. Given that we had not observed a composite effect for body postures in behavioural performance in a previous investigation (Soria Bauser *et al.*, 2011), we expected ERPs for aligned and misaligned bodies to be similar. Similar ERPs for misaligned and aligned bodies would seem to provide evidence that holistic processing and second-order relational information are not important for successful body perception.

Method

Subjects

Twenty-four right-handed subjects participated in this study (twelve female; mean age 29.3 years, *SD* = 6.0; age range 21–35 years). None of the participants reported a history of neurological or psychiatric problems, and all subjects reported normal or corrected-to-normal vision. The study was performed in accordance with the ethic standards laid down in the declaration of Helsinki (Varga, 1975) and was approved by the Ethics Committee of the of Psychological Faculty of the Ruhr University Bochum, Germany. Written informed consent was obtained from all subjects prior to participation.

Stimuli

Stimuli and experimental design were adopted from Soria Bauser *et al.* (2011). Greyscale photographic illustrations of 30 different subjects (15 female) were used as stimuli. All of these 30 subjects that were photographed to create the current stimulus set wear the same black T-shirt (in different sizes) and darkish trousers to avoid that participants might use some specific features of the T-shirts to distinguish between the presented body picture. The factors faces versus bodies, inverted versus upright and aligned versus misaligned were manipulated to create eight stimulus categories (bodies aligned upright, bodies misaligned upright, bodies aligned inverted, bodies misaligned inverted, faces aligned upright, faces misaligned upright, faces aligned inverted, faces misaligned inverted). Each stimulus category consisted of 30 pictures of approximately 3° × 3° of visual angle per item. In accordance with previous studies, the faces of the body stimuli were masked in order to minimize face processing (Minnebusch *et al.*, 2009, 2010). It is a matter of debate whether bodies should be presented with or without heads when investigating similarities and differences in face and body processing mechanisms (see Minnebusch & Daum, 2009). It has been argued that bodies with heads might activate face and body processing mechanisms (see, Cox, Meyers & Sinha, 2004; Morris, Pelphrey & McCarthy, 2006). However, recent studies reported that omission of the head abolished the inversion effect (Minnebusch *et al.*, 2009; Yovel, Pelc, & Lubetzky, 2010). The head thus seems to be an important feature aiding the identification of a stimulus as a body and the activation of processes related to configural body processing (Brandman & Yovel, 2010; Reed, Stone, Grubb, & McGoldrick, 2006; Yovel *et al.*, 2010). In accordance with this notion, bodies were presented with heads but with masked faces in the current study (see Figure 1).

Human bodies were presented in an aligned and a misaligned version. Based on previous studies investigating the face composite effect (e.g., Rossion & Boremanse, 2008), an aligned version of each body picture was created by separating the upper and lower body parts by a small gap (1.8 mm). A misaligned version was created by additionally shifting the lower body part to the right, starting in the middle of the upper body part (see Figure 1). The top part of each body picture was then paired with a lower body part of another person of the same gender to create new stimuli. The same body stimuli (aligned and misaligned) were presented in upright and inverted versions (see Figure 1).

In addition, 15 female and 15 male face stimuli which were created in our lab were presented (see Figure 1). The upper and lower parts of each face were separated by a small gap (1.8 mm) to create aligned illustrations of each face. Misaligned faces were created by shifting the lower face part to the right. The nose was used as a reference point (see Figure 1). To create aligned and misaligned faces with different bottom parts, the top part of each face was further paired with a lower face part of another person of the same gender (Figure 1). Misaligned and aligned face and body stimuli were used in a delayed matching-to sample task.

Procedure

Participants were instructed to face a computer monitor at a viewing distance of 80 cm in a sound attenuated room. Trials involving face and body stimuli were presented in random order. Each trial consisted of two face or body pictures. The first and the second picture of each trial belonged to the same category (faces or bodies) and the same gender (male or female). They were presented in the same orientation (upright or inverted) and were both either aligned or misaligned.

Each trial started with a fixation cross-presented at the centre of the screen for 100 ms (see Figure 2). The first picture then appeared for 400 ms followed by a scrambled mask for 200 ms. The second stimulus was presented for 400 ms after an inter-trial-interval of about 550 ms (range 400–700 ms). Subjects then had to respond within 1,000 ms: While ignoring the lower part of each face/body, they had to decide whether the top part of the first and second picture was the same (same condition/repeated) or different (different condition/non-repeated). Subjects were specifically asked to concentrate on the top part of the picture on the screen. They had to respond as fast and as accurately as possible (using two response keys) in the interval between the onset of the second stimulus and the end of the inter-trial interval. Stimulus presentation was controlled using ERTS.

