Neural Correlates of Human Body Perception

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Abstract

■ The objective of this study was to investigate potential sex differences in the neural response to human bodies using fMRI carried out in healthy young adults. We presented human bodies in a block-design experiment to identify body-responsive regions of the brain, namely, extrastriate body area (EBA) and fusiform body area (FBA). In a separate event-related "adaptation" experiment, carried out in the same group of subjects, we presented sets of four human bodies of varying body size and shape. Varying levels of body morphing were introduced to assess the degree of morphing required for adaptation release. Analysis of BOLD signal in the block-design experiment revealed significant Sex × Hemisphere interactions in the EBA and the FBA responses to human bodies. Only women showed greater BOLD response to bodies in the right hemisphere compared with the left hemisphere for both EBA and FBA. The BOLD response in right EBA was higher in women compared with men. In the adaptation experiment, greater right versus left hemisphere response for EBA and FBA was also identified among women but not men. These findings are particularly novel in that they address potential sex differences in the lateralization of EBA and FBA responses to human body images. Although previous studies have found some degree of right hemisphere dominance in body perception, our results suggest that such a functional lateralization may differ between men and women. ■

INTRODUCTION

Significant sex differences exist in the perception and evaluation of one's own body. Women, when compared with men, demonstrate (a) greater overestimation of body size (Bergstrom, Stenlund, & Svedjehall, 2000), (b) greater sensitivity to changes in body size (Aleong et al., unpublished results), and (c) greater dissatisfaction with their bodies (Kostanski, Fisher, & Gullone, 2004; Rosenblum & Lewis, 1999; Wood, Becker, & Thompson, 1996). Several studies have also reported sex differences in desired (or ideal) body size, with women and men describing their ideal body size as, respectively, smaller or thinner (Williamson & Delin, 2001; Ambrosi-Randic, 2000; Tiggemann & Wilson-Barret, 1998; Brodie, Bagley, & Slade, 1994) or larger, leaner, and more muscular (Parkinson, Tovee, & Cohen-Tovee, 1998; Cohn et al., 1987) than their real body size.

On the basis of the above evidence of sex differences in body satisfaction and body-size perception, we set out to investigate the possible neural mechanism underlying sex differences in the perception of variations in body size and shape. Recently, a number of neuroimaging studies identified two regions in the extrastriate cortex that show greater response to human bodies and body parts compared with the neural response to objects, namely, the extrastriate body area (EBA) located in the lateral occipito-temporal cortex (Downing, Wiggett, & Peelen, 2007; Taylor, Wiggett, & Downing, 2007; Downing, Chan, Peelen, Dodds, & Kanwisher, 2006; Peelen & Downing, 2005b; Downing, Jiang, Shuman, & Kanwisher, 2001) and the fusiform body area (FBA) located in the lateral posterior fusiform gyrus (Peelen & Downing, 2005a; Schwarzlose, Baker, & Kanwisher, 2005). Transcranial magnetic stimulation and fMRI studies implicated EBA in the local processing of bodies, particularly that of individual body parts, regardless of whether the bodies are static (Taylor et al., 2007; Urgesi, Calvo-Merino, Haggard, & Aglioti, 2007; Urgesi, Candidi, Ionta, & Aglioti, 2007; Urgesi, Berlucchi, & Aglioti, 2004) or in motion (Downing, Peelen, Wiggett, & Tew, 2006; Grossman & Blake, 2002). Although FBA has been studied to a much lesser extent, fMRI studies have identified this region as distinct from other nearby functional regions including the fusiform face area (FFA) while showing selective responses to images of bodies and body parts (Schwarzlose et al., 2005). In comparing EBA and FBA responses to body images, Taylor et al. (2007) also reported that FBA may aide in the deciphering of body form through the configuration of individual parts into a whole body.

EBA has been consistently regarded as instrumental in the processing of the static body form. Nevertheless, the question remains as to whether EBA is responsive to subtle changes in the size of human bodies and whether this responsiveness depends on the sex of the observer. The two primary goals of this study were to investigate (a) whether EBA and FBA are responsive to changes in body size as determined by a release of the adaptation effect and (b) whether the neural response to human bodies and/or to changes in body size is different in men

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and women. To answer this question, we used an fMRI-adaptation paradigm, which is based on the premise that repeated presentation of an identical visual stimulus is associated with a reduction in the fMRI signal in a given neuronal population (Grill-Spector & Malach, 2001; Buckner et al., 1998; Stern et al., 1996; Martin et al., 1995). In our study, adaptation was induced through repeated presentation of an identical body. Recovery from adaptation was assessed after introducing subtle changes in body size and shape.

We also took advantage of the natural variations in the body mass index (BMI) in our sample to investigate whether the neural response to human bodies varies as a function of the observer's BMI. BMI is a measure that takes into account subjects' height and weight to provide a crude indicator of adiposity. In a previous behavioral study, we have observed that individuals with higher BMI show reduced sensitivity to changes in body size (Aleong et al., unpublished results). Given these findings, we predicted that individuals with high BMI would have lower EBA and FBA responses to bodies.

Our results provide evidence of a significant relationship between an observer's sex and BMI and the neural response to human bodies as well as evidence of EBA and FBA sensitivity to subtle changes in body size and shape. Our study is particularly novel in that we are among the first to examine the functional characteristics of EBA and FBA using an adaptation paradigm and report significant sex differences in hemispheric asymmetry in EBA and FBA responses to human body images.

METHODS

Subjects

All protocols were granted approval by the Ethics Committee of the University of Nottingham Medical School. Adult volunteers were recruited using advertisements posted at the University of Nottingham. Upon initial contact, subjects were screened for (a) past and present diagnosis of a neurological, psychiatric, or behavioral disorder; (b) past or presently prescribed medications that may affect brain function (e.g., antidepressants); and (c) MRI contraindications.

Subjects who fulfilled the initial screening criteria were then asked to come to the laboratory for a single testing session lasting approximately 3 hr. Informed consent was obtained from all participants. Subjects then completed the computerized quick Diagnostic Interview Schedule Screening Instrument (Bucholz et al., 1991) that was used to screen them for psychiatric, neurological, and behavioral disorders, including anorexia nervosa, bulimia nervosa, depression, anxiety disorders, and substance abuse disorders. Upon completion, subjects viewed a brief practice session of the task used in the fMRI-adaptation experiment.

A total of 21 subjects (11 men, 10 women) were tested, but three subjects (2 men, 1 woman) were subsequently excluded due to excessive head motion during scanning (1 man), faulty MRI acquisition (1 man), and positive symptoms for an eating disorder (1 woman). Of the remaining 18 eligible subjects (9 men, 9 women), the mean age and BMI were as follows: men, 23.7 years (range = 19–32 years, *SEM* = 1.4 years) and 22.7 kg/m^2 (range = 18.7–30.4 kg/m^2, *SEM* = 1.1 kg/m^2); women, 23.4 years (range = 20–27 years, *SEM* = 0.9 years) and 20.7 kg/m^2 (range = 18.5–22.4 kg/m^2, *SEM* = 0.4 kg/m^2). Independent samples t tests revealed no significant differences between men and women for either age or BMI, $p > .1$.

All but one (woman) of the subjects were right-handed and had normal or corrected-to-normal vision. None of the subjects tested positive for a psychiatric, neurological, or behavioral disorder as indicated by the Diagnostic Interview Schedule Screening Instrument.

