

Privileged detection of conspecifics: Evidence from inversion effects during continuous flash suppression

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ARTICLE INFO

Article history:

Received 18 August 2011

Revised 14 May 2012

Accepted 13 June 2012

Available online 7 July 2012

Keywords:

Bodies

Faces

Conspecifics

Inversion

Awareness

Binocular rivalry

Continuous flash suppression

ABSTRACT

The rapid visual detection of other people in our environment is an important first step in social cognition. Here we provide evidence for selective sensitivity of the human visual system to upright depictions of conspecifics. In a series of seven experiments, we assessed the impact of stimulus inversion on the detection of person silhouettes, headless bodies, faces and other objects from a wide range of animate and inanimate control categories. We used continuous flash suppression (CFS), a variant of binocular rivalry, to render stimuli invisible at the beginning of each trial and measured the time upright and inverted stimuli needed to overcome such interocular suppression. Inversion strongly interfered with access to awareness for human faces, headless human bodies, person silhouettes, and even highly variable body postures, while suppression durations for control objects were not (inanimate objects) or only mildly (animal faces and bodies) affected by inversion. Furthermore, inversion effects were eliminated when the normal body configuration was distorted. The absence of strong inversion effects in a binocular control condition not involving interocular suppression suggests that non-conscious mechanisms mediated the effect of inversion on body and face detection during CFS. These results indicate that perceptual mechanisms that govern access to visual awareness are highly sensitive to the presence of conspecifics.

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1. Introduction

The perception of other individuals is of unique biological and social significance, rendering other human beings perhaps the single most important class of objects in our visual world. Both the face and the body provide a wealth of information about another person's identity, age, gender, actions, attractiveness, direction of attention and emotional state (e.g., Slaughter, Stone, & Reed, 2004). Accordingly,

there is evidence that both faces and bodies are processed with higher priority than other objects. For example, visual attention is directed preferentially to both faces and bodies (Bindemann, Burton, Hooge, Jenkins, & de Haan, 2005; Downing, Bray, Rogers, & Childs, 2004; Langton, Law, Burton, & Schweinberger, 2008; Lavie, Ro, & Russell, 2003; Ro, Friggel, & Lavie, 2007) and neuroimaging studies have described distinct cortical areas in the ventral visual pathway specialized for processing faces (Kanwisher & Yovel, 2006) and human bodies (Peelen & Downing, 2007). In the present study we tested whether perceptual mechanisms that govern access to visual awareness are particularly sensitive to visual input that resembles the upright human form.

To measure access to visual awareness we employed a recently developed continuous flash suppression (CFS)

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paradigm, introduced by Jiang, Costello, and He (2007), that allows for the investigation of visual processes that precede (and lead to) stimulus awareness. CFS is a variant of binocular rivalry in which high-contrast patterns flashed to one eye render a stimulus presented to the other eye invisible for a couple of seconds (Tsuchiya & Koch, 2005). Potency in gaining access to awareness is quantified as the time observers need to detect an initially suppressed stimulus. As a means to study stimulus detectability, this method offers a number of advantages over other paradigms such as visual search, or paradigms using briefly presented or degraded stimuli. During CFS, single target stimuli compete against random masks, thus ruling out potential differences in target-distractor similarity that can complicate the interpretation of visual search studies (Duncan & Humphreys, 1989; also see Hershler & Hochstein, 2005; VanRullen, 2006). Furthermore, the strong suppression induced by the CFS masks (Tsuchiya, Koch, Gilroy, & Blake, 2006) obviates the need for artificially degraded stimuli or very short presentation durations, and permits stimulus presentation at natural contrast levels for comparably long periods of time.

Importantly, however, because visual detection is strongly influenced by a stimulus's low-level physical properties, differences in detection performance for different object categories that differ widely in physical low-level properties, such as pictures of people versus cars, cannot be taken as a direct measure of category-specific processing (VanRullen, 2006). To illustrate, the perceptual dynamics during interocular suppression are primarily determined by "stimulus strength" (Levelt, 1965; also see, e.g., Arnold, Law, & Wallis, 2008; Blake, 1977; Fox & Rasche, 1969; Shimaoka & Kaneko, 2011; Tsuchiya & Koch, 2005; Tsuchiya et al., 2006; Yang & Blake, 2012), that is, by a stimulus's low-level physical stimulus properties, including overall luminance, global contrast, local contrast relationships, the contrast and luminance relative to the background and relative to the elements of the CFS masks, the spatial frequency of the stimulus and the mask elements, and the interactions of all of these factors. Moreover, not all physical factors that may influence suppression durations are actually known. Because it is currently unknown how physical stimulus properties influence detection during CFS, overall differences in suppression durations between object categories could reflect any of these low-level physical stimulus differences and thus cannot provide evidence for category-preferences in visual detection.

To circumvent this problem, previous studies have used stimulus inversion to test for category preferences in the detection of objects. As physical stimulus properties are identical for upright and inverted stimuli, inversion effects in detection are assumed to reflect the sensitivity of the mechanisms involved in access to awareness to the stimulus's global structure (e.g., Lewis & Edmonds, 2003; Lewis & Ellis, 2003; Purcell & Stewart, 1988; VanRullen, 2006). Importantly, studies using CFS have found that initially invisible upright faces break into consciousness more quickly than inverted faces (Jiang et al., 2007; Stein, Senju, Peelen, & Sterzer, 2011; Yang, Zald, & Blake, 2007; Zhou, Zhang, Liu, Yang, & Qu, 2010), which is true even for highly

schematic faces (Stein, Peelen, & Sterzer, 2011). The FIE observed during CFS has been taken as evidence that the global facial structure is processed even before faces reach conscious awareness (Jiang et al., 2007; Zhou, Zhang, et al., 2010).

While these studies demonstrated privileged detection of upright faces and face-like stimuli, inversion effects during CFS have, thus far, not been found for non-face objects (Zhou, Zhang, et al., 2010). However, the behavioral benefits of specialized detection of faces only, rather than people more generally, are not immediately obvious considering that in our daily visual environment the awareness of the presence of another person often occurs through the detection of body form, for example when a person is viewed from a distance, in low-light, or from behind. Under these conditions, facial features may be poorly or not at all visible. In the present study we therefore tested the hypothesis that the privileged access to awareness found for upright (versus inverted) faces is similarly present for upright versus inverted person silhouettes and headless bodies, relative to non-person objects.

To measure the potency of upright and inverted faces, bodies, and other objects in gaining access to awareness, we adopted the CFS technique from previous studies on face detection (Jiang et al., 2007; Zhou, Zhang, et al., 2010). If detection mechanisms were not only preferentially tuned to the structure of upright faces, but also to upright bodies and person silhouettes, we would expect inversion effects during CFS to be larger for these stimuli than for other objects (Maurer, Le Grand, & Mondloch, 2002).

Our study can be partitioned into five parts. The first part was aimed at providing initial evidence for an effect of inversion on the detection of conspecifics during interocular suppression, both for photographs of headless human bodies and faces (Experiment 1) and for person silhouettes (Experiment 2). In the second part, we asked whether the body inversion effect (BIE) during CFS extends to highly variable, less prototypical person silhouettes that cannot be easily anticipated from trial to trial (Experiment 3). Third, we tested whether inversion effects would be restricted to human bodies and faces or whether a similar inversion effect would exist for animal bodies and faces (Experiments 4 and 5). Fourth, we attempted to shed some light on the features that are key for eliciting a BIE by measuring inversion effects for scrambled body silhouettes (Experiment 6). Finally, we ran control experiments testing whether the effect of inversion on the detection of conspecifics was specific to CFS (Jiang et al., 2007; Zhou, Zhang, et al., 2010), or whether a comparable effect of inversion would be present without interocular suppression (Experiment 7).

To foreshadow the results, we found that (a) both body and face inversion severely interferes with access to awareness, (b) the inversion effects for headless bodies and person silhouettes are of similar size as the inversion effect for isolated faces, (c) both the body and the face inversion effect are larger than inversion effects for a wide range of other object categories, and (d) body and face inversion effects are significantly larger during CFS than during a binocular control condition. Taken together, these

findings provide the first evidence that upright depictions of conspecifics have privileged access to conscious awareness.

2. General method

2.1. Sample characteristics

All participants were paid volunteers, most of them undergraduate or graduate students, with normal or corrected-to-normal vision, who were naïve as to the purpose of the study.

2.2. Apparatus and stimuli

Visual displays were presented on a 19-in CRT monitor (1024 × 768 pixels resolution, 60 Hz refresh rate) with a black background. As the precise luminance was not critical to our research question (i.e. the comparison of identical stimuli in upright and inverted orientations), we did not linearize the monitor output. Therefore, all luminance and contrast values refer to the monitor's input values and are referred to in terms of "percentage black", i.e. "50% black" refers to a gray value of 128. Observers viewed the screen dichoptically through a custom-built mirror stereoscope, with the participants' heads stabilized by a chin-and-head rest at a viewing distance of 50 cm. The mirrors were adjusted for each observer to promote stable binocular fusion and correct binocular fusion was verified before each experimental block. Visual stimuli were presented with MATLAB (The MathWorks, Natick, MA) using the Cogent 2000 toolbox functions (www.vislab.ucl.ac.uk/cogent.php).

