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A face inversion effect without a face

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A B S T R A C T

Numerous studies have attributed the face inversion effect (FIE) to configural processing of internal facial features in upright but not inverted faces. Recent findings suggest that face mechanisms can be activated by faceless stimuli presented in the context of a body. Here we asked whether faceless stimuli with or without body context may induce an inversion effect as large as the FIE. In Study 1 participants performed a sequential matching task for upright and inverted faces, faceless heads with full, minimal or no body context, headless bodies and bodies viewed from the back. Results show inversion effects as large as the FIE for faceless heads with full or minimal body context, but not for faceless heads without body context, headless bodies or bodies viewed from the back. These findings remarkably show that in contrast to the well-established configural explanation for the FIE, the FIE does not necessarily depend on the processing of internal facial features, but can be also triggered for faceless stimuli presented in body context. In Study 2 participants rated the extent to which they detected a face in stimuli presented with or without faces briefly followed by a mask. We found that faceless stimuli that generated a large inversion effect were rated higher for the existence of a face than faceless stimuli that generated small or no inversion effects. These findings further suggest that the FIE can be generated by a contextually induced face percept at the face detection stage rather than the face identification stage.

1. Introduction

The face inversion effect (FIE) is the disproportionate drop in recognition for inverted relative to upright faces, in comparison to other visual stimuli (Yin, 1969) and has been considered a well-established marker for specialized face processing mechanisms. This extensively studied phenomenon has been typically attributed to disruption in the representation of spatial relations among internal facial features, reflecting a unique mechanism of holistic processing that is either absent or weaker in inverted relative to upright faces (Farah, Wilson, Drain, & Tanaka, 1998; Maurer, Grand, & Mondloch, 2002; McKone & Yovel, 2009; Richler, Mack, Palmeri, & Gauthier, 2011; Tanaka & Farah, 2003; Young, Hellawell, & Hay, 1987). More recent studies further showed that this FIE is strongly linked with face-selective neural mechanisms (Mazard, Schiltz, & Rossion, 2006; Yovel & Kanwisher, 2005). These findings highlight the importance of the FIE as a useful tool for understanding special cognitive and neural mechanisms of face perception.

Recent studies of face-body cross-category processing have introduced the fascinating idea that face-processing mechanisms can be activated by faceless stimuli presented in the context of a body (Andrews, Davies-Thompson, Kingstone, & Young, 2010; Cox, Meyers, & Sinha, 2004; Ghuman, McDaniel, & Martin, 2009). In particular, an fMRI study by Cox et al. (2004) presented participants with faces, headless bodies, degraded faces with no internal features and contextually defined faces, which were

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composed of the same degraded face figures presented in natural configuration on top of the body figures. They reported that the response of the fusiform face area (FFA) to contextually-defined faces was as strong as the response to intact faces and stronger than the response to degraded faces alone. Importantly, the response of the FFA to degraded faces with no body context was similar to its response to non-preferred stimuli such as natural scenes and headless bodies. These findings indicate that face areas are not only selective to internal facial features, but also to faceless heads presented in body context. Additional evidence for the link between the representation of faces and bodies is reported in a recent behavioral adaptation study by Ghuman et al. (2009), who used a cross-category adaptation paradigm to measure the aftereffect of body processing on the representation of faces (see also Lai, Oruc, & Barton, 2011). Remarkably, they found that prolonged viewing of a headless body shifts the perceptual tuning curve for faces, suggesting that an inference about a missing face is sufficient to induce adaptation to faces, even in the absence of the facial features themselves.