Brain Imaging

All brain imaging was completed using a 1.5-T Phillips Achieva scanner (Eindhoven, Netherlands). An initial high-resolution T1-weighted structural image (matrix = 160 × 256 × 256; 1 mm^3 voxels) was acquired for all subjects for localization and registration purposes with the functional data. A series of BOLD T2*-weighted gradient-echo, echo-planar images were then acquired. Two different functional acquisitions were used, respectively, for the rapid event-related design adaptation experiment and block-design experiment. All subjects completed the adaptation experiment first, followed by the block-design experiment.

Rapid Event-related Body Size Adaptation Experiment

The aim of the adaptation experiment was to assess whether EBA and FBA were sensitive to changes in body size as determined by a release of the adaptation effect. In addition, we wished to determine the level of body morphing required to trigger such a release of adaptation. BOLD images were acquired using the following parameters: matrix size = 64 × 64; echo time = 50 msec; repetition time = 1500 msec; slice thickness = 4 mm; and voxel size = 4 × 4 × 4 mm. A total of 159 nineteen-slice volumes were collected for each run after the gradients had reached steady state (acquisition time of 28 min).

Subjects were presented with a series of real and morphed body images derived from the Adolescent Body-Shape Database (AdoBSD; Aleong, Duchesne, & Paus, 2007). Real body images (front view) were distorted by manipulating the size and shape of various identified body parts using a preselected principal component (PC4) with levels of distortion defined by the standard deviation (*SD*) of the mean of the PC (Aleong et al., 2007). PC4-derived morphing (e.g., 0.1, 0.2, 0.3, 0.4 *SD*) involved predominantly the hips, the thighs, and the calves.

The experiment involved a total of 364 trials divided into seven separate runs, each run lasting 3 min and 57 sec.

Trial order was randomized across all runs. A single trial consisted of four body images each presented for 200 msec with 100 msec of blank screen following each body image, for a total of 1200 msec. After each trial, one of three intertrial intervals, namely, 1800, 3300, or 4800 msec, was randomly used. During the intertrial interval, a white fixation cross appeared on the screen (Figure 1). Body images were presented at a visual angle of approximately 2.5° × 5° (width × height).

To maintain the subject's attention during the scan, we used an incidental task that required the subject to detect changes in the contrast of either a body or the fixation cross. These events occurred only rarely (3 of 52 trials in a given run). The extent of the change was demonstrated to the subjects during the practice session. Images positive for a contrast change were dimmed by 30% using Adobe Photoshop 7.0 (Adobe Systems Incorporated, San Jose, CA). The dimmed body image was randomly selected to be the second, third, or fourth image in a trial. Similarly, the fixation cross was dimmed for an equal duration as a body during a trial. Subjects were instructed to press, with the right hand, a button of an MRI-compatible button box as quickly as possible when they detected a change in image contrast.

A total of seven types of trials (conditions) were used in the adaptation experiment: (1) identical, (2) different, (3) 0.1 morphing, (4) 0.2 morphing, (5) 0.3 morphing, (6) 0.4 morphing, and (7) fixation. Fifty-two repetitions of each condition were included in the experiment for a total of 364 trials. The identical trial/condition consisted of four identical real body images, all of the same AdoBSD adolescent. The different condition consisted of the real body images of four different AdoBSD adolescents of the same sex. The four morphing conditions involved the presentation of two real body images and two morphed body images, all of a single AdoBSD adolescent (e.g., two real images + two 0.4-morphed images). The order of the four morphed images was randomized within each trial. The fixation condition involved the continuous presentation of a fixation cross for the duration of the trial.

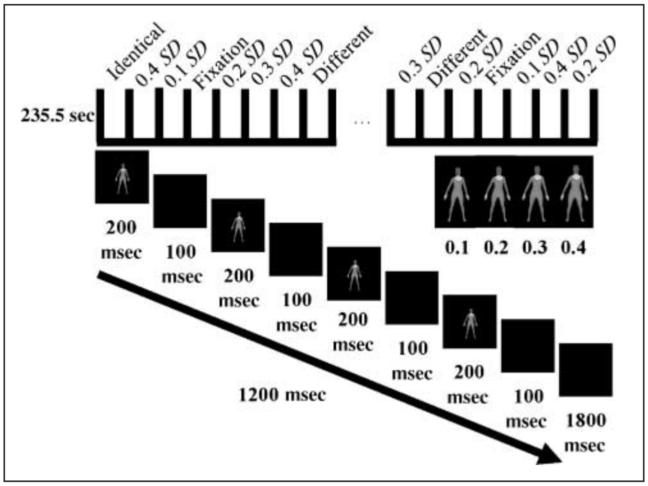


Figure 1. Rapid event-related adaptation experiment. The experiment was conducted to establish whether EBA and FBA are sensitive to changes in body size and shape. Subjects were randomly presented with a total of 364 trials divided into seven separate runs (i.e., 52 trials/run). Each trial consisted of four randomly presented body images conforming to one of seven testing conditions. For the identical and different conditions, four identical and different undistorted body images were presented, respectively. For each of the four morphing conditions (e.g., 0.1 *SD*, 0.2 *SD*, 0.3 *SD*, 0.4 *SD*), two real bodies and two morphed bodies were randomly presented. Subjects were instructed to indicate when they detected a change in image contrast.

For the identical and the morphed conditions, the images of 26 different adolescents from the AdoBSD (13 boys, 13 girls) were used. Male and female AdoBSD adolescents were age matched (five 15-year-olds; six 16-year-olds; two 17-year-olds) and were selected to reflect older age ranges so as to present the most adult-like images. Body images were presented in the front view only. Given the positive range (*SD*) of morphing conditions, morphed body images were larger than the real body images. Each of the 26 AdoBSD adolescents was presented twice across the four morphing and identical conditions for a total of 260 trials.

For the different condition, the images of 18 different adolescents from the AdoBSD (9 boys, 9 girls) were used. Four AdoBSD adolescents (4 boys or 4 girls) were selected randomly for each trial. Again, boys and girls were age matched (five 15-year-olds; three 16-year-olds; one 17-year-old). Unlike the adolescents used for the identical and morphed conditions, the height differences between the adolescents used for the different condition were controlled. In presenting the real images of these different AdoBSD adolescents, we wished to minimize the natural height differences between the AdoBSD images and, therefore, preselected the nine male and nine female AdoBSD adolescents so that the maximum height differential did not exceed the maximum height difference between a real body image and a 0.4 morph (i.e., 4% of height; 62 pixels). Fifty-two different trials were presented along with 52 fixation trials and 260 morphing/identical trials resulting in a grand total of 364 trials.

Block-Design Experiment

The primary goal of this experiment was to localize body-responsive (i.e., EBA and FBA) cortical regions in each subject. The block-design experiment was completed for each subject during which BOLD images were acquired using the following parameters: matrix size = 64 × 64; echo time = 50 msec; repetition time = 3000 msec; slice thickness = 4 mm; and voxel size = 4 × 4 × 4 mm. A total of eighty-two 32-slice volumes were collected after the gradients had reached steady state (acquisition time of 25 min).