Throughout each experiment, two red fusion frames (Experiment 5: $10.0^\circ \times 10.0^\circ$ of visual angle; all other experiments: $12.0^\circ \times 12.0^\circ$) were displayed side by side on the screen such that one frame was shown to each eye (distance between the centers of both frames 21.2°). To further support stable binocular fusion, textured fusion contours (width 0.8°) consisting of randomly arranged

black and white pixels were drawn within the red frames. In all experiments apart from Experiment 5 in which the background was dark, stimuli were presented against a white background within these contours (see Fig. 1). In the center of each frame a red fixation dot (diameter 0.7°) was displayed. Participants were asked to maintain stable fixation during each experimental block.

Test stimuli differed between experiments and are described in the respective methods section of each separate experiment. For each experiment, we created inverted versions of all test stimuli by flipping the images vertically. To induce interocular suppression, we generated high-contrast CFS masks (Experiment 5: $8.4^\circ \times 8.4^\circ$; all other experiments: $10.4^\circ \times 10.4^\circ$) consisting of randomly arranged grayscale circles (diameter 0.4–1.8°; see Fig. 1).

2.3. Procedure

Each trial started with a 1-s fixation period. Subsequently, CFS masks updated every 100 ms were presented to one randomly selected eye. Concurrently, a test stimulus was introduced to the other eye. To avoid abrupt transients, test stimuli were gradually faded in over the first second of each trial and then remained constant until the end of the trial. Depending on the nature of the test stimuli (e.g., photographs or silhouettes) we used different methods for fading in which are described separately for each experiment. In all experiments apart from Experiment 5 in which we used a slightly different procedure which is described in the respective methods section, test stimuli were presented until response or for a maximum of 10 s either to the left or to the right of the fixation dot, at jittered vertical positions. The range of possible vertical and horizontal test stimulus positions differed between experiments, due to differences in stimulus size. Participants were simply required to indicate on which side of the fixation dot the test stimulus emerged from perceptual suppression by pressing the left or the right arrow key on the keyboard. They were instructed to respond as soon as any part of the test stimulus became visible and to respond

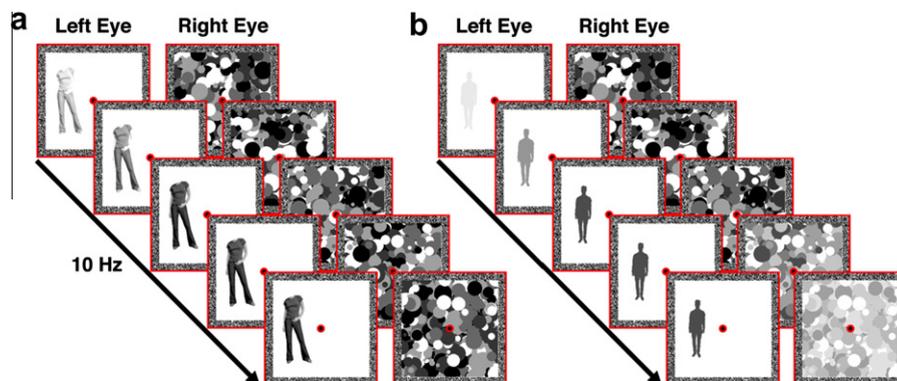


Fig. 1. Schematics of example trials from Experiment 1 (a) and Experiment 2 (b). To induce interocular suppression, high contrast CFS masks flashing at 10 Hz were presented to one eye, while a test stimulus was gradually introduced to the other eye. Participants were asked to indicate on which side of fixation the test stimulus or any part of the test stimulus became visible. (a) In Experiment 1, CFS masks were displayed at full contrast until the end of the trial. (b) In Experiments 2–7, the contrast of the CFS masks was slowly ramped down over the course of each trial to reduce the number of trials in which the test stimulus did not overcome interocular suppression.

as fast and as accurately as possible. Throughout all experiments, stimulus category and stimulus orientation (upright, inverted) were manipulated within subjects.

2.4. Analysis

We excluded trials with incorrect responses from the computation of mean suppression durations. In all experiments and for all stimulus categories, errors occurred in less than 3% of all trials, respectively. Trials in which the test stimulus was not consciously perceived, i.e. trials without a response, were assigned a suppression duration of 10 s (i.e. the maximum length of a trial) to estimate the lower bound of suppression duration in these trials (Stein, Senju, et al., 2011). There were less than 1% of such miss trials, except for Experiment 1 in which misses were more frequent (due to differences in the strength of the CFS masks, see below).

3. A body inversion effect during CFS (Experiments 1 and 2)

In the first part of the present study, we tested for an effect of body inversion on the duration of perceptual suppression and compared the effect of inversion between bodies, faces and other familiar object categories. In Experiment 1, we presented upright and inverted photographs of bodies (without heads), faces, and chairs. In this first experiment, we used headless bodies to test whether inversion had an effect even in the complete absence of head-and face-related visual information. We included chairs as another highly familiar object category that is typically encountered in upright orientation. In Experiment 2, we replaced photographs by silhouettes of bodies to remove all texture information. Having tested for an inversion effect for headless bodies in Experiment 1, from Experiment 2 on we used bodies with heads (with facial information erased) to increase the stimuli's ecological validity. To control for the effects of symmetry (e.g., Sasaki, Vanduffel, Knutsen, Tyler, & Tootell, 2005), in Experiment 2 table lamps were used as control category. Like bodies, table lamps are typically encountered in upright orientation, are symmetrical along the vertical axis, and are easily recognized when presented as silhouettes. We also included

face photographs in Experiment 2. If inversion affected suppression durations for all kinds of familiar object categories that are usually seen in upright orientation, we would expect similar effects of inversion for all categories. Alternatively, inversion effects during CFS may be restricted to faces (Zhou, Zhang, et al., 2010). Finally, the detection of both faces and bodies may be disproportionately affected by inversion relative to other object categories, suggesting that perceptual mechanisms tuned to the detection of conspecifics may exist.

3.1. Experiment 1: Body photographs

3.1.1. Method

3.1.1.1. Participants. Thirteen individuals (11 female, age range 19–28 years) participated in Experiment 1.

3.1.1.2. Stimuli. Test stimuli were grayscale photographs of faces, bodies (with heads removed), and chairs (see Fig. 2a). We selected 20 pictures for each category. Photographs of emotionally neutral faces ($3.7^\circ \times 4.5\text{--}5.2^\circ$) were taken from the Nimstim stimulus set (Tottenham et al., 2009). Pictures of bodies ($2.3\text{--}4.3^\circ \times 6.9^\circ$) and chairs ($2.2\text{--}4.3^\circ \times 4.4^\circ$) were similar to those previously used to localize body-selective visual areas (e.g., Downing, Wiggett, & Peelen, 2007).

3.1.1.3. Procedure. Gradual fading in of the test stimuli was achieved by linearly decreasing the test stimulus luminance from white to the respective original luminance within a period of 1 s from the beginning of each trial (see Fig. 1a). Test stimuli were presented to the left or to the right of the fixation dot (horizontal center-to-center distance 2.7°) at a random vertical position relative to the fixation dot (maximum vertical center-to-center distance 1.1°).

Face, body and chair stimuli were presented in separate blocks consisting of 80 trials each. Within a block each combination of two test stimulus orientations (upright, inverted), two eyes for test stimulus presentation and 20 test stimulus identities occurred once and the trial order was randomized. Prior to each block observers were informed about the upcoming test stimulus category and about the

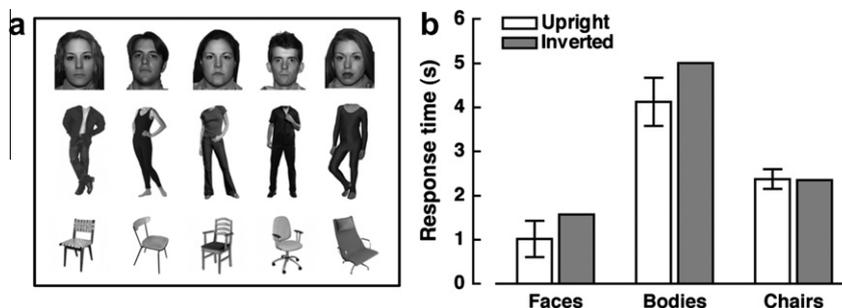


Fig. 2. (a) Example stimuli and (b) results from Experiment 1. (b) Bar plots show mean response times for faces, bodies, and chairs emerging from interocular suppression, separately for upright and inverted stimulus orientations. In this and all further plots depicting raw response times, positive and negative error bars denote 95% confidence intervals for the mean difference between upright and inverted test stimuli within each stimulus category, respectively.

occurrence of both upright and inverted stimulus versions. Block order was randomized across participants.