This body-induced activation of face mechanism by faceless stimuli may also account for recent findings of an inversion effect for faceless body stimuli, which was as large as the inversion effect for faces (Minnebusch, Suchan, & Daum, 2009; Reed, Stone, Bozova, & Tanaka, 2003; Yovel, Pelc, & Lubetzky, 2010). Although this body inversion effect (BIE) was at first attributed to specialized body processing mechanisms (Reed, Stone, Grubb, & McGoldrick, 2006), the BIE was not associated with body-selective neural mechanisms, but rather was found to be associated with face-selective brain areas (Brandman & Yovel, 2010). Furthermore, the behavioral BIE is abolished for headless bodies, but not for other types of incomplete bodies, reflecting a central role of the head in the generation of the BIE (Minnebusch et al., 2009; Yovel et al., 2010). Taken together, these findings suggest that unlike the FIE, which has been shown to be associated with face-selective mechanisms (Mazard et al., 2006; Yovel & Kanwisher, 2005), the BIE is not a marker of specialized processing of its stimulus category (bodies). Instead, the BIE is associated with face or head processing mechanisms, and may therefore reflect a head or face inversion effect.

Taken together the BIE and the recently found body-induced activation of face mechanisms, we hypothesized that the inversion effect found for whole faceless bodies reflects a FIE resulting from contextual processing of body cues rather than an effect of body-selective processing. More specifically, we asked what type of body context is necessary to induce an inversion effect as large as the FIE for faceless stimuli. To test our hypothesis, we conducted a series of behavioral experiments comparing the magnitude of the inversion effect for faces and various types of faceless stimuli to determine whether a *full inversion effect* can be induced for faceless stimuli. For future reference throughout this paper, a full inversion effect is defined as an inversion effect that is as large as the FIE. In addition, we asked if the same faceless stimuli that produce a full inversion effect also generate a percept of a face in a briefly masked face detection paradigm. In other words, we asked whether a full inversion effect could be the result of contextually-induced detection of a face that activates the face system.

2. Study 1: inversion effect

In Study 1 participants were allocated to one of seven sequential matching tasks for upright and inverted stimuli. Each task measured the magnitude of inversion effect for a stimulus category that differed in either face identity, body pose or head pose.

2.1. Materials and methods

2.1.1. Participants

Ninety-eight participants (age 20–27, females: $n = 79$) with normal or corrected to normal vision took part in the study in exchange for course credit. Fourteen participants were allocated to each of the seven tasks. Each participant performed only one of the tasks, in order to avoid possible perceptual influences among the different categories. All participants signed a consent form approved by the Tel-Aviv University ethics committee. Six additional participants were removed from analysis due to near-chance performance in the upright condition.

2.1.2. Stimuli

The body and head stimuli were created from gray-scale male figures generated with Poser 7.0 software (e frontier America Inc.), used in a previous study by Yovel et al. (2010). The Poser figures were used to create images of whole bodies, headless bodies (Fig. 1a), heads with shoulders, heads alone (Fig. 1b) and bodies viewed from the back (Fig. 1c). All body and head stimuli were of the same identity, and differed only in pose. A set of 18 physically possible upright body poses were constructed, and a set of 18 different-body pairs was created by altering the positions of one arm, one leg, and the head of each figure. Face stimuli were (Fig. 1a) created with FACES software (IQ Biometrix, Inc.), used in a previous study by Yovel et al. (2010). Face stimuli included 18 different-face pairs that differed in the shape of the eyes, nose and mouth.

To hide facial features, the faces of the Poser figures were covered by a gray ellipsoid. Headless bodies were created by removing the heads from the whole body images. Body parts were removed from the neck down to create faceless head stimuli, and from the chest down to create images of faceless heads in minimal body context. Additionally, body figures were rotated in depth 180° to generate whole bodies viewed from the back. The size of the body and face images was approximately 220×330 pixels. The size of the faceless head stimuli was approximately 90×120 pixels. The size of the heads with minimal body context was approximately 220×160 pixels. Head size was identical between the two types of faceless head stimuli in order to avoid potential differences in face visualization due to different head size. The inverted stimuli were in plane rotations (180°) of the same stimuli used in the upright trials.

