

Bodies are Represented as Wholes Rather Than Their Sum of Parts in the Occipital-Temporal Cortex

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Behavioral studies suggested that bodies are represented as wholes rather than in a part-based manner. However, neural selectivity for body stimuli is found for both whole bodies and body parts. It is therefore undetermined whether the neural representation of bodies is configural or part-based. We used functional MRI to test the role of first-order configuration on body representation in the human occipital-temporal cortex by comparing the response to a whole body versus the sum of its parts. Results show that body-selective areas, whether defined by selectivity to headless bodies or body parts, preferred whole bodies over their sum of parts and successfully decoded body configuration. This configural representation was specific to body stimuli and not found for faces. In contrast, general object areas showed no preference for wholes over parts and decoded the configuration of both bodies and faces. Finally, whereas effects of inversion on configural face representation were specific to face-selective mechanisms, effects of body inversion were not unique to body-selective mechanisms. We conclude that the neural representation of body parts is strengthened by their arrangement into an intact body, thereby demonstrating a central role of first-order configuration in the neural representation of bodies in their category-selective areas.

Keywords: body perception, body selectivity, configural processing, extrastriate body area, functional magnetic resonance imaging

Introduction

Bodies, like faces, are important and prevalent visual stimuli that provide us with rich social information, including the identity, gender, emotions, attractiveness, and intentions of others. It is therefore fitting that the processing mechanisms of bodies may be different from those of general object processing. Particularly, it has been suggested that bodies, like faces, are represented as wholes rather than in a part-based manner (Reed et al. 2006). Indeed, behavioral studies have shown that the visual perception of bodies is mediated by the spatial configuration of body parts (Seitz 2002; Neri 2009; Ramm et al. 2010; Robbins and Coltheart 2012). These include effects of both first-order configuration, defined by the general layout of body parts (i.e., head attached to neck, arms attached to shoulders, legs attached to hip, etc.) and second-order configuration, defined by interactive processing between body parts. Specifically, evidence for first-order configural processing has shown that bodies are best perceived in natural configuration rather than in part-scrambled configuration in which the limbs are displaced (Neri 2009; Ramm et al. 2010; Soria Bauser and Suchan 2013).

In contrast to evidence for configural processing of human bodies, neural selectivity has been found not only for whole bodies (Wachsmuth et al. 1994; Downing et al. 2001; Tsao et al. 2003; Peelen and Downing 2005; Schwarzlose et al. 2005;

Taylor et al. 2007; Brandman and Yovel 2010; Popivanov et al. 2012) but also for isolated body parts (Gross et al. 1969; Desimone et al. 1984; Bell et al. 2009, 2011; Pinsk et al. 2009; Chan et al. 2010; Weiner and Grill-Spector 2010, 2011a, 2011b). These areas are characterized by a highly selective response to bodies or to body parts over other visual objects, and have been proposed to process descriptive information about the form and structure of the body (Downing and Peelen 2011). In an attempt to reveal whether the representation of bodies in body-selective areas is part- or whole-based, Taylor et al. (2007) examined whether the response of body-selective areas increases with the amount of body information (e.g., finger, hand, arm, torso). They found that the response increased linearly in the extrastriate body area (EBA) and in a step-like manner in the fusiform body area (FBA). These findings led to the conclusion that the EBA is selective for body parts and the FBA for larger body configurations (Taylor et al. 2007). However, because the amount of body information was confounded with the intactness of body configuration, it is unclear whether the FBA was selectively responding only to large amounts of body information or also to the intact spatial configuration of this information.

Given the behavioral evidence for configural processing of bodies, it is important to determine whether neural representations of bodies are configural, that is, based on the arrangement of body parts into a whole, or whether whole bodies are represented as the sum of their parts such that body parts are represented independently from one another. Thus, in the current study, we investigated the role of first-order spatial configuration in the neural representation of bodies. To this end, we presented images of whole bodies or spatially scattered their parts, resulting with the same amount of body information in whole or part-scrambled configuration (Fig. 1A). Thereby, using fMRI, we tested whether object category-selective areas in the occipital-temporal cortex are tuned to a whole body over the sum of its parts and code the difference between them. Specifically, greater response to whole bodies over their sum of parts would reflect selectivity for whole-body configuration, while pattern discrimination between whole bodies and their sum of parts would reflect neural representation of configural body information. In a second experiment, we further examined whether the processing of body configuration occurs also in brain areas that were defined by selectivity to isolated body parts. In addition, to examine whether the differences in response to whole bodies versus their sum of parts are specific to body stimuli, Experiment 2 included control stimuli of faces and their sum of parts. Finally, given that the body inversion effect was shown for whole bodies but not body parts (Reed et al. 2006), we also examined the extent to which inverted bodies are represented in a configural manner.

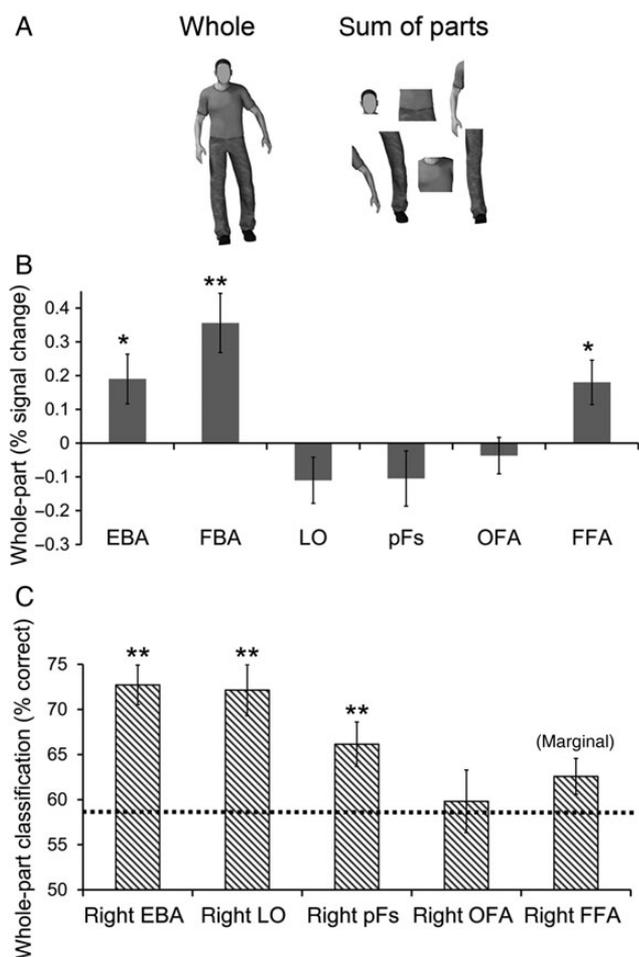


Figure 1. The response to whole bodies versus their sum of parts presented in Experiment 1. (A) Sample stimuli—a whole body and the sum of its parts. (B) The difference between the response to whole and sum of parts in body, object, and face areas. Body-selective areas and the FFA, but not object areas or the OFA, showed a significant preference for whole bodies over their sum of parts. (C) MVPA revealed above chance discrimination between whole bodies and their sum of parts in all examined areas, except the OFA. Chance level is presented by the dotted line indicating the average 95th percentile of permutation test. * $P < 0.05$; ** $P < 0.01$.

Materials and Methods

To assess whether bodies are represented as wholes or as their sum of parts, we first measured the selectivity for intact versus part-scrambled bodies in overall signal. In addition, multivoxel pattern analysis (MVPA) (Haxby et al. 2001) was used to test whether body configuration is coded in the neural response. The use of MVPA was further motivated by the weak responses of object and face areas to body stimuli, in which the superior sensitivity of MVPA (Norman et al. 2006) may expose effects not visible in overall signal.

Subjects

Twelve healthy volunteers (5 males, age 22–31 years) were included in Experiment 1. Experiment 2 included 13 healthy volunteers (7 males, age 20–43 years), who had not participated in Experiment 1. All subjects had normal or corrected-to-normal vision and gave informed consent, which was approved by the ethics committee of the Tel Aviv Sourasky Medical Center. Three additional subjects were excluded from data analysis due to excessive head motion during scanning.

Stimuli

In Experiment 1, stimuli of the functional localizer were 80 grayscale images per category of headless bodies, faces, objects, and scrambled

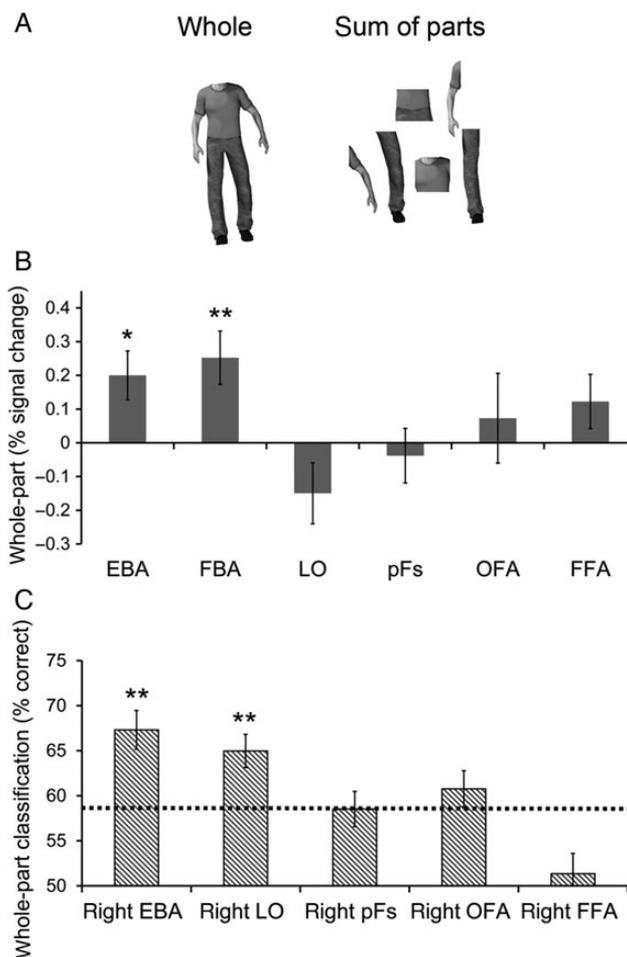


Figure 2. The response to headless bodies versus their sum of parts presented in Experiment 1. (A) Sample stimuli—a headless body and its sums of parts. (B) The difference between the response to whole body and sum of its parts in body, object, and face areas. Only body-selective areas showed a significant preference for headless bodies over their sum of parts. (C) MVPA revealed above chance discrimination between bodies and their sum of parts in the right EBA and LO. Chance level is presented by the dotted line indicating the average 95th percentile of permutation test. * $P < 0.05$; ** $P < 0.01$.

