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It's All in Your Head: Why Is the Body Inversion Effect Abolished for Headless Bodies?

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It has been recently argued that human bodies are processed by a specialized processing mechanism. One evidence was that body inversion reduces recognition abilities (body inversion effect; BIE) as much as it does for faces, but more than for other objects. Here we showed that the BIE is markedly reduced for headless bodies and examined the reason for this unexpected finding. Two alternative hypotheses were examined. Either the BIE is reduced for any type of incomplete body, or the head plays a special role in discrimination of body posture. Results show that omission of other body parts (leg or arms) did not influence the magnitude of the BIE relative to complete bodies. Analogous manipulations with faces did not influence the magnitude of the face inversion effect. Importantly, similar to effects we found for headless bodies, discrimination abilities for upright bodies and the BIE were markedly reduced for complete bodies that did not differ in head posture. We conclude that intact discrimination of body posture relies heavily on the head position. Our findings also imply that the BIE and the face inversion effect may be generated by different mechanisms.

AQ: 1

Keywords: inversion effect, face, body, part-based, holistic

Recent studies provide evidence regarding a specialized mechanism for the visual processing of human bodies. Functional magnetic resonance imaging (fMRI) studies have reported brain regions in the occipital-temporal cortex that show a much stronger response to human bodies or body parts in relation to objects, faces, tools, and scenes (for a review, see Peelen & Downing, 2007). Furthermore, behavioral studies have shown that discrimination of inverted bodies, similar to that of faces, is worse than the discrimination of upright bodies (body inversion effect, or BIE). Importantly, the body inversion effect has been shown to be as large as the well-established inversion effect for faces and much larger than the inversion effect for other object categories (Reed, Stone, Bozova, & Tanaka, 2003) such as houses (Reed et al., 2003).

The face inversion effect has long been considered a marker of specialized holistic processing of faces (Farah, Wilson, Drain, & Tanaka, 1998; Maurer, Le Grand, & Mondloch, 2002). Although the face inversion effect by itself is not a direct measure of holistic processing, many studies have shown that upright but not inverted faces are processed by holistic mechanisms (Tanaka & Farah, 2003; Young, Hellawell, & Hay, 1987), although the exact nature of these mechanisms is still under debate (Maurer et al., 2002; McKone & Yovel, 2009; Murray, 2004; Richler, Gauthier, Wenger, & Palmeri, 2008; Richler, Tanaka, Brown, & Gauthier, 2008; Robbins & McKone, 2007; Rossion, 2008; Sekuler, Gaspar, Gold, & Bennett, 2004). Only a few studies have directly examined whether, like faces, the representation of upright bodies is holistic. Reed, Stone, Grubb, and McGoldick (2006) showed no inversion effect for isolated body parts and for horizontally cut half bodies, but a face-sized inversion effect for complete bodies. The only study, which directly examined holistic processing, used the whole-part paradigm (Seitz, 2002), which had been used previously to demonstrate holistic representation of faces (Tanaka & Farah, 1993). Findings showed better recognition of body parts in the context of the whole body than in isolation. However, unlike the similar face whole-part studies, the body whole-part effect was not examined with inverted or scrambled bodies to assess whether it is specific for intact upright bodies. Thus, there is still no direct convincing evidence that upright but not inverted bodies are processed as nondecomposable wholes.

Whereas the face inversion effect has been extensively examined in the past four decades, there are only handful of studies that examined the BIE and whether it exists for any type of body stimuli (Reed et al., 2003, 2006). The current study focuses on a recent surprising finding that demonstrates that bodies without heads (hence, headless) yielded no inversion effect in relation to complete bodies (Minnebusch, Suchan, & Daum, 2009). There are two possible explanations to the absence of a BIE for headless bodies: The first alternative is that a BIE is not obtained for incomplete bodies, in which a body part is missing. This explanation is consistent with the findings that the BIEdisappears for incomplete bodies (Reed et al., 2006) or unnatural body postures (Reed et al., 2003). A second alternative is that the head has a special status in the processing of the human body and its presence is critical for intact body discrimination. Such a finding is especially important for fMRI studies exploring brain areas involved in the perception of human bodies, which often use headless bodies

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to ensure that effects reported are specific to the body system but not to the face system (e.g., Peelen & Downing, 2005; Schwarzlose, Baker, & Kanwisher, 2005).

In a series of experiments, we attempted to decide between these two alternative explanations for the absence of inversion effect for headless bodies by assessing the effect of part omission on the BIEand the possible special role that the head may have in the discrimination of body posture. In addition, we examined whether the same effects that we got with bodies are also found for faces. It is noteworthy that this study does not provide any direct test to the question of whether body stimuli are processed holistically. The goal of these studies was to assess the extent to which the head plays a special role in the discrimination of body posture.

General Method

Participants

All participants had normal or corrected-to-normal vision and received course credit for their participation. All participants signed a consent form that was approved by the Tel Aviv University ethics committee.