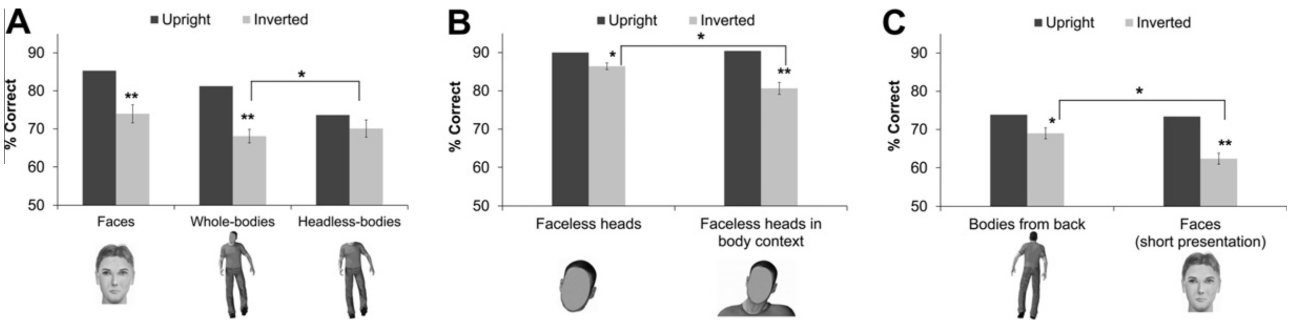

Fig. 1. Accuracy for matching upright and inverted stimuli in Study 1: (a) faces, faceless whole bodies and headless bodies; (b) faceless heads with and without minimal body context; and (c) bodies from the back and faces matched for performance in upright. Error bars indicate the standard error of the difference between upright and inverted stimuli. * <0.05, ** <0.01.

2.1.3. Apparatus and procedure

Stimuli were presented using Psychtoolbox implemented in MATLAB (Brainard, 1997). A chin rest was used to keep the distance between the participants and the monitor constant at 45 cm. The design of the tasks was the same as in a previous study by Yovel et al. (2010). Participants were asked to determine whether two subsequently presented stimuli were the same or different with respect to identity for faces and pose for bodies and heads. Each trial started with a fixation cross presented in the center of the screen for 750 ms. The first stimulus was presented for 250 ms, followed by a blank screen for 1000 ms. The second stimulus appeared on the screen until a response was made. Upright and inverted trials were presented in an interleaved random manner. The experimental task contained 144 trials (2 presentations × 18 pairs × 2 [same/different] × 2 [upright/inverted]). Two mandatory breaks of at least 20 s each were given every 50 trials.

2.2. Results and discussion

Accuracy was computed as the proportion of correct responses. Mean reaction times were computed for correct responses (Table 1). We first report replication of previous findings with faces, whole bodies and headless bodies (Minnebusch et al., 2009; Yovel et al., 2010) and obtain a baseline measure of the FIE to which all other inversion effects are compared. We then examine the magnitude of the inversion effect for faceless heads and faceless heads with body context. In addition, to assess the extent to which an inversion effect may depend on the likelihood that a stimulus contains internal facial features, we examined the inversion effect for bodies from the back that are not expected to contain internal facial features. Finally, because bodies from the back yielded lower performance rate, the inversion effect for faces was measured again using shorter exposure, to match with upright performance for bodies from the back.

Table 1
Mean reaction times and standard deviations of correct responses for upright and inverted stimuli in Study 1 show no evidence for speed–accuracy trade-off.

Stimuli	Upright (s)	Inverted (s)
Faces	0.93 (0.20)	0.97 (0.19)
Whole bodies	0.95 (0.30)	1.05 (0.36)
Headless bodies	0.95 (0.29)	0.94 (0.26)
Faceless heads	0.73 (0.16)	0.75 (0.16)
Faceless heads in context	0.77 (0.15)	0.77 (0.13)
Bodies from the back	0.90 (0.16)	0.96 (0.21)
Faces (short presentation)	1.10 (0.31)	1.21 (0.40)