3.1.1.4. Analysis. Trials in which the test stimulus was not consciously perceived, i.e. trials without a response, were more frequent in Experiment 1 (faces: 2.4%, bodies: 20.2%, chairs: 4.7%) than in subsequent experiments. This was due to the fact that CFS masks were presented at full contrast throughout each trial, whereas in the other experiments the contrast of the CFS masks was gradually reduced over the course of each trial (compare the CFS masks in Fig. 1a and b; further details are given in Section 3.2.1).

3.1.2. Results and discussion

As can be seen from Fig. 2b, there were large overall differences in suppression duration between categories, resulting from differences between categories in low-level physical stimulus properties (e.g., Blake, 1977; Fox & Rasche, 1969; Levelt, 1965). Bodies yielded the longest overall suppression durations and the largest proportion of miss trials in which stimuli did not overcome CFS at all, indicating that in Experiment 1 the body photographs had lower “stimulus strength” (Levelt, 1965) than the face and chair photographs. As explained in the Introduction, these overall differences in suppression durations cannot be taken as a measure of category-preferences in visual detection. Of interest here are the effects of test stimulus orientation on suppression durations *within* each category. A two-way repeated measures ANOVA on mean suppression duration, with the factors category (bodies, faces, chairs) and orientation (upright, inverted), revealed a significant main effect of category, $F(2,24) = 31.44$, $p < .001$, and a significant main effect of orientation, $F(1,12) = 24.36$, $p < .001$. Crucially, these main effects were qualified by a significant interaction between category and orientation, $F(2,24) = 5.11$, $p = .014$, meaning that inversion prolonged suppression durations for bodies, $t(12) = 3.52$, $p = .004$, and faces, $t(12) = 2.94$, $p = .012$, but not for chairs, $t < 1$ (see Fig. 2b). Furthermore, inversion had a stronger effect on suppression durations for bodies and faces than for chairs, $F(1,12) = 10.61$, $p = .007$, and $F(1,12) = 6.13$, $p = .029$, respectively, but the effect of inversion did not significantly differ between bodies and faces, $F < 1$.

These results provide the first evidence for an effect of body inversion on the duration of perceptual suppression. Interestingly, the effect of inversion on face and body detection was of similar size, although the large differences in overall suppression durations between categories preclude firm conclusions at this point. Importantly, both the FIE and the BIE were larger than the inversion effect for a familiar control category, thus fulfilling an important criterion for inferring category-specific detection mechanisms (Maurer et al., 2002). For chairs, suppression durations were virtually unaltered by inversion, suggesting that large inversion effects on access to awareness may be relatively specific to faces and bodies. It should be noted, however, that chairs may not constitute an optimal category. For example, pictures of chairs tended to be more variable and less symmetrical than pictures of faces and

bodies (see Fig. 2a). Subsequent experiments were designed to address these concerns.

We obtained a BIE on simple stimulus *detection* using bodies with heads removed. By contrast, recent studies investigating the effect of body inversion on posture *discrimination* using sequential matching tasks have revealed a crucial role for head information in mediating the effect of inversion on body discrimination. For headless bodies, the advantage in discriminating between upright compared to inverted body postures was either reduced (Yovel, Pelc, & Lubetzky, 2010), fully abolished (Brandman & Yovel, 2010) or even reversed (Minnebusch, Suchan, & Daum, 2009). The discrepant results regarding the role of the head illustrate that body discrimination tasks and the present measure of interocular suppression tap into different processes. Fine discrimination and sequential matching may be strongly affected by top-down attentional allocation to the most diagnostic information, which includes the head (see Minnebusch et al., 2009). By contrast, the present findings show that perceptual mechanisms governing simple stimulus detection during interocular suppression are tuned to upright body postures, irrespective of head presence.

3.2. Experiment 2: Body silhouettes

In Experiment 2, we sought to replicate the effect of body inversion on the duration of perceptual suppression using a new set of stimuli. We selected table lamps as a new control category, as these are usually seen upright, are fairly symmetrical and have a clear vertical organization with an aspect ratio similar to bodies. In addition, we controlled for potential differences in within-category physical variability and sought to approximate overall suppression durations between categories.

3.2.1. Method

3.2.1.1. Participants. A new group of 12 individuals (nine female, age range 20–50 years) participated in Experiment 2.

3.2.1.2. Stimuli. Body silhouettes ($1.5\text{--}2.7^\circ \times 5.9^\circ$) were generated on the basis of eight emotionally neutral body photographs previously used by Atkinson, Heberlein, and Adolphs (2007). Table lamps ($1.8\text{--}3.4^\circ \times 4.8^\circ$) were selected from the image collection software Photo-Object 2.07 (Hemera Technologies Inc., www.hemera.com). To obtain comparable overall suppression durations for body and lamp silhouettes, they were assigned different luminance values (bodies: 60% black, lamps: 80% black), resulting in different effective contrasts relative to the white background against which the test stimuli were presented. These luminance values had been determined during initial pilot testing. In addition, we also included eight emotionally neutral grayscale face photographs ($2.7\text{--}3.1^\circ \times 3.7\text{--}4.0^\circ$), again taken from the Nimstim set. In order to induce suppression durations comparable to the other categories, we first blurred these face stimuli using a Gaussian filter to remove very high spatial frequencies and subsequently assigned them a lower global contrast

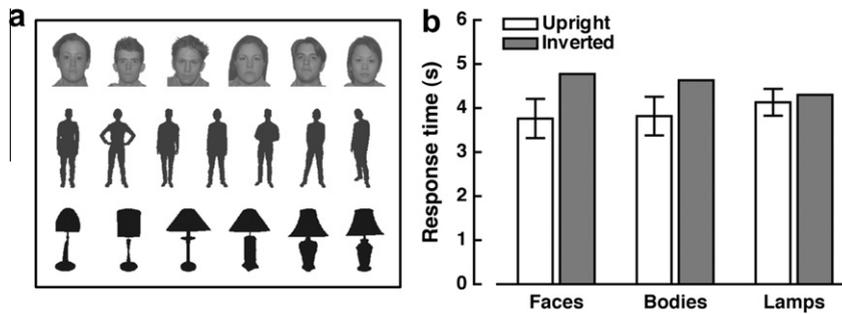


Fig. 3. (a) Example stimuli and (b) results from Experiment 2.

than in Experiment 1 (compare the face photographs depicted in Figs. 2a and 3a).

We carefully ensured that the stimulus categories did not differ in within-category physical variance and calculated interstimulus pixel-wise correlations within each test stimulus category (e.g., Thierry, Martin, Downing, & Pegna, 2007). Correlation coefficients were converted using Fisher's Z-transformation before averaging and then transformed back. Mean pixel-wise correlations were $r = .63$ for bodies, $r = .69$ for lamps, and $r = .69$ for faces. Please note that these correlation coefficients represent a measure of physical similarity only and do not necessarily correlate with perceptual similarity.

3.2.1.3. Procedure. Test stimuli were centered at a random horizontal position between 2.5° and 3.3° to the left or to the right of the fixation dot, and at a random vertical position relative to the fixation dot (maximum vertical center-to-center distance 0.8°). Body and lamp silhouettes were faded in as in Experiment 1, i.e. their luminance was reduced from full white to the respective original luminance over a period of 1 s. To prevent very short suppression durations for faces, we now gradually blended them in using a combined luminance/contrast ramp in which the faces' contrast was ramped up linearly from 0% to 100% within the first second of each trial, while the faces' luminance was reduced linearly from full white to the original luminance within the same period. Starting 1.1 s after trial onset, the contrast of the CFS masks was decreased linearly to 0% (i.e. full white as the background) over a period of 7.0 s. This contrast ramp was implemented to reduce the number of trials in which the test stimulus was not perceived at all (Tsuchiya, Moradi, Felsen, Yamazaki, & Adolphs, 2009; Yang et al., 2007) and was used in all subsequent experiments.

Observers completed three blocks containing 96 trials each. Within a block each combination of three test stimulus categories, two test stimulus orientations, two eyes for test stimulus presentation and eight stimulus identities occurred once and the trial order was randomized. Thus, in contrast to Experiment 1, trials from all categories were intermixed within blocks. Before the experiment started, participants were informed about the upcoming test stimulus categories and about the occurrence of both upright and inverted stimulus versions.

3.2.2. Results and discussion

There were no differences in overall suppression durations between categories, as shown in Fig. 3b. Correspondingly, a two-way repeated measures ANOVA with the factors category (bodies, faces, lamps) and orientation yielded no significant main effect of category, $F(2,22) < 1$, but a significant main effect of orientation, $F(1,11) = 33.90$, $p < .001$, and a significant category-by-orientation interaction, $F(2,22) = 6.41$, $p = .006$. As in Experiment 1, inversion prolonged suppression durations for bodies, $t(11) = 4.08$, $p = .002$, and faces, $t(11) = 5.01$, $p < .001$, but not for lamps, $t(11) = 1.22$, $p = .250$, and the effect of inversion was significantly larger for bodies and faces than for lamps, $F(1,11) = 11.68$, $p = .006$, and $F(1,11) = 9.22$, $p = .011$. Finally, there was again no significant difference between the effects of inversion on bodies and faces, $F < 1$.