Stimuli

The body stimuli were gray-scale male figures created with the AQ: 2 Poser 7.0 software (e frontier America, Inc., Tokyo, Japan). All body poses were physically possible but did not convey any meaningful body posture. To make sure that facial features are not used for discrimination, we covered the faces with a gray ellipsoid. A set of 18 upright postures was constructed. Each pose was paired with an identical pose to create 18 identical-body pairs. Different-body pairs were created by altering the positions of three body parts of the original stimulus: An arm, a leg, and the head of the figure were F1 placed at a different angle or in a different position (see Figure 1A). The inverted body stimuli were the same stimuli used in the upright trials, rotated 180° in picture plane. The size of the body stimuli was approximately 8 cm in width and 10 cm in height.

The same number of pairs of face stimuli was created. Different-face pairs differed in the identities of the eyes, nose, and mouth (see Figure 1B). The size of the face stimuli was approximately 6 cm in width and 9 cm in height.

Apparatus and Procedure

Stimuli were presented using Psychtoolbox implemented in MATLAB (Brainard, 1997). A chin rest was used to keep the distance between the subjects and the monitor constant at 45 cm.

The design of the experiment was similar to the procedure described in a previous study by Reed and colleagues (Reed et al., 2006). Participants were asked to determine whether two subsequently presented faces or bodies were the same or different with respect to identity for faces and posture for bodies. Participants were not informed in advance in what way the face and body pairs would differ and therefore were free to attend to any information that they found to be relevant for the task. In all experiments, the first stimulus was presented for 250 ms, followed by a blank screen for 1,000 ms, and then a second stimulus was presented and remained on the screen until the participant responded. Both stimuli were presented at the same orientation, either both upright or both inverted. Participants pressed one key when the two stimuli were identical and another key when the stimuli were different. For all trials, participants were asked to respond as accurately as possible. Each pair was presented twice in an upright orientation and twice in an inverted orientation. Upright and inverted trials were presented in an interleaved random manner.

After reading the instructions, participants were presented with a practice session of five trials. The experimental task contained 144 trials: 2 × 18 pairs × 2 (Same/Different) × 2 (Upright/Inverted). Two mandatory breaks of 20 s each were given every 50 trials. Participants pressed the space bar whenever they were ready to continue at the end of the 20-s break. The entire testing session lasted approximately 15 min.

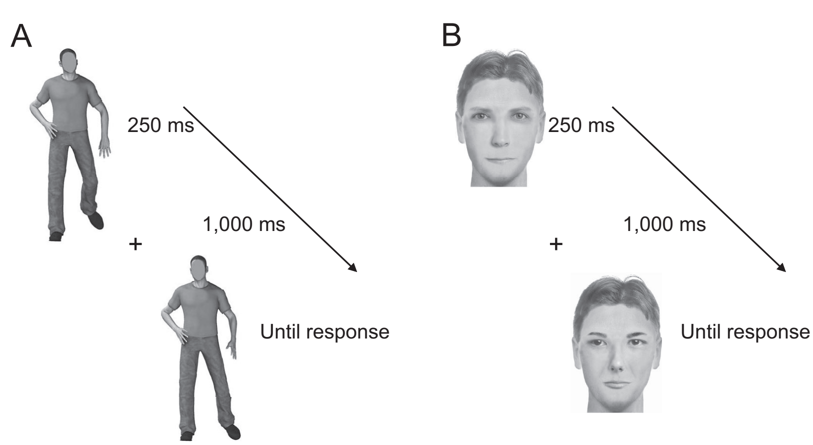

Figure 1. A sequential matching task was used in all experiments. Pairs of faces or bodies were presented either in an upright or inverted orientation. The first stimulus was presented for 250 ms, followed by 1,000 ms of blank screen. The second stimulus was either identical or different and was presented until response. Body stimuli differed in head, hand, and leg position. Face stimuli differed in eye, nose, and mouth.

Data Analysis

We computed the proportion of correct responses for different and same trials and calculated a d' score and criterion shift (C), in which hits were correct responses to different-pair stimuli and false alarms were incorrect responses to identical-pair stimuli. Mean reaction times for correct responses were also computed. Analyses performed on reaction times showed no evidence for a speed–accuracy trade-off (see Table 1).

Experiment 1

In Experiment 1, we attempted to replicate previous reports that the body inversion effect is as large as the face inversion effect.

Method

Participants. Ten subjects (age: 20–27 years; 7 women) participated in Experiment 1.

Stimuli and procedure. The face and body trials were presented in separate blocks. The order of the blocks was counterbalanced across subjects. Subjects were asked to discriminate between the sequentially presented faces or bodies.

Results

Discrimination of upright stimuli was better than that of inverted stimuli for both faces and bodies (Figure 2). A repeated-measures analysis of variance (ANOVA) with orientation (upright or inverted) and category (face or body) as within-subject factors revealed a main effect of orientation, $F(1, 9) = 24.1$, $p < 0.001$, $\eta^2_{\text{par}} = 0.73$, no main effect of category, and no interaction between these factors ($F < 1$). These findings replicate previous reports of inversion effects for faces and bodies that are of similar magnitudes.