Note that the bottom parts of the first and second stimuli were different on all trials. The top parts differed in 50% of the trials. Each first stimulus was used once in the same and once in the different condition. In total, two blocks of 240 trials were administered.

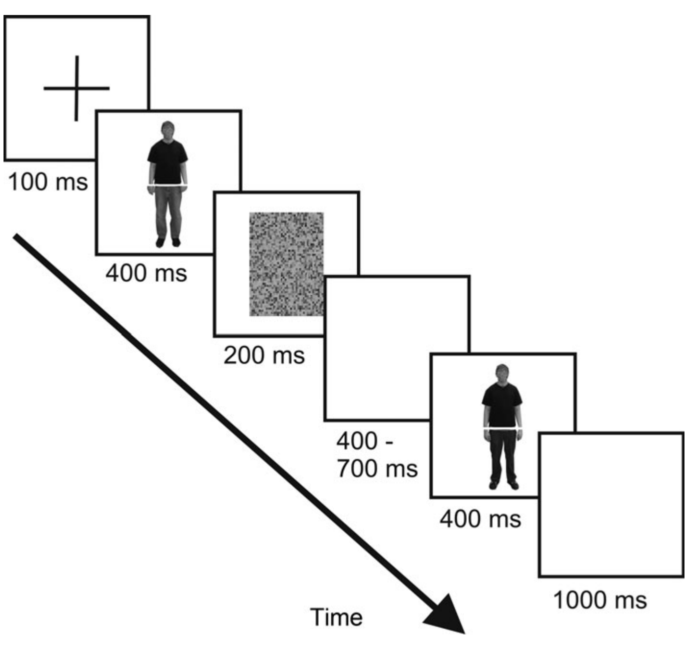

Figure 2. Experimental design.

Electroencephalography recordings

Electroencephalography (EEG) recordings were obtained using 30 silver-silver chloride (F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, PO7, PO3, POz, PO4, PO8) electrodes which were mounted to an electrode cap according to the 10–20 standard setup (Jasper, 1958). We used a Brain Products BrainAmp Standard Amplifier (Brain Products, Munich, Germany). Electrode impedance was kept below 5 kΩ, and all active electrodes were referenced to linked mastoid electrodes. Fpz was used as the ground electrode. EEG was digitized at a sampling rate of 500 Hz, and signals were filtered offline before averaging with a band pass filter of 0.05–35 Hz (12 db/oct, zero phase shifts). Analysis was conducted using Brain Vision Analyzer 2.0 (Brain Products, Munich, Germany). Trials with EEG voltage steps exceeding 50 μV were excluded by means of an automatic artefact detection algorithm. EEG artefacts resulting from eye movements and blinks were corrected by using independent component analysis (ICA) as implemented in Brain Vision Analyzer 2. Data were re-referenced to a common average reference.

Data analyses

Behavioural data

In accordance with other studies using the composite illusion (e.g., Goffaux & Rossion, 2006; de Heering, Rossion, Turati, & Simion, 2008; Soria Bauser *et al.*, 2011), analyses focused on the performance in the 'same' condition in which upper face or body parts were identical while lower face or body parts differed between the first and second picture of each trial. Behavioural results for the different trials are also reported to verify that the CFI does not represent a kind of unexpected bias effect (i.e., a tendency to press same for misaligned and different for aligned stimuli. For each condition and each subject, the percentage of correct responses and reaction times (RTs; for correct reactions) was determined. Percentage of correct responses and RTs were entered into separated $2 \times 2 \times 2$ repeated-measure ANOVA with the factors Stimulus Category (bodies vs. faces), Alignment (aligned vs. misaligned) and Orientation (upright vs. inverted).