objects (i.e., a random mixture of pixels of each of the object images). The main experiment included whole bodies (Fig. 1A) and bodies without heads (Fig. 2A) in intact or scrambled configuration. Additional control stimuli for the headless stimuli were bodies without arms or without a leg in intact or scrambled configuration. The stimuli consisted of 40 grayscale body images, created from one computer-generated male human figure. A set of 10 different physically possible nonmeaningful body poses was constructed using Poser 7.0 software (e frontier America, Inc.) (Yovel et al. 2010). The whole-body images were then processed in Adobe Photoshop CS2 as follows. To hide facial features, the face was covered by a gray oval. The head was removed to create headless bodies. Body parts were separated and put in scrambled configuration to create the sum of parts for whole and for headless bodies.

In Experiment 2, stimuli of the functional localizer were 80 grayscale images per category of headless bodies, body parts, faces, objects, and scrambled objects. The images of headless bodies and body parts were created from body figures generated with Poser 7.0 software (e frontier America, Inc.). The main experiment included 8 stimulus categories of bodies and faces and their sum of parts, in upright or inverted orientation. Body stimuli consisted of 20 images of whole bodies in intact or scrambled configuration used in Experiment 1. Face stimuli consisted of 20 grayscale face images, generated from 10 different faces created with FACES software (IQ Biometric, Inc.),

previously used by Yovel et al. (2010). Face parts were separated using Adobe Photoshop CS2 and put in scrambled configuration (Fig. 4A).

Apparatus and Procedure

High-resolution fMRI data were collected in a 3T GE MRI scanner, using an 8-channel coil. Echo planar imaging sequence was used to collect fMRI data with a TR of 2 s, TE of 35 ms, 23–26 slices per TR, slice thickness of 2.4 mm no-gap (matrix 96 × 96) and FOV of 20 cm. Stimuli were presented with Matlab (Psychtoolbox; Brainard, 1997), and projected onto a screen viewed by the subjects through a mirror located in the scanner. Anatomical data were collected in a spoiled gradient echo (SPGR) scan (oblique).

Experiment 1 included 2 functional localizer sessions consisting of 4 blocks per category and 5 baseline fixation blocks (336 s) and 4 main experiment sessions consisting of 2 blocks per category and 5 baseline fixation blocks (336 s). Experiment 2 included 6 functional localizer sessions consisting of 2 blocks per category and 3 baseline fixation blocks (220 s) and 5 main experiment sessions consisting of 2 blocks per category and 5 baseline fixation blocks (336 s). Condition block order was counterbalanced within and across sessions. Each block lasted 16 s and included 20 stimuli, each presented for 350 ms with a 450-ms interstimulus interval. To maintain vigilance in the localizer sessions, subjects were instructed to press a response box button, whenever 2 identical images appeared consecutively (a 1-back task). In the main experiment sessions, subjects were instructed to press a response box button each time the background color of the body image slightly darkened from white to light gray (247, 247, 247).

Data Analysis of Category-Selective Areas

fMRI data analysis was accomplished using statistical parametric mapping (SPM) and MarsBar toolbox for SPM. The first 6 volumes were acquired during a blank screen display and were discarded from the analysis. Preprocessing included slice-timing correction, realignment, and spatial smoothing with a 4 × 4 × 4 mm full-width at half-maximum Gaussian kernel. Echo planar imaging (EPI)-SPGR co-registration was performed and a general linear model haemodynamic response function model was estimated for each subject.

ROI Selection

Anatomical masks were drawn for each subject in the left and right fusiform gyrus and extrastriate cortex, using MRIcron (Chris Rorden). The extrastriate mask included the area lateral to the calcarine sulcus, posterior–lateral to the fusiform gyrus, and posterior–inferior to the parieto-occipital sulcus. On its lateral side, it is inferior to the superior-temporal sulcus. Thereafter, localizer data were used to locate category-selective activations within each anatomical mask. By limiting statistical analysis to the predefined anatomical masks, we were able to largely reduce the number of voxels tested for significance relative to when testing the entire brain, thereby reducing multiple comparisons. We used combinations of t-contrasts to assure their specific selectivity among all localizer categories as well as their positive BOLD response to the selected category. For body areas defined by selectivity for headless bodies, body-selective voxels were extracted from a full conjunction of headless bodies > objects, headless bodies > scrambled objects, and headless bodies > 0 t-contrast maps. The EBA and FBA were defined as body-selective voxels within the extrastriate and fusiform masks, respectively (false discovery rate, FDR $q=0.05$), excluding voxels of faces > objects t-contrast (uncorrected $P<0.01$). Body areas defined by selectivity for body parts included voxels extracted from a full conjunction of body parts > objects, body parts > scrambled objects, and body parts > 0 t-contrast maps. The extrastriate body part area (EBpA) and fusiform body part area (FBpA) were defined as body part-selective voxels within the extrastriate and fusiform masks, respectively (FDR $q=0.05$), excluding voxels of faces > objects t-contrast (uncorrected $P<0.01$). Similarly, object-selective voxels of the lateral occipital complex (LOC) were extracted from a full conjunction of objects > scrambled objects and objects > 0 t-contrast maps. The LO and posterior fusiforms (pFs) were defined as object-selective voxels within the extrastriate and fusiform masks, respectively (FDR $q=0.05$),

excluding voxels of both headless bodies > objects and faces > objects t-contrasts (uncorrected $P<0.01$). Finally, face-selective voxels were extracted from a full conjunction of faces > objects, faces > scrambled objects, and faces > 0 t-contrast maps. The occipital face area (OFA) and fusiform face area (FFA) were defined as face-selective voxels within the extrastriate and fusiform masks, respectively (FDR $q=0.05$), excluding voxels of headless bodies > objects t-contrast (uncorrected $P<0.01$).

Overall BOLD Response

Average time courses across voxels of each region of interest (ROI) were extracted for each of the main experiment conditions. The dependent measure was the average of time points 3–10 (from block onset). Whole-part effect was defined as the difference between the fMRI response to whole bodies and their sum of parts.

In Experiment 1, there were no interactions with hemisphere in any of the ROIs ($P>0.19$). Therefore, results were collapsed across hemispheres using a weighted average based on the relative volumes of the ROI in each hemisphere (see supplementary Figures for results of both hemispheres). To examine the magnitude of the whole-part effect in different brain areas, we used repeated-measures ANOVA with whole-part (whole, sum of parts), region (extrastriate, fusiform), and ROI category (face, body, and object areas) as within-subject factors.

In Experiment 2, there were no interactions with hemisphere in any of the ROIs ($P>0.06$) except in the response to inverted faces, with generally larger whole-part effects in the right hemisphere of the extrastriate ROIs (EBA, OFA, LO). Therefore, results were collapsed across hemispheres using a weighted average based on the relative volumes of the ROI in each hemisphere, except for the analysis of inverted face stimuli that was performed separately for left and right hemispheres (see supplementary Figures for results of both hemispheres). In addition to the factors examined in Experiment 1, we also tested the effects of stimulus (body, face) and orientation (upright, inverted) in the repeated-measures ANOVA.

Multivoxel Pattern Analysis

Pattern classification was used to assess whether category-selective areas represent a whole-body configuration. A whole-part classification effect was measured by the level of classification between the whole and sum of parts conditions. In each ROI, a maximum of 50 voxels that were the most significant of the main contrast (preferred-category > objects or objects > scrambled objects) were selected for MVPA (Axelrod and Yovel 2012). This was done to avoid dimensionality effects on classifier performance and prevent any potential over fitting (Hastie et al. 2001), while ensuring a sufficient amount of data for effective classification. Raw intensity values after preprocessing were extracted and separated into data folds of half-sessions, resulting in 8 data folds in Experiment 1 (halves of the 4 main experiment sessions) and 10 data folds in Experiment 2 (halves of the 5 main experiment sessions). Each fold included 1 whole block (10 volumes) per condition. The voxel data were detrended and normalized (mean and STD) across the time course of each fold to minimize dependencies. In addition, we subtracted the global average of each time-point across voxels to base classifications exclusively on pattern information rather than on the average ROI signal. The time-course data were shifted 2 volumes (4 s) to account for the hemodynamic lag.

MVPA of intact versus scrambled configuration was performed separately for each of the stimulus types (whole bodies, headless bodies, faces) in an $n - 1$ cross-validation procedure. A linear SVM network was trained on $n - 1$ folds and tested on the leftover fold using Bioinformatics toolbox for Matlab. This was repeated for every fold and the accuracy ratios of the classifier were averaged. The distribution of classifier performance was collected using a permutation test, in which each classification pair was classified 10 000 times using randomly permuted class labels. For each subject, to find out whether a given ROI can discriminate between whole bodies and their sum of parts, we measured whether classification of the 2 types of body configurations was above chance level, given by the 95th percentile of permutation tests. At group level, single-sample t -tests (one-tailed) were performed against the average chance level. Additionally, we calculated the proportion of subjects who individually showed above chance classification.