In Experiment 2, we examined whether the omission of heads from human bodies would abolish the BIE, as has been recently reported (Minnebusch et al., 2009). It is noteworthy that the BIE for complete bodies that was reported by Minnebusch and colleagues was small (92% for upright faces and 90% for inverted faces) in relation to effects reported in previous studies. In fact, a significant inversion effect for complete bodies was found only with efficiency scores (a combined accuracy and reaction time measure). It is possible that the lack of inversion effect for headless bodies is specific to a task that yielded weak effects even for complete bodies. It is therefore important to first replicate this effect with a task that generates a massive inversion effect in accuracy scores, similar to the one previously reported in the literature (Reed et al., 2006).

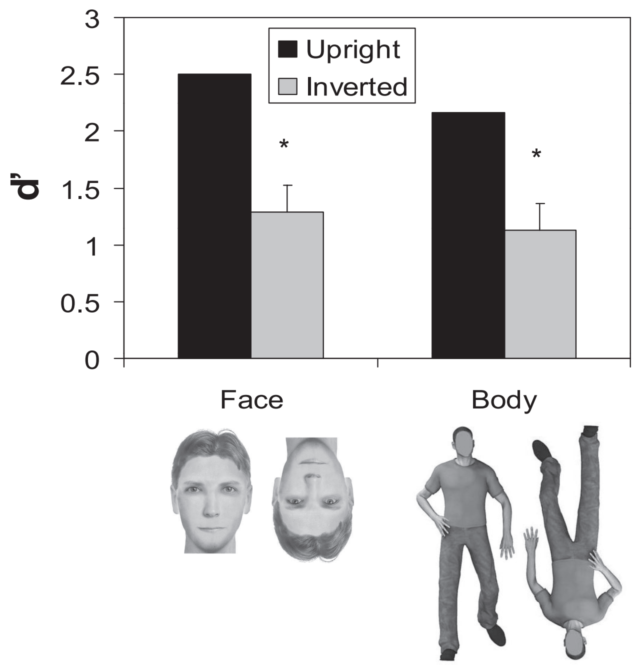

Figure 2. Performance level (d') for upright and inverted faces and bodies yielded similar inversion effects (i.e., better performance for upright than for inverted stimuli). Error bars indicate the standard error of the difference between upright and inverted stimuli, that is, the variance of the body inversion effect. * $p < .001$.

Experiment 2

Method

Participants. Twelve subjects (age: 22–26 years; 6 women) were presented with a headless body task. Ten additional subjects (age: 21–23 years; 4 women) participated in a complete body task similar to the one used in Experiment 1 but without an additional face task. The reason we chose to perform the two conditions in a between-subjects design was to minimize the likelihood that participants would fill in the missing information of the incomplete bodies following exposure to their complete body version.

Table 1
Reaction Time to Upright and Inverted Body or Face Stimuli Used in Experiments 1–5 Show No Evidence for Speed–Accuracy Trade-Off

Stimuli	Upright (ms)	Inverted (ms)	Inversion effect (ms)	t	p
Whole bodies (Experiment 1)	869	918	49	$t(9) = 2.29$	.04
Headless bodies (Experiment 2)	959	955	−3	$t(11) = 0.13$	.89
Armless bodies (Experiment 3A)	968	1,002	34	$t(9) = 1.53$	.16
Legless bodies (Experiment 3B)	950	1,009	59	$t(11) = 2.22$	.04
Whole face (Experiment 4A)	1,005	1,053	48	$t(11) = 1.26$	.23
Eyeless faces (Experiment 4B)	992	998	6	$t(9) = 0.15$	.88
Mouthless faces (Experiment 4C)	924	953	29	$t(9) = 1.21$	.25
Head fixed bodies (Experiment 5)	843	875	32	$t(9) = 0.96$	.36

Stimuli and procedure. The headless bodies used in this task were the same body stimuli that were presented in Experiment 1, but we removed the heads from the bodies (Figure 3). The complete body stimuli used in this experiment were identical to the stimuli used in Experiment 1. The two groups of subjects who participated in Experiment 2 were only presented with a body posture discrimination task (headless or complete bodies) without an additional face task. We used the same sequential matching task described above.

Results

A two-way mixed ANOVA with body type (complete or headless) as a between-subjects factor and orientation as a within-subject factor revealed a significant interaction of body type and orientation, $F(1, 20) = 9.91$, $p < 0.005$, $\eta^2_{par} = 0.33$. Paired t tests showed a significant inversion effect for complete bodies, $t(9) = 6.74$, $p < 0.0001$, $d = 4.6$, but not for headless bodies, $t(11) = 0.78$, $p = .45$.