2.2.1. Inversion effects for face, whole body and headless body stimuli

Performance for upright stimuli was better than for inverted stimuli for both faces and whole bodies, but not for headless bodies (Fig. 1a). Notably, the face and whole body tasks were matched for performance in the upright condition ($t(26) = 1.51$, $p = 0.142$). A repeated-measures ANOVA of accuracy with category (face, whole body, headless body) as a between-subjects factor and orientation (upright, inverted) as a within-subjects factor revealed a main effect of category ($F(1,39) = 5.74$, $p = 0.006$, $\eta_p^2 = 0.227$), a main effect of orientation ($F(1,39) = 56.28$, $p < 0.001$, $\eta_p^2 = 0.591$), and an interaction between these factors ($F(2,39) = 5.58$, $p = 0.007$, $\eta_p^2 = 0.222$). Paired t-tests of accuracy showed a significant inversion effect for faces ($t(13) = 4.77$, $p < 0.001$), and for whole-bodies ($t(13) = 7.35$, $p < 0.001$), but not for headless-bodies ($t(13) = 1.57$, $p = 0.141$). Independent sample t-tests showed no difference between the magnitude of the inversion effects (upright–inverted) for faces and whole-bodies ($t(26) = 0.62$, $p = 0.543$), whereas the inversion effect for headless bodies was smaller than the effects found for whole bodies ($t(26) = 3.32$, $p = 0.003$) and for faces ($t(26) = 2.37$, $p = 0.025$). A repeated-measures ANOVA of reaction times revealed a similar main effect of orientation, with longer reaction times for inverted than upright ($F(1,39) = 15.81$, $p < 0.001$, $\eta_p^2 = 0.288$) and an interaction between orientation and category ($F(2,39) = 9.65$, $p < 0.001$, $\eta_p^2 = 0.331$). Paired t-tests of reaction time showed a significant inversion effect for whole-bodies ($t(13) = 5.06$, $p < 0.001$) and for faces ($t(13) = 2.76$, $p = 0.016$), but not for headless-bodies ($t(13) = 0.66$, $p = 0.521$). These findings replicate previous reports of a full inversion effect for whole but not for headless bodies (Yovel et al., 2010). Furthermore, they provide us with a baseline inversion effect measure to compare with results of subsequent experiments.

The inversion effect for whole faceless bodies but not for headless bodies together with previous findings that the BIE is associated with face-selective rather than body-selective brain areas (Brandman & Yovel, 2010), suggest that the inversion effect found for whole bodies is not mediated by body processing mechanisms but by face or head processing mechanisms. It is therefore important to determine whether the inversion effect for whole bodies is generated by the head alone or is an effect of contextual face processing of body information as was previously seen in the FFA (Cox et al., 2004). To answer this question, we measured the magnitude of the inversion effect induced by faceless heads compared to the inversion effect induced by faceless heads with minimal body context. Furthermore, to examine whether these stimuli induced a full inversion effect we compared results to the face and whole body inversion effects.

2.2.2. Inversion effects for faceless heads with and without body context

Performance for upright stimuli was better than for inverted stimuli in both tasks. However, this effect was significantly stronger for faceless heads in-context than for faceless heads (Fig. 1b).

A repeated-measures ANOVA of accuracy with category (faceless head, faceless head in-context) as a between-subjects factor and orientation (upright, inverted) as a within-subjects factor revealed no main effect of category ($F(1,26) = 1.44$, $p = 0.242$, $\eta_p^2 = 0.052$), a main effect of orientation ($F(1,26) = 54.74$, $p < 0.001$, $\eta_p^2 = 0.678$), and an interaction between these factors ($F(1,26) = 1.77$, $p = 0.002$, $\eta_p^2 = 0.312$), indicating a larger inversion effect for faceless heads in-context than for faceless heads. A similar ANOVA of reaction times revealed no significant effects ($p > 0.11$).

To compare the magnitude of inversion effects to the effect that we obtained for whole bodies and faces, independent sample t-tests were performed, showing no difference in the magnitude of inversion effects between whole-bodies and heads in-context ($t(26) = 1.42$, $p = 0.169$) and between faces and heads in-context ($t(26) = 0.54$, $p = 0.592$). The inversion effect for faceless heads was significantly smaller compared to whole-bodies ($t(26) = 4.80$, $p < 0.001$) and compared to faces ($t(26) = 3.06$, $p = 0.005$). Tukey's HSD post-hoc tests revealed similar effects at a significance level of 0.05. These results demonstrate a full inversion effect for faceless heads with minimal body context, as opposed to a diminished effect for faceless heads alone. Thus, corresponding with previous indications of face processing that is triggered by contextual body cues (Cox et al., 2004; Ghuman et al., 2009).