To ensure sufficient data for effective classification while preserving an optimal number of ROIs for testing, MVPA was performed on ROIs of size of at least 46 voxels, thus ROI size for MVPA was 46 voxels (minimum ROI size for inclusion) to 50 voxels (the maximum number of tested voxels as explained earlier). Smaller ROIs were excluded from the analysis to minimize dimensionality effects. Subsequently, ROIs in which <9 subjects reached 46 voxels were excluded altogether. The excluded ROIs were the left and right FBA, the left OFA and left FFA in Experiment 1 and the left FBA and left FBpA in Experiment 2. As most excluded ROIs were in the left, and left and right hemispheres showed similar result patterns, classification results are presented only for the right hemisphere (see supplementary Figures for results of left hemisphere). Notably, classification accuracy in Experiment 1 did not differ between hemispheres in the LO and pFs ($P > 0.27$), while the EBA showed overall higher classification accuracy in the right than in the left hemispheres ($F_{1,11} = 14.28$, $P = 0.003$) with no interaction between hemisphere and body type ($P > 0.28$). In Experiment 2, overall higher classification accuracy was found for upright bodies and faces in the right than in the left hemisphere in the EBpA ($F_{1,12} = 5.55$, $P = 0.036$) and LO ($F_{1,12} = 5.44$, $P = 0.038$), but not in the EBA, pFs, OFA, and FFA ($P > 0.08$), with no interactions between hemisphere and stimulus ($P > 0.3$). No other effects of hemisphere or interaction of hemisphere and stimulus were significant.

To compare the magnitude of whole-part classification across different category-selective areas, we performed paired *t*-tests of classification accuracy between ROI pairs. In Experiment 2, to compare the magnitude of whole-part classification between body and face stimuli, we report below the results of repeated-measures ANOVA with region (extrastriate, fusiform), stimulus (body, face), and ROI category (body areas, face areas) as within-subject factors. To examine the effect of stimulus inversion, we also included orientation (upright, inverted) as another factor in the ANOVA.

Controlling for Multiple Comparisons

FDR of *t*-tests presented below in each of the result sections revealed similar effects at a significance level of 0.05, except where otherwise noted in corrected *P* value.

Results

Accuracy in detecting brightness changes in the background did not differ across conditions in either experiment ($P > 0.1$). Therefore, the following fMRI responses cannot be attributed to differences in task difficulty or engagement across the different stimulus conditions. In the following subsections, for each category-selective area, we report the analysis of overall responses (percent signal change) followed by results obtained with MVPA.

Experiment 1

Whole Bodies versus the Sum of Their Parts

The level of fMRI responses to whole bodies versus their sum of parts are summarized in Figure 1.

Body-selective areas. Averaged fMRI response: Body-selective areas showed higher overall responses to whole bodies than their sum of parts. Paired *t*-tests of percent signal change revealed higher responses to whole ($M = 0.93$ SD = 0.43) versus sum of parts ($M = 0.74$, SD = 0.36) in the EBA ($t_{(11)} = 2.59$, $P = 0.025$) as well as higher responses to whole ($M = 1.12$, SD = 0.41) versus sum of parts ($M = 0.73$, SD = 0.36) in the FBA ($t_{(10)} = 4.58$, $P = 0.001$).

Pattern classification: MVPA revealed successful discrimination between whole versus sum of parts in the right EBA ($t_{(11)} = 6.30$, $P < 0.001$), and was significantly above chance level in all subjects (100%). The FBA was excluded from pattern

classification analysis because of its relatively small size (see Materials and Methods and Experiment 2 where we found larger FBA activations and report classification results). These findings suggest that body-selective areas code the layout of body parts and are tuned to whole-body configuration. However, it is also possible that the higher response to whole bodies reflects the higher attention to the familiar image of a whole body than the image of scattered body parts. Such effect of attention would lead to higher response to whole bodies also in other brain areas that are not body-selective. To assess whether these findings are unique to body areas, we also examined the response of general object areas and face-selective areas to the body stimuli.

Object-selective areas. Averaged fMRI response: In contrast to body areas, the LOC object-general areas, showed no difference in overall responses to whole bodies versus their sum of parts in the LO ($t_{(11)} = 1.61$, $P = 0.136$) and pFs ($t_{(11)} = 1.28$, $P = 0.227$). The preference for whole bodies that was found in the body areas (EBA, FBA) was significantly larger than found in object areas (LO, pFs) as indicated by an interaction between whole-part (whole, sum of parts) and ROI category (body areas, object areas) ($F_{1,10} = 78.23$, $P < 0.001$). These findings suggest that the higher response to whole bodies is specific to body areas and does not reflect a general attentional or low-level preference for whole bodies over their sum of parts.

Pattern classification: In contrast to the overall fMRI response, MVPA revealed discrimination between whole bodies and their sum of parts in object areas. Specifically, above chance discrimination was found in the right LO ($t_{(11)} = 4.67$, $P < 0.001$), and was significantly above chance level in 83% of subjects, as well as in the right pFs ($t_{(11)} = 2.93$, $P = 0.007$), and was significantly above chance level in 75% of subjects. Comparison of the magnitude of discrimination between the body and object areas showed no difference in whole-part classification between the right EBA and right LO ($t_{(11)} = 0.16$, $P = 0.876$) and marginally significant better classification in the right EBA than the right pFs ($t_{(11)} = 2.32$, $P = 0.040$, corrected $P = 0.067$).

Face-selective areas. Averaged fMRI response: face-selective areas responded differently by region. In contrast to body areas, and similar to object areas, the OFA did not exhibit any differences in response to whole bodies versus sum of parts ($t_{(11)} = 0.68$, $P = 0.508$). However, the FFA showed higher responses to whole bodies than their sum of parts ($t_{(11)} = 2.74$, $P = 0.019$). This whole-part effect in the face areas was smaller than the whole-part effects found in body areas, as revealed by an interaction between whole-part (whole, sum of parts) and ROI category (body areas, face areas) ($F_{1,10} = 16.98$, $P = 0.002$) and no 3-way interaction with region (extrastriate, fusiform) ($F_{1,10} = 0.13$, $P = 0.720$).

Pattern classification: Similar to the averaged fMRI response, MVPA in face areas revealed successful discrimination in FFA but not OFA. Specifically, discrimination of whole versus sum of parts was marginally above chance in the right FFA ($t_{(10)} = 1.71$, $P = 0.059$, corrected $P = 0.088$) and significantly above chance level in 82% of subjects, and below chance in the right OFA ($t_{(8)} = 0.25$, $P = 0.404$) and only 56% of the subjects showed significant discrimination. Importantly, whole-part classification was better in the body-selective area than in both face-selective areas. Paired *t*-tests of accuracy revealed better classification of whole bodies versus their sum of parts in the

right EBA than in the right OFA ($t_{(8)} = 2.96$, $P = 0.018$) and right FFA ($t_{(10)} = 6.16$, $P < 0.001$).

In sum, results indicate neural selectivity to whole bodies over the sum of their parts in body-selective areas but not in object-general areas, as revealed by the higher fMRI responses for whole versus sum of parts. This indicates that greater attention or familiarity for whole bodies is unlikely to account for the higher response to whole bodies relative to sum of parts in the body areas. In contrast to the clear dissociation found between body and object areas in overall responses, MVPA revealed similar whole-part classification in the EBA and LO. In face-selective areas, the OFA showed no effects of whole part, whereas the FFA showed preference for whole versus sum of parts as well as a marginal effect of whole-part classification, which was significantly smaller than the effect in body areas. The sources of the effects found in the LO and FFA are clarified in the following sections.

Headless Bodies versus the Sum of Their Parts

Body areas have been commonly defined in previous studies as well as our study with headless bodies. We therefore examined the response to a body versus the sum of its parts also without the head. A second motivation to include headless bodies was to further examine the preference we found in the FFA for whole bodies over their sum of parts, given earlier reports that the FFA is tuned to whole bodies but not to headless bodies (Cox et al. 2004; Brandman and Yovel 2010). The level of fMRI responses to headless bodies versus their sum of parts are summarized in Figure 2.

Body-selective areas. Averaged fMRI response: Body-selective areas showed a preference for headless bodies over their sum of parts as they did for whole bodies. Specifically, higher overall responses to headless bodies than their sum of parts were found in the EBA ($t_{(11)} = 2.77$, $P = 0.018$) and FBA ($t_{(10)} = 2.48$, $P = 0.006$).

Pattern classification: MVPA revealed successful discrimination between headless bodies and their sum of parts in the right EBA ($t_{(11)} = 3.84$, $P = 0.001$), and was significantly above chance level in 92% of subjects. These findings are consistent with a recent fMRI-adaptation study that showed similar adaptation effects for whole and headless bodies in the body areas (Brandman and Yovel 2010), suggesting that body areas generate similar representation of whole and headless bodies.

Object-selective areas. Averaged fMRI response: The LOC showed no significant difference in overall responses to headless bodies versus sum of parts in the LO ($t_{(11)} = 1.65$, $P = 0.127$) and pFs ($t_{(11)} = 0.47$, $P = 0.646$). The preference for headless bodies over their sum of parts, which was found in the body areas (EBA, FBA), was significantly larger than the difference in response to headless bodies versus their sum of parts in object areas (LO, pFs) as indicated by an interaction between whole-part (whole, sum of parts) and ROI category (body areas, object areas) ($F_{1,10} = 71.42$, $P < 0.001$).