Results showed better performance for posture discrimination of upright bodies than of inverted complete bodies, similar to Experiment 1. In contrast, performance for upright headless bodies did not differ from performance for posture discrimination of inverted bodies (Figure 4). Note that performance for upright headless bodies was significantly lower than for upright complete bodies, as confirmed by an independent sample t test, $t(20) = 2.87$, $p < 0.01$, $d = 1.28$, but there was no difference between performance levels for complete and headless inverted bodies, $t(20) = -0.58$, $p = .55$.

Analysis of the criterion shift (C) revealed no difference in response criterion between upright and inverted bodies, neither for complete bodies, $t(9) = 1.4$, $p = .2$, nor for headless bodies, $t(11) = .57$, $p = .57$.

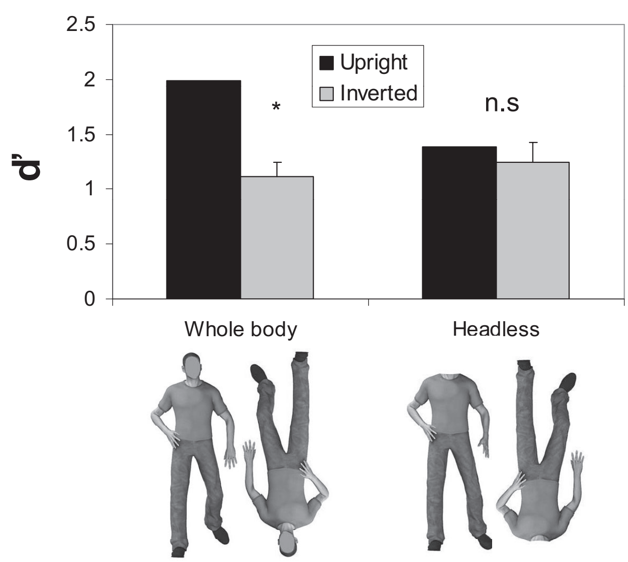

Figure 3. Performance level (d') for bodies without heads (headless). Headless bodies yielded no inversion effect and a much lower performance for the upright orientation than did complete bodies. Error bars indicate the standard error of the difference between upright and inverted stimuli, that is, the variance of the body inversion effect. * $p < .001$.

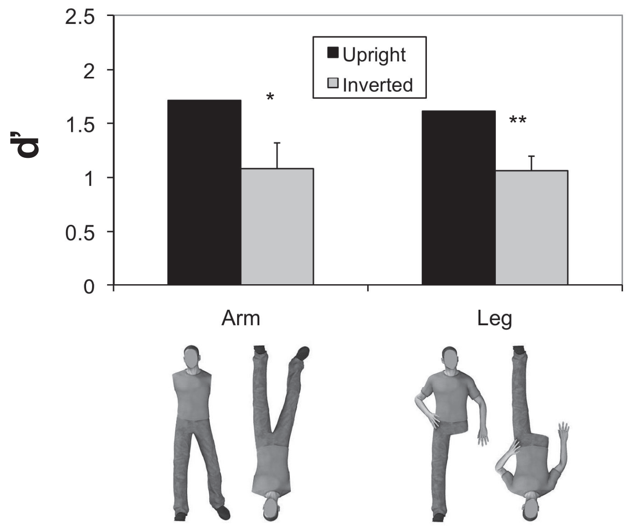

Figure 4. Performance level (d') for bodies without hands or a leg show a significant inversion effect for these incomplete bodies that include heads, in contrast to headless bodies that showed no inversion effect (see Figure 3). Error bars indicate the standard error of the difference between upright and inverted stimuli, that is, the variance of the body inversion effect. * $p < .01$. ** $p < .001$.

Discussion

Experiment 2 showed that the removal of the head significantly reduced the BIE. Thus, posture discrimination of headless bodies was not significantly better for upright bodies than for inverted bodies. This effect may suggest that a BIE is found for posture discrimination of only complete bodies. Alternatively, the head may have a special status in the processing of body posture, and thus removal of another body part will not influence the magnitude of the BIE. In order to answer this question, in Experiments 3A and 3B we presented the same body stimuli without arms (armless bodies) or without a leg (legless bodies) in a similar sequential matching task. If the BIE depends on the completeness of the body stimuli, we would expect the inversion effect to be abolished or reduced also for armless and legless bodies. However, if the BIE depends on the existence of the head, armless and legless bodies would yield a significant inversion effect as complete bodies.

Our findings also show that performance for upright headless bodies was lower than that for complete bodies. This finding may reflect the fact that the pairs of headless body stimuli differ in only two body parts (arm and leg), whereas complete body stimuli differ in three body parts (head, arm, and leg). By removing the arm or the leg, we are also able to examine whether the impaired discrimination of headless bodies in relation to complete bodies is due to the smaller number of part differences in incomplete bodies.

Experiment 3

Method

Participants. Ten subjects (age: 21–25 years; 5 women) participated in Experiment 3A (armless), and 13 (age: 24–26 years; 8 women) participated in Experiment 3B (legless).