EEG data

EEG analysis focused on the ERP response to the second picture of each pair as we did not find significant differences between the ERP responses to the first and second picture. Additionally, we focused on the second picture of each trial because response patterns are associated with the second picture. Only correct trials were included in the analysis. Only trials depicting same upper halves are included in the analysis of the P100, N170 and P200 as the composite illusion refers only to the same trials. After artefact removal, raw data were segmented offline. For each subject, average epochs ranging from 200 ms prior to stimulus onset and ending 450 ms after stimulus presentation were determined for each stimulus condition. Activity in the time range 200 ms before stimulus onset served as baseline. Visual inspection showed a pattern which seems to be typical for visual evoked ERPs reflecting the P100, N170 and P200 components. Previous investigations focused predominantly on the first two components (Jacques & Rossion, 2010; Letourneau & Mitchell, 2008), while the present study focused on all three of them. The P100 amplitude was determined as the peak amplitude between 80 and 120 ms after stimulus onset at electrode positions P7/P8 and PO7/PO8. The N170 amplitude was assessed as the peak amplitude within the 140–180 ms post-stimulus latency window relative to baseline at electrode positions P7/P8 and PO7/PO8. The P200 amplitude was determined as the peak amplitude between 180 and 250 ms after stimulus onset at electrode positions P7/P8 and PO7/PO8. Amplitude maxima were used to determine P100, N170 and P200 latencies. Visual inspection suggested that the maximum amplitudes emerged at these electrode positions in all conditions. P100, N170 and P200 amplitudes and latencies were submitted to separate repeated-measure ANOVAs with Category (bodies vs. faces), Alignment (aligned vs. misaligned), Orientation (upright vs. inverted), Electrode Position (P7/P8 vs. PO7/PO8) and Hemisphere (right vs. left) as within-subject factors.

Results

Behavioural data for the same trials

Percentages of correct responses and RTs for same trials are presented in Table 1.

Percentage of correct responses

For percentage of correct responses, analysis revealed main effects of Category ($F_{1,23}$ = 16.6, p = .001) and Orientation ($F_{1,23}$ = 34.36, p < .001) with better performances for faces compared to bodies and upright compared to inverted stimuli. In addition, the analysis showed significant Category × Alignment ($F_{1,23}$ = 12.1, p = .002) Category × Orientation ($F_{1,23}$ = 54.2, p < .001), Alignment × Orientation ($F_{1,23}$ = 15.9, p = .001) and Category × Alignment × Orientation ($F_{1,23}$ = 36.1, p < .001) interactions. To resolve the three-way interaction, separated analyses were conducted for faces and bodies.

For bodies, we found a main effect of Orientation ($F_{1,23}$ = 51.1, p < .001) with better performances for upright compared to inverted bodies (see Table 1). The current results are consistent with the pattern described for the classical inversion effect indicating that bodies are processed configurally. None of the other comparisons reached significance (all p > .08) pointing out that misalignment did not affect the perception of bodies.

For faces, ANOVA yielded main effects of Alignment ($F_{1,23}$ = 20.5, p < .001) and Orientation ($F_{1,23}$ = 5.9, p = .024) as well as a significant interaction between Alignment and Orientation ($F_{1,23}$ = 59.0, p < .001). Performances were better for misaligned compared to aligned faces and upright compared to inverted faces.

Table 1. RTs (a) and percentage of correct responses (b) for same trials. Standard deviations are presented in brackets

	Upright		Inverted	
	Aligned	Misaligned	Aligned	Misaligned
(a)				
Bodies	600 (112)	606 (106)	618 (117)	614 (121)
Faces	620 (103)	606 (97)	601 (102)	616 (104)
(b)				
Bodies	94.7 (4.2)	92.7 (3.8)	82.4 (9.5)	81.7 (9.4)
Faces	90.0 (3.3)	96.4 (3.7)	91.7 (4.4)	90.0 (6.0)

Post-hoc paired comparisons revealed better performances for upright misaligned compared to upright aligned faces ($T_{1,23} = 77.4$, $p < .001$). This pattern supports the assumption that holistic processing is necessary for face perception. However, the opposite pattern emerged for inverted faces with better performances for aligned compared to misaligned faces ($T_{1,23} = 7.8$, $p = .010$) indicating that the effect of misalignment is modulated by stimulus inversion.

RTs

For RTs, none of the main effects or interactions in the ANOVA reached significance (all $p < .08$).

Behavioural data for the different trials

Percentages of correct responses and RTs for different trials are presented in Table 2.

Percentage of correct responses

For percentage of correct responses, ANOVA yielded main effects of Category ($F_{1,23} = 82.2$, $p < .001$), Orientation ($F_{1,23} = 102.8$, $p < .001$) and Alignment ($F_{1,23} = 6.8$, $p = .015$). Performance was better for faces compared to bodies, upright compared to inverted stimuli and aligned compared to misaligned stimuli. In addition, there was a significant interaction between the factors Category and Orientation ($F_{1,23} = 50.8$, $p < .001$).

