Title: Gender differences in the neural underpinning of perceiving and appreciating the beauty of the body

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Abstract:

Although previous studies have suggested a certain degree of right hemisphere dominance for the response of extrastriate body area (EBA) during body perception, recent evidence suggests that this functional lateralization may differ between men and women. It is unknown, however, whether and how gender differences in body perception affect appreciating the beauty of the body conspecifics. Here, we applied five 10-Hz repetitive transcranial magnetic stimulation (rTMS) pulses over left and right EBA and over the vertex to investigate the contribution of visual body representations in the two hemispheres on esthetic body perception. Female and male healthy volunteers were requested to judge how much they liked opposite- and same-gender virtual model bodies or to judge their weight, thus allowing us to compare the effects of right- and left-EBA rTMS on esthetic (liking) and perceptual (weight) judgments of human bodies. The analysis of the esthetic judgments provided by women revealed that right-EBA rTMS increased the liking judgments of opposite- vs. same-gender models, as compared to both vertex and left EBA stimulation. Conversely, in