Pattern classification: MVPA revealed discrimination between whole bodies and their sum of parts in the LO but not pFs. Specifically, above chance discrimination was found in the right LO ($t_{(11)} = 3.25$, $P = 0.004$), and was significantly above chance level in 67% of subjects. Classification performance in the pFs did not exceed chance level ($t_{(11)} = -0.18$, $P = 0.571$), and was significantly above chance level in only 42% of

subjects. Similar to whole bodies, comparison of the magnitude of discrimination of headless bodies and their sum of parts between the body and object areas showed no difference in whole-part classification between the right EBA and right LO ($t_{(11)} = 1.20$, $P = 0.254$) and better classification in the right EBA than the right pFs ($t_{(11)} = 4.06$, $P = 0.002$).

Face-selective areas. Averaged fMRI response: Interestingly, the whole-part effect that was found for whole bodies was abolished for headless bodies. The FFA and OFA showed no difference between the fMRI responses to headless bodies and their sum of parts (right FFA: $t_{(11)} = 1.52$, $P = 0.157$; right OFA: $t_{(11)} = 0.55$, $P = 0.595$).

Pattern classification: Similar to the averaged fMRI response, classification analysis revealed no discrimination between headless bodies and sum of parts in the right FFA ($t_{(10)} = -3.32$, $P = 0.996$), with only 18% of subjects showing above chance classification and in the right OFA ($t_{(8)} = 0.91$, $P = 0.196$). Thus, whereas body-selective areas showed consistent selectivity for whole bodies and whole-part classification for both whole and headless bodies, the effects in the FFA disappeared when the head was removed.

Comparison to armless and legless bodies. Recent studies have defined body-selective areas by limbs only and named them limb areas (Weiner and Grill-Spector 2010, 2011a, 2011b). By examining the configural representation of armless and legless bodies, we can also ask if indeed limbs play a special role in the representation of bodies. Results show similar whole-part effects for armless and legless bodies as for headless bodies. Specifically, overall responses show a general preference for headless, armless, and legless bodies over their sum of parts, as revealed by a main effect of whole part (whole, sum of parts) in the EBA ($F_{1,11} = 26.32$, $P < 0.001$) and the FBA ($F_{1,10} = 39.97$, $P < 0.001$). This preference for whole over parts was as large as for headless bodies, as revealed by no interactions between body type (headless, armless, legless) and whole part ($P > 0.311$). Similarly, MVPA revealed successful discrimination of whole versus sum of parts for both armless ($t_{(11)} = 4.09$, $P < 0.001$) and legless bodies ($t_{(11)} = 4.04$, $P < 0.001$), and no effect of body type on classification accuracy ($F_{2,22} = 0.43$, $P = 0.654$). Thus, the head or limbs had no special role in the representation of bodies in the body areas.

In sum, these findings show that body-selective areas prefer a body over the sum of its parts, and discriminate between them, regardless of the presence of the head or limbs. Object areas also exhibited overall similar patterns of response to whole bodies as to headless bodies compared with their sum of parts. In contrast, the preference for whole bodies over their sum of parts in the FFA was abolished for headless bodies. Thus, the FFA represented configural information only when the head was present. These findings are consistent with a recent finding of fMRI-adaptation to whole bodies but not to headless bodies in the FFA (Brandman and Yovel 2010), suggesting that the FFA is sensitive to whole bodies that include a head, even without a face, but not to headless bodies.

Experiment 2

In Experiment 1, we revealed that body-selective areas defined with headless bodies show greater selectivity for whole or headless bodies than their sum of parts. Experiment 2 addresses 4 remaining questions. First, a central question is

whether body configuration is represented only in areas that are selective for headless bodies, or also in body areas defined by selectivity for isolated body parts. Thus, in Experiment 2, we defined 2 different types of body areas, based on their selectivity to either headless bodies, as in Experiment 1, or a variety of isolated body parts. A second important question is whether the higher response to whole bodies than their sum of parts in body-selective areas is unique for bodies or whether it may reflect a preference for any other stimulus that is presented in its intact configuration. In addition, an alternative explanation for the classification of whole bodies and their sum of parts found in body and object areas is that they may discriminate a single stimulus from multiple stimuli. To address these 2 alternative explanations, in addition to their response to body stimuli, we examined the response of body-selective areas and general object areas to whole faces versus their sum of parts. If body areas are generally selective for whole or single stimuli, they will show the same discrimination between a whole face and the sum of its parts. Third, we asked whether whole-part effects found in Experiment 1 are unique for upright bodies or can also be found for inverted bodies, as it has been previously suggested that first-order configural processing is unique for upright bodies (Reed et al. 2006). Fourth, we re-examined the configural effect that we found for whole bodies in face-selective areas and compared that with the configural representation these areas generate for faces.

Replication of Whole-Body Preference in Headless Body Areas but Not Object Areas

Body-selective areas. Averaged fMRI response: We first examined the response to whole bodies versus their sum of parts in headless body areas and in object areas as in the first experiment. Replicating the results of Experiment 1, a preference for whole bodies over their sum of parts was found in headless body areas but not in object areas. In body areas, paired t -tests of percent signal change revealed higher overall responses to whole bodies versus their sum of parts in the EBA ($t_{(12)} = 4.09$, $P = 0.001$) and in the FBA ($t_{(11)} = 3.98$, $P = 0.002$) (Fig. 3A, 2 left bars).

Pattern classification: MVPA replicated the discrimination found in Experiment 1 between whole bodies and their sum of parts. Specifically, above chance discrimination was found in the right EBA ($t_{(12)} = 9.63$, $P < 0.001$), and was significantly above chance level in 100% of subjects, and in the right FBA ($t_{(8)} = 2.61$, $P = 0.015$), and was significantly above chance level in 78% of subjects (Fig. 3B, 2 left bars).

Object-selective areas. Averaged fMRI response: As in Experiment 1, object areas showed no preference for whole bodies over their sum of parts. Overall responses were similar for whole bodies and their sum of parts in the LO ($t_{(12)} = 0.47$, $P = 0.648$) and pFs ($t_{(12)} = 0.11$, $P = 0.910$). Furthermore, the whole-part effect was significantly larger in body areas than in object areas, as revealed by an interaction between whole-part (whole, sum of parts) and ROI category (headless body, object) ($F_{1,11} = 79.38$, $P < 0.001$).

Pattern classification: Further replicating results of Experiment 1, MVPA revealed discrimination between whole bodies and their sum of parts in object areas. Specifically, above chance discrimination was found in the right LO ($t_{(12)} = 6.14$, $P < 0.001$), and was significantly above chance level in 100% of subjects, and in the right pFs ($t_{(12)} = 4.99$, $P < 0.001$), and was significantly above chance level in 100% of subjects.

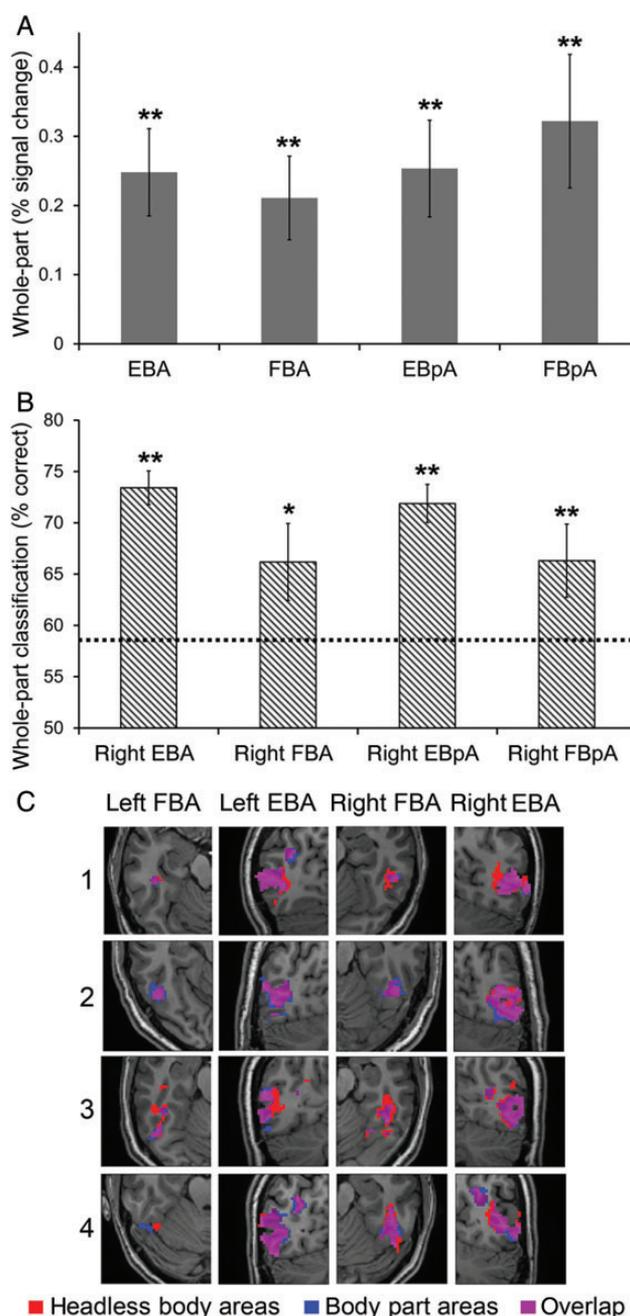


Figure 3. Body areas defined by headless bodies or body parts. (A) The difference between the response to a whole body and the sum of its parts in body areas defined by selectivity to headless bodies (2 right bars) or body parts (2 left bars) showed a similar significant preference for whole bodies over their sum of parts. (B) MVPA revealed above-chance discrimination between whole bodies and their sum of parts similarly in headless body areas (2 left bars) and body part areas (2 right bars). (C) Body-selective areas defined as voxels showing higher responses to headless bodies than objects and scrambled objects (red) or higher responses to body parts than objects and scrambled objects (blue) and their overlapping voxels (purple) in 4 representative subjects. Chance level is presented by the dotted line indicating the average 95th percentile of permutation test. * $P < 0.05$; ** $P < 0.01$.