Stimuli and procedure. We used the same body stimuli that were used in Experiment 1. In Experiment 3A, we cut out both arms (Figure 4). Thus, discrimination of different poses was based on the different positions of the head, the legs, or both. In Experiment 3B, we removed one leg (Figure 4). The remaining leg was similar in position for both bodies in the different-posture pairs. Thus, discrimination of legless bodies was based on the hand or head position. The reason we removed both arms and not one of the arms was because one-armless bodies did not look like incomplete bodies but as complete bodies with a hidden arm. Importantly, only one of the arms in complete bodies differed in posture across each pair of different bodies. Thus, removing both arms did not remove more information about posture differences in relation to removal of only one arm.

Results

Performance for inverted bodies was significantly lower than for upright bodies in both the armless and legless conditions (Figure 4). A paired *t* test revealed better performance for upright bodies than for inverted armless bodies, $t(9) = 2.65$, $p < 0.05$, $d = 1.7$, and for upright bodies than for inverted legless bodies, $t(12) = 3.37$, $p < 0.01$, $d = 1.9$. To assess whether the magnitude of the inversion effect for incomplete bodies differs from that of the inversion effect for complete bodies, we compared these data with whole bodies' data collected in Experiment 2 and performed a two-way mixed ANOVA with body type (complete or armless) as a between-subjects factor and with orientation as a within-subject factor. This analysis revealed a main effect of orientation, $F(1, 18) = 31.0$, $p < 0.0001$, $\eta^2_{par} = 0.63$, and no significant interaction of body type and orientation ($F < 1$). A similar analysis with complete and legless bodies revealed a main effect for orientation, $F(1, 20) = 42.7$, $p < 0.0001$, $\eta^2_{par} = 0.67$, and no interaction between body type and orientation, $F(1, 20) = 2.3$, $p = .17$. Furthermore, unlike the much lower performance level that we found for upright headless bodies in comparison with upright complete bodies, performance for armless upright bodies did not differ from performance for complete bodies, $t(18) = 1.21$, $p = .24$. Similarly, performance for legless bodies did not differ from performance for complete upright bodies, $t(20) = 1.5$, $p = .13$. These findings suggest that in contrast to the head, which seems to be critical for intact discrimination of human body posture, the omission of the hands or leg does not significantly impair discrimination of body posture.

A possible explanation for the large effect of head omission on body discrimination is that the difference in head posture across each pair of stimuli is larger than the difference in hand or leg position. In order to assess this suggestion, we calculated the correlations between the pixels of each pair of images for whole bodies, headless bodies, armless bodies, and legless bodies. This correlation reflects the similarity between each pair of stimuli and is smallest for complete bodies that differ in three body parts. Removal of each body part is expected to increase this correlation (bodies differ by only two parts). The largest increase in comparison to whole bodies would indicate which body part position difference was largest. For example, if the head posture difference is largest, removal of the head would increase the correlations more than would removal of other body parts, such that the difference in correlations between the whole body and the headless bodies should be largest in relation to the legless and armless bodies. Results, however, show exactly the opposite. The difference between the correlations for heads and headless bodies was minimal and significantly smaller than was the difference between the correlations of whole bodies and armless bodies ($p < .001$) and the difference between whole bodies and legless bodies ($p < .0005$), which were mostly different. Thus, although the image differences between leg posture were largest and those between head posture were minimal in our stimulus set, discrimination levels were reduced when the head was missing but not when an arm or leg was missing.

Analysis of the criterion shift (C) revealed no difference between upright and inverted bodies, neither those for armless bodies, $t(9) = -.48$, $p = .64$, nor those for legless bodies, $t(12) = 1.8$, $p = .10$.

Discussion

Our findings show that the BIE is not abolished for all types of incomplete bodies but only when the head is removed. A significant BIE was found when hands were removed or when a leg was removed. Furthermore, removal of hand or leg information was less detrimental to discrimination of upright bodies than was the removal of head information. Although similar to headless bodies—armless and legless bodies differed only in two body parts (head and leg for armless, and head and arm for legless)—performance level for armless and legless bodies was reduced in relation to complete bodies, which differed in all three body parts. Furthermore, image-based analysis showed that the magnitude of the head position difference between bodies was significantly smaller than was the magnitude of leg or arm difference. These findings suggest that subjects primarily attend to the head region or rely on head information in a posture discrimination task for both complete and incomplete bodies. Performance is significantly reduced when such information is not available, even though discrimination information can still be extracted from the positions of the hands and legs.