Since faceless heads in body context, but not faceless heads alone, induced a full inversion effect, we conclude that head processing mechanisms cannot explain the full inversion effect found for whole bodies. Together with the lack of an inversion effect for headless bodies, these results support the hypothesis that these inversion effects are mediated by face processing mechanisms activated by body context, rather than by independent body or head processing mechanisms. These findings therefore imply that heads in body context may activate the face system, generating a full inversion effect similar to the FIE, even though there is no visible face in the image. Importantly, these findings suggest that the FIE may not necessarily require the presence of internal facial features and can be similarly induced by faceless heads with minimal body context. The faceless heads alone may not have included sufficient contextual cues to activate the face system, and therefore did not generate a full FIE. Thus, additional body context may be required to induce a FIE. One-way in which body context could trigger a FIE would be by inducing imagery of the internal features of a face within the faceless head. If this hypothesis is correct, we would expect no or smaller inversion effect for bodies shown from the back as these body images are not expected to include internal facial features. To examine this hypothesis we turned the same whole body stimuli from front to back and presented them in the same sequential matching task.

2.2.3. Inversion effect for bodies presented from the back

On a discrimination task of bodies viewed from the back, performance for upright stimuli was better than for inverted stimuli, as shown by paired t-tests of accuracy ($t(13) = 3.36$, $p = 0.005$) and reaction time ($t(13) = 2.99$, $p = 0.010$). However, the magnitude of the inversion effect for bodies from the back was significantly smaller than the inversion effect for whole-bodies ($t(26) = 3.61$, $p = 0.001$). Thus, there is a diminished inversion effect for bodies viewed from the back. Notably, performance level for upright bodies from the back was significantly lower than performance for whole bodies and faces. To assure that this smaller inversion effect is not due to scaling effect, we compared the inversion effect on this task to the effect for faces on a task that generated a similar performance level for upright faces as for bodies from the back (Fig. 1c). To obtain this we used the same face task reported above but presented the first face stimulus of each pair of sequentially presented faces for 50 ms instead of 250 ms. The inversion effect in the more difficult face task was larger than for bodies from the back ($t(26) = 3.01$, $p = 0.006$). Importantly, the magnitude of inversion effect for the new face task did not differ significantly from the inversion effect for faces presented for longer duration used in the original face task ($t(26) = 0.11$, $p = 0.913$). Tukey's HSD post-hoc tests revealed similar effects at a significance level of 0.05.

The diminished inversion effect produced by bodies from the back is consistent with the idea that a full inversion effect is generated only when internal facial features can be easily visualized in the faceless image. Such visualization may result from activation of face processing mechanisms by heads in body context, which generates a full inversion effect. To further examine this hypothesis we conducted a face detection study that measured the extent to which each type of faceless body stimuli may induce a percept of a face.

3. Study 2: a face detection task

In Study 2, participants were given a face detection task, in which they were asked to rate their perceived presence

Table 2
Ratings of face presence in the face detection task show differences in illusory face detection between the different faceless stimuli.

	Stimuli	Whole Bodies	Faceless Heads in Context	Faceless Heads	Headless Bodies	Bodies from the Back
Ratings M, (SD)		5.52 (1.32)	3.74 (1.58)	3.03 (1.27)	2.70 (1.23)	1.71 (1.08)
Fisher LSD	Whole Bodies		$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
MSE = 1.19	Faceless Heads in Context			$p = 0.048$	$p = 0.007$	$p < 0.001$
df = 76	Faceless Heads				$p = 0.295$	$p < 0.001$
	Headless Bodies					$p < 0.001$
	Bodies from Back					

of a face. Body and head figures from Study 1 were briefly presented followed by a mask either with or without a face when possible (for heads, heads with minimal body context and whole bodies) or without a face for headless bodies and bodies from the back.

3.1. Materials and methods

3.1.1. Participants

Twenty participants (age 20–27, females: $n = 20$) who did not participate in Experiment 1, took part in the study in exchange for course credit. All participants had normal or corrected to normal vision and signed a consent form approved by the Tel-Aviv University ethics committee.