These findings support and extend the results from Experiment 1 in multiple ways. First, the disproportionately large effect of inversion on bodies and faces appears not to be caused by differences regarding within-category physical variance. Second, vertical symmetry and aspect ratio could not explain the strong inversion effects observed for bodies and faces, as table lamps shared these properties. Third, the existence of a strong inversion effect for body silhouettes demonstrates that the detection advantage of upright bodies can be induced by the mere outline of a human body and does not depend on detailed texture information from the skin or from the clothes. Fourth, the fact that the size of the FIE did not exceed the size of the BIE when controlling for overall suppression duration suggests that the perceptual mechanisms mediating body detection are similarly sensitive to inversion as those underlying face detection (Jiang et al., 2007; Stein, Peelen, et al., 2011; Yang et al., 2007; Zhou, Zhang, et al., 2010).

4. A body inversion effect for highly variable postures (Experiment 3)

Having established the existence of a detection advantage for upright bodies and faces during CFS in the first part of the study, we next asked whether the BIE would persist when using a large set of diverse body postures depicting various, mostly asymmetrical, poses. Bodies, unlike faces and most other object categories, dramatically change

shape when shown in different poses. This provides a great challenge for perceptual systems that detect these stimuli, raising the possibility that the body detection effects observed so far are limited to canonical views of bodies. Yet, for a body detection mechanism to be useful, it would need to generalize across the different poses we encounter in daily life. In Experiment 3, we tested this prediction using variable body silhouettes, comparing the size of the BIE to the effect of inversion on house plants as another highly familiar control category.

4.1. Experiment 3: Variable body silhouettes

4.1.1. Method

4.1.1.1. Participants. These were the same 12 participants who had taken part in Experiment 2 before.

4.1.1.2. Stimuli. We selected 40 body silhouettes ($1.7\text{--}4.0^\circ \times 4.5\text{--}5.3^\circ$) and 40 silhouettes of house plants ($1.7\text{--}4.0^\circ \times 5.3^\circ$) from various sources. To increase within-category physical variability body silhouettes depicted various poses, for example standing, dancing, exercising, sitting and jumping individuals, seen from different viewing angles (see Fig. 4a). Mean pixel-wise correlations within each category were $r = .48$ for bodies and $r = .45$ for plants.

4.1.1.3. Procedure. Test stimuli could appear at a random position centered between 2.8° and 3.0° to the left or to the right of the fixation dot and between 0° and 0.8° above or below the fixation dot. Silhouettes were faded in by reducing the luminance from 100% to 50% white over the first second of a trial.

Experiment 3 consisted of 160 trials (separated by a break after 80 trials) in which each test stimulus was presented twice, once upright and once inverted. The eye to which the test stimulus was presented was randomized, with the constraint that both the upright and inverted versions of a given test stimulus were displayed to the same eye. This was done because observers with pronounced eye dominance exhibit large baseline differences in suppression durations depending on the eye to which the test stimulus is presented (e.g., Yang, Blake, & McDonald, 2010). Finally, trial order was randomized. In Experiment 3 and in all subsequent experiments, participants were both informed about the to-be-presented stimulus category

and they were shown printouts depicting thumbnails of all test stimuli, both upright and inverted versions, prior to the experimental session.

4.1.2. Results and discussion

Inspection of Fig. 4b reveals that variable body silhouettes induced a body inversion effect, while there was no effect of inversion on detecting house plants. Accordingly, a two-way repeated measures ANOVA with the factors category (bodies, plants) and orientation yielded a significant category-by-orientation interaction, $F(1,11) = 6.48$, $p = .027$. There was also a significant main effect of orientation, $F(1,11) = 13.03$, $p = .004$, while the main effect of category was not significant, $F(1,11) = 1.91$, $p = .194$. Inversion prolonged suppression durations for bodies, $t(11) = 4.12$, $p = .002$, but not for plants, $t < 1$.

These results again show that the mere shape of a body suffices to induce a BIE that is substantially larger than the effect of inversion on silhouettes from a familiar control category. Moreover, Experiment 3 demonstrates that even highly variable and asymmetrical upright body silhouettes take precedence over inverted body silhouettes in accessing awareness. The robustness of the BIE to posture variation suggests that the perceptual mechanisms underlying the advantage of upright bodies are tuned to a wide range of upright bodies and not limited to prototypical postures or canonical views.

5. Effect of animacy (Experiments 4 and 5)

So far, our findings could be interpreted as demonstrating that the detection of animate objects (bodies, faces) is more strongly affected by inversion than the detection of inanimate objects (chairs, lamps, house plants), possibly reflecting detection mechanisms specialized for animate objects in their common upright position (New, Cosmides, & Tooby, 2007; Tipples, Young, Quinlan, Broks, & Ellis, 2002). Indeed, at the level of conceptual knowledge about objects, distinct domain-specific subsystems have been proposed for animate and inanimate object categories (Caramazza & Shelton, 1998) and spatial patterns of neural responses in object-sensitive inferior temporal cortex show a sharp division between animate and inanimate objects (Kriegeskorte et al., 2008). While most previous studies investigating the effect of inversion on face detection and body posture discrimination included only inanimate

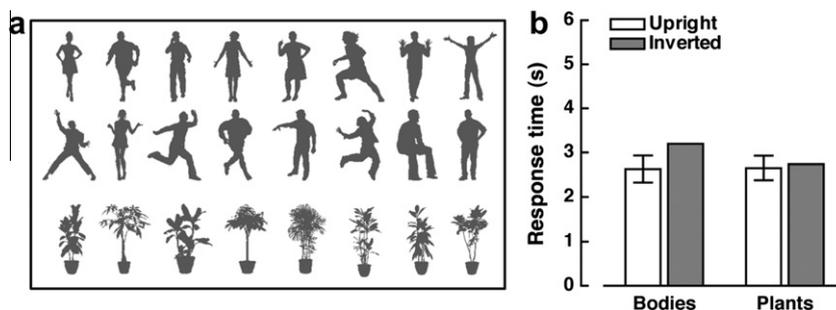


Fig. 4. (a) Example stimuli and (b) results from Experiment 3.

control categories such as houses (e.g., Reed, Stone, Bozova, & Tanaka, 2003; Reed, Stone, Grubb, & McGoldrick, 2006; Zhou, Zhang, et al., 2010), evidence from recognition tasks hints at the existence of inversion effects for certain species of animals. Inversion has been found to impair recognition performance for dogs, and to a lesser degree for birds (Diamond & Carey, 1986; Gauthier, Skudlarski, Gore, & Anderson, 2000; Minnebusch et al., 2009; Robbins & McKone, 2007), although these effects were smaller than for faces, even in dog and bird experts (except for Diamond & Carey, 1986). Furthermore, humans are worse in recognizing inverted as compared to upright chimpanzee faces, while recognition of other animal faces is unimpaired by inversion (Taubert, 2009). In Experiment 4, we compared the effect of inversion on suppression durations for variable body silhouettes to silhouettes of dogs and birds. We also included silhouettes of trees as an additional inanimate control category. In Experiment 5, we compared inversion effects for human and chimpanzee faces.

5.1. Experiment 4: Human vs. animal bodies

5.1.1. Method

5.1.1.1. Participants. A new set of 10 individuals (six female, age range 19–42 years) participated in Experiment 4.

5.1.1.2. Stimuli. We used the same 40 variable body silhouettes as in Experiment 3 ($1.7\text{--}4.0^\circ \times 4.5\text{--}5.3^\circ$). In addition, we included 40 silhouettes of dogs ($2.7\text{--}4.4^\circ \times 2.9\text{--}3.5^\circ$), birds ($2.3\text{--}4.3^\circ \times 2.3\text{--}3.7^\circ$), and trees ($2.3\text{--}4.0^\circ \times 3.9\text{--}5.3^\circ$) as an additional control category, respectively (see Fig. 5a). All silhouettes were assigned the same luminance value (70% black). Mean pixel-wise correlations were matched for all four test stimulus categories (bodies $r = .48$, dogs, birds and trees $r = .49$, respectively).

5.1.1.3. Procedure. Test stimuli were displayed at the same positions as in Experiment 3. Gradual fading-in of the test stimuli was achieved by implementing the same luminance ramp as in Experiment 3. Participants completed 320 trials, interrupted by a break every 80 trials. Each test stimulus was presented twice, once upright, once inverted. Randomization adhered to the same rules as described for Experiment 3.