Similar to the attention bias towards the head region in bodies that may underlie our findings, many studies have reported that face recognition primarily depends on examination of the eye region (Blais, Jack, Scheepers, Fiset, & Caldara, 2008; Henderson, Williams, & Falk, 2005). Moreover, individuals who have difficulty in face recognition, such as prosopagnosic individuals (Barton, Radcliffe, Cherkasova, & Edelman, 2007) or autistic individuals (Jones, Carr, & Klin, 2008), tend to focus on the mouth rather than on the eye region. We were therefore interested in assessing whether part omission in faces would result in analogous effects to those we found with bodies. Specifically, we asked whether omission of the eyes but not the mouth would reduce performance for upright faces or abolish the face inversion effect, in the same way that removal of the head but not the leg reduced posture discrimination abilities for upright bodies and the magnitude of the body inversion effect.

Experiment 4

Method

Participants. Ten subjects (age: 19–26 years; 7 women) participated in Experiment 4A, in which eyes were covered (eyeless faces) in the faces that were used in Experiment 1. Ten additional subjects (age: 21–25 years; 6 women) participated in Experiment 4B, in which the mouth was covered (mouthless faces), and 12 subjects (age: 21–25 years; 9 women) participated in a whole-face study similar to the face task used in Experiment 1.

Stimuli and procedure. We used the face stimuli that were presented in Experiment 1. In eyeless stimuli, the region of the eyes and eyebrows was covered. For the mouthless stimuli, the region of the mouth was covered (Figure 5). We used the same sequential matching task that was described above.

Results

Performance level was higher for upright faces than for inverted faces for all face types (Figure 5). To assess whether the inversion effects for eyeless or mouthless faces differed from the inversion effect for complete faces, a two-way mixed ANOVA with face type (complete or eyeless) as a between-subjects factor and orientation as a within-subject factor revealed a main effect of orientation, $F(1, 18) = 28.5$, $p < 0.0001$, $\eta^2_{\text{par}} = 0.58$, and no significant interaction of face type and orientation ($F < 1$). Similar analysis comparing complete and mouthless faces revealed similar findings of a main effect of orientation, $F(1, 18) = 26.9$, $p < 0.0001$, $\eta^2_{\text{par}} = 0.59$, and no significant interaction of face type and orientation ($F < 1$). Paired t tests revealed a significant face inversion effect for whole faces, $t(11) = 3.48$, $p < 0.001$, $d = 2.3$, for eyeless faces, $t(9) = 5.12$, $p < 0.001$, $d = 3.4$, and for mouthless faces, $t(9) = 5.51$, $p < 0.005$, $d = 3.67$.

Analysis of the criterion shift (C) revealed no difference in this measure between upright and inverted faces for complete faces, $t(9) = .19$, $p = .85$, for eyeless faces, $t(9) = 1.8$, $p = .11$, or for mouthless faces, $t(9) = -1.6$, $p = .14$.

Discussion

Experiment 4 examined the effect of the removal of a face part on the magnitude of the face inversion effect. We specifically asked whether removal of the eye region, to which we attend when we process faces, would generate the similar effect that removal of the head generated with bodies. Unlike headless bodies, which show no inversion effect, the removal of eyes from faces does not reduce the well-established face inversion effect. These findings suggest that unlike bodies, in which omission of the head but not the hands or a leg abolished the inversion effect, the face inversion effect is not influenced by omission of a single face part, even the eyes, which are primarily examined in face recognition tasks. These findings suggest that we cannot directly infer—from the extensive knowledge that we acquired over the past 40 years regarding the face inversion effect—how picture-plane inversion will affect the processing of human bodies.

In the final experiment, we further examined the reason for the lack of inversion effect for headless bodies. It has been suggested that the BIE is reduced for impossible body postures (Reed et al., 2003). Here, we specifically asked whether performance for headless bodies and the BIE are reduced because a headless body is an unrealistic body image, or because information about the position of the head is critical for intact discrimination of body posture. To that effect, we measured discrimination abilities for complete human bodies that differed in hand and leg position but not in head position (hence, fixed-head bodies). A significantly lower discrimination level of these fixed-head body stimuli would suggest that the reduced performance level and inversion effect for headless bodies is not because they are unnatural body figures, but because we primarily use the head position to discriminate between different human poses.

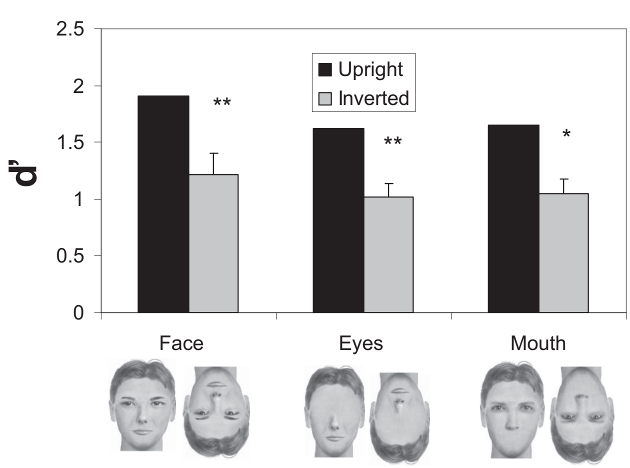

Figure 5. The inversion effect for faces without eyes or without a mouth did not differ from the inversion effect for whole faces. Error bars indicate the standard error of the difference between upright and inverted, that is, the variance of the face inversion effect. * $p < .001$. ** $p < .0001$.

