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Body inversion effect without body sense: Insights from deafferentation

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Abstract

Like faces, human bodies are recognized via the configuration of their parts; their recognition is impaired by inversion. Processing of configural relations has been shown to depend on perceptual expertise with certain classes of objects. Because people see their own body and others' bodies frequently, humans are experts in the visual processing of human body postures. In addition, the observer's own on-line, multimodal body representation which heavily relies on current proprioception may play a crucial role in recognizing human body postures. We investigated whether static body posture recognition relied on current proprioceptive inputs or whether visual familiarity and stored body representations were sufficient. IW, who is deafferented (lost cutaneous touch and proprioception from his body), was tested on the recognition of upright and inverted human body postures, faces, and houses. As controls, IW showed an inversion effect for abstract, common, and rare human body postures as well as faces, but not houses. Results rule out a strong contribution of current afferent inputs to the recognition of human postures. The findings are discussed in terms of the role of the body schema in body posture recognition and how other contributions from one's own body may be involved in the visual processing of human bodies.

Keywords: Body inversion effect; Configural processing; Embodiment; Mental simulation; Body schema; Deafferentation

1. Introduction

A well-established observation is that face recognition is impaired when faces are presented upside down (Valentine, 1988; Yin, 1969). This finding is regarded as evidence that the visual system uses special perceptual processing for faces different from the processing of other non-face objects. Face recognition is mainly driven by processing of configural relations, whereas processing of non-face objects is based on local features and therefore, less disrupted by inversion (cf. Farah, Tanaka, & Drain, 1995; Tanaka & Farah, 1993). It has been argued that with experience, people develop a face prototype providing the basis for encoding certain characteristic abstract properties of faces (cf. Diamond & Carey, 1986). Diamond and Carey (1986) further suggested that the processing of configural relations underlies all "expert" recognition of objects for which prototypical spatial configurations can be defined. In line with this hypotheses Tanaka and Gauthier (1997) demonstrated that dog experts, for instance, showed an inversion effect for dog pictures and car enthusiasts showed an inversion effect for pictures of cars.

Recently, Reed, Stone, Bozava, and Tanaka (2003; cf. Stekelenburg & de Gelder, 2004) showed that inversion effects are also found for pictures of human body postures. Discriminating two upright body postures is much easier than discriminating two inverted body postures. In line with the above interpretation, one could argue that the frequent observation of other bodies results in visual expertise. More specifically, as a result of perceiving bodies frequently observers might extract specific configural relations present in human bodies such as the typical organization of head, trunk, arms and legs. In other words, the body inversion effect may be due to visual processing during which the perceptual input is mapped onto a spatial representation that captures specific structural relations present when

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one observes other bodies. These relations are disrupted when bodies are presented upside-down leading to a decrease in discrimination performance for inverted bodies (cf. also Pavlova & Sokolow, 2000; Sumi, 1984).

The importance of long-term spatial body representations for the body inversion effect was shown in Reed, Stone, Grubb, and McGoldrick (2006). The body inversion effects disappears when the normal configuration of the body parts are scrambled. The processing of configural relations of a body posture seems to rely on the structural hierarchy of body parts, not on the isolated parts themselves. Structural hierarchy refers to the organization of isolated body parts in terms of the overall object and the spatial relationship of each part relative to each other (cf. Marr, 1982). For instance, bodies are recognized not only by the fact that the shoulder and arms are below the head but also from the fact that the shoulder and arms are in a particular position relative to the overall structure of the body, that is, they are always attached to the same part of the trunk and above the feet.

1.1. *Viewing others' bodies: a matter of embodiment?*

However, humans have extensive expertise moving their own bodies to perform certain actions. The resulting bodily experiences may result in a form of multimodal expertise that could influence visual recognition mediated by a multimodal, spatial body representation (Reed, Stone, & McGoldrick, 2005). In other words, visual expertise with human bodies might be acquired not only from frequently viewing other bodies but also from feeling one's own body. In particular, we might be able to use proprioceptive information about our own body when perceiving the bodies of others. Thus, configural body processing may be unique and different from the configural processing of other inanimate objects. In line with this argument are findings demonstrating that human bodies are indeed special objects of perception. There is evidence that specific brain areas are activated when bodies are observed, in particular, the extrastriate body area in the lateral occipitotemporal cortex. This area seems to selectively respond to visual images of human bodies or body parts (Astafiev, Stanely, Shulman, & Corbetta, 2004; Downing, Jiang, Shuman, & Kanwisher, 2001).