Subjects were presented with real body images derived from the AdoBSD (Aleong et al., 2007), emotionally neutral human faces derived from a set of standardized face stimuli by Schneider, Gur, Gur, and Muenz (1994) and Erwin et al. (1992) and scrambled versions of the same body and face stimuli. The experiment consisted of six runs with 16 blocks per run. Block types included human bodies, human faces, scrambled human bodies, scrambled human faces, and fixation. Within each run, block order was pseudorandomized with three minisets of blocks, each set containing one block per condition followed by a final block of fixation. Within each miniset, the five blocks were randomized (Figure 2). Each 15-sec block was composed of 20 presentations of a given stimulus. Body, face, and scrambled images were each presented on the screen for 300 msec followed by a blank screen for 450 msec. During fixation, a cross was presented in the middle of the screen for 750 msec. All body images were presented at a visual angle of approximately 2.5° × 5° (width × height).

For the blocks of human bodies, 20 real body images of adolescents from the AdoBSD (10 boys, 10 girls) were randomly selected from those AdoBSD adolescents ranging in age from 16 to 17 years. Similarly, for the blocks of human faces, 20 emotionally neutral faces (10 men, 10 women) were randomly selected. The same 20 body images and 20 faces were used in all body and face blocks, but the image order was completely random within each block. These body and face images were scrambled using a Matlab-based script (A. Mignault, personal communication, March 28, 2007) that divided an image into approximately 325 and 525 image squares, respectively (10 × 10 pixels per square). The location of the image squares were then randomly sorted creating a scrambled image. As in the adaptation experiment, an incidental task was used to maintain subjects' attention. In this case, 2 of the 20 images (in each block) were randomly selected to contain a red circle in one of nine physical locations overlaying the image. Subjects were instructed to press, with the right hand, a button when they detected the presence of the red circle.

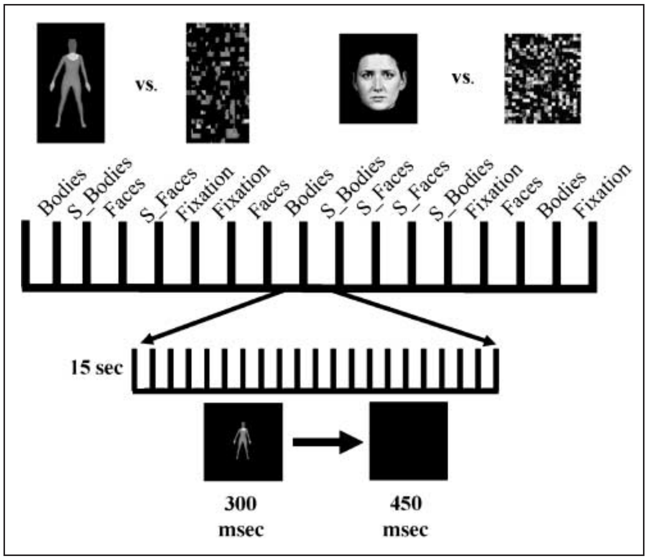


Figure 2. Block-design experiment. The experimental protocol was used to identify body-responsive (i.e., EBA, FBA) brain regions for each subject. Subjects were presented with blocks of images representing five different conditions [i.e., bodies, scrambled bodies (s_bodies), faces, scrambled faces (s_faces), fixation]. Six runs were completed by each subject with each run consisting of 16 pseudorandomized condition blocks. Each condition block was composed of 20 images of the respective condition. Subjects were asked to indicate when a red circle appeared on the screen.

Behavior: Body Discrimination Task

After completion of the fMRI experiments, subjects were asked to perform a task outside the scanner. The design of the task was identical to the rapid event-related adaptation experiment. This time, however, subjects were asked to indicate whether the four bodies in a single trial were the same or different.

Analysis

Image Processing

All images were first assessed for head motion and functional images underwent motion correction and low-pass filtering using in-house correction tools (fmr_preprocess. runs: R. Hoge, 1996). Images were then smoothed spatially using a 6-mm FWHM Gaussian filter. All functional images were realigned to the third frame of the first run of the event-related experiment. All statistical analyses were completed using fmristat, a Matlab-derived (The Mathworks, Natick, MA) toolbox (Worsley et al., 2002). A model of each experimental design was created and convolved with a hemodynamic response function to generate experimental time-series (Glover, 1999).

For each run, a general linear model with correlated errors was used to calculate regression coefficients for every voxel. Initially, autocorrelation parameters were calculated for each voxel and then smoothed spatially using a 15-mm FWHM Gaussian filter. The linear model was then reestimated to produce estimates of effects and standard errors (Worsley et al., 2002). Multiple runs within task and within subject were combined using a fixed-effects analysis and subsequently transformed into a common standardized space (MNI 305; Collins, Neelin, Peters, & Evans, 1994). t statistic maps were created for each individual for the following subtractions in our analysis of the block-design and event-related adaptation experiments: block design—bodies minus scrambled bodies and faces minus scrambled faces; adaptation—different minus fixation, 0.1 morph minus fixation, 0.2 morph minus fixation, 0.3 morph minus fixation, 0.4 morph minus fixation, and identical minus fixation.

Individual multirun t statistic maps (bodies minus scrambled bodies) were then overlaid on individual high-resolution T1-weighted anatomical images to identify, in each subject, stereotaxic coordinates of EBA and FBA in standardized space. Localization of EBA and FBA was completed in accordance with previously published reports of relevant anatomy and mean coordinates in standardized space (Downing, Chan, et al., 2006; Peelen & Downing, 2005b; Downing et al., 2001) and through the use of established brain atlases (Duvernoy, 1999; Talairach & Tournoux, 1988). We anticipated EBA and FBA to be localized, respectively, within the lateral occipito-temporal cortex and lateral posterior fusiform gyrus. A minimum *t* value of 2.0 was used for the identification of EBA and FBA in each subject. We used this less stringent criterion for localizing these regions in each subject in light of the strong responses in these regions in the group average *t* statistic maps (see below) and the a priori nature of our hypotheses. Although faces and scrambled faces were used as stimuli categories, our primary hypotheses involved body perception, and for that reason, the face data will not be discussed further.

Once individual coordinates of EBA and FBA were identified from the block-design experiment, these peak voxel coordinates were used as the center of a sphere (5-mm radius) from which mean percent change in BOLD signal was extracted from the comparison of bodies minus scrambled bodies for each subject. The same EBA and FBA coordinates determined in the block-design experiment were then used to extract percent change in BOLD signal from each subject's rapid event-related adaptation subtractions.

Average group *t* statistic maps for the comparison bodies minus scrambled bodies were generated by combining the individual multirun *t* statistic maps transformed into standardized space using a mixed-effects model, as defined by the multistat function in the fmristat toolbox. The mixed-effects model refers to an analysis that was midway between a fixed-effects and random-effects model in which the final degrees of freedom of the effect was arbitrarily set equal to 100 to minimize smoothing bias (Worsley et al., 2002). The group *t* statistic maps were thresholded at a p value of 0.05 (t statistic of 5.08) corrected for multiple comparisons. Average group *t* statistic maps were overlaid onto a group anatomical image that was generated by averaging individual T1-weighted anatomical images previously transformed into standardized space (MNI 305; Collins et al., 1994).

Percent BOLD Change Statistics

In the analysis of the block-design experiment, a repeated measures ANOVA was completed with percent change in BOLD signal as the dependent variable, observer's sex as the between-subjects factor, and cerebral hemisphere as the within-subjects factor. Separate ANOVAs were completed for EBA and FBA. Repeated measures ANOVAs were also used to investigate percent change in BOLD signal extracted from the adaptation subtractions, with percent change in BOLD signal as the dependent measure, sex as the between-subjects factor, and hemisphere and condition (i.e., different minus fixation, 0.1 morph minus fixation, 0.2 morph minus fixation, 0.3 morph minus fixation, 0.4 morph minus fixation, identical minus fixation) as the within-subjects factors. All post hoc analyses were corrected for multiple comparison using a Bonferroni correction. Given the significant age and the BMI results described in our previous behavioral study of adolescent body perception (Aleong et al., unpublished results), we conducted exploratory analyses using age and BMI as covariates in separate ANCOVA analyses.