Discrimination was as large as in body areas, with no effect of ROI category ($F_{1,8} = 0.37$, $P = 0.561$).

Body Part-Selective Areas Prefer Whole Bodies Over the Sum of Their Parts

One of the main objectives of Experiment 2 was to determine whether the preference for whole-body configuration is

Table 1
The proportion of overlap between body areas defined with headless bodies and body parts

Subjects	Left hemisphere				Right hemisphere			
	% EBA overlapping EBpA	% EpBA overlapping EBA	% FBA overlapping FBpA	% FpBA overlapping FBA	% EBA overlapping EBpA	% EpBA overlapping EBA	% FBA overlapping FBpA	% FpBA overlapping FBA
1	76.65	86.14	70.97	64.71	74.20	97.35	59.89	94.12
2	92.39	66.55	98.18	20.93	91.01	68.30	86.60	57.14
3	81.13	68.62			84.51	68.46		0.00
4	70.74	78.72			12.28	100.00	15.09	100.00
5	65.47	86.34	41.67	76.92	66.32	94.51	37.14	100.00
6	85.67	68.71	5.00	1.96	85.83	75.22	78.31	60.68
7	74.93	95.01	3.39	66.67	50.09	99.09	0.00	
8	91.11	76.84			72.23	85.58	57.89	33.33
9	42.24	82.58	50.00	100.00	54.66	94.22	22.50	83.72
10	73.96	94.42	80.95	85.00	71.99	76.32	42.33	83.49
11	66.60	97.05	71.29	93.51	53.25	96.72	18.18	96.00
12	76.22	85.80			74.61	93.56	62.96	67.11
13	70.04	89.05	65.22	100.00	79.10	87.12	56.67	54.84
M (SD)	74.39 (12.88)	82.76 (10.31)	54.07 (32.64)	67.74 (34.74)	66.93 (20.75)	87.42 (11.60)	44.80 (26.80)	69.20 (30.38)

exclusive for body areas defined with headless bodies or also found in areas defined with isolated body parts. We therefore examined the response to whole bodies versus their sum of parts in body areas defined by their selectivity for body parts alone. Responses of body-selective areas defined with body parts or with headless bodies to whole bodies versus their sum of parts are summarized in Figure 3.

Interestingly, the body part areas largely overlapped with the headless body areas (Fig. 3C). Specifically, 85% of the EBpA overlapped with the EBA, and 67% of the FBpA overlapped with the FBA (for proportion of overlap between body areas, see Table 1). Averaged fMRI response: Similar to headless body areas, body part areas showed higher overall responses to whole bodies than their sum of parts, both in the EBpA ($t_{(12)} = 3.77$, $P = 0.003$) and FBpA ($t_{(12)} = 3.47$, $P = 0.005$) (Fig. 3A, 2 right bars). Furthermore, this preference for whole bodies over their sum of parts was as large as in headless body areas, as no interaction was found between whole-part (whole, sum of parts) and ROI category (headless body areas, body part areas) ($F_{1,11} = 0.89$, $P = 0.366$).

Pattern classification: MVPA revealed discrimination between whole bodies and their sum of parts in body part areas. Specifically, above chance discrimination was found in the right EBpA ($t_{(12)} = 6.82$, $P < 0.001$), and was significantly above chance level in 100% of subjects, as well as in the right FBpA ($t_{(9)} = 3.29$, $P = 0.005$), and was significantly above chance in 90% of subjects (Fig. 3B, 2 right bars). Furthermore, discrimination was as large as in headless body areas, with no effect of ROI category ($F_{1,7} = 0.01$, $P = 0.913$). These results show that configural body processing is a general feature of body-selective areas in the occipital-temporal cortex regardless of whether they are defined with headless bodies or body parts.

To test whether there are areas that are solely selective for isolated body parts that may not process body configuration, we examined subregions of the EBpA and FBpA that excluded voxels of headless body > objects t-contrast (uncorrected $P < 0.01$), and that were at least 3 voxels in size. MVPA was not performed on these ROIs, as they reached 46 voxels in only 4 subjects or less ($M = 44.23$, $SD = 73.34$). These purely part-selective areas comprised only 10% of the EBpA and 14% of the FBpA. Indeed, these areas did not show a preference for whole bodies over their sum of parts in the extrastriate ($t_{(12)} = 1.36$, $P = 0.198$) or in the fusiform ($t_{(7)} = 1.57$, $P = 0.160$).

Thus, small subregions of body-selective areas may represent body parts independently of their spatial configuration.

Is the Selectivity for Whole Configuration Specific to Body Stimuli?

To test whether the preference of body-selective areas for whole configuration is specific to body stimuli, we examined the response of body-selective areas to whole faces versus their sum of parts. Given that body part areas generated the same results as headless body areas in the previous section, the tests in the remaining sections were performed only on body-selective areas defined with headless bodies, which are comparable with Experiment 1. Responses to whole bodies and faces versus their sums of parts in body- and object-selective areas are summarized in Figure 4.

Body-selective areas. Averaged fMRI response: Unlike their response to the body stimuli, body-selective areas showed no preference for whole faces over their sum of parts. Specifically, body-selective areas showed no difference in overall responses to whole faces and their sum of parts, both in the EBA ($t_{(12)} = 0.39$, $P = 0.701$) and FBA ($t_{(11)} = 0.98$, $P = 0.348$). The whole-part effects for body stimuli were significantly larger from those found with face stimuli as revealed by an interaction between whole-part (whole, sum of parts) and stimulus (bodies, faces) ($F_{1,11} = 6.83$, $P = 0.024$).

Pattern classification: MVPA revealed no discrimination between whole faces and their sum of parts in body-selective areas. Specifically, discrimination was below chance in the right EBA ($t_{(12)} = 0.92$, $P = 0.187$), and was significantly above chance level in 54% of subjects, and below chance in the right FBA ($t_{(8)} = 0.07$, $P = 0.471$), and was significantly above chance in 67% of subjects. Discrimination of whole versus sum of parts was significantly smaller for face stimuli than for body stimuli, as revealed by a main effect of stimulus ($F_{1,8} = 20.18$, $P = 0.002$).

Object-selective areas. Unlike body areas that showed selectivity and decoded configural information for bodies but not faces, object areas showed no difference in their representation of configural information of faces and bodies.

Averaged fMRI signal: Overall responses revealed no preference for whole faces over their sum of parts. Specifically,

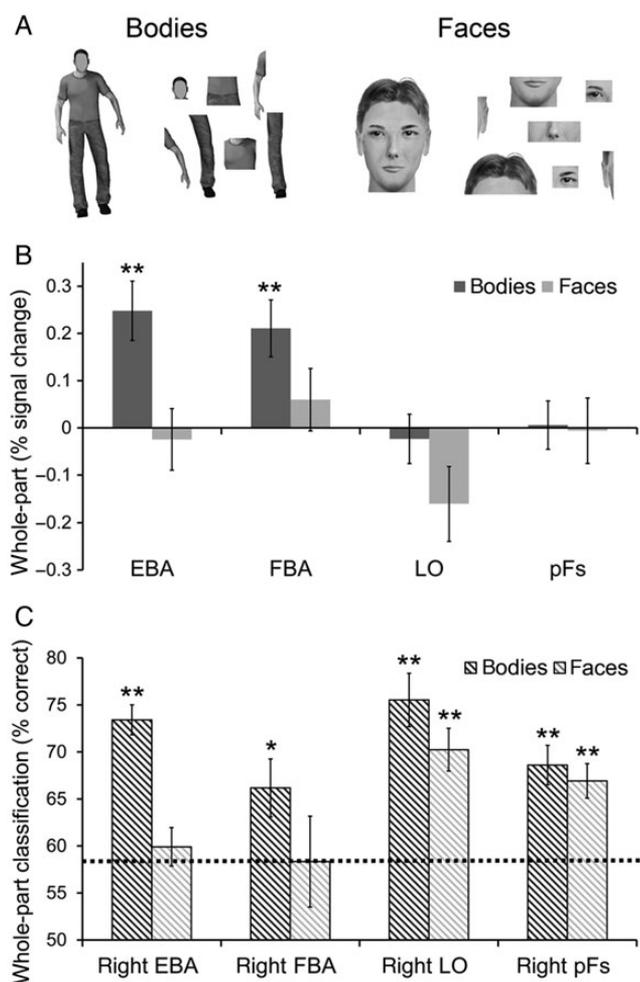


Figure 4. The response to whole bodies or faces versus their sums of parts presented in Experiment 2. (A) Sample stimuli—a body and a face versus their sums of parts. (B) The difference between the response to whole bodies and faces and their sum of parts in body and object areas. Body-selective areas, but not object areas, showed a significant preference for whole bodies over their sum of parts. Neither body nor object areas showed a difference in response to whole faces versus their sum of parts. (C) MVPA revealed that whereas body-selective areas discriminated between bodies and their sum of parts, but not between faces and their sum of parts, object areas similarly discriminated between faces and their sum of parts and between bodies and their sum of parts. Chance level is presented by the dotted line indicating the average 95th percentile of permutation test. * $P < 0.05$; ** $P < 0.01$.

responses did not differ significantly for whole faces and their sum of parts in the LO ($t_{(12)} = 2.12$, $P = 0.055$, corrected $P = 0.165$) and the pFs ($t_{(12)} = 0.09$, $P = 0.928$).

Pattern classification: MVPA revealed that in contrast to body areas, which decoded whole from parts for bodies but not face stimuli, object areas decoded whole from parts of both bodies and faces. In particular, similar to body stimuli, MVPA revealed successful discrimination between whole faces and their sum of parts in object areas. Above chance discrimination was found in the right LO ($t_{(12)} = 4.69$, $P < 0.001$), and was significantly above chance level in 92% of subjects, as well as in the right pFs ($t_{(12)} = 4.27$, $P < 0.001$), and was also significantly above chance level in 92% of subjects. Furthermore, discrimination was as large as for body stimuli, with no effect of stimulus (body, face) ($F_{1,12} = 1.66$, $P = 0.222$).