3.1.2. Stimuli

Stimuli included eight types of images generated from the 18 body figures used in the inversion tasks: heads with/without faces, heads-in-context with/without faces, whole bodies with/without faces, headless bodies and bodies-from-back. The stimuli that included faces were the original stimuli we created for the body experiments before covering their face with an oval mask. All figures had the same identity in body and face, and differed between them only in pose. As in Study 1, the size of the body stimuli was approximately 220 × 330 pixels. To keep head and face size roughly similar in all conditions, head and head-in-context stimuli were reduced in size so that the head occupied 60 × 90 pixels. All stimuli were phased-scrambled to create mask images.

3.1.3. Procedure

Participants viewed a rapidly presented stimulus followed by a mask. In each trial, a fixation cross appeared for 1000 ms, followed by a target image presented for 27 ms followed immediately by a mask of 250 ms. Participants were then asked to rate how certain they were that they had seen a face in the image, on a scale between 1 (certain they had not seen a face) and 8 (certain they had seen a face).

Head and body stimuli were separated into two blocks in order to avoid body visualization in the head conditions. One block included the whole body (with and without faces), headless body and body-from-back stimuli, whereas the head and head-in-context stimuli (with and without faces) were presented on a different block. Each block contained 144 trials in random order (18 images × 4 conditions × 2 repetitions). The order of the blocks was counterbalanced across participants.

3.2. Results and discussion

We computed the mean ratings of perceived face presence for each of the eight types of stimuli. Overall, ratings were higher when the face was present than when it was covered, as revealed by a repeated-measures ANOVA with category (whole body, head, head in-context) and face (present, covered) as within-participant factors ($F(1,19) = 66.13$, $p < 0.001$, $\eta_p^2 = 0.777$). With respect to the five faceless stimuli, a one-way repeated-measures ANOVA revealed differences between categories ($F(4,76) = 33.95$, $p < 0.001$, $\eta_p^2 = 0.641$). Post-hoc Fisher LSD tests (see Table 2) revealed that faceless whole bodies and faceless heads with minimal body context were given significantly higher ratings than faceless heads alone, headless bodies and bodies from the back. Furthermore, faceless heads with no body context were rated as low as headless bodies. In sum, integration of these findings with the results of Study 1 shows that faceless stimuli that generated full inversion effects (whole bodies, heads in minimal body context) were given higher ratings than faceless stimuli that showed diminished inversion effects (faceless heads, headless bodies and bodies from the back), as shown in Fig. 2.

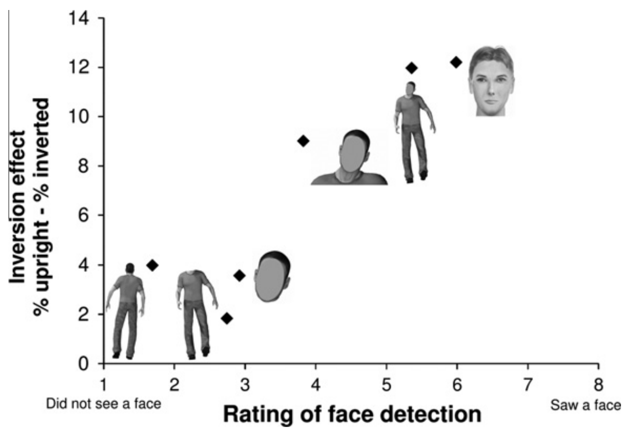

Fig. 2. A scatter-plot indicating the strong relationship between the magnitude of the inversion effect (y-axis) and the detection rating (1–8) of the degree to which subjects perceived a face for the same stimuli when they were briefly presented followed by a mask.

4. General discussion

The current study shows that faceless stimuli may generate an inversion effect that is as large as the inversion effect for faces. In particular, a full inversion effect was found for faceless stimuli that are composed of a head within the context of a body, both with full (i.e. whole bodies) or minimal (i.e. neck and shoulders) body context. In contrast, diminished or no inversion effects were measured for faceless heads without body context, headless bodies and whole bodies viewed from the back. Furthermore, we found that when presented in a briefly masked face detection task, the same faceless stimuli with full or minimal body context induced stronger face percepts than faceless heads without context, headless bodies and bodies from the back (Fig. 2). These findings suggest that faceless stimuli that generate a percept of internal facial features also generate a full inversion effect.