Behavior: fMRI Scanning

As described above, subjects were asked to indicate the presence of a red circle or a change in image contrast during the block-design and event-related adaptation experiments, respectively. In examining subject performance, we assessed the following dependent variables: (a) hits, (b) misses, (c) false positives, and (d) RT. Separate independent samples *t* tests were completed with subject sex as the fixed factor for each of the dependent variables.

Behavior: Body Discrimination Task

Subjects performed a same–different discrimination task after fMRI scanning was completed. Repeated measures ANOVAs were used to examine subject performance with the mean percentage of different responses or RT as the dependent measure, condition (i.e., identical, 0.1 morph, 0.2 morph, 0.3 morph, 0.4 morph, different) as the within-subjects factor, and sex as the between-subjects factor. Post hoc analyses were corrected using the Bonferroni correction.

RESULTS

Bodies versus Scrambled Bodies

As shown in Figure 3, we observed a significantly higher BOLD response to human bodies, as compared with scrambled bodies, at several locations in the extrastriate cortex and fusiform gyrus (Table 1). These locations correspond to the previously identified EBA (Downing, Chan, et al., 2006; Downing, Peelen, et al., 2006; Peelen & Downing, 2005b; Downing et al., 2001) and FBA (Peelen & Downing, 2005a; Schwarzlose et al., 2005). Additional anatomical locations that showed significant BOLD response are listed in Table 1.

In examining individual functional data, EBA was present in the left and right hemisphere for all 18 subjects. In contrast, left or right FBA were found in only 16/18 subjects. The EBA and the FBA responses (i.e., percent change in BOLD signal in the bodies-minus-scrambled-bodies subtraction) were quantified in each subject. Repeated measures ANOVAs revealed significant Hemisphere × Sex interactions for EBA, $F(1,16) = 6.8$, $p < .05$, and

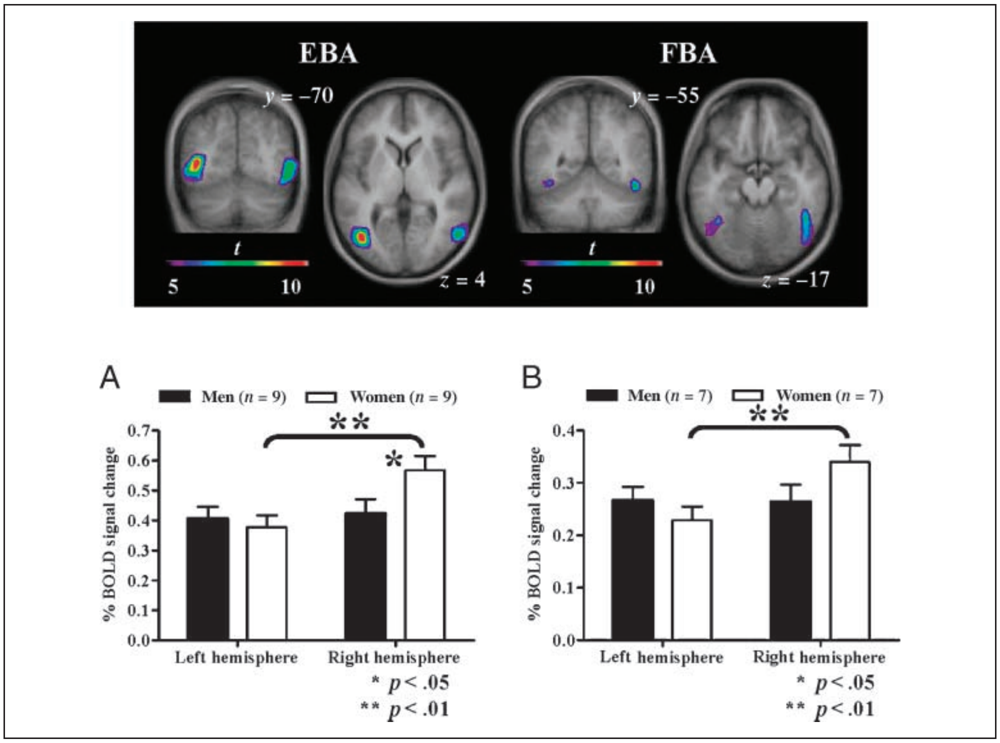


Figure 3. EBA and FBA response to human body images. Average group t statistic maps for the comparison of bodies minus scrambled bodies revealed significant BOLD response in bilateral EBA and FBA. Percent change in BOLD signal was extracted from a sphere (5-mm radius) centered at each subject's EBA and FBA coordinates for the subtraction of bodies minus scrambled bodies. Repeated measures ANOVAs were completed separately for EBA and FBA. Significant Sex × Hemisphere interactions were detected for both EBA (A) and FBA (B), $p < .05$. Women demonstrated a greater right than left hemisphere response for EBA and FBA, $p < .01$, as well as greater right EBA response compared with men, $p = .05$.

FBA, $F(1,12) = 7.2$, $p < .05$. Simple main effects analysis revealed that women showed greater response in the right than left hemisphere for both EBA and FBA, $p < .01$ (Figures 3A and 3B). In addition, women demonstrated greater response than men in the right EBA, $p = .05$. All simple main effects and post hoc analyses were corrected for multiple comparison using the Bonferroni correction.

Exploratory analyses revealed no significant main effect or interaction effects with respect to subject age for EBA or FBA, $p > .1$. No main effect of subject BMI was found with respect to the BOLD response in EBA or FBA, $p > .2$. A significant interaction between hemisphere and BMI, however, was identified for EBA, $F(1,14) = 7.9$, $p < .05$. Further examination of the data revealed that subjects with relatively large BMI were generally men. To address this potential confounding effect of subject sex, separate analyses were conducted for male and female groups. A laterality index (LI) was calculated for men and women [LI = (Right EBA %BOLD signal change − Left EBA %BOLD change) / Right EBA %BOLD signal change] and subsequently correlated with observer BMI. Significant correlations were found for both men, $r = -0.881$, $p < .01$ (Figure 4A) and women, $r = -0.733$, $p < .05$ (Figure 4B). Thus, the results indicate that reduced right hemisphere dominance was associated with higher BMI values.

Adaptation Effects

We used the individual coordinates of EBA and FBA, identified in the block-design experiment, to quantify the BOLD response in each subject's multirun t statistic maps obtained for each of the adaptation-related subtractions. Repeated measures ANOVAs revealed a significant main effect of hemisphere for both EBA, $F(1,16) = 6.5$, $p < .05$ (Figure 5A), and FBA, $F(1,12) = 6.4$, $p < .05$ (Figure 6A), with the right hemisphere showing greater BOLD response than the left hemisphere. This is consistent with the findings obtained in the block-design experiment, as described above. Although the Sex × Hemisphere interactions for EBA, $F(1,16) = 1.3$, $p = .3$, and FBA, $F(1,12) = 3.2$, $p = .1$, were not significant, post hoc analyses were conducted in light of the strong Sex × Hemisphere interactions observed in the block-design experiment. Post hoc comparisons with Bonferroni correction revealed that women, and not men, showed greater BOLD response in the right

Table 1. Stereotaxic Coordinates of Regions with Significant BOLD Response in the Comparison of Human Bodies versus Scrambled Human Bodies

		Coordinates			
Region	*Hemisphere*	*x*	*y*	*Z*	*t*
Middle occipital gyrus (EBA)	L	−43	−70	4	10.0
	R	55	−68	−3	8.4
Fusiform gyrus (FBA)	L	−40	−55	−17	6.4
	R	48	−51	−21	8.2
Superior parietal gyrus	L	−30	−60	51	5.5

versus left hemisphere in both EBA and FBA, $p < .05$ (Figures 5B and 6B).