Further research suggests that, a multimodal representation of one's own body might be involved in the perception of other people's bodies (Keysers et al., 2004; Knoblich, Thornton, Grosjean, & Shiffrar, 2005; Reed, 2002; Reed & Farah, 1995; Shiffrar & Freyd, 1990, 1993; Wilson, 2001). For instance, Reed and Farah (1995) showed that one can better detect a postural change in another person's arms when one concurrently moves one's arms, but not when one moves one's legs (and vice versa). This finding indicates that the proprioceptive representation of one's own body position contributes to the visual perception of others' body postures. Moreover, in the study of Reed et al. (2003) the body inversion effect was diminished when impossible rather than possible human postures were used (impossible postures violated biomechanical limitations of the body). This result supports the assumption that perceiving a human posture might be an active process in which the perceived body figure is mapped onto the observer's body representation.

A more specific claim is that perceiving a human body in a certain posture causes an internal or imagined replication of this posture in the observer (cf. Gallese, 2001, 2005; Gallese & Goldman, 1998; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Wilson, 2001). In line with this hypothesis, Reed, Nyberg, and Grubb (2006) reported larger inversion effects for human figures compared to canine figures. In addition, they demonstrated that for human postures the size of the body inversion is independent of the familiarity with the observed posture, challenging purely visual accounts.

Another variant of a theory claiming bodily contribution to visual perception is that others' bodies are covertly imitated using the observer's own body representation (Wilson & Knoblich, 2005). Evidence for this theory is provided by studies showing that people tend to automatically mimic other's behavior such as facial expressions (Bavelas, Black, Lemery, & Mullett, 1986; Wallbott, 1991), gestures or postures (Bernieri, 1988; Boker & Rotondo, 2002; Shockley, Santana, & Fowler, 2003; for a review see Wilson & Knoblich, 2005). Covert imitation requires the use of implicit knowledge of one's own body. This knowledge is thought to encompass afferent somatosensory information from certain body parts such as proprioceptive feedback (i.e., peripheral body representation or proprioceptive awareness of one's own body) as well as efferent motoric information (i.e., central body representation because actions are centrally generated). For instance, one could argue that observing others leads to a covert imitation of the motor program which predicts the sensory consequences of an observed action (cf. e.g., Blakemore, Frith, & Wolpert, 1998, 2002; Wolpert, 1997). In addition, it has been demonstrated that both afferent and efferent components contribute to body awareness (cf. Tsakiris & Haggard, in press). So far the relative contributions of afferent and efferent components are not clarified and difficult to investigate in healthy subjects.

1.2. *The present study: visual perception of body postures without proprioception*

The aim of the present study was to test whether afferent feedback from one's own body is necessary for static body posture recognition and expertise or whether one's long-term representations of the body can suffice. In other words, does processing of body postures elicit an internal (partly unconsciousness) simulation of the perceived body part that hinges on an on-line, multimodal representation of one's own body (cf. e.g., Gallese, 2001, 2005; Wilson, 2001; Wilson & Knoblich, 2005)? Or does body posture recognition result in the activation of a long-term multimodal, spatial body schema established during frequent visual and motoric exposure to the specific characteristics of human bodies?

To investigate these two possibilities we examined IW, a man who has lost his afferent inputs to his internally based body representations (cf. Head and Holmes, 1911) after he had suffered from an extremely rare viral infection. More specifically, at the age of 19, IW became completely and selectively deafferented below the neck for tactile and proprioceptive information. That is, he lost completely and irreversibly kinaesthetic, cutaneous and muscular input from all of his body parts except the head and neck. When prevented from seeing his body, IW is unable to locate or move any of his body parts. However, he has recovered a remarkable degree of control of his movements solely relying on visual feedback and cognitive control. IW requires constant vision of his body in order to know where his body parts are and how to move them. Note that peripheral sensory input is not only relevant for movement control, but also contributes to the phenomenal experience of having, or rather, of being a body. To illustrate, during the first weeks of his illness, IW reported the feeling of being alienated from his body. If he is brought into a certain body posture, he can (visually) locate his body parts in space but he lacks the experience of feeling his bodily position.