The inversion effect was greater for bodies compared to faces (bodies: $T_{1,23} = 98.0$, $p < .001$; faces: $T_{1,23} = 10.5$, $p = .004$).

RTs

For RTs, analysis revealed main effects of Category ($F_{1,23} = 9.9$, $p = .005$) and Orientation ($F_{1,23} = 43.0$, $p < .001$) with slower RTs for bodies compared to faces and inverted compared to upright stimuli.

Table 2. RTs (a) and percentage of correct responses (b) for different trials. Standard deviations are presented in brackets

	Upright		Inverted	
	Aligned	Misaligned	Aligned	Misaligned
(a)				
Bodies	657 (78)	677 (88)	713 (99)	705 (101)
Faces	636 (73)	649 (82)	679 (67)	675(64)
(b)				
Bodies	90.3 (7.4)	86.7 (6.0)	69.0 (13.5)	66.8 (15.1)
Faces	95.1 (4.2)	94.4 (4.0)	91.8 (6.4)	90.1 (5.7)

Electrophysiological data

Grand average maps for faces and bodies are depicted in Figures 3 and 4. Mean amplitudes over the four electrode positions are illustrated in Figure 5.

P100 amplitude

Analysis of the P100 amplitude showed main effects of Category ($F_{1,23}$ = 30.6, p < .001), Orientation ($F_{1,23}$ = 13.2, p = .001), Electrode Position ($F_{1,23}$ = 29.0, p < .001) and Hemisphere ($F_{1,23}$ = 36.6, p < .001). P100 amplitudes were larger for faces compared to bodies, for inverted compared to upright presented stimuli, at electrode position PO7/PO8 compared to P7/P8, and over the right compared to the left hemisphere.

P100 latency

There were main effects of Category ($F_{1,23}$ = 7.6, p = .021) and Orientation ($F_{1,23}$ = 34.2, p < .001), with delayed P100 latencies for faces compared to bodies and inverted compared to upright stimuli. All other effects failed to reach statistical significance.

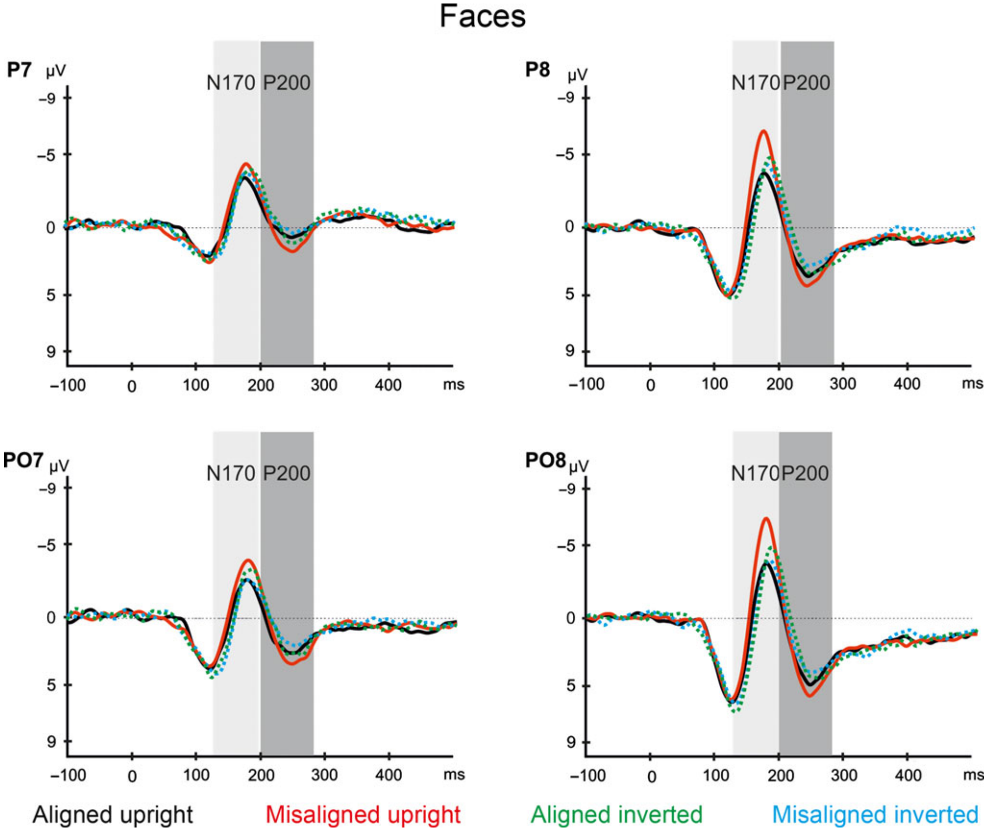

Figure 3. Grand average wave forms at electrode positions P7, P8, PO7 and PO8 for faces.