A significant effect of condition was also identified in both EBA, $F(5,80) = 23.1$, $p < .001$, and FBA, $F(5,60) = 8.8$, $p < .001$. Pairwise comparisons with Bonferroni correction for multiple comparisons revealed a clear adaptation effect in both regions; significant differences between the different fixation and the identical fixation conditions were observed, $p < .001$. EBA also showed a greater sensitivity to changes in body size and shape: No significant differences were detected between the identical, the 0.1, and the 0.2 conditions, $p > .9$. The BOLD signal at the 0.3 and the 0.4 morphing conditions was higher relative to the 0.2 and the 0.1 conditions, $p < .01$, but lower relative to the different condition, $p < .01$. These progressive increases in BOLD response and significant signal recovery at the 0.3 morphing level reflect a clear sensitivity to small changes in the size and shape of the body images (Figure 5C).

In the case of FBA, adaptation effects were also observed (Figure 6C). A recovery from adaptation was identified at the 0.3 morphing level, $p < .05$. No significant differences were identified between the identical, the 0.1, and the 0.2 conditions, $p > .9$. The BOLD signal at the 0.3 and the 0.4 morphing conditions did not differ significantly from the 0.1 and the 0.2 conditions, $p > .06$, nor from the different condition, $p > .4$, indicating that FBA showed reduced sensitivity to body size changes when compared with EBA.

A main effect of subject age was found across hemispheres and morphing conditions for EBA only, $F(1,14) = 7.3$, $p < .05$. Subject BMI was also related to the BOLD response across hemispheres for EBA, $F(1,14) = 4.6$, $p < .05$, and FBA, $F(1,10) = 5.5$, $p < .05$. A significant Hemisphere × BMI interaction was found for EBA only, $F(1, 14) = 5.0$, $p < .05$. As described for the block-design experiment, separate BMI analyses were conducted for men and women. Correlation of the LI index with observer BMI across all six subtractions revealed a significant negative correlation for men, $r = -0.722$, $p < .05$ (Figure 4C), and a near-significant correlation for women, $r = -0.612$, $p = .08$ (Figure 4D). Thus, like in the block-design experiment, individuals of higher BMI showed reduced right-hemisphere dominance.

Behavior: fMRI Scanning

Mean performance scores for the red circle and the image-contrast detection tasks are listed in Table 2. Independent samples *t* tests revealed no significant differences between men and women for any performance variable for both

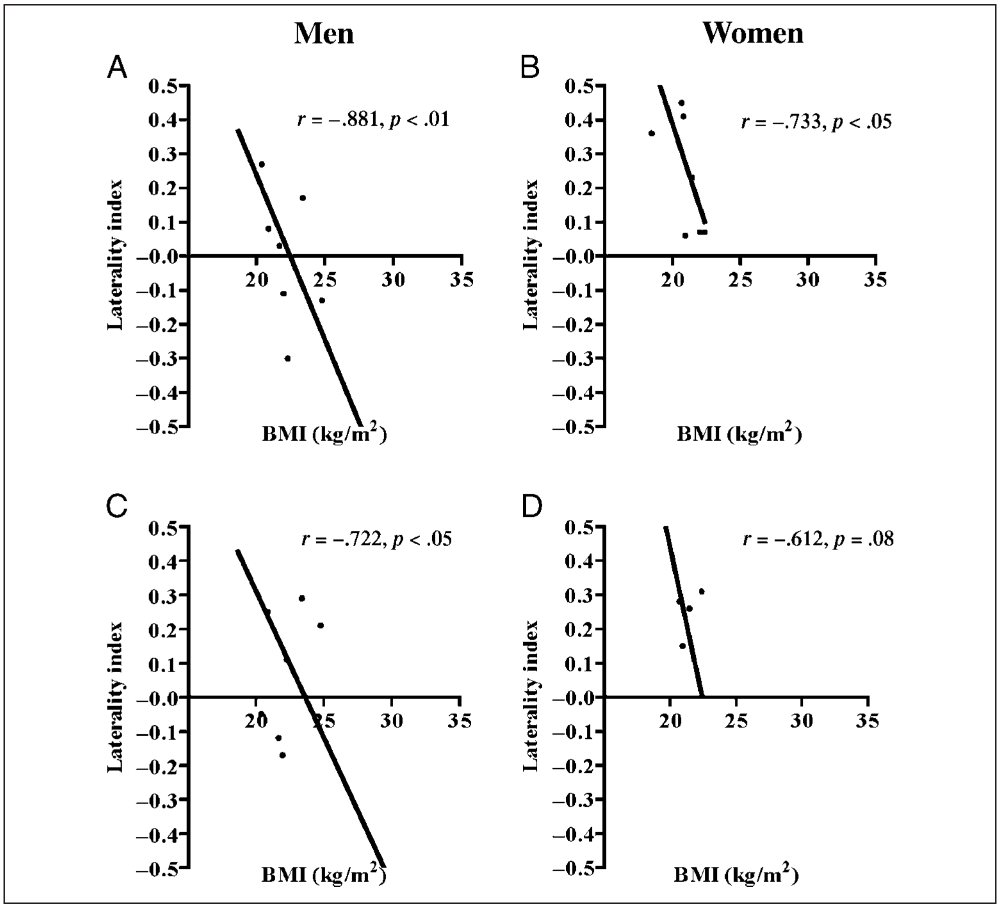
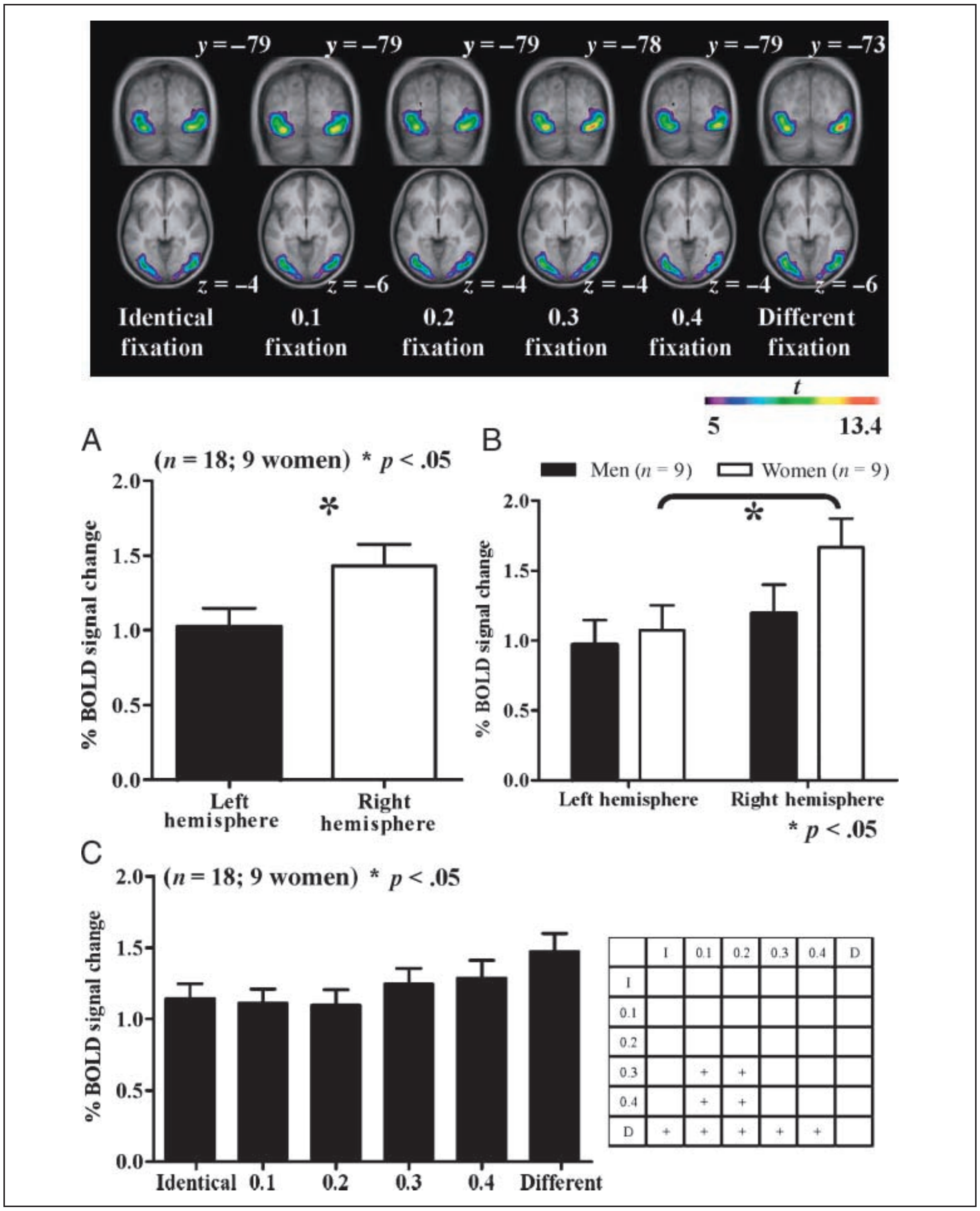