Testing IW provides a unique opportunity to address whether the configural processing of body postures requires access to an on-line, multimodal representation of one's own body or whether a long-term multimodal, spatial body representation is sufficient. Most people probably use both a current proprioceptive representation of one's own body as well the long-term body representation when viewing other people, whether they are moving or not. However, because IW does not have afferent inputs but does have long-term body representations, we can determine if the ability to perceive afferent inputs are a necessary precondition for configural body processing. If such configural processing depends on an on-line multimodal body representation, IW should not show the body inversion effect, because he lacks such a representation. If IW shows the normal body inversion effect this would support configural body processing originating in the visual system and stored multimodal body representations.

2. Experiment 1

Experiment 1 used Reed et al. (2003) paradigm. IW and healthy control subjects observed stimuli showing pictures of human body postures, faces or houses in upright or inverted orientation (cf. Fig. 1). Houses were included as a class of control stimuli because they do not evoke inversion effects. The inclusion of the house stimuli permits the inversion effects for faces and body postures to be compared directly with the inversion effects, or lack thereof, for houses. In addition, the embodiment hypothesis can be applied to both faces and bodies, but not for houses. Houses are necessary to demonstrate the importance of the sensorimotor contributions. In addition, the comparison of inversion effects for faces, body postures, and houses confirms that in typical populations, faces and bodies are processed differently from other inanimate objects, that not all objects pro-

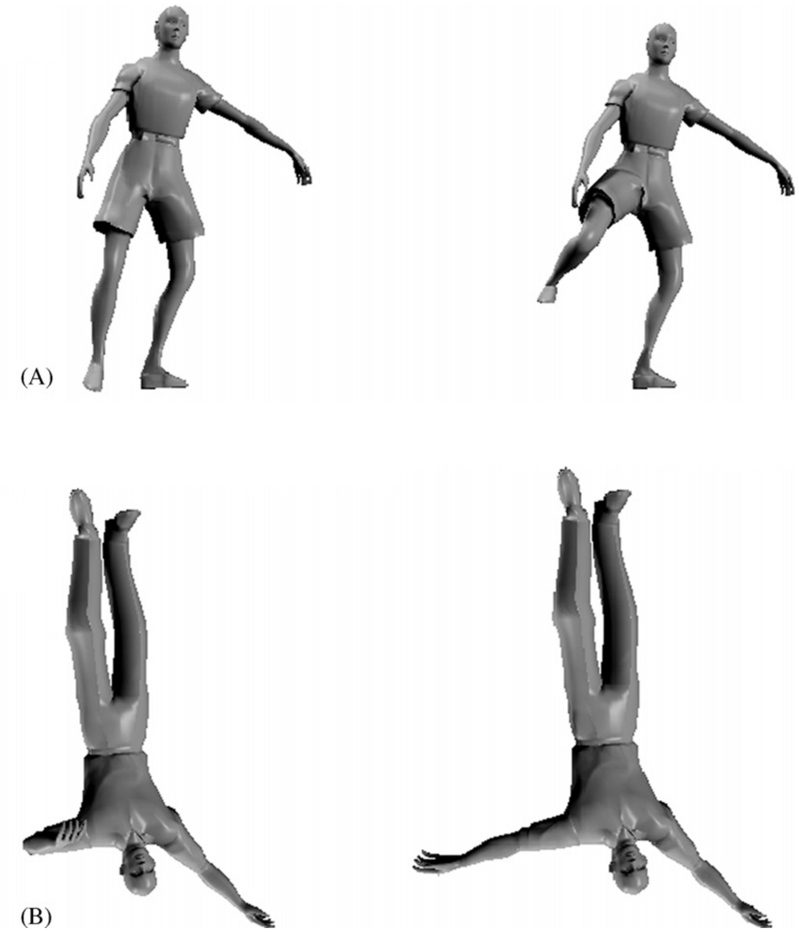

Fig. 1. Examples of upright and inverted body stimuli used in the first experiment. The correct response for each stimulus pair is "different". (A) Body posture stimuli: example of an upright "different" trial. (B) Body posture stimuli: example of an inverted "different" trial.

duce inversion effects, and that the magnitude of the inversion effect for faces and bodies is significantly different from that of houses.

The task was to decide whether two pictures were same or different. From the findings of Reed et al. (2003), we expected that controls would show an inversion effect (better recognition of upright than inverted objects) for faces and body postures, but not for houses. If embodied simulation and current afferent input is necessary for the recognition of static body postures, IW should show inversion effects for faces but not for body postures and houses because he has afferent inputs for his face but not for his body. However, if he can use visual experience and stored spatial body representations to recognize body postures, then he should also show a body inversion effect.