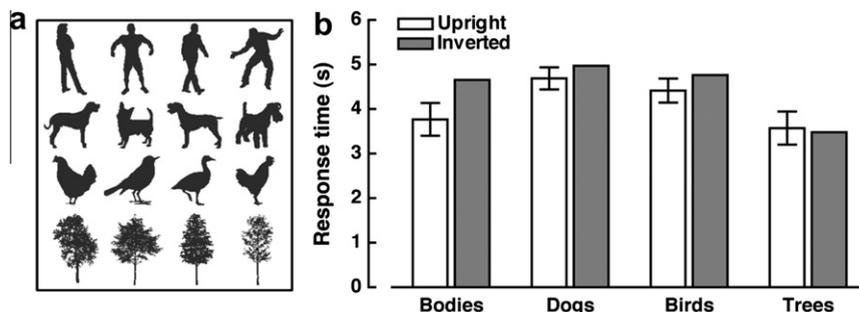


Fig. 5. (a) Example stimuli and (b) results from Experiment 4.

5.1.2. Results and discussion

Fig. 5b indicates that there were significant effects of inversion on suppression durations for dogs and birds, but these appeared to be smaller than the BIE. A two-way repeated measures ANOVA with the factors category (bodies, dogs, birds, trees) and orientation revealed significant main effects of category, $F(3,27) = 28.90$, $p < .001$, and orientation, $F(1,9) = 11.34$, $p = .008$, and a significant category-by-orientation interaction, $F(3,27) = 14.06$, $p < .001$. Inversion induced longer suppression durations for bodies, $t(9) = 5.47$, $p < .001$, dogs, $t(9) = 2.56$, $p = .031$, and birds, $t(9) = 2.92$, $p = .017$, but not for trees, $t < 1$. Crucially, reduced ANOVAs demonstrated that the effect of inversion was larger for bodies than for all other categories, smallest $F(1,9) = 9.62$, all $p < .05$.

These results show that inversion can also interfere with the detection of animal bodies. Still, the BIE for variable body silhouettes again exceeded the effects of inversion on detection for all other animate object categories. Thus, a general detection advantage of upright animal bodies cannot fully account for the advantage of upright human bodies in overcoming suppression. Rather, these results demonstrate that the mechanisms underlying the detection of human bodies exhibit an increased sensitivity to inversion, suggesting that these mechanisms are preferentially tuned to the shape of upright human bodies.

5.2. Experiment 5: Human vs. chimpanzee faces

5.2.1. Method

5.2.1.1. Participants. There were 10 new participants (all female, age range 20–35 years).

5.2.1.2. Stimuli. We selected 10 frontal face views of chimpanzees from the internet and 10 emotionally neutral frontal face views of humans from the Ekman and Friesen (1976) face set. All faces were cropped to remove external facial features and resized to fit a rectangle ($3.2^\circ \times 3.9^\circ$). The facial outlines were smoothed into the background by applying a circular averaging filter to the outer edges (see Fig. 6a). All faces had the same contrast and were assigned the same mean luminance as the background against which they were presented (75% black). We chose this low luminance level in order to preserve the brightness of the original chimpanzee faces that were considerably darker than the original human faces.

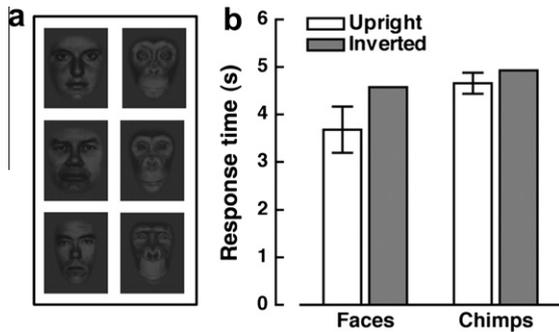


Fig. 6. (a) Example stimuli and (b) results from Experiment 5.

5.2.1.3. Procedure. Test stimuli were displayed in the four quadrants (centered at eccentricities of 2.8°). The contrast of the test stimuli was ramped up from 0% to 100% over the first second of each trial and the contrast of the CFS masks was linearly decreased to 25% black over a period of 7.0 s starting 1.1 s after trial onset. In Experiment 5, participants used four keys (“F”, “V”, “J”, “N”) on a QWERTY keyboard to indicate as fast and accurately as possible in which quadrant the test stimulus or any part of the test stimulus appeared (Sterzer, Hilgenfeldt, Freudenberg, Bermppohl, & Adli, 2011; Yang et al., 2007). There were 160 trials, separated by a break after 80 trials. Each combination of category (human face, chimpanzee face), orientation, eye to which the test stimulus was presented and face exemplar was presented equally often and trial order was randomized. The location of the test stimulus was selected at random for each trial.

5.2.2. Results and discussion

A two-way repeated measures ANOVA with the factors category (human face, chimpanzee face) and orientation yielded significant main effects of orientation, $F(1,9) = 16.57$, $p = .003$, and category, $F(1,9) = 27.79$, $p = .001$, with overall shorter suppression durations for human faces. Most importantly, there was a significant category-by-orientation interaction, $F(1,9) = 12.85$, $p = .006$. While post hoc comparisons revealed a significant effect of orientation not only for human faces, $t(9) = 4.15$, $p = .002$, but also for chimpanzee faces, $t(9) = 2.74$, $p = .023$, from Fig. 6b it is evident that the inversion effect was considerably larger for human faces.

Thus, the perceptual mechanisms mediating face detection appear to be optimally tuned to upright human faces and to respond less to faces of other animals. Interestingly, the specificity of the FIE to human faces dovetails with a recent study demonstrating that newborns preferentially look at human faces when paired with faces of non-human primates (Heron-Delaney, Wirth, & Pascalis, 2011). This may point to a resemblance between the mechanisms governing access to awareness under CFS and inborn attention biases (Stein, Peelen, et al., 2011). In sum, the FIE during CFS is largely specific to faces of conspecifics, just as the mechanisms involved in body detection are tuned to upright bodies of human conspecifics.

6. Visual information critical for the body inversion effect during CFS (Experiment 6)

What key information contained in upright bodies may be read out by the perceptual mechanisms involved in body detection? To shed some light on this question, we adopted the strategy used by Reed et al. (2006) to characterize the kind of configural information that governs the BIE on recognition performance. When the positions of the body parts were “shuffled”, i.e. randomly rearranged, Reed et al. found no effect of inversion on body discrimination and concluded that the spatial positions of the body parts relative to the trunk, i.e., the first-order spatial relations, were critical for eliciting a BIE. In Experiment 6, we asked whether the upright body advantage in accessing awareness would be similarly dependent on the relative spatial positions of the body parts or whether the upright orientation of the body parts and the trunk, regardless of their spatial relationship, would be sufficient to drive the detection mechanisms mediating the BIE during CFS.

6.1. Experiment 6: Shuffled body silhouettes

6.1.1. Method

6.1.1.1. Participants. A new group of 12 observers (nine female, age range 20–35 years) took part in Experiment 6.

6.1.1.2. Stimuli. We employed a subset of the variable body silhouettes used in Experiment 3. Each shuffled body stimulus was created by detaching the head, arms and legs from the trunk of an upright body silhouette and then reattaching these body parts to other positions of the trunk, leaving all parts fully visible in their original upright orientation (see Fig. 7a). This shuffling procedure was possible for 19 of the original body stimuli, resulting in 19 intact bodies ($1.8\text{--}4.0^\circ \times 4.5\text{--}5.3^\circ$) and their respective 19 shuffled counterparts ($1.7\text{--}4.0^\circ \times 3.7\text{--}6.0^\circ$). The luminance was the same for all stimuli (50% black).

6.1.1.3. Procedure. We presented test stimuli at the same positions as in Experiment 3, using the same luminance ramp and randomization procedure. The experiment contained 152 trials, divided by a break after 76 trials. Each

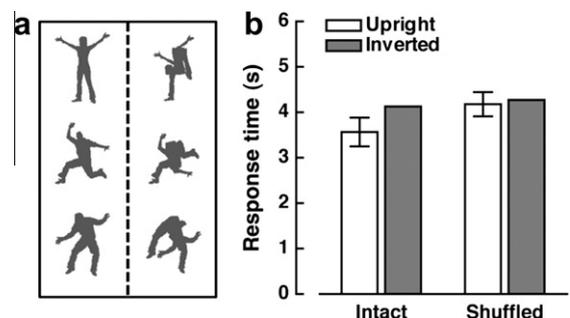


Fig. 7. (a) Example stimuli and (b) results from Experiment 6. ‘Intact’ refers to unmodified body silhouettes. ‘Shuffled’ refers to reassembled body silhouettes for which we detached the head, arms and legs from the trunk and subsequently reattached these body parts at other locations of the trunk, thereby disrupting the normal spatial relations between parts.

test stimulus was presented four times, twice upright, twice inverted.