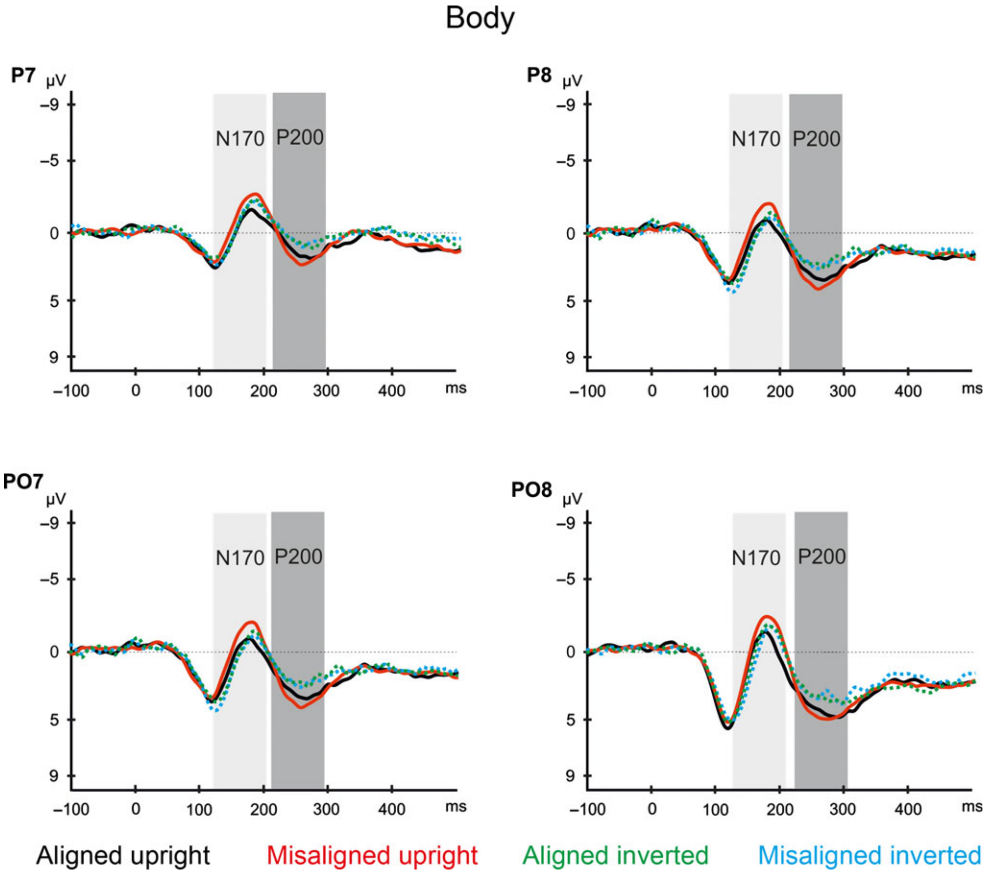

Figure 4. Grand average wave forms at electrode positions P7, P8, PO7 and PO8 for bodies.

N170 amplitude

Analysis revealed main effects of Category ($F_{1,23}$ = 41.2, p < .001), with enhanced N170 amplitudes for faces compared to bodies, and Alignment ($F_{1,23}$ = 85.5, p < .001), with enhanced N170 amplitudes for misaligned stimulus presentation compared to aligned stimulus presentation (see Figure 4) as well as Hemisphere ($F_{1,23}$ = 8.7, p = .007) with enhanced N170 amplitudes in the right, compared to the left hemisphere. In addition, there were significant interactions between Category and Alignment ($F_{1,23}$ = 22.9, p < .001), Alignment and Orientation ($F_{1,23}$ = 67.0, p < .001) as well as Category, Alignment and Orientation ($F_{1,23}$ = 4.8, p = .039).