2.1. Method

2.1.1. Participants

IW (male, 52 years) and twelve neurologically healthy, age-matched controls (five men; four left handed; mean age = 52.42 years, range 41–66 years) took part in this experiment. IW had suffered a complete large sensory-fibre peripheral neuropathy about 33 years previously. The illness resulted in a complete loss of the senses of movement or position, cutaneous touch or proprioceptive or cutaneous reflexes below the neck down. Nociceptive and thermoceptive afferents were largely spared as well as his motor fibres. As a result, IW depends heavily on visual feedback to control his movements. The control of his movements is achieved at the cost of a large attentional demand. For a detailed description of IW's clinical history, see Cole (1995) and Cole and Sedgwick (1992).

2.1.2. Apparatus and stimuli

All stimuli were three-dimensional figures of human bodies, faces or houses (cf. Reed et al., 2003 for more details of creating stimuli). Body stimuli contained 16 male and 16 female figures in different postures. They were created by using Fractal Design Poser 2.0$^{\text{TM}}$. The size of each picture was approximately 14 cm × 10 cm. For each stimulus, a "different" stimulus, or distractor, was created varying the position of one or two body parts: arm, leg, or head. Face stimuli were 16 black-and-white photographs of male or female Caucasian, African-American, or Asian faces. Size of each face was about 8 cm × 9 cm. Each face distractor stimulus matched the stimulus with which it was paired in both gender and ethnicity, but differed in one or two features (e.g., facial hair). House stimuli were line drawings of houses created on a Macintosh computer. Each of 16 different houses measured approximately 12 cm × 17cm. House distractor stimuli were created by altering the following elements: position of door, steps, chimney, main or small window. Stimulus presentation and data acquisition were controlled by PsyScope 1.2.5 PPC running on a Macintosh computer (MAC OS DA-9.2.2), permitting a pixel resolution of 1024 × 768 pixels. The visual stimuli were presented centrally on a 21-in. (53.34 cm) monitor with a vertical refresh rate of 100 Hz.

2.1.3. Design and procedure

Body, face and house stimuli were presented in separate 32-trial blocks in pseudorandomized order. Each participant received 128 trials of each stimulus type, for a total of 384 trials. In each block, 16 stimuli pairs were presented in upright orientation and the other 16 stimuli pairs were presented in inverted orientation. Stimulus orientation varied randomly within each block. Further, on half of the trials two stimuli were same, on the other half of the trials they were different. The first experimental block started with four practice trials for each stimulus type that were different from the ones used in the critical experimental trials. Participants sat at a distance of about 75 cm from screen and were instructed to determine as quickly and accurately as possible whether two faces, two bodies or two houses were same or different. On each trial and for all types of stimuli, the first stimulus was presented for 250 ms, than a blank screen appeared for 1000 ms, followed by the second stimulus that was shown until the participant responded. Half of the participants pressed the left key on a button box with their left index finger if the stimuli were different and the right key with their right index finger if the stimuli were the same. The other half of participants received the reverse judgment-key mapping. After each block participants had the opportunity to rest.

2.2. Results and discussion

For IW and each control participant, we calculated median reaction times (RTs) and the mean proportion of correct responses for each condition. The results are summarized in Table 1 and in Fig. 2. Only correct trials were included in the analysis of response times.

2.2.1. Data analysis of controls

Separate analyses of variances (ANOVAs) on median RT data as well as on proportion of correct responses were carried out for each stimulus type. Faster reaction times and a higher proportion of correct responses to stimuli presented in upright orientation than in inverted orientation indicate the presence of an inversion effect. For the median RT data, a significant body inversion effect, $F(1, 11) = 6.46$, $p = .027$, and a significant face inversion effect, $F(1, 11) = 29.92$, $p < .001$ occurred. The ANOVAs on proportion of correct responses also confirmed a significant body inversion effect, $F(1, 11) = 17.22$, $p = .002$ and a significant face inversion effect, $F(1, 11) = 40.85$, $p < .001$. The inversion effect for houses was not significant for either median RTs ($p = .068$) or proportion correct ($p = .442$). In sum, age-matched controls replicated the pattern inversion effects reported by Reed et al. (2003). Recognition performance of body postures was faster and more accurate when presented in upright than in inverted orientation.