6.1.2. Results and discussion

Fig. 7b shows that the BIE was restricted to intact body silhouettes. Accordingly, a two-way repeated measures ANOVA with the factors intactness (intact, shuffled) and orientation revealed a significant main effect of orientation, $F(1,11) = 9.38$, $p = .011$, and a significant intactness-by-orientation interaction, $F(1,11) = 8.11$, $p = .016$, while the main effect of intactness was not significant, $F(1,11) = 2.08$, $p = .177$. Inversion significantly prolonged suppression durations for intact bodies, $t(11) = 3.85$, $p = .003$, but not for shuffled bodies, $t < 1$. Thus, the upright orientation of individual body parts or the trunk does not suffice to elicit shorter suppression durations. Rather, these results suggest that the correct relative spatial positions of the body parts and the trunk are necessary to activate detection mechanisms mediating the BIE during CFS. One caveat to this interpretation is that rearranging the body parts did not only disrupt the first-order relations, but also reduced the stimuli's meaningfulness, which may have also reduced the impact of inversion.

7. Specificity to CFS (Experiment 7)

Finally, we probed whether the strong effects of inversion on body and face detection revealed during the previous experiments would be specific to detection during CFS, or whether similar effects would be present without interocular suppression under normal binocular viewing conditions. Previous studies using faces have interpreted an increased effect of inversion during CFS compared to a binocular control condition as evidence for non-conscious face processing under interocular suppression (Jiang et al., 2007; Zhou, Zhang, et al., 2010). A stronger non-conscious representation of upright faces could bias the competition between the conflicting input from both eyes in favor of the face representation and thus pave the way for earlier detection of upright faces. Because the FIE was greatly enhanced during CFS compared to a control condition not involving interocular suppression, Jiang et al. (2007) concluded that a non-conscious processing advantage of upright faces under CFS caused faster detection. Following this reasoning, in Experiment 7 we measured the effect of inversion on body detection both during CFS and during a perceptually similar binocular control condition.

7.1. Experiment 7

7.1.1. Method

7.1.1.1. Participants. A total of 28 new observers (22 female, age range 19–42 years) participated in Experiment 7. Ten subjects were assigned to Experiments 7a and 7c, respectively, and eight observers took part in Experiment 7b.

7.1.1.2. Stimuli and procedure. We presented the same 40 variable body silhouettes at the same spatial positions as in Experiment 4. In the CFS conditions, the stimuli were gradually faded in using the same luminance ramp as in

Experiment 4. In addition to the CFS condition, we now included a control condition that was designed to emulate the perceptual experience of the CFS condition, but did not involve interocular suppression. In this control condition, we presented the exact same stimuli at the same positions and participants performed the same task as in the CFS condition, but the test stimuli and the CFS masks were displayed to both eyes and the test stimuli were gradually blended into the masks using alpha blending (e.g., Jiang et al., 2007; Stein, Senju, et al., 2011; Zhou, Zhang, et al., 2010). In pilot testing, we determined the length of the transparency ramp needed to yield mean detection times that roughly approximated the mean suppression durations obtained in the CFS condition of Experiment 4. This yielded a transparency ramp that linearly reduced the body silhouettes' transparency from 100% to 0% within 19.2 s.

In Experiment 7a, for each subject 40 different ramp durations were randomly drawn from a normal distribution ($\mu = 19.2$ s, $\sigma = 3.6$ s) to decrease the predictability of test stimulus appearance. These 40 ramps were then randomly assigned to the 40 body silhouettes, with the constraint that both the upright and the inverted version of a given test stimulus were presented using the same ramp duration. For Experiment 7b, we used the same procedure to sample 40 ramp durations from an ex-Gaussian distribution, which typically provides an excellent fit to RT data from a wide range of experiments (e.g., Heathcote, Popiel, & Mewhort, 1991; Hockley, 1984; Ratcliff & Murdock, 1976). The parameters for this ex-Gaussian distribution ($\mu = 10.4$ s, $\sigma = 3.8$ s, $\tau = 6.6$ s) were chosen to more closely match mean detection times in the control and CFS conditions, on the basis of results in Experiment 7a and pilot testing. In Experiment 7c, we sought to match the variability of detection times in the control and CFS conditions (based on results of Experiment 7b), by randomly selecting 40 ramp durations from an ex-Gaussian distribution with a larger spread and a longer right tail ($\mu = 10.4$ s, $\sigma = 15.6$ s, $\tau = 26.0$ s). Ramp durations shorter than 2.5 s were set to 2.5 s to replace negative values and to avoid potential floor effects.

Experiments 7a–7c comprised 160 trials each, separated by a break after 80 trials. Trials from the CFS and the control condition were intermixed and occurred equally often. Each test stimulus exemplar was shown twice in both the CFS and in the control condition, once upright, once inverted. In the CFS condition upright and inverted versions of a particular test stimulus exemplar were presented to the same eye. Trial order was randomized.

7.1.2. Results and discussion

For Experiment 7a a repeated-measures ANOVA with the factors condition (CFS, control) and orientation yielded a significant main effect of condition, $F(1,9) = 14.82$, $p = .004$, reflecting faster responses in the CFS than in the control condition. There was also a significant main effect of orientation, $F(1,9) = 19.21$, $p = .002$, and, most importantly, a significant condition-by-orientation interaction, $F(1,9) = 11.00$, $p = .009$. Thus, body inversion significantly prolonged suppression durations during CFS, $t(9) = 4.45$,

$p = .002$, but did not significantly modulate detection times in the control condition, $t(9) = 1.75$, $p = .114$ (see Fig. 8a). Before drawing firm conclusions from these findings, we first sought to rule out the possibility that differences in overall RTs could have caused the specificity of the large BIE to the CFS condition.

In Experiment 7b, we successfully matched overall RTs, as indicated by a non-significant main effect of condition, $F < 1$ (see Fig. 8b). There was a significant main effect of orientation, $F(1,7) = 27.25$, $p = .001$, as well as a significant condition-by-orientation interaction $F(1,7) = 19.08$, $p = .003$, meaning that upright bodies overcame CFS significantly more quickly than inverted bodies, $t(7) = 4.77$, $p = .002$, whereas detection times in the control condition did not significantly differ between upright and inverted bodies, $t < 1$. Thus, differences in overall RTs cannot account for the specificity of large body inversion effects to CFS. However, further exploration of the data revealed that although mean RTs were matched, RT variability was increased during CFS, probably due to the stochastic dynamics of binocular rivalry (e.g., Blake & Logothetis, 2002). In the CFS condition, the mean SD of individual responses (excluding trials with no or erroneous responses) was larger than in the control condition (Experiment 7a, CFS: 2.22 s, Control: 0.74 s; Experiment 7b, CFS: 2.30 s, Control: 1.16 s).

In Experiment 7c, we reduced these differences in mean SDs (CFS: 2.46 s, Control: 2.12 s, not statistically different, $t(9) = 1.02$, $p = .334$). Still, the pattern of results was similar to the previous experiments. There was a significant main effect of condition, $F(1,9) = 7.08$, $p = .026$, reflecting slightly prolonged RTs in the control condition (see Fig. 8c) and a significant main effect of orientation, $F(1,9) = 30.57$, $p < .001$, as well as a significant interaction between the two factors, $F(1,9) = 37.93$, $p < .001$. Again, inversion strongly interfered with the detection of bodies during CFS, $t(9) = 6.16$, $p < .001$, while there was no significant effect in the control condition, $t(9) < 1$. Taken together, the results from Experiments 7b and 7c show that neither differences in overall RTs nor differences in RT variability can explain the increased impact of inversion on body detection during CFS.

Thus, the large BIE during CFS appears to be caused by processes that are largely specific to CFS. Following the conclusions drawn by previous studies (Jiang et al., 2007; Zhou, Zhang, et al., 2010; also see Costello, Jiang, Baartman, McGlennen, & He, 2009; Mudrik, Breska, Lamy, & Deouell,

2011; Stein & Sterzer, 2012; Stein, Senju, et al., 2011; Sterzer et al., 2011; Stewart et al., 2012; Tsuchiya et al., 2009; Yang & Yeh, 2011; Zhou, Jiang, He, & Chen, 2010), this suggests that preferential access to awareness for upright bodies may be mediated or amplified by non-conscious body processing under interocular suppression. Thus, perceptual mechanisms involved in detecting both faces and human bodies appear to be able to operate on stimuli outside of conscious awareness.

8. General discussion

In the present study, we asked whether visual cues of conspecifics would have privileged access to awareness, relative to other familiar object categories. We used CFS to render bodies, faces, and a variety of matched control categories invisible and measured the time upright and inverted stimuli needed to overcome such interocular suppression and break into awareness (Jiang et al., 2007). We assumed that detection mechanisms preferentially tuned to upright bodies and faces would manifest themselves in larger effects of inversion on suppression durations for these categories as compared to other familiar object categories. Across six experiments bodies accessed awareness considerably more quickly when presented in upright orientation, regardless of whether they were depicted as photographs or silhouettes. Furthermore, this body inversion effect (BIE) during CFS was not restricted to prototypical body postures, but persisted at full strength for highly variable and asymmetrical body postures seen from various viewpoints. Importantly, in all experiments the BIE was significantly larger than the effect of inversion on the detection of stimuli from a wide range of animate and inanimate control categories (see Fig. 9). In three separate experiments, the impact of inversion on emergence from suppression was similarly strong for human bodies and faces (Fig. 9). Finally, the BIE and the face inversion effect (FIE) were stronger for the CFS condition than for a perceptually similar binocular control condition, indicating that non-conscious visual processing of upright bodies and faces contributed to the effects observed under CFS (Jiang et al., 2007). These results suggest that detection mechanisms that mediate access to awareness are preferentially tuned to both human faces and bodies (see Fig. 10), i.e. to cues that signal the presence of conspecifics.