Experiment 5

Method

Participants. Ten subjects (age: 20–24 years; 6 women) participated in Experiment 5.

Stimuli and procedure. We used the same stimuli we presented in Experiments 1 and 2 but kept only the hand and leg position difference, whereas the head position remained similar for the different-posture pairs (Figure 6). These complete body figures then differed in the position of the leg and arm but not the head. A sequential matching task was used as described in the previous experiments. Subjects were not informed about the nature of difference between the body postures used in the task.

Results

The inversion effect for bodies in which head position was fixed was significant, $t(9) = 3.3$, $p = 0.01$, $d = 2.1$. However, a comparison between the magnitude of the inversion effect of fixed-head bodies and complete bodies used in Experiment 2 ($n = 10$), in which head position varied, revealed a much larger inversion effect for complete bodies than for fixed-head bodies (Figure 6). A two-way mixed ANOVA with body type (head position fixed or head position varied) as a between-subjects factor and orientation as a within-subject factor revealed a main effect of orientation, $F(1, 18) = 56.1$, $p < 0.0001$, $\eta^2_{\text{par}} = 0.78$, but a significant interaction of body type and orientation, $F(1, 18) = 12.8$, $p < 0.0001$, $\eta^2_{\text{par}} = 0.42$. The BIE was significantly larger for bodies in which the head position varied, $t(9) = 6.74$, $p < 0.0001$, $d = 4.5$,

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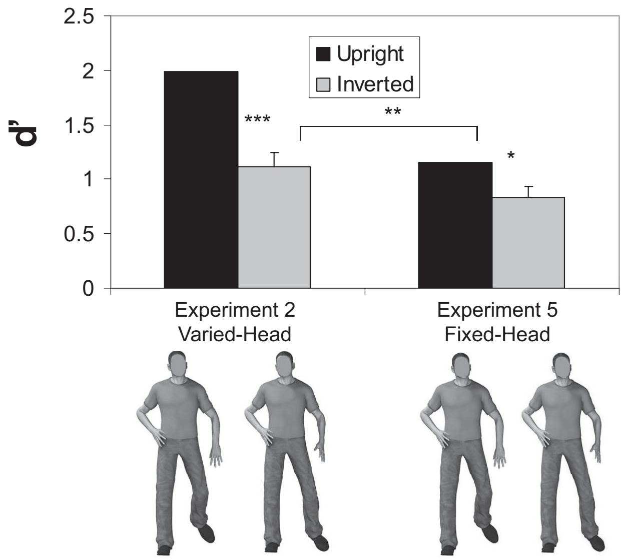

Figure 6. The inversion effect is abolished and performance for upright bodies is reduced for complete bodies in which the head position is fixed and therefore not informative to discrimination of body posture. Data for head-varied bodies was collected in Experiment 2. Error bars indicate the standard error of the difference between upright and inverted stimuli, that is, the variance of the body inversion effect. * $p < .01$. ** $p < .001$. *** $p < .0001$.

than for bodies in which the head position was fixed. Furthermore, a two-sample t test confirmed that the performance for fixed-head upright bodies was significantly lower than performance for upright bodies in which head position varied, $t(18) = 3.9$, $p < 0.001$, $d = 1.8$. Thus, discrimination of body posture was more difficult for complete bodies that did not differ in head position.

The small but significant inversion effect for fixed-head bodies is inconsistent with the lack of inversion effect for headless bodies. To assess whether fixed-head bodies indeed generated a larger inversion effect than did headless bodies, we compared the magnitude of the inversion effect for the fixed-head position and the headless bodies that we examined in Experiment 2. A two-way mixed ANOVA with body type (head position fixed or headless) as a between-subjects factor and with orientation as a within-subject factor revealed no significant interaction between the two body types ($F < 1$) and no difference between performances for the upright stimuli, $t(20) = 1.18$, $p = .25$. Thus, performance for upright bodies and the inversion effect are reduced when the head cannot be used to discriminate body posture for both complete and incomplete bodies.

Analysis of the criterion shift (C) revealed a stronger tendency to make same responses for upright bodies than for inverted bodies of the fixed-head bodies, $t(9) = 2.48$, $p < .05$. This pattern was significantly different from the absence of the effect that was found for complete bodies, an interaction of body type (complete or fixed head) by orientation, $F(1, 20) = 5.83$, $p < .05$, $\eta^2_{par} = .22$. Furthermore, independent sample t test showed that the tendency to make same responses was marginally significantly larger for fixed-head bodies than for varied-head bodies, $t(9) = 1.95$, $p = .07$. This finding suggests that when the head position is identical, subjects tend to see the full body as similar, even if it differs by arm and leg positions.