Table 1

Median reactions times (MD RT), percentage proportion of correct responses (PC) and respective standard errors (S.E.) for controls and IW as a function of stimulus type and stimulus orientation

	Bodies		Faces		Houses	
	Inverted	Upright	Inverted	Upright	Inverted	Upright
MD RT (S.E.)						
Controls ($n = 12$)	921 (44.7)	880 (44.0)	926 (41.4)	839 (37.8)	1029 (30.9)	975 (39.1)
IW	813	781.5	738	683	949	838
PC (S.E.)						
Controls ($n = 12$)	80.8 (3.0)	89.3 (1.9)	83.4 (1.8)	94.5 (1.2)	73.3 (2.8)	76.1 (3.0)
IW	81.3	81.3	85.9	90.6	57.8	65.1

Note: Only the control group allows for calculating standard errors.

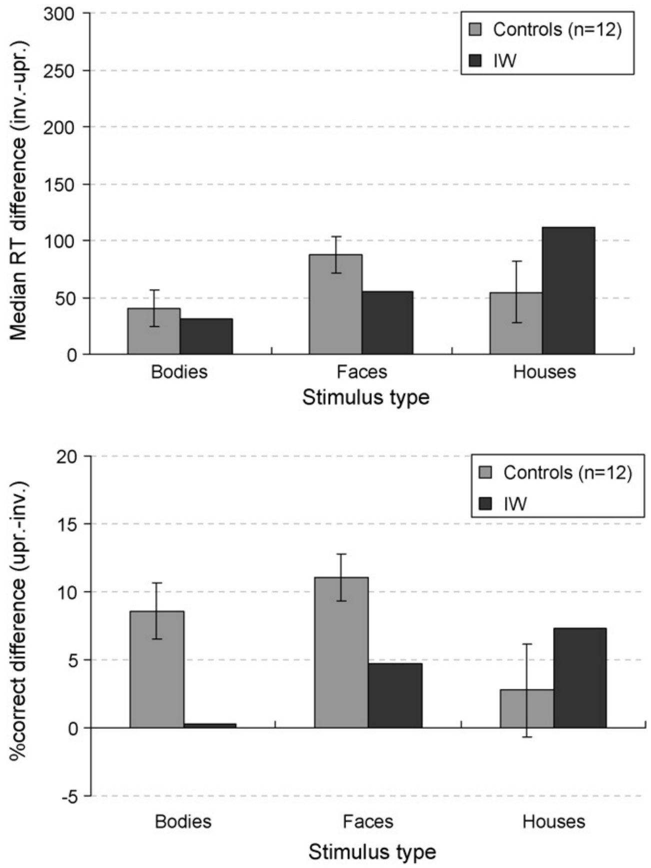

Fig. 2. Difference in median reaction times (top panel) and percentage proportion of correct responses (bottom panel) between inverted and upright body, face and house stimuli for IW and controls.

2.2.2. *Comparison of IW with controls*

The analysis of IW's data revealed that his performance did not differ from controls. In order to compare the IW's inversion effects with those of controls we used a modified *t*-test developed by Crawford and Howell (1998). This test allows one to compare an individual's score against a norm derived from a small sample of control participants and more importantly, provides an unbiased estimate of the abnormality of an individual's score. This test uses the *t*-distribution rather than the standard normal distribution and the sample statistics are treated as sample statistics and not as a population parameter. In other words, in this method the individual is treated as a sample of $n = 1$, and therefore does not contribute to the estimate of the within group variance. The problem of using the standard (*z*-score) method is that with small samples the abnormality of an individual's score might be exaggerated (cf. Crawford & Garthwaite, 2002). There were neither significant differences between IW and controls regarding the inversion effect on median RTs for bodies, faces, and houses (all t's < 1.2 and p's > .2) nor for the inversion effects on the proportion of correct responses for all types of stimuli (all t's < 1 and p's > .5).

To summarize, there was little difference between IW and neurologically healthy controls regarding the inversion effect for human bodies, faces, and houses. Like the controls, IW used configural processing to recognize human body postures and faces, but not houses. Given that IW has afferent information for his face but not his body, this result suggests that the recognition of human body postures does not require a current afferent input to the on-line multimodal representation of one's own body and that long-term body multimodal body representations may be sufficient for recognizing static human body postures.