Figure 4. Influence of observer BMI on the perception of human bodies. An LI was calculated for men and women for both the block-design and the adaptation experiments. Significant negative correlations were found between observer BMI and LI for men (A) and women (B) for the block-design experiment as well as the men (C) and women (D) for the adaptation experiment. Thus, individuals of higher BMI showed reduced right hemisphere dominance in their response to human body images.



	I	0.1	0.2	0.3	0.4	D
I						
0.1						
0.2						
0.3		+	+			
0.4		+	+			
D	+	+	+	+	+	

Figure 5. EBA adaptation results. Percent change in BOLD signal was extracted from EBA coordinates derived from the block-design experiment for each subject. A repeated measures ANOVA revealed significant main effects for brain hemisphere (A), $p < .05$, and body-morphing condition (C), $p < .001$. Greater right EBA BOLD response was identified compared with left EBA, $p < .05$. Post hoc analyses revealed that women, but not men, showed a greater right versus left EBA response (B), $p < .05$. A significant adaptation effect was observed as evidenced by a significant reduction in BOLD signal for the identical-fixation condition compared with the different-fixation condition, $p < .001$. A significant recovery from adaptation was also found at the 0.3 *SD* morphing level, indicating that EBA was sensitive to changes in body size and shape. The associated table (C) indicates significant differences between the various body-morphing conditions, $p < .05$.

the red circle ($p > .4$) and the image-contrast ($p > .2$) detection tasks.

Behavior: Body Discrimination Task

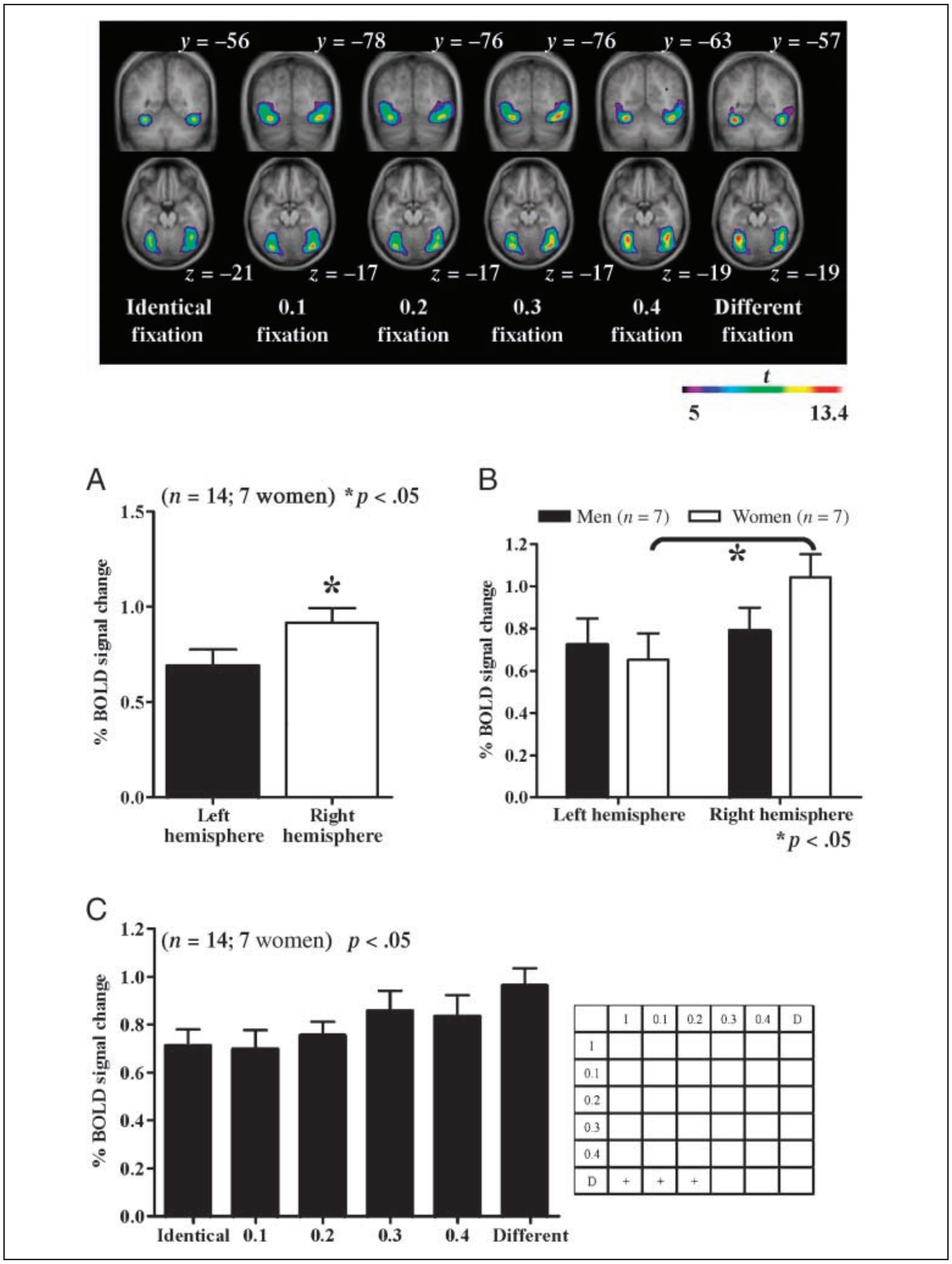
Separate repeated measures ANOVAs revealed significant main effects of condition for both RT, $F(5,80) = 13.0$, $p < .001$, and percent "different" responses, $F(5,80) = 171.2$, $p < .001$. Pairwise comparisons with Bonferroni correction for multiple comparisons revealed significant differences between conditions for mean percent "different" responses with an increasing number of "different" responses with increasing degree of morphing, $p < .01$ (Figure 7A). Similarly, pairwise comparisons demonstrated that the mean RTs for the 0.4 morph and different conditions were significantly lower than for the other conditions, $p < .05$ (Figure 7B). We found no effect of Sex or Sex × Condition interaction, $p > .2$.