To resolve the three-way interaction, separate analyses were performed for bodies and faces. For both categories, there were main effects of Alignment yielding reduced amplitudes for aligned compared to misaligned bodies and faces (bodies: $F_{1,23}$ = 40.1, p < .001; faces: $F_{1,23}$ = 83.3, p < .001). Furthermore, there were significant Alignment × Orientation interactions (bodies: $F_{1,23}$ = 39.5, p < .001; faces: $F_{1,23}$ = 33.5, p < .001), indicating enhanced amplitudes for misaligned compared to aligned stimuli. The effect of alignment was larger for upright compared to inverted stimuli and the interaction between Alignment and Orientation was larger for bodies compared to faces (bodies upright: $F_{1,23}$ = 76.4, p < .001; bodies inverted: $F_{1,23}$ = 10.1, p = .004; faces

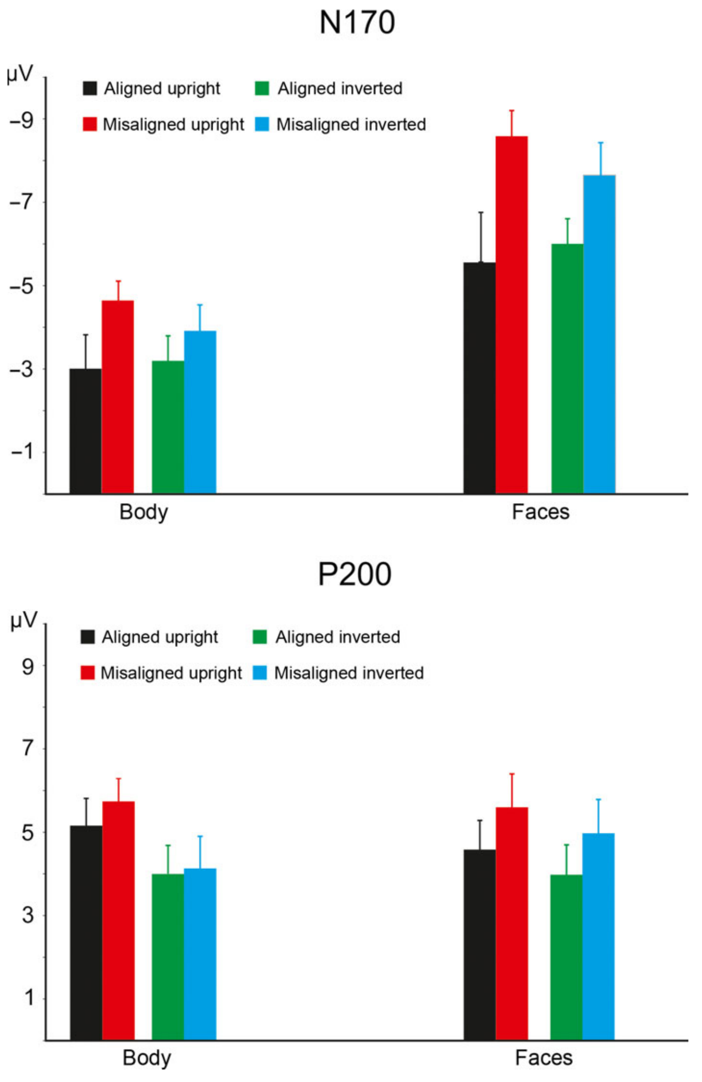

Figure 5. N170 and P200 amplitudes (with between subject standard errors) over the four electrode positions for faces and bodies.

upright: $F_{1,23} = 141.4, p < .001$; faces inverted: $F_{1,23} = 24.6, p < .001$). All other effects did not reach statistical significance.

N170 latency

ANOVA revealed main effects of Alignment ($F_{1,23} = 5.7, p = .026$) and Orientation ($F_{1,23} = 42.0, p < .001$), with delayed N170 amplitudes for misaligned compared to aligned stimuli and inverted compared to upright stimulus presentation. All other effects failed to reach statistical significance.

P200 amplitude

Analysis yielded main effects of Orientation ($F_{1,23} = 18.6$, $p < .001$), Alignment ($F_{1,23} = 16.9$, $p = .001$), Electrode Position ($F_{1,23} = 25.7$, $p < .001$) and Hemisphere ($F_{1,23} = 18.5$, $p < .001$), with greater P200 amplitudes for upright compared to inverted stimuli, misaligned compared to aligned stimulus presentation, at electrode position PO7/PO8 compared to P7/P8 and over the right compared to the left hemisphere. Additionally, there was a significant interaction between Category and Alignment ($F_{1,23} = 7.4$, $p = .013$) as well as Category, Alignment, Orientation and Electrode position ($F_{1,23} = 7.4$, $p = .013$). Subsequent paired comparisons showed reduced P200 amplitudes for aligned compared to misaligned faces ($F_{1,23} = 23.7$, $p < .001$). This effect could not be observed for bodies ($p = .16$; see Figure 4).