3. Experiment 2

One issue not addressed by Experiment 1 was whether the use of non-meaningful, abstract body postures might have biased IW to use a vision-based strategy he had to acquire to compensate his lack of an on-line body representation. Abstract postures may not have evoked a strong need to simulate the postures and to map his body onto the stimulus' postures. In Experiment 2 we address this concern. We compare the body inversion effect for meaningful body postures that might more strongly evoke the need for on-line body representations to interpret and evaluate the postures. In addition, we manipulate the familiarity of the meaningful postures to further accentuate the potential need to use current bodily inputs for the visual processing of human body postures. If meaningful body postures require the use of afferent inputs to create a simulation of that meaningful posture, then IW may not show configural processing for meaningful stimuli in general. However, afferent inputs and simulation processes may be even more important for rare postures for which IW has less visual experience viewing the postures and less prior bodily experience assuming the postures. As a result, current afferent input and embodied simulation may be more important for the configural processing of rare body postures for which IW has less expertise. If this is the case, IW should produce greater inversion effects for common than for rare body postures and the need for embodied simulation would be demonstrated for the recognition of unfamiliar body postures. In contrast, IW's performance would be different from control subjects who can use their on-line body representation to simulate the rare postures. Control subjects should show equivalent inversion effects for common and rare postures (Reed, Nyberg et al., 2006).

IW and age-matched control participants observed images of common and rare human body postures (cf. Fig. 3) in upright and inverted orientations. Additionally, this experiment uses a slight variation on the paradigm of Experiment 1: the target image was rotated 90° along its vertical axis, relative to the stimulus image, to reinforce the need to create a three-dimensional representation of the body posture.

3.1. *Method*

3.1.1. *Participants*

IW and 12 neurologically healthy, age-matched controls (6 men; 2 left handed; mean age = 58.17 years, range 46–70 years) took part in this experiment. Five of the controls also participated in Experiment 1.

3.1.2. *Apparatus and stimuli*

Similar body posture stimuli as in Experiment 1 were used, displaying human bodies in common or rare postures. Stimuli were pre-rated by volunteers on a 10-point scale as to how common each posture was for humans. Mean highest

Fig. 3. Examples of familiar and unfamiliar human posture stimuli used in the second experiment. The second posture is rotated 90° from the orientation of the first posture. The correct response for the familiar stimulus pair is "same" and the correct response for the unfamiliar stimulus pair is "different": (A) familiar human posture and (B) unfamiliar human posture.

and mean lowest rated postures were selected (see Reed, Nyberg et al., 2006 for details). To minimize low-level visual differences between the two types of stimuli, they were both presented in mono-chromatic gold tones.

3.1.3. Design and procedure

Rare and common stimuli were presented in four separate 24-trial blocks in pseudo-randomized order, resulting in a total of 192 trials. In each block, 12 stimuli pairs were presented in upright orientation, the other 12 stimuli pairs in inverted orientation. Stimulus orientation varied randomly within each block. On half of the trials the two stimuli were "same," on the other half they were "different." The first experimental block started with four practice trials for each stimulus type that contained stimuli not included in the experimental blocks. The procedure was the same as in Experiment 1 with the following exceptions. After an inter-stimulus interval of 1000 ms, on each trial the second picture appeared until participants indicated whether the two postures were the same or different by pressing a key. Furthermore, the second stimulus appeared rotated 90° along its vertical axis (cf. Fig. 3). As in Experiment 1 speed and accuracy were recorded.

3.2. Results and discussion

As in Experiment 1 for IW and each control participant, median RTs and mean proportion of correct responses were calculated for each condition. Results are summarized in Table 2 and in Fig. 4. Again the RT analysis was based only on correct responses.

3.2.1. Data analysis of controls

Two viewing frequency (common, rare) X orientation (inverted, upright) ANOVAs were carried out on median RTs

Table 2
Median reactions times (MD RT), percentage proportion of correct responses (PC) and respective standard errors (S.E.) for controls and IW as a function of stimulus type and stimulus orientation

	Familiar bodies		Unfamiliar bodies	
	Inverted	Upright	Inverted	Upright
MD RT (S.E.)				
Controls ($n = 12$)	1120 (49.1)	1068 (42.7)	1115 (28.5)	1052 (40.4)
IW	1286	990	1049	922
PC (S.E.)				
Controls ($n = 12$)	69.3 (3.8)	81.3 (3.0)	72.3 (2.4)	83.1 (2.3)
IW	77.1	75.0	68.8	68.8

Note: Only the control group allows for calculating standard errors.