Thus, whereas body areas are specifically tuned to whole-body configuration and not face configuration, object areas

discriminate between whole stimuli and their sum of parts similarly for body and face stimuli (Fig. 4C). This indicates that while the response of body areas reflects specific processing of body configuration, object areas represent differences between whole and sum-of-parts of any object stimulus.

Is the Preference for Whole-body Configuration Unique for Upright Bodies?

Behavioral studies report an inversion effect for whole-body stimuli (Reed et al. 2003). This body inversion effect has been proposed to result from first-order configural processing of upright but not inverted bodies (Reed et al. 2006). However, recent findings suggest that the inversion effect for whole-body stimuli is not associated with body-selective mechanisms as it is abolished for headless bodies (Minnebusch et al. 2009; Yovel et al. 2010) and is found in face-selective areas, not body-selective areas (Brandman and Yovel 2010). We therefore examined the effects of inversion on configural representation of bodies in body-, object-, and face-selective areas. Specifically, we compared the magnitude of whole-part effects induced by upright versus inverted bodies in body-, object-, and face-selective areas. We report here the analysis of body- and object-selective areas (Fig. 5) and, in the next section, the analysis of face-selective areas (Figs 6 and 7).

Averaged fMRI signal: Results show that in both body- and object-selective areas, body inversion had no effect on overall response, yet it reduced decoding. Specifically, body areas preferred whole bodies over their sum of parts similarly for upright and inverted bodies, as revealed by a main effect of whole-part (whole, sum of parts) on percent signal change ($F_{1,11} = 23.49$, $P < 0.001$) and no interactions between orientation (upright, inverted) and whole-part ($P > 0.879$). Object areas showed no difference in response to whole bodies versus their sum of parts for both upright and inverted bodies, as revealed by no effect of whole part ($F_{1,12} = 0.03$, $P = 0.857$), nor interactions between orientation and whole part ($P > 0.713$) (Fig. 5B).

Pattern classification: In contrast to the averaged fMRI signal, MVPA revealed that discrimination of whole versus sum of parts was worse for inverted than upright bodies in both body- and object-selective areas (Fig. 5C), as revealed by a main effect of orientation in body-selective areas ($F_{1,8} = 10.94$, $P = 0.011$) and in object-selective areas ($F_{1,12} = 15.72$, $P < 0.001$), and no interactions with region (extrastriate, fusiform) ($P > 0.417$). Importantly, this effect was of similar size in body- and object-selective areas, as revealed by no interactions with ROI category (body areas, object areas) ($P > 0.239$). Thus, although the decoding of whole bodies versus their sum of parts was reduced with inversion, this effect was similar across body- and object-selective areas. This shows that the effect of body inversion on whole-part classification is not unique to body-selective areas, and may reflect general effects of lower perceptual experience for inverted than upright bodies in the occipital-temporal cortex.

Are Face-Selective Areas Tuned to the Configuration and Orientation of Face and Whole Body Stimuli?

While the main motivation to include face stimuli was as a control for body stimuli in body- and object-selective areas, an additional question the data we collected allowed us to ask is whether face-selective areas, similar to body-selective areas, are tuned to the first-order configuration of their preferred stimuli. Furthermore, previous studies have shown that face-selective areas are associated with the inversion effect of both

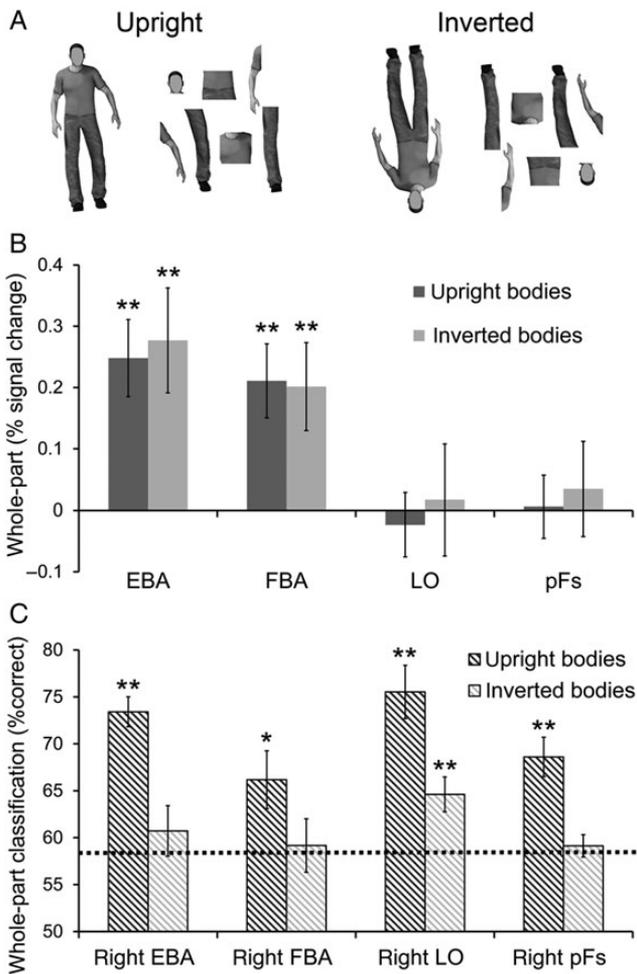


Figure 5. The response to upright or inverted bodies versus their sums of parts presented in Experiment 2. (A) Sample stimuli—an upright body and an inverted body and their sums of parts. (B) The difference between the response to upright and inverted whole bodies and their sum of parts in body and object areas. The whole-part difference was similar for upright and inverted bodies in body and object areas. (C) MVPA revealed better discrimination of upright than inverted bodies versus their sum of parts in both body- and object-selective areas. Chance level is presented by the dotted line indicating the average 95th percentile of permutation test. * $P < 0.05$; ** $P < 0.01$.

faces and whole bodies (Yovel and Kanwisher 2005; Brandman and Yovel 2010). We therefore examined the responses of face-selective areas to whole faces and their sum of parts as well as to whole bodies and their sum of parts (Fig. 6). Finally, we examined the effect of inversion on the configural representation of these stimuli (Fig. 7).

Configural representation of faces and bodies. Averaged fMRI response: face-selective areas showed higher response to whole than sum of parts for face stimuli in both the FFA and OFA. Specifically, face-selective areas showed higher overall responses to whole faces ($M = 0.97$, $SD = 0.52$) than their sum of parts ($M = 0.56$, $SD = 0.26$) in the FFA ($t_{(12)} = 3.37$, $P = 0.005$) as well as higher responses to whole faces ($M = 0.90$, $SD = 0.56$) than their sum of parts ($M = 0.57$, $SD = 0.35$) in the OFA ($t_{(12)} = 2.97$, $P = 0.012$). For body stimuli, overall responses were higher for whole than for sum of parts in the FFA ($t_{(12)} = 3.36$, $P = 0.006$) but not in the OFA ($t_{(12)} = 1.43$, $P = 0.177$). This effect was marginally smaller for body stimuli

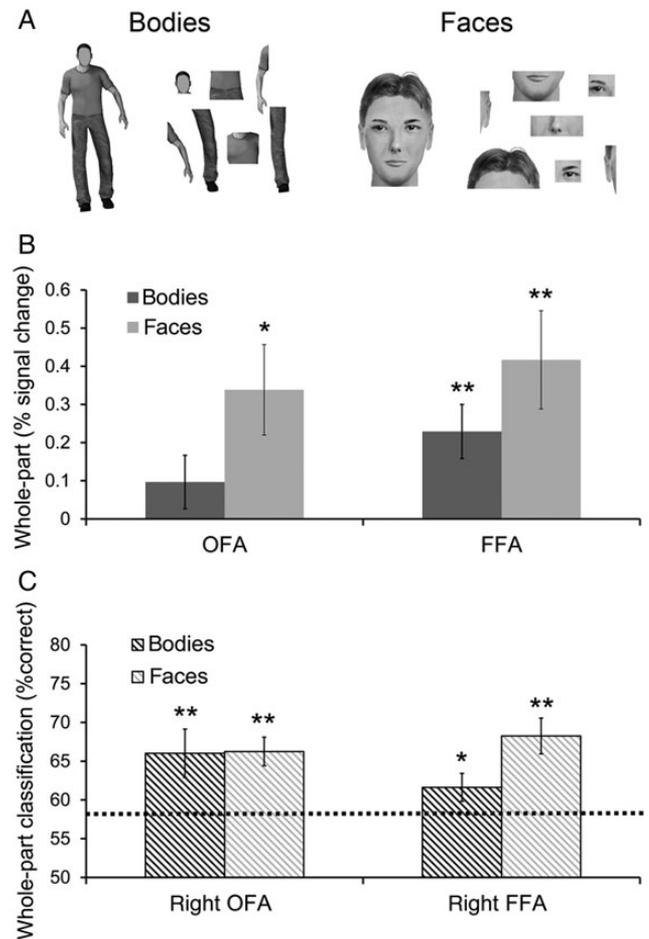


Figure 6. The response of face-selective areas to bodies and faces presented in Experiment 2. (A) Sample stimuli—a face and a body and their sums of parts. (B) The difference between the response to whole body and faces and their sum of parts in face-selective areas. Face-selective areas show a marginally larger preference for whole faces over their sum of parts than for whole bodies over their sum of parts. (C) MVPA revealed above chance discrimination between both faces and bodies versus their sum of parts in face-selective areas. Chance level is presented by the dotted line indicating the average 95th percentile of permutation test. * $P < 0.05$; ** $P < 0.01$.

than for face stimuli, as revealed by an interaction between stimulus (bodies, faces) and whole part (whole, sum of parts) ($F_{1,12} = 4.02$, $P = 0.068$) (Fig. 6B).