Discussion

The findings of Experiment 5 show that even when bodies are complete but the head position is fixed and therefore not informative for posture discrimination, discrimination of upright bodies and the inversion effects are markedly reduced. These findings replicate findings with headless bodies and suggest that the elimination of the BIE for headless bodies and the significant decrease in discrimination for upright headless bodies is not because they are incomplete or unnatural body figures that do not exist in the real world. Indeed, a criterion shift analysis revealed that fixed-head bodies generated a bias to make same responses in relation to bodies that differ in head position. These findings suggest that the head has a special role in the processing of body posture, and when it cannot be used for discrimination, performance is significantly reduced.

General Discussion

The goal of the current study was to shed light on mechanisms that underlie the body inversion effect. We found that the BIE is abolished for headless bodies (see also Minnebusch et al., 2009) and examined two possible explanations for this finding: Either the BIE is abolished for any type of incomplete bodies, or the head position plays a unique role in the discrimination of body posture. Our findings show that the BIE is not reduced when other body parts, such as arms or a leg, are removed. Furthermore, performance for upright bodies and the BIE are also significantly reduced for complete bodies in which the head position is fixed and is therefore not informative for discrimination of body posture. Taken together, these findings suggest that the discrimination of body posture is reduced whenever the head position cannot be used for discrimination and not because headless bodies are incomplete or unnatural type of body figures. One important implication of the major role that the head information plays in body discrimination is that it may also account, at least to some extent, for the BIE. In other words, performance for inverted bodies may be lower than for upright bodies, because heads are less visible when bodies are presented upside down. Although this idea was not directly tested in our studies, it does suggest that more research is needed in order to reveal the underlying mechanisms of the BIE and whether they indeed reflect holistic processing of upright but not inverted faces (Reed et al., 2006; Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007). As aforementioned, direct measures of holistic processing have hardly been used to assess the nature of processing of upright (Seitz, 2002) and inverted bodies.

The inversion effect for incomplete bodies has been tested recently in a study by Reed et al. (2006), who examined the inversion effect for body parts and "half bodies" in comparison to complete bodies. They reported no inversion effect for body parts and for horizontally divided bodies, but a significant inversion effect for vertically divided bodies. A BIE for vertically divided bodies is consistent with the importance of head position for discrimination of upright bodies, because head information can be extracted from vertically divided stimuli. The absence of an inversion effect for horizontally divided

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bodies is expected for the lower body half, which similar to headless bodies, does not include a head. Furthermore, Reed et al. (2006) found better performance for the upper part than for the lower part of the body, which is consistent with the special role that the head plays in body discrimination tasks. Inconsistent with our findings, no inversion effect was found for the upper part of the body, which includes head, torso, and arm information. These stimuli are somewhat similar to our legless stimuli, which did generate a significant inversion effect in our study. Future studies may directly compare these two experimental conditions to account for this discrepancy.

Unlike the face inversion effect, which has been extensively studied in the past 40 years, very few studies have examined the underlying cognitive and neural mechanisms of the BIE. Our study challenges the idea that the BIE reflects the same kind of holistic mechanisms that are thought to account for the face inversion effect. Similar to the critical role heads seem to have in body discrimination, eyes play a central role in face discrimination. Still, the inversion effect is not reduced for faces without eyes but is significantly reduced for bodies without heads. Thus, the extensive understanding that we have about mechanisms that may underlie the face inversion effect may not be necessarily applicable to account for the BIE, until further research is completed with human bodies.

The finding that headless bodies are processed dramatically differently from complete bodies is also highly relevant for neuroimaging studies of the body-selective system, which typically use headless bodies in order to study the areas that respond to body stimuli in isolation from areas that process face stimuli. In fact, a recent fMRI study found that the response of the body-selective area to complete bodies was lower than that for bodies in which the head was occluded by a book (Morris, Pelphrey, & McCarthy, 2006). Taken together with our findings, it seems that removal of head information may significantly modify the body representation, and therefore findings with headless bodies may not be informative about the processing of complete bodies. Interestingly, a recent study showed that recognition of face expression is significantly influenced by the body emotional expression (Aviezer et al., 2008), which also suggests a close interaction between the representation of the head and the rest of the body.

In summary, the current study suggests that the head plays a central role in the discrimination of body posture. When head position is not informative about the position of the rest of the body (i.e., headless and fixed-head bodies), not only discrimination abilities go down, but also the body inversion effect is markedly reduced. It is possible that reduced performance for inverted bodies that we observed for bodies that do differ in head position may, at least to some extent, reflect the difficulty in discriminating head postures in upside-down bodies, a hypothesis that should be directly tested in future studies. The difference between the effect of part omission on the face inversion effect and the body inversion effect suggests that we cannot infer from the extensive knowledge that we have about the mechanisms underlying the face inversion effect about the mechanisms that underlie the body inversion effect. The possible role of holistic processing in the body inversion effect should be assessed in future studies that will directly measure the extent to which upright bodies but not inverted bodies are processed as nondecomposable wholes.

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