DISCUSSION

Our study revealed that female, but not male, observers exhibited greater response in the right than left hemisphere to images of human bodies for both EBA and FBA; this finding was obtained in both block-design and adaptation experiments. EBA and FBA showed a clear recovery from adaptation following the introduction of small changes in body size and shape, thus arguing in favor of a fine-grained neural mechanism underlying the perception of human bodies involving these two regions. EBA showed greater sensitivity to human bodies compared with FBA, as indicated by the ability of EBA to discriminate between 0.3 and 0.4 conditions relative to the different condition. Observers' BMI also modulated the hemispheric effects in both experiments; women with larger BMI showed no difference in the BOLD response between left and right EBA, whereas men with low BMI did show hemispheric asymmetry in EBA response.

It is important to note that subjects were not asked to make any explicit judgments about the body images; incidental tasks were used instead to ensure participants' attention during the presentation of the stimuli. With no differences in subject performance having been observed, we conclude that attention was sufficiently maintained by both sexes.

A key finding of our study is the *sex difference* in the hemispheric asymmetry of EBA and FBA responses to images of human bodies. Overall, the presence of such hemispheric asymmetry is consistent with a number of previous studies. Note, however, that none of the studies mentioned below examined possible sex differences in brain asymmetry. Previous fMRI studies have described greater consistency in the localization of right EBA (Downing et al., 2001), greater selectivity for bodies in right EBA compared with left EBA (Downing, Chan, et al., 2006), and greater whole-body selectivity in the right hemisphere compared with the left hemisphere (Downing et al., 2007). Distortion of the body form, such as displacing an arm or



	I	0.1	0.2	0.3	0.4	D
I						
0.1						
0.2						
0.3						
0.4						
D	+	+	+			

Figure 6. FBA adaptation results. Percent change in BOLD signal was extracted from FBA coordinates derived from the block-design experiment for each subject. A repeated measures ANOVA revealed a significant main effect of hemisphere (A) with greater right versus left FBA response, $p < .05$. Post hoc analyses revealed that women, but not men, showed a greater right versus left FBA response (B), $p < .05$. A significant main effect of condition (C) was also found, $p < .001$. A significant reduction in BOLD signal was detected upon presentation of identical bodies when compared with the presentation of different bodies, $p < .001$. A recovery from adaptation was found at the 0.3 *SD* level, $p < .05$. The associated table (C) indicates significant differences between the various body-morphing conditions, $p < .05$.

Table 2. fMRI—Behavioral Results

	Block-Design Experiment				*Adaptation Experiment*			
	Men		*Women*		*Men*		*Women*	
	Mean	*SEM*	*Mean*	*SEM*	*Mean*	*SEM*	*Mean*	*SEM*
Hits	98.6	0.4	98.1	0.9	87.8	6.1	84.7	2.8
Misses	1.5	0.4	1.9	0.9	12.2	6.1	15.3	2.8
False positives	0.05	0.02	0.06	0.02	0.8	0.4	2.3	1.0
RT (msec)	443.0	18.1	455.4	14.8	654.5	89.3	594.5	20.3

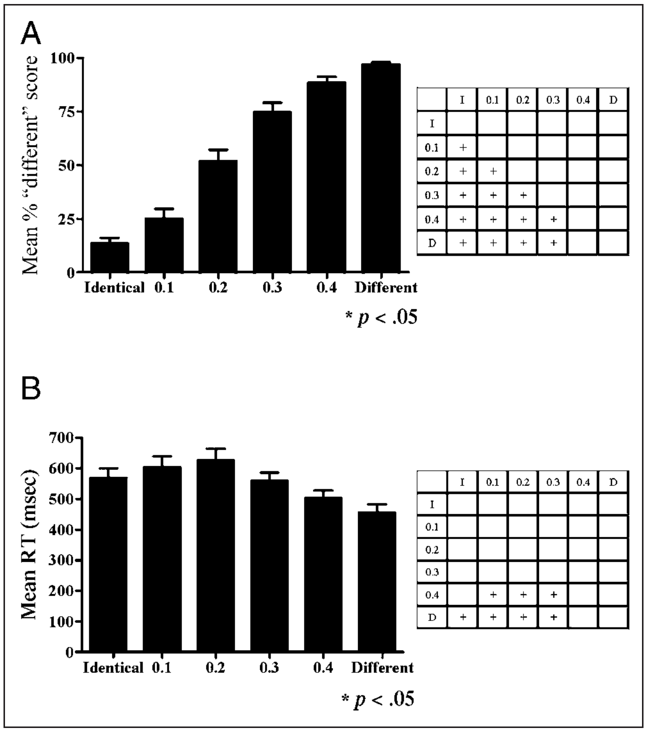
leg onto the neck, resulted in a greater reduction of the N1 amplitude recorded over the right versus left hemisphere (Gliga & Dehaene-Lambertz, 2005).

Hemispheric differences have also been described in patients with brain damage and patients with eating disorders (Frassinetti, Maini, Romualdi, Galante, & Avanzi, 2008; Uher et al., 2005). Patients with lesions in the right hemisphere showed significantly greater deficits in self–body part matching when compared with those with left hemisphere lesions and with controls (Frassinetti et al., 2008). In response to real and distorted body shapes, healthy women and women with eating disorders showed stronger and/or more extensive BOLD response in the right, compared with left, EBA (Uher et al., 2005).

Some clues as to the functional significance of greater right EBA and FBA engagement may be derived from face-perception studies, which have described right hemisphere dominance in the FFA response to faces (Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996). A case has been made regarding the potential similarities between the perception of human faces and bodies, as both types of stimuli are biologically important classes of objects that show behavioral inversion effects (Reed, Stone, Grubb, & McGoldrick, 2006; Reed, Stone, Bozova, & Tanaka, 2003; Farah, Tanaka, & Drain, 1995; Valentine, 1988; Yin, 1969) and are processed in category-selective brain regions (Downing et al., 2001, 2007; Downing, Chan, et al., 2006; Peelen & Downing, 2005a; Schwarzlose et al., 2005; Kanwisher et al., 1997; McCarthy et al., 1997; Puce et al., 1996; Puce, Allison, Gore, & McCarthy, 1995). Hemispheric differences in face perception (i.e., greater right than left hemisphere) may be explained, in part, by face configuration and familiarity. The right FFA showed greater response when matching whole faces compared with face parts, whereas the left FFA demonstrated the reverse pattern (Rossion et al., 2000). In addition, right FFA and occipital face area exhibited greater levels of activity for unfamiliar versus familiar faces (Rossion, Schiltz, & Crommelinck, 2003).