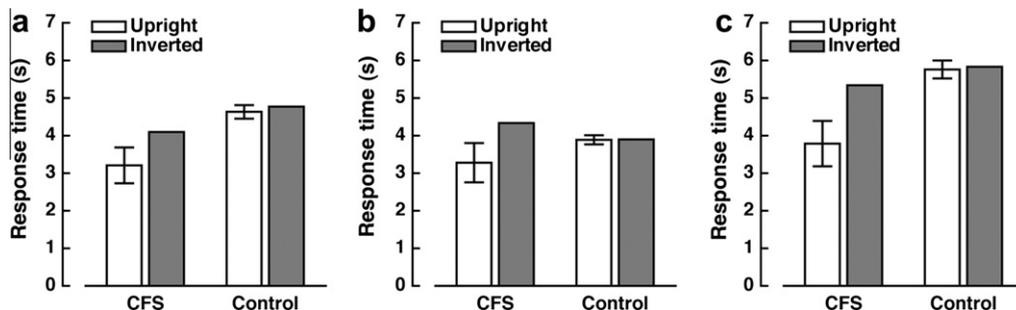


Fig. 8. Results from (a) Experiment 7a, (b) Experiment 7b, and (c) Experiment 7c.

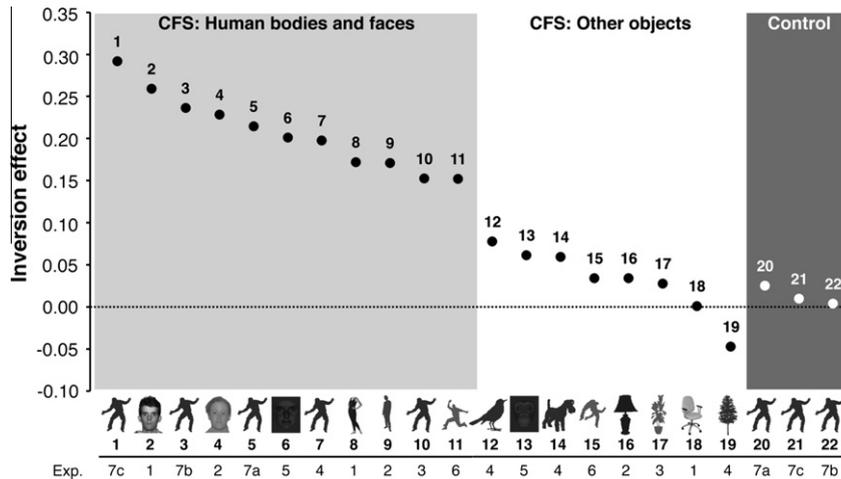


Fig. 9. Overview of the normalized effects of inversion for all stimulus categories from all experiments. For each subject and each category, normalized effects were obtained by dividing the difference between mean RTs for upright and inverted test stimuli by the mean RT for inverted stimuli (Tsuchiya et al., 2009). Points denote the respective inversion effect averaged across subjects. Thumbnails depict an example stimulus from each category. Numbers below the points refer to the numbers below the associated thumbnails. Please note that this overview is simply intended to serve illustrative purposes and that some values were obtained with the same subjects, while others were obtained using independent samples.

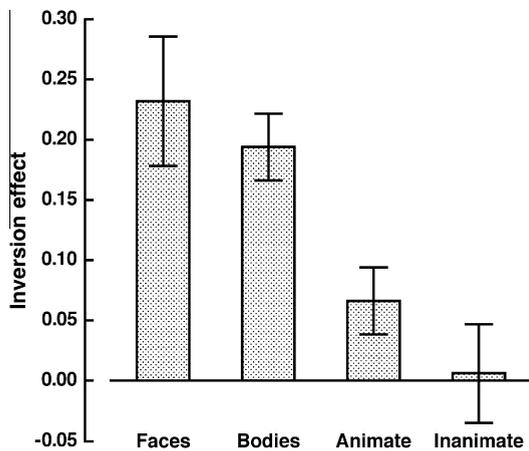


Fig. 10. Normalized inversion effects collapsed across multiple experiments, separately for suppression durations of bodies (Experiments 1–4, 6, and 7), human faces (Experiments 1, 2, and 5), and other animate (Experiments 4 and 5; including chimpanzee faces) and inanimate (Experiments 1, 2, and 3) objects. Error bars represent 95% confidence intervals. Please note that the figure is simply intended to serve illustrative purposes and that some participants who took part in more than one experiment contributed more than one data point.

8.1. Inversion effects on person detection vs. person discrimination

While the present study constitutes the first attempt to systematically explore the effect of inversion on person detection, a number of previous studies have examined the effect of inversion on body or face discrimination (Brandman & Yovel, 2010; McKone, Kanwisher, & Duchaine, 2007; Minnebusch et al., 2009; Reed et al., 2003, 2006; Robbins & McKone, 2007; Yin, 1969; Yovel et al., 2010). Evidently, discrimination tasks tap into perceptual and cognitive processes that are at least partially distinct from

those involved in simple detection (de Gelder, Frissen, Barton, & Hadjkhani, 2003; Duchaine & Nakayama, 2006; Johnson, 2005). To illustrate, a sequential posture discrimination task requires observers to encode the exact posture of the sample stimulus, to hold this information in visual short-term memory during a delay period, and to compare or match it to the exact posture of the ensuing comparison stimulus. Thus, in such tasks the BIE most likely reflects inversion-induced interference at multiple levels of the body processing hierarchy, ranging from reduced stimulus encoding to weakened visual short-term memory representations and differences in the deployment of attention (see Minnebusch et al., 2009). By contrast, the detection task used in the present experiments did not require participants to discriminate individual body postures (or even to categorize stimuli as bodies), but simply to detect and localize the presence of a stimulus. The present results show that remarkably strong and specific inversion effects can be observed for such simple detection tasks.

The effect of body inversion on simple stimulus detection appears to differ in two important ways from the effect of inversion on body discrimination. First, while the effect of inversion on discrimination performance is strongly dependent on head presence (Brandman & Yovel, 2010; Minnebusch et al., 2009; Yovel et al., 2010), in the present study the BIE during CFS was of virtually equal strength for headless body photographs and for body silhouettes with head contours only. Thus, while body discrimination crucially relies on information about the position of the head relative to the body, possibly because the head is the most diagnostic body part for discriminating the body postures used in previous experiments (Minnebusch et al., 2009), the mechanisms underlying body detection are tuned to upright bodies independently of head presence. Second, whereas the discrimination of individual faces is typically more strongly affected by inversion than body posture discrimination (Minnebusch

& Daum, 2009), across three of the present experiments the effect of inversion was of virtually equal strength for bodies and faces (see Figs. 9 and 10). We can only speculate about potential reasons for these differences. For example, to discriminate other individuals, humans may rely mainly on facial information when this information is available, as suggested by the strong effect of head presence on the BIE in discrimination tasks (Brandman & Yovel, 2010; Minnebusch et al., 2009; Yovel et al., 2010). We have become experts in utilizing configural information from upright faces (Diamond & Carey, 1986), which may be supported by perceptual mechanisms dedicated to face recognition (Farah, Wilson, Drain, & Tanaka, 1998; McKone et al., 2007). Thus, one possibility is that the larger effect of inversion on the discrimination of faces reflects our greater expertise in face than body discrimination. By contrast, the simple detection of another person can rely on the detection of both faces and bodies (Bindemann, Scheepers, Ferguson, & Burton, 2010). In fact, depending on viewing distance and viewpoint, the body may be the most important visual cue for detecting the presence of another person. The similar size of the BIE and the FIE during CFS suggests that the mechanisms guiding simple detection are similarly tuned to both upright faces and human bodies.

8.2. *Category specificity of inversion effects during CFS*

Why does inversion have such disproportionately large effects on access to awareness for bodies and faces relative to other familiar object categories? In our experiments, successful detection of a target stimulus solely required the detection of an object feature that was not part of the background or the CFS masks. As the features contained in upright and inverted stimuli were identical, the inversion effects revealed by the present methodology must reflect the impact of the spatial arrangement of those features. This means that information about the structure of the stimulus was available to the visual system before conscious detection (Lewis & Ellis, 2003; Purcell & Stewart, 1988). The present findings imply that if the non-consciously extracted structure conforms to an upright human body or face, the stimulus is more likely to be detected. A functional mechanism for specialized face detection has been outlined by Lewis and Ellis (2003). While being agnostic about the role of visual awareness, their model assumes that visual input is matched to a deformable internal representation of a prototypical face. The better the fit between this face representation and the visual input, the faster the stimulus is detected. A poor fit between the (upright) face representation and inverted faces would then account for the FIE.