P200 latency

There were main effects of Category ($F_{1,23} = 16.9$, $p < .001$), with delayed P200 amplitudes for bodies compared to faces. None of the other comparisons reached significance.

Discussion

In the current investigation, we compared the composite illusion for faces and bodies in order to further elucidate whether faces and bodies are processed by similar or different mechanisms (for review see, Minnebusch & Daum, 2009). The CFI is associated with a subtype of configural processing termed holistic processing. In addition, second-order relational information are also manipulated by the CFI. A previous behavioural study from our department pointed out that holistic processing and second-order relational information seem to be necessary for the successful perception of faces but not bodies (Soria Bauser *et al.*, 2011). While subjects performed a matching-to sample task with aligned and misaligned faces and bodies, we explored different ERP components (P100, N170 and P200). In addition, we were interested how the effect of misalignment is modulated by the effect of stimulus inversion.

In accordance with previous studies, we found better performance for misaligned and upright compared to aligned and upright faces (see Table 1; Hole, George, & Dunsmore, 1999; Le Grand, Mondloch, Maurer, & Brent, 2004; Rossion & Boremanse, 2008; Young *et al.*, 1987). As expected, we did not observe an effect of misalignment for the different trials (see, Table 2). Additionally, there was no unexpected response bias. Thus, the current data show the CFI: two identical top halves of a face are perceived as being different if they are presented with different bottom parts. This pattern indicates that upright faces undergo integrative processing, and that it is difficult to ignore some parts of a face while processing other parts. In other words, faces are perceived as wholes. The current data support the assumption that holistic processing as well as second-order relational information are necessary for successful face processing. The effect of better performances for misaligned compared to aligned faces disappeared when faces were presented upside down (see Table 1). However, we observed the opposite pattern with better accuracy scores for aligned and inverted compared to misaligned and inverted faces. A possible explanation for this effect might be that inversion disrupts the three subtypes of configural processing so that inverted faces have to be processed feature based. In this context it might be easier to process aligned compared to misaligned faces.

The current results support the assumption that for faces the effect of misalignment is modulates by stimulus inversion. By contrast, we observed no effect of misalignment for human body shapes. In other words, for the accuracy scores, we found an effect of misalignment for upright faces but not for upright bodies. This result pattern are consistent with a previous study conducted in our department (Soria Bauser *et al.*, 2011) which indicated that holistic processing as well as second-order relational information might be more important for the perception of faces than for the perception of bodies. Furthermore, there was an effect of stimulus inversion for aligned and misaligned bodies. As inversion is thought to disturbed configural processing mechanisms the present data support the notion that bodies are processed configurally. The present data show that body perception relies on first-order relational information but not on holistic or second-oder relational information. It might be that the position of the head or the upper body part is more important for body processing than the lower body part (see, Tao & Sun, 2013; Yovel *et al.*, 2010). In addition, the position of the head might even be more important than holistic processing mechanisms. Thus, misalignment did not affect mechanisms associated with body processing as subjects might focus on the upper body part while ignoring the lower body part. According to that, we did not find differences between aligned and misaligned bodies but between upright and inverted bodies. Alternatively, it might be that it is easier to compare two upper halves of a body when they are presented in the upper part of the picture than to compare two upper halves of a body presented in the lower part of a picture.

Based on the behavioural data, we searched for an ERP component also yielding differences between misaligned and aligned faces but not between misaligned and aligned bodies. As was also reported in previous studies (Jacques & Rossion, 2010; Kuefner *et al.*, 2010; Letourneau & Mitchell, 2008), alignment did not modulate the P100 for either faces or bodies (see Figures 3 and 4). For both categories, N170 amplitudes were enhanced and delayed for misaligned compared to aligned stimuli (see Figures 3 and 4). However, the effect of misalignment seemed to be larger for faces compared to bodies (see Figures 3 and 4). The present data are consistent with the studies by Jacques and Rossion (2010) and Letourneau and Mitchell (2008), indicating that dividing a face into two parts leads to a disruption of holistic processing which is assumed to be reflected by the N170. However, we observed the same effect for misaligned bodies with enhanced N170 amplitudes for misaligned compared to aligned bodies. This result pattern did not fit to the behavioural data. Thus, the effect of misalignment seems to take place in a later time window. A possible explanation for this effect in the time window of the N170 might be that bodies are processed holistically but this kind of holistic body processing is not obligatory for upright bodies.