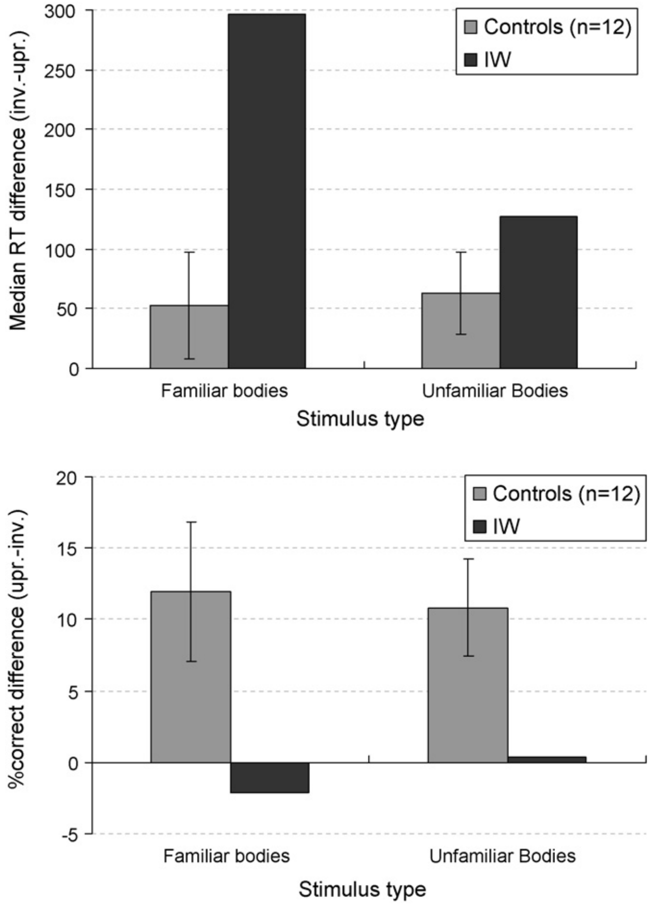

Fig. 4. Difference in median reaction times (top panel) and percentage proportion of correct responses (bottom panel) between inverted and upright familiar and unfamiliar human postures for IW and controls.

and proportion correct. The ANOVA for median RT did not reveal an effect of viewing frequency ($p = .681$) but a significant main effect of orientation, $F(1, 11) = 5.23$, $p = .043$ occurred. Response times in the upright condition were faster than the RTs in the inverted condition (1060 ms versus 1118 ms). The interaction was not significant ($p = .867$). The second ANOVA for proportion correct also did not reveal a significant effect of viewing frequency ($p = .197$), but a significant main effect of orientation, $F(1, 11) = 19.63$, $p = .001$. Accuracy was better for upright postures (0.82 versus 0.71 proportion correct). Again, the interaction between viewing frequency and orientation did not reach significance ($p = .865$). Consistent with Reed, Nyberg et al. (2006), control participants showed inversion effects for human body postures regardless of viewing frequency.

3.2.2. *Comparison of IW with controls*

IW's data showed the same pattern as controls' data (cf. Table 2 and Fig. 4). Crawford and Howell's modified *t*-tests (1998) revealed no significant difference between IW and controls with regard to median RTs (all t's < 1.6 and p's > .16) and proportion accuracy (all t's < 1 and p's > .4).

In sum, IW showed again the same pattern of results as the controls—his recognition performance was faster and more accurate for human postures presented in an upright orientation, regardless of viewing frequency. The use of common and rare meaningful postures as stimuli did not change IW's use of configural processing from the abstract postures used in Experiment 1. One alternative explanation for this lack of effect for viewing frequency is that the manipulation was not sensitive enough to produce differences in inversion effects. However, in Reed, Nyberg et al. (2006) this manipulation did produce inversion effect differences for the recognition of common and rare dog postures. Thus, the overall pattern of results from Experiments 1 and 2 and prior findings lead to the conclusion that IW used his long-term body representations and knowledge obtained prior to his illness to perform this task. It does not appear that current afferent inputs are necessary to recognize even rare human postures, such as humans in dog postures.