Pattern classification: MVPA revealed similar whole-part classification for faces and bodies in face-selective areas (Fig. 6C). Specifically, above chance discrimination of whole faces versus their sum of parts was found in the right OFA ($t_{(10)} = 3.67$, $P = 0.002$), and was significantly above chance level in 82% of subjects, as well as in the right FFA ($t_{(9)} = 3.58$, $P = 0.003$), and was also significantly above chance level in 90% of subjects. For body stimuli, above chance discrimination was found in the right FFA ($t_{(9)} = 1.95$, $P = 0.041$, corrected $P = 0.064$), significantly above chance level in 70% of subjects, as well as in the right OFA ($t_{(10)} = 3.83$, $P = 0.002$), significantly above chance level in 91% of subjects. Whole-part classification did not differ between body and face stimuli in face-selective areas, as revealed by no effects of Stimulus ($P > 0.121$).

These findings show that face-selective areas are specifically tuned to the configuration of faces and prefer a whole face over the sum of its parts. Face-selective areas are also tuned to the configuration of whole bodies. However, the results of

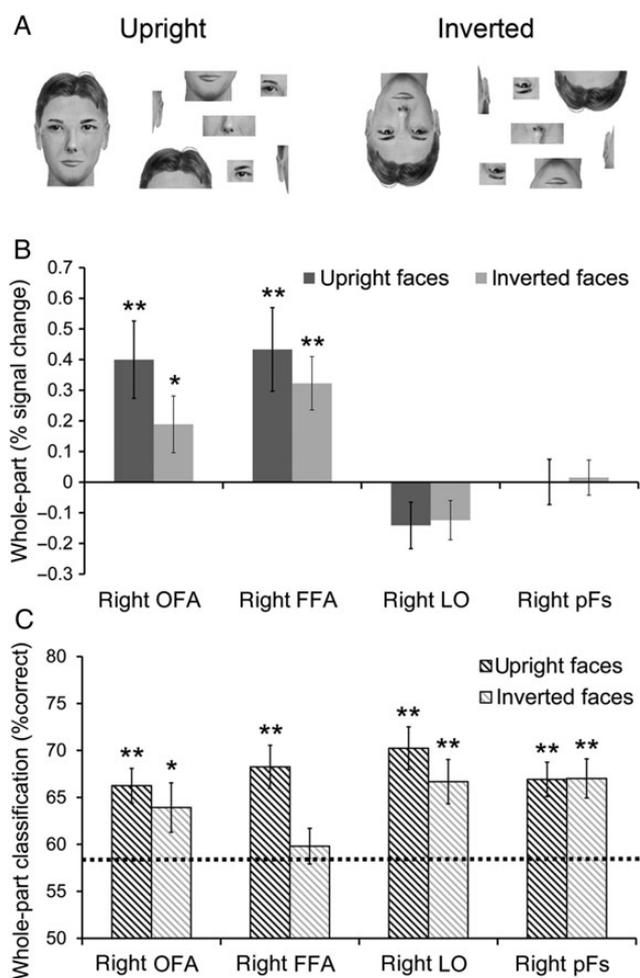


Figure 7. The response to upright or inverted faces versus their sums of parts presented in Experiment 2. (A) Sample stimuli—an upright and an inverted face and their sums of parts. (B) The difference between the response to upright and inverted faces and their sum of parts in face and object areas. A marginally larger preference for whole faces over their sum of parts was found in face areas but not in object areas. (C) MVPA revealed better discrimination of upright than inverted bodies versus their sum of parts in the FFA, but not in the OFA or in object-selective areas. Chance level is presented by the dotted line indicating the average 95th percentile of permutation test. * $P < 0.05$; ** $P < 0.01$.

Experiment 1 show that they disappear for headless bodies, suggesting that face-selective areas are more sensitive to the presence of the head rather than to body configuration in general. Furthermore, when comparing the response of body- and face-selective areas to body and face stimuli, the pattern of response in face areas mirrors the whole-part effects found in body areas (Fig. 4), showing that each category-selective area is tuned to the configuration of its preferred stimulus more than the nonpreferred stimulus. Specifically, results show a three-way interaction between ROI category (face areas, body areas), stimulus (bodies, faces), and whole part (whole, sum of parts) in overall responses ($F_{1,11} = 21.38$, $P < 0.001$) and an interaction between ROI category and stimulus in MVPA accuracy ($F_{1,5} = 37.22$, $P = 0.002$), with whole-part effects larger for faces than bodies in face-selective areas, and larger for bodies than faces in body-selective areas.

Face inversion. We examined the effect of inversion on the configural representation of faces in the face areas and compared it with object areas (Fig. 7).

Averaged fMRI response: In overall response, the preference found for whole faces over their sum of parts in face-selective areas was slightly larger for upright than inverted faces, as revealed by a marginal interaction between orientation (upright, inverted) and whole-part (whole, sum of parts) ($F_{1,11} = 3.89$, $P = 0.074$). In object areas, no differences were found in the size of whole-part effect between upright and inverted faces, as revealed by no interactions between orientation and whole-part ($P > 0.833$). The effect of larger whole-part preference in upright than inverted faces was significantly stronger in face- than in object-selective areas, as revealed by a three-way interaction between ROI category (face areas, object areas), orientation and whole-part ($F_{1,11} = 10.29$, $P = 0.008$) (Fig. 7B).

Pattern classification: MVPA revealed similar whole-part classification for upright and inverted faces in object areas and in the OFA, whereas in the FFA configural representation was found for upright but not inverted faces (Fig. 7C). Specifically, above chance discrimination of inverted faces versus their sum of parts was found in the right OFA ($t_{(10)} = 2.02$, $P = 0.035$, corrected $P = 0.061$), and was as large as for upright faces ($t_{(10)} = 0.97$, $P = 0.355$). However, whole-part classification of inverted faces was below chance in the right FFA ($t_{(9)} = 0.99$, $P = 0.174$), and was significantly worse than for upright faces ($t_{(9)} = 0.284$, $P = 0.019$). No difference was found in whole-part classification between upright and inverted faces in the LO ($t_{(12)} = 1.50$, $P = 0.158$) or pFs ($t_{(12)} = 0.03$, $P = 0.973$). Furthermore, the effect of better whole-part classification in upright than inverted faces was significantly larger in face- than in object-selective areas, as revealed by an interaction between ROI category (face areas, object areas) and orientation (Upright, Inverted) ($F_{1,8} = 6.12$, $P = 0.038$), and particularly larger in the FFA than in the OFA, as revealed by a marginal three-way interaction between ROI category, orientation, and region (extrastriate, fusiform) ($F_{1,8} = 4.15$, $P = 0.076$). These findings show that unlike the inversion effect for bodies that was found in both the body and object areas (Fig. 5), configural representation of faces was found for upright but not inverted faces only in the FFA. These findings are consistent with a previous study showing that the face inversion effect is specifically associated with the FFA but not the OFA or object areas (Yovel and Kanwisher 2005).

Body inversion. Face-selective areas showed no effects of body inversion on whole-part in percent signal change ($P > 0.394$) or classification accuracy ($P > 0.100$).

Discussion

Body-Selective Areas are Tuned to Whole-Body Configuration

Body perception has been shown to depend on the spatial configuration of the body in behavioral studies (Seitz 2002; Neri 2009; Ramm et al. 2010; Robbins and Coltheart 2012). Nevertheless, it has been unknown whether the neural representation of bodies is based on their spatial configuration or whether bodies are represented in a part-based manner. We therefore examined how first-order body configuration is represented in object category-selective cortex. Our findings reveal that body-selective areas prefer whole bodies over the sum of their parts and code the first-order configuration of bodies (Fig. 1) regardless of the presence of the head (Fig. 2).

This configural representation for whole bodies was found both in areas defined by selectivity for headless bodies and in areas defined by selectivity for body parts (Fig. 3). Importantly, this preference for whole-body configuration in body-selective areas does not reflect general preference or greater attention to the familiar body configuration, as no such preference was found in general object areas (Fig. 1). Furthermore, MVPA revealed that configural representation was found only for body stimuli in body-selective areas, whereas object areas were sensitive to configural information of both bodies and faces (Fig. 4). Compared with body areas, face-selective areas showed weaker sensitivity to configural information of bodies, and unlike body areas, were not sensitive to the configuration of headless bodies (Fig. 2). Altogether, these findings suggest that the tuning to whole-body configuration in body areas is a unique body-selective mechanism, not a result of general object processing mechanisms. On a broader level, our findings demonstrate a central role of first-order configuration in the neural representation of bodies.

The current study is the first to show that body areas prefer a whole body over the sum of its parts. This finding expands on a previous report by Taylor et al. (2007), who found a gradual increase in the selectivity of the EBA as a function of the amount of body shown, and a step-like increase in the selectivity of the FBA for larger body parts. Our current findings suggest that the response of both the EBA and FBA does not merely reflect an additive part-based response to multiple body parts, but rather a preferred response to whole-body configuration. Furthermore, whereas, in Taylor et al. (2007), the amount of body information varied between configurations, here we show that given the same amount of body information, the configuration itself is coded in both the EBA and FBA. Given that such configural representation was specific to body stimuli in these areas, our findings suggest that body-selective neural mechanisms are inherently configural.