Our newly found inversion effects for faceless stimuli in body context as well as the results of the face detection study are fully consistent with the fMRI study of Cox et al. (2004), which presented participants with images of degraded faces that are similar to our faceless head stimuli in that they lack internal facial features. The FFA response to degraded faces attached to a body was as high as the response to intact faces and significantly higher than to headless bodies and degraded faces alone. Importantly, the FFA response to degraded faces in body context was as large as its response to intact faces. Here we show that the same type of stimulus that activated the FFA as much as faces in Cox et al. also yielded an inversion effect as large as the FIE. Our study also shows that these same stimuli also induced a face percept when presented in a brief masked face detection task. Altogether, these findings suggest that the inversion effect found for such faceless stimuli is generated by face processing mechanisms rather than head or body processing mechanisms.

A critical question is how could a FIE occur without the presence of a face? This is especially striking given that the FIE has been typically attributed to disruptions in detecting relations among internal facial features (Farah et al., 1998; Maurer et al., 2002; McKone & Yovel, 2009; Tanaka & Farah, 2003; Young et al., 1987). Given that a full inversion effect can be found even when internal facial features are absent suggests that the FIE can no longer be fully explained by configural processing of internal facial features. Our findings suggest that additional factors may activate the face system and generate a full inversion effect. Such activation of the face system is possible if the FIE, which has been typically associated with face identification mechanisms, is generated already at the face detection stage. Once a stimulus is detected as an upright face, face processing mechanisms are activated (Cox et al., 2004) and the processing of the same inverted stimulus is deteriorated. This hypothesis is in line with Tsao and Livingstone (2008) who suggested that holistic face processing can be explained by an obligatory detection stage that uses a coarse upright template of internal facial features (e.g. a T shape or a top-heavy configuration shape) and gates the activation of face-selective modules. Inverted faces, which do not fit well the T shape template, do not pass the detection gate as well as upright faces and therefore generate weaker face-selective activations. Our current findings of the face detection task, together with the fMRI findings of Cox et al. (2004), extend the type of stimuli that may efficiently pass the face-detection gate and activate these face mechanisms. These stimuli include faceless heads in body context, but do not include body images such as bodies from the back or headless bodies, which do not trigger visualization of facial features. Interestingly, it also does not include faceless heads with no body context as such stimuli do not activate the FFA (Cox et al., 2004), did not induce a face percept in our face detection task and did not generate a full FIE. Thus, faceless heads as presented here and in Cox et al. (2004) did not include sufficient contextual cues for the presence of a face. We therefore propose an additional template that may cross the face-detection gate, which does not require the presence of internal facial features or a T-like shape, but relies on the combination of external and contextual information (i.e. a faceless head in body context). Once such an image passes the face detection gate, it activates face mechanisms and a full inversion effect is observed.

A number of alternative explanations for the role of body cues in the generation of the FIE may be suggested but can be ruled out. First, it could be argued that face-selective areas represent not only faces but also body information associated with a face. Second, the detection of a body in other visual processing areas (e.g. body-selective areas) may trigger the activation of the face system. However, based on our finding that contextual cues alone (i.e. headless bodies) were not enough to induce a FIE, both these explanations seem insufficient. Furthermore, the fact that headless bodies generate much lower responses than faces in the FFA (Cox et al., 2004; Schwarzlose, Baker, & Kanwisher, 2005), and that face-selective areas are not sensitive to differences in headless bodies (Brandman & Yovel, 2010) make the above accounts even more unlikely. A third mechanism that may be suggested as an alternative to the automatic generation of a face percept during face detection, is activation of the face system by semantic information associated with faces. This may be relevant, as a face is likely to be found when viewing a head, but not when viewing a headless body or person from the back. However, in our study, heads alone did not generate a full inversion effect even though participants were told they were matching positions of heads and the external features (e.g. hair, ears) were exposed. Thus, although participants knew they were looking at human heads, this knowledge was not enough to induce a FIE for faceless head stimuli in our study or a face-sized FFA response in Cox et al. (2004). This is also in line with Ghuman et al. (2009) who found no behavioral face adaptation to semantically gender-related objects such as males' and females' shoes. Therefore, preliminary semantic knowledge alone cannot explain the FIE found for faceless stimuli.