4. General discussion

The purpose of this study was to investigate whether current afferent inputs and on-line body representations were necessary for recognizing human body postures or whether long-term body representations would suffice. We took advantage of the condition of a haptically deafferented subject, IW, who selectively lost the senses of touch and proprioception from all of his body and is therefore deprived of all proprioceptive experience (except neck and head). If processing of human bodies in the external world requires a mental simulation that makes use of an on-line multimodal body representation and afferent inputs, IW should differ from controls in his processing of human body postures; in particular, he should not show the body inversion effect. However, he should show body inversion effects if he were able to use long-term, multimodal body representations for recognition.

In Experiment 1, we presented IW and controls with pictures of human bodies, faces or houses in upright or inverted orientation. IW produced a body inversion effect that was similar to faces and unlike houses. Like the control participants he was faster in judging whether two abstract postures were the same or different when they were presented in upright than inverted orientation. These findings confirmed that IW processed body postures configurally and that the configural processing of static human postures may make use of long-term body representations in the absence of current afferent inputs. It appears that embodied simulation may not be necessary for body posture recognition. In Experiment 2, we emphasized the need for an on-line body representation by comparing inversion effects for common and rare postures. The rationale was that rare body postures would rely more on current body inputs and simulation; IW should show a difference in configural processing between common and rare because he would not be able to rely as much on stored body representations acquired prior to his illness for these rare postures. Similar to the results for the control group, IW showed inversion effects for human bodies presented in both common and rare postures. Even under conditions in which the potential need for embodied simulation was emphasized, IW's use of long-term spatial body representations that include both visual and proprioceptive information (Reed, 2002) appear to be sufficient for both common and rare body posture recognition and embodied simulation does not appear to be necessary.

The recognition of static human body posture does not require embodied simulation in which an active mental reconstruction of a posture is created via an on-line multimodal body representation that relies on current proprioceptive input. However, this does not mean that people do not use embodied simulation when viewing others in more naturalistic conditions. Recent studies have demonstrated that our bodily self-awareness is not only constituted by afferent (i.e., peripheral) information but also by efferent (i.e., central) information (cf. Bermúdez, Marcel, & Eilan, 1998; Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005). Thus, typical visual processing of human bodies may still be mediated by a representation that contains efferent motoric information which is intact in IW. Such efferent signals generated along with motor commands could provide sufficient information for maintaining a multimodal body representation that supports perceiving others' bodies.

Although IW does not receive any sensorimotor feedback about his body movements, he is still able to produce body movements using constant visual control. In fact, in order to execute a body movement he highly relies on predictions of feedforward mechanisms, which are assumed to be derived from copies of efferent signals (cf. Cole & Paillard, 1995; Stenneken, Aschersleben, Cole, & Prinz, 2002). Thus, IW is still able to build the efferent motor commands for overtly or covertly performing body movements.

One could test the hypothesis that visual processing of human bodies is mainly mediated by efferent motoric information by investigating the body inversion effect in long-term tetra- or quadriplegic patients who are deprived from both afferent and efferent information. First support for this hypothesis is provided by the data of a quadriplegic patient we have tested. A quadriplegic since she was 9-year-old, this now 20-year old showed no body inversion effects for the tasks used in Experiments 1 and 2.

Further, in another recent study we did find evidence that peripheral bodily sensations can play a role in the recognition of acting bodies, that is, actions performed by other people (Bosbach, Cole, Prinz, & Knoblich, 2005). The deafferented patients IW and GL both showed a selective deficit in detecting the expectation of weight of another person when seeing him/her lifting a box. One obvious difference between this study and the present study is that dynamic action information (videos) was provided in the former. Thus, there is a possibility that the observation of *dynamic* action information, but not the observation of *static* posture information, leads to the activation of processes in the observer's motor system that simulate the observed action (cf. Fischer, 2005).

To conclude, the results of this study rule out a necessary contribution of *current* afferent, somatosensory information about one's own body, and thus the involvement of a dynamic, immediate body representation when recognizing static human body postures. Instead, our results can be interpreted as evidence that prior visual and proprioceptive experience with human bodies contributes to the configural processing of static human body postures (cf. Diamond & Carey, 1986; Tanaka & Gauthier, 1997). The visual system is tuned to the structural characteristics of upright but not inverted bodies; thus it has learned to extract the typical configural relations characterizing human bodies. In addition, our findings suggest that knowledge of the biomechanical limitations and possibilities of a human body also contribute to the configural processing of visual body images (cf. Reed, Nyberg et al., 2006; Shiffrar & Freyd, 1990, 1993).

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