The role of configuration and familiarity, as described in face perception, may also be relevant for hemispheric differences in body perception. For example, EBA showed a gradual increase in selectivity as a function of the number of body parts displayed, indicating that EBA may code for body parts more so than for the whole body (Taylor et al., 2007). The right EBA dominance that we observed in women may, therefore, be representative of sex differences in the relative sensitivity to individual body parts.

All body image stimuli used in the block-design and adaptation experiments were of unfamiliar bodies presented



	I	0.1	0.2	0.3	0.4	D
I						
0.1	+					
0.2	+	+				
0.3	+	+	+			
0.4	+	+	+	+		
D	+	+	+	+		

	I	0.1	0.2	0.3	0.4	D
I						
0.1						
0.2						
0.3						
0.4		+	+	+		
D	+	+	+	+		

Figure 7. Body discrimination behavioral results. Subjects were asked to perform a behavioral task following fMRI acquisition. The design of the behavioral task was identical to the fMR-adaptation experiment, but subjects were asked to indicate if the four bodies presented in a single trial were the same or different. Repeated measures ANOVAs revealed significant main effects of body-morphing condition for the percentage of different responses (A), $p < .001$, and RT (B), $p < .001$. An increasing number of "different" responses were identified with increasing body morphing, $p < .01$. Subjects also responded faster with the 0.4 *SD* and different body conditions, $p < .05$. The associated tables (A and B) indicate significant differences between the various body-morphing conditions, $p < .05$.

from an allocentric viewpoint. Previous studies reported a greater right EBA response to allocentric body images when compared with egocentric body images (Saxe, Jamal, & Powell, 2006; Chan, Peelen, & Downing, 2004). Left EBA, in contrast, failed to distinguish between the two image perspectives (Saxe et al., 2006; Chan et al., 2004). Thus, greater right EBA activity may be related, in part, to the viewpoint of the bodies used.

The more robust response to human bodies present in right EBA in women, but not men, may represent a neural substrate of the sex differences in the perceptual and cognitive processes described previously. For example, we found greater overestimation of body size and greater detection sensitivity to changes in body size when comparing female with male adolescents (Aleong et al., unpublished results). Others found that women, but not men, show an increased bias in identifying bodies as fatter than their real body size when presenting body images in the left visual field (Mohr, Porter, & Benton, 2007). Previous neuroimaging studies of sex differences in the response to human bodies focused mostly on emotional processing and used explicit tasks involving words related to body image (Shirao, Okamoto, Mantani, Okamoto, & Yamawaki, 2005) or images of bodies (Kurosaki, Shirao, Yamashita, Okamoto, & Yamawaki, 2006). In these studies, brain regions such as the amygdala and the prefrontal cortex showed a differential response in women and men (Kurosaki et al., 2006; Shirao et al., 2005).

The results of our rapid event-related experiment also support the proposal that EBA and FBA may be involved in the neural processing of human body size, as we observed significant adaptation effects and, most importantly, recovery from adaptation with subtle changes in body size. We found that EBA was more sensitive to changes in the size and shape of human bodies because EBA, and not FBA, was able to distinguish between the 0.3, 0.4, and different conditions.

Sensitivity to object size has been explored previously in object-specific brain regions, including the monkey inferotemporal complex (Ito, Tamura, Fujita, & Tanaka, 1995; Logothetis, Pauls, & Poggio, 1995; Desimone, Albright, Gross, & Bruce, 1984; Schwartz, Desimone, Albright, & Gross, 1983; Sato, Kawamura, & Iwai, 1980) and the human lateral occipital cortex and FFA (Ewbank, Schluppeck, & Andrews, 2005; Sawamura, Georgieva, Vogels, Vanduffel, & Orban, 2005; Vuilleumier, Henson, Driver, & Dolan, 2002; Grill-Spector et al., 1999; Malach, Grill-Spector, Kushnir, Edelman, & Itzchak, 1998; Malach et al., 1995). Although previous studies have reported a mixed pattern of size invariance in lateral occipital cortex, particularly in response to faces, we described a clear sensitivity to human body size in the body-responsive regions of EBA and FBA. This specific divergence in size variance suggests that human bodies may be a special category of objects for which sensitivity to body size is necessary. Processing of body size in EBA and FBA may permit greater efficiency in interacting with the external environment through the positioning of one's body relative to another body or the assessment of external threats.

The different recovery patterns demonstrated by EBA and FBA in the adaptation experiment are also consistent with previous neuroimaging results describing differential responses of EBA and FBA as a function of the amount of body figure visible to the observer (Taylor et al., 2007). We described a greater EBA sensitivity to changes in body size when compared with FBA. Similarly, Taylor et al. (2007) described a gradual increase in response by EBA as the amount of body visible increased; FBA showed a more step-like increase in response when torsos were presented. The authors proposed that EBA is biased toward the representation of individual body parts and shows greater selectivity for individual body parts compared with FBA, which preferentially represents larger portions of the human body (Taylor et al., 2007). In light of this hypothesis, our results may be indicative of EBA processing of changes in the body size of individual parts, whereas FBA may process larger scale changes in body size.

One additional finding was that of a significant interaction between observer BMI and EBA response in both experiments. This finding should be interpreted with caution due to the low variability in BMI among our participants and the relatively low number of subjects. Nevertheless, men and women with higher BMI showed reduced hemispheric asymmetry in the BOLD response of EBA. This result is consistent with our previous behavioral study in which we observed a negative correlation between subject BMI and detection sensitivity for body-morphing changes (Aleong et al., unpublished results). Functional neuroimaging results have also revealed weaker responses in EBA among women with an eating disorder compared with healthy women (Uher et al., 2005). In addition, men with low BMI did show greater hemispheric asymmetry in EBA response, indicating that men with low BMI show similar perceptual patterns of response to human bodies when compared with women of lower BMI.

In our study, individuals of relatively healthy BMI were shown images within the same range of their own BMI. Furthermore, presented body images did not reflect subjects' own bodies. Thus, one must question whether individuals with relatively high BMI failed to show any hemispheric asymmetry in EBA response merely because the presented body images did not match the size and shape of their bodies. Or could this BMI-modulated suppression effect in the perception of human bodies be linked to differences in emotional/motivational investment regarding human bodies between obese and healthy individuals? To investigate these issues, future experiments must use larger scale changes in body size and shape as well as image stimuli that match the observer's BMI and measure potential differences in the top–down attentional modulation of perceptual processes between obese and healthy groups.

Our findings may also offer some insight into the underlying neural mechanisms of eating disorders. As EBA and FBA are sensitive to subtle changes in body size, future studies of patients with eating disorders should explore EBA and FBA as potential sources of neural dysfunction in this clinical population. Furthermore, the demonstrated hemispheric asymmetry in the neural response to human body images in women may provide some insight into the greater incidence of anorexia and bulimia nervosa in women as compared with men.

In conclusion, our study offers direct evidence of the influence of cerebral hemisphere, sex, and BMI on the perception of human bodies. Women showed (a) greater response to human bodies in the right versus left EBA and FBA and (b) greater right EBA response compared with men. Both EBA and FBA are sensitive to changes in body size with EBA showing greater sensitivity than FBA. Observer BMI modulated the response of EBA to human bodies. Application of our methodology among adolescents, patients diagnosed with an eating disorder, or obese individuals could prove helpful in identifying developmental trends and neural underpinnings of the perception of human bodies.

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