In a similar vein, an internal representation of a prototypical human body could provide a simple model accounting for the BIE. The findings from the present study impose a number of constraints on the characteristics of such a body representation. First, as we did not obtain an inversion effect for bodies with randomly rearranged body parts (Experiment 6), the body representation would have to contain information about the possible configuration of body parts relative to the trunk (i.e., first-order relational

information, cf. Reed et al., 2006). Second, similar to the internal face representation proposed by Lewis and Ellis (2003), the body representation would have to be sufficiently deformable to fit the highly variable postures employed in the present study (Experiments 3, 4, 6, and 7). Finally, the head appears not to be a critical part of this internal body representation (Experiment 1).

It could be argued that the inversion effects for faces and bodies we observed were due to top-down anticipation of upright depictions of these (but not other) categories. For example, faces have a highly consistent and predictable arrangement of features. Participants may thus have anticipated detecting upright face-like patterns, perhaps more so than other categories (Lewis & Ellis, 2003), leading to faster detection of upright faces. We think this explanation is unlikely to fully account for the present results, for several reasons. First, participants were instructed to respond as soon as they saw any part of an object irrespective of its category, and were not instructed to detect, search for, or even recognize a particular category. Second, while in Experiment 1 object categories were presented in separate blocks, in all subsequent experiments object categories were presented intermixed within the same block (upright and inverted versions were always intermixed and equiprobable). Previous research has shown that visual search for multiple targets simultaneously is less efficient than visual search for one target (e.g., Los, 1996; Menneer, Cave, & Donnelly, 2009). If our results reflect top-down search for, or anticipation of, upright faces or bodies, we would therefore expect stronger inversion effects when upright faces or bodies made up a larger proportion of trials within a block. We did not find this pattern of results, with similarly strong body inversion effects when bodies were presented in separate blocks (Experiment 1; BIE = 881.9 ms), in blocks of two categories (Experiments 3 and 6; mean BIE = 563.0 ms), three categories (Experiment 2; BIE = 814.2 ms), or even four categories (Experiment 4; BIE = 885.9 ms). Note that in Experiment 4 only 12.5% of trials showed an upright person silhouette, making it unlikely that participants were actively anticipating this stimulus. Third, we did not obtain comparable inversion effects in the binocular control condition, although in these blocks participants were presented exclusively with body silhouettes. Fourth, during CFS we observed strong inversion effects for highly variable body postures. These postures were not predictable from trial to trial, and were not consistent in shape. These characteristics would make it difficult to anticipate specific shapes, yet inversion effects were of similar size for highly variable person silhouettes (Experiments 3 and 4; mean BIE = 711.2 ms) and for silhouettes that did not vary much in posture (Experiment 2; BIE = 814.2 ms). Nonetheless, although we think it is unlikely that top-down anticipation can fully explain our results, it would be interesting to test the degree to which anticipation or expectation can influence suppression durations during CFS.

A question of great interest is whether face and body detection mechanisms are innate or experience-dependent. Because our experiments were not designed to distinguish between these accounts, at this stage we can only speculate. On the one hand, it appears likely that fre-

quent exposure to conspecifics and ample perceptual experience with bodies and faces contribute to the formation (or at least to the elaboration) of visual mechanisms tuned to upright bodies and faces. Another, not mutually exclusive, possibility is that the interplay between innate orienting biases and experience gives rise to perceptual mechanisms supporting the fast detection of upright bodies and faces. Directly relevant to this notion are findings from studies showing that neonates direct attention to visual stimuli that are diagnostic for conspecifics, such as faces and face-like patterns (Farroni et al., 2005; Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991; Valenza, Simion, Macchi Cassia, & Umiltà, 1996), direct gaze (Farroni, Csibra, Simion, & Johnson, 2002), and bodily movement (Bardi, Regolin, & Simion, 2011; Simion, Regolin, & Bulf, 2008). Interestingly, inverted faces or inverted body motion fail to elicit these inborn looking preferences (Farroni et al., 2005; Simion et al., 2008). For the developmental time course of static body detection, results vary depending on the exact stimuli and methodology used. While some studies suggest that infants do not recognize the normal human body configuration before nine (Heron & Slaughter, 2010; Zieber et al., 2010), 12 (Slaughter & Heron, 2004), or even 18 months of age (Slaughter, Heron, & Sim, 2002), there is also evidence for a much earlier onset (Gluga & Dehaene-Lambertz, 2005; Heron-Delaney et al., 2011). Still, it is unclear whether these reflex-like orienting systems in infancy then become suppressed by matured cortical circuits, or whether they continue to serve as detectors for conspecifics throughout life (Pascalis & Kelly, 2009; Stein, Peelen, et al., 2011; Tomalski, Csibra, & Johnson, 2009).

In most experiments of the present study, inversion effects were specific to bodies and faces and were not found for other familiar objects categories such as chairs, table lamps, house plants, or trees. However, two experiments provided evidence for slowed detection of inverted animate stimuli other than human bodies and faces; inversion effects reached statistical significance for chimpanzee faces and for silhouettes of birds and dogs (Experiments 4 and 5), although they were considerably smaller than those for human bodies and faces (see Fig. 9). Still, these inversion effects suggest that person detection mechanisms may generalize somewhat to other animal species. A more general animate detection advantage is in line with the idea of an animate monitoring bias (Tipples et al., 2002), perhaps reflecting ancestral priorities (New et al., 2007).

8.3. Putative neural mechanisms

What neural structures could underlie the person-specific inversion effects during CFS? One possibility is that the disproportionate inversion effects for faces and bodies observed here reflect processing in subcortical pathways. Neural responses to perceptually suppressed stimuli are diminished throughout the geniculostriate pathway (Haynes, Deichmann, & Rees, 2005; Polonsky, Blake, Braun, & Heeger, 2000; Tong & Engel, 2001; Wunderlich, Schneider, & Kastner, 2005) and virtually abolished in object-sensitive areas of the ventral visual pathway (Fang & He, 2005; Hesselmann & Malach, 2011; Pasley, Mayes, &

Schultz, 2004; Sheinberg & Logothetis, 1997; Tong, Nakayama, Vaughan, & Kanwisher, 1998; Williams, Morris, McGlone, Abbott, & Mattingley, 2004). In fact, many prominent models of the processing of socially or emotionally relevant stimuli suppose an important role of a subcortical pathway involving the superior colliculus, pulvinar and amygdala in rapidly conveying coarse information about ecologically significant stimuli (de Gelder et al., 2003; Phelps & LeDoux, 2005; Tamietto & de Gelder, 2010; Vuilleumier, 2005; Öhman & Mineka, 2001; but see Pessoa & Adolphs, 2010).

Alternatively, on a multi-level account of binocular rivalry (Nguyen, Freeman, & Alais, 2003; Sterzer, Kleinschmidt, & Rees, 2009; Tong, Meng, & Blake, 2006) some residual activity induced by an invisible stimulus may transpire along the ventral stream and carry sufficient face- and body-related information to give rise to the inversion effects observed in the present study. Indeed, recent fMRI, MEG and EEG studies that traced the neural processing of faces rendered invisible by CFS have revealed residual neural responses in high-level visual areas including the fusiform face area (FFA; Jiang & He, 2006; Jiang et al., 2009; Sterzer, Haynes, & Rees, 2008; Sterzer, Jalilainen, & Rees, 2009). Thus, the advantage of upright faces and bodies in gaining access to awareness might be mediated by preserved activity in category-selective cortical areas such as the FFA (Kanwisher, McDermott, & Chun, 1997) and the adjacent and spatially overlapping fusiform body area (FBA; Peelen & Downing, 2005; Schwarzlose, Baker, & Kanwisher, 2005). Future experiments are needed to distinguish between these possibilities.

8.4. Conclusion

In summary, the strong effects of inversion on access to awareness for human bodies and faces revealed in the present study provide the first evidence for the privileged detection of conspecifics. As we obtained these inversion effects using a measure of perceptual suppression during CFS, this suggests that visual mechanisms that mediate access to awareness exhibit a striking sensitivity to visual information diagnostic for the presence of other individuals. An important challenge for future research will be to reveal the precise neural mechanisms underlying the detection of conspecifics, to delineate the role of visual experience, and to understand the functional and neural relation of these mechanisms to putative innate detection mechanisms in infants of both our own and other species.

Acknowledgments

We thank Martin Hebart for help with stimulus programming, Silvia Ubaldi for help with data collection, and Andrea Heberlein for kindly providing us with the body stimuli employed in Experiment 2.

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