Notably, our findings show that a full inversion effect and a face percept are not found for headless bodies and bodies from the back. These results may seem inconsistent with the recent study by Ghuman et al. (2009) who showed that a behavioral face adaptation aftereffect can occur for headless bodies and bodies from the back. However, our study differs from Ghuman et al. in several ways. First, Ghuman et al. examined adaptation for familiarized faces and bodies, whereas our body stimuli were of unfamiliar persons. It is possible that cross-adaptation was caused by the activation of person identification mechanisms in bodies and faces, and not by face detection mechanisms. Support for this hypothesis can be found in a recent study by Robbins and Coltheart (2012a), who found a larger inversion effect for familiarized headless bodies (that were initially learned with a face) than for unfamiliar headless bodies. This suggests that a familiar headless body may activate the face system by cross-category identification of the familiar bodies and faces, rather than by face detection from body context. In subsequent experiments Ghuman et al. (2009) used a gender adaptation task with headless bodies and bodies from the back. It is again possible that a gender task activates different mechanisms of body and face perception, independent of face detection. Thus, Ghuman et al.'s findings may not contradict our hypothesis that as long as the stimuli activate the face system either by detection or identification mechanisms, a full inversion effect is expected to be found. Future studies are needed to directly investigate these hypotheses.

Our findings should be also discussed in the context of the body inversion effect. The lack of a full inversion effect for headless bodies and for bodies from the back suggest that the inversion effect reported for whole bodies (Reed et al., 2003, 2006) is in fact mediated by face processing mechanisms rather than by body processing mechanisms. This suggestion has been directly demonstrated in an fMRI study which revealed similar discrimination for upright and inverted bodies in body areas, but better discrimination for upright than inverted bodies in face areas (Brandman & Yovel, 2010). The latter effect disappeared for headless bodies, similar to the behavioral inversion effect. We therefore conclude that current data suggest no evidence for a BIE mediated by body processing mechanisms. Furthermore, previous studies that reported a BIE suggested that it reflects holistic processing of bodies. Although our findings suggest that the BIE does not appear to reflect body processing mechanisms but face processing mechanisms, they do not directly address the question of whether bodies are processed holistically. Given that the inversion effect is not a direct measure of holistic processing, the lack of a BIE cannot be taken as evidence for the absence of holistic body processing and this question should be examined in studies that directly measure holistic processing. Indeed, support for the idea that bodies are processed holistically is shown in a study by Seitz (2002), who reported a whole-part effect for upright bodies similar to the one found for upright faces (Tanaka & Farah, 1993). It should be noted that inverted bodies were not examined by Seitz. Therefore, the question of whether the whole-part effect is specific for upright bodies is still open. In addition, a recent study by Robbins and Coltheart (2012b) found a composite effect for both upright and inverted body stimuli (but see Soria Bauser, Suchan, & Daum, 2011), though unlike faces (Hole, 1994), the effect was stronger for left–right than up-down composites. In sum, unlike the numerous studies that established the idea that faces are processed holistically, body stimuli have not been extensively studied and therefore the question of holistic body processing should be further examined in future studies.

To conclude, our study is the first to show that a FIE can be found not only for intact faces, but also for stimuli with no internal facial features as long as the faceless head is presented in the context of a body. These findings further highlight that the previously reported body inversion effect actually reflects a FIE. Taken together with previous evidence, the current findings support the idea that the detection of an upright head in relevant context automatically triggers face processing mechanisms. Strikingly, this contextually induced face percept may be enough to produce the most well-established marker of face processing, the face inversion effect, which so far has been attributed to configural processing of internal facial features in upright faces.

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