Further differences between both categories emerged for a later ERP, the P200, and these differences seem to mirror the behavioural pattern (see Table 1 and Figures 3 and 4). Misaligned faces elicited enhanced P200 amplitudes compared to aligned faces. This pattern could not be observed for bodies, suggesting that configural processes related to the effect of misalignment emerged 200 ms after stimulus onset. Furthermore, inversion seemed to affect the face and body specific P200 in a similar way. For both categories, we observed enhanced P200 amplitudes for upright compared to inverted stimulus presentation. This is the first study investigating how the effect of misalignment modulates the P200 and the present data pointed out that holistic face processes might take place 200 ms after stimulus onset. Until now, the P200 has been associated with different functions. A previous study reported differences between faces and cars in the time window of the P200, indicating that the P200 is associated with face-specific brain processes (Boehm *et al.*, 2011). In addition, the P200 seems to be modulated by the degree of familiarity of a face (Caharel *et al.*, 2002), and is thus regarded as an index of learning and more elaborate processing mechanisms (Latinus & Taylor, 2005). Finally, the P200 seems to mirrors processes associated with second-order relational information. Further studies are needed to clarify the specific function of the P200 for holistic face processing.

The current data support the assumption that face and body perception might rely on different types of configural processing. Previous investigations pointed out that first-order relational information might be important for both stimulus classes, whereas holistic processing seemed to be more important for the successful perception of faces rather than body postures (Maurer *et al.*, 2002; Minnebusch & Daum, 2009; Reed *et al.*, 2006; Soria Bauser *et al.*, 2011). First-order relational information refers to the position of features in space (e.g., the head is located above the torso), whereas holistic processing refers to the fact that a stimulus is processed as one gestalt. If a stimulus is processed holistically, it is very difficult to process a single stimulus feature while ignoring the other features. These differences between face and body processing seem to occur in the time window of the N170 and P200.

Furthermore, N170 latencies were longer for faces compared to bodies, suggesting that body forms are processed faster than faces. This notion has already been reported previously (Righart & De Gelder, 2007; Stekelenburg & De Gelder, 2004). The current data stand in contrast to Thierry *et al.* (2006) reporting delayed N170 amplitudes for bodies compared to faces. A possible explanation for this effect might be that each study has used different stimulus sets. For instance, Thierry *et al.* (2006) used bodies without heads where the present study presented bodies with masked faces (see Figure 1). Previous studies pointed out that the head seem to play an important role for configural body processing (Minnebusch *et al.*, 2009; Tao & Sun, 2013; Yovel *et al.*, 2010). A recent study pointed out that subjects used the position of the head as reference point to process upright body postures. In addition, headless bodies are artificial stimuli as we will never see a body without head in daily life. Therefore, it might be that headless bodies provoke delayed N170 as they did not fit to the general body template. Furthermore, the current investigation used whole bodies. Thierry *et al.* (2006) showed different body pictures including torsos without legs or only legs. Another difference between the current study and the study by Thierry *et al.* (2006) referred to the experimental task. Thierry *et al.* (2006) used a one-back task while the subjects of the current investigation performed a matching-to sample task. Therefore it would be preferable to have a common stimulus set and the same experimental task which could be used in different studies.

Conclusion

Taken together, this study aimed to compare the well-known CFI with the effect of misalignment for human body shapes in order to explore further processing differences between both stimulus categories. Since a previous investigation had reported differences between both categories related to the composite illusion, we searched for ERP components mirroring the observed behavioural pattern. Differences between both categories emerged 170 and 200 ms after stimulus onset in occipitotemporal areas. However, the behavioural pattern fits to the results of the P200 indicating that processes associated with the effect of misalignment seem to take place in this time window. Furthermore, this study support the assumption that that face and body perception might rely on different types of configural processing. Holistic processes and second-order relational information are necessary for the successful perception of face while first-order relational information might be important for faces and bodies. Thus, both stimulus classes are processed configurally, but faces are located at the end of the configural processing steam where bodies seem to be located in the middle between objects and faces (see, also Reed *et al.*, 2006).

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