Previous studies have reported body selectivity in the human brain both for whole bodies (with and without the head) (Downing et al. 2001; Peelen and Downing 2005; Schwarzlose et al. 2005; Taylor et al. 2007; Brandman and Yovel 2010) and for isolated body parts (Bracci et al. 2010; Chan et al. 2010; Op de Beeck et al. 2010; Orlov et al. 2010; Weiner and Grill-Spector 2010, 2011a, 2011b). Here, we show that not only areas selective for whole bodies, but also areas selective for isolated body parts, process the entire body layout and prefer whole-body configuration. Thus, while body-selective neural responses can be induced by body parts alone, the response of these areas to multiple body parts is strengthened by their arrangement into an intact body, suggesting that selectivity for body parts is secondary to the whole-body configuration. Notably, only small subregions of body part areas (10–14%), defined specifically by no selectivity for headless bodies, lacked the preference for whole-body configuration. Beyond these small clusters, the large overlap of areas defined with body parts and areas defined with headless bodies (Fig. 3C) suggests that body-selective mechanisms are, tuned to the spatial configuration of the whole body. A direct implication of these findings is that the preferred stimuli of occipital-temporal body-selective areas are whole or headless bodies, not body parts. Furthermore, these findings show that the definition of body selectivity so far, as stronger response to any body or body part stimuli than to nonbody stimuli, provides only a partial understanding of the nature of selective

mechanisms, as it does not necessarily reflect tuning to the preferred stimuli.

While configural processing of human bodies has been previously reported in behavioral studies, here we provide the first evidence for body-selective neural mechanisms that are tuned to whole-body configuration. Perceptual effects of first-order configuration have been demonstrated by better recognition of bodies in natural configuration than when limbs were displaced (Neri 2009; Ramm et al. 2010). Furthermore, a recent study showed that electrophysiological responses, specifically the N170, were enhanced by whole-body and face configuration compared with scrambled configuration (Soria Bauser and Suchan 2013). In the current study, we show that first-order body configuration is represented by body-selective neural mechanisms. Notably, both in previous studies manipulating first-order configuration as well as the current study, the displacement of limbs not only changed the configuration of the body but also eliminated some natural junctions between body parts, such as the junction between the arm and shoulder. The role of these junctions in the effects of part-scrambling of bodies remains open for future investigation.

Although our study only examined first-order configuration for body stimuli, behavioral studies also provide evidence for interactive processing between body parts (i.e., holistic processing), which cannot be directly inferred from part-scrambling of body configuration. Specifically, Seitz (2002) showed that body parts are recognized better in the context of the whole body than in isolation, similar to a whole-part effect that is well established for faces (Tanaka and Farah 1993). More recent reports show a composite effect (cf. Young et al. 1987) for bodies, in which recognition of one half of the body was affected by the other half when they were naturally aligned, but not misaligned (Robbins and Coltheart 2012). Taken together, these studies suggest that the visual processing of bodies engages cognitive mechanisms that are better tuned to the whole body than to its parts. Future studies should examine whether second-order configuration and holistic processing are also represented in body-selective areas, as was demonstrated for faces in face-selective areas (Schiltz and Rossion 2006; Axelrod and Yovel 2010).

Importantly, we show that the configural representation of bodies in body-selective areas reflects a unique body-selective mechanism. The configural representation of bodies that we found in body areas differed in 2 ways from the representation that was found in general object areas. First, unlike body areas that showed higher response to whole bodies than their sum of parts, object areas showed a nonsignificant trend of higher response to parts than wholes. Given that greater attention to objects alone may increase the response of category-selective areas to both preferred and nonpreferred stimuli (Haxby et al. 1999), these findings rule out the possibility that the preference for whole bodies in body areas reflect preference to familiar configuration or greater attention to familiar body configuration than the less meaningful scattered parts. Second, whereas object areas, in particular IO, decoded whole bodies from their sum of parts as much as body areas did, unlike body areas, object areas discriminated to the same extent whole faces from their sum of parts. Thus, object areas show general sensitivity to first-order configuration nonspecific to bodies, whereas body areas are tuned exclusively to body configuration.

The Effects of Inversion on Configural Representation of Bodies

Whereas the inversion effect for faces was attributed to configural processing of upright but not inverted faces (Young et al. 1987; Farah et al. 1998; Maurer et al. 2002; Tanaka and Farah 2003; McKone and Yovel 2009) and associated with face-selective neural mechanisms (Yovel and Kanwisher 2005; Mazard et al. 2006), the inversion effect for bodies was not found in body-selective mechanisms (Brandman and Yovel 2010). Consistent with these findings, our current results show that body inversion resulted in a decrease in discrimination of wholes versus sum of parts, which was similar in body- and object-selective areas (Fig. 5). Thus, the effect of body inversion is not specifically associated with configural body representation in body-selective areas, but rather reflects a general configural representation that is also found in object-general areas. This contrasts with our findings in face-selective areas, discussed in more detail below, which show that the effect of face inversion is a unique face-selective mechanisms reflecting stronger configural representation of upright than inverted faces in the FFA but not in body- or object-selective areas.

Discrimination of Whole Objects from Their Sum of Parts in the LOC

In addition to body- and face-selective mechanisms of configural processing, the current results may reveal general object representation of configural information in the LOC. Particularly, despite the lack of preference for wholes or parts in overall responses, multivariate pattern analysis revealed that object-selective areas coded the difference between whole stimuli and their sum of parts, similarly for bodies and faces (Fig. 4). Since this effect disappeared when bodies were inverted, we rule out the possibility that it was driven by sensitivity to single (whole) versus multiple (sum of parts) objects. Thus, our results suggest that the LOC represents information regarding the configuration of an object, nonspecific to category. This finding is related with previous studies showing configural object representation in the LOC (for review see Taylor and Downing 2011). Specifically, 2 studies showed that the response of the LOC was stronger for whole than for scrambled cars and faces (Lerner et al. 2001) and animal line drawings (Lerner et al. 2002). However, these effects were found for highly scrambled images that had lost much of their perceptual meaning. In contrast, here we compared the response to whole objects versus their sum of meaningful parts, as part-scrambled images maintained their perceptual integrity as body parts (head, limbs, torso, hip) and face parts (eyes, nose, mouth, hair, ears). Finally, it is important to note that while the LOC discriminated between whole bodies or faces and their sums of parts, it did not show a significant response-magnitude preference. This highlights the difference between the 2 types of information represented by response magnitude and response pattern in the occipital-temporal cortex, suggesting that whereas a preference for whole over sum of parts is found in specialized category-selective mechanisms for their preferred categories, pattern discrimination may reflect configural object information that is represented nonspecific to category in general object areas.

Configural Representation of Faces and Whole Bodies in Face-Selective Areas

The current study provides evidence not only for configural body processing in body areas, but also for configural face

processing in face areas. Specifically, we asked whether face-selective areas, similar to body-selective areas, are tuned to the first-order configuration of their preferred stimuli. We found that face-selective areas prefer a whole face over the sum of its parts and code the first-order configuration of faces. In addition, an interesting finding of this study confirms the role of body and head configuration in the activation of face-selective mechanisms. Although the internal facial features in the head of the body stimuli were completely covered, face-selective areas, and particularly the FFA, were tuned not only to the configuration of faces, but also to the configuration of bodies with heads (Figs 1 and 6). Specifically, face areas preferred whole bodies over their sum of parts and discriminated between them. However, these effects were abolished when the head was removed (Fig. 2). Thus, whereas body-selective areas were tuned to whole-body configuration regardless of the head, face-selective areas were tuned to an image of a head attached to a body, but not to whole-body configuration in general.

This response pattern of sensitivity to bodies with heads in face-selective areas corresponds with previous findings by Cox et al. (2004), showing higher response of the FFA to a faceless head attached to a body than to a faceless head presented beneath a body or in isolation. Furthermore, an inversion effect for whole bodies but not headless bodies was reported both in behavioral findings (Minnebusch et al. 2009; Yovel et al. 2010; Brandman and Yovel 2012) and in an fMRI study showing an fMR-adaptation inversion effect for whole but not headless bodies in face-selective areas (Brandman and Yovel 2010). Taken together with previous reports, our current findings support the hypothesis that face-selective mechanisms, and particularly the FFA, are activated by the contextual processing of a faceless head attached to a body. These findings suggest that studies interested in dissociating between face-selective and body-selective mechanisms should present headless bodies rather than whole bodies (with a faceless head), as the latter activate both body and face mechanisms.

The Effect of Inversion on Configural Representation of Faces

Unlike the effect of inversion on representation of body configuration, which was found in both body- and object-selective areas, configural face representation was reduced by inversion exclusively in face-selective areas but not in object areas. Particularly, the FFA was more sensitive to the configuration of upright than inverted faces, whereas the OFA and object areas similarly discriminated upright and inverted faces from their sums of parts (Fig. 7). This is consistent with a previous finding that the face inversion effect is specifically associated with the FFA and not with the OFA and object areas (Yovel and Kanwisher 2005). Importantly, the current study is a direct measure of configural processing and therefore is the first to provide direct support for the hypothesis that the face inversion effect is mediated by mechanisms of configural representation of upright but not inverted faces in the FFA.

Conclusions

Our results provide clear evidence for first-order configural processing of bodies in the occipital-temporal cortex. First, we have shown that body-selective areas, as defined with headless bodies or with body parts, show clear neural selectivity to

whole-body configuration. This configural representation was not found for whole faces and is therefore specific to body stimuli. Furthermore, we have shown that this configural body representation is specifically found in body-selective areas and does not extend to object or face-selective areas. The response of body-selective areas therefore reflects body-specific configural processing, not a general preference for whole-object configuration. Second, the configural representation of bodies was reduced for inverted bodies, yet this effect was not specific to body areas but also found in object-general areas, suggesting that the effect of body inversion does not reflect the operation of body-selective mechanisms. This contrasts with faces, for which the configural representation was reduced by inversion only in the FFA, indicating the specific face-selective mechanisms of face inversion. Third, unlike the specific configural representations that were found for faces and bodies in their category-selective areas, general object areas coded the difference between a whole object and the sum of its parts, non-specific to category. In sum, we suggest that body-selective neural mechanisms uniquely represent information about the spatial configuration of their preferred stimuli, and are specifically tuned to their intact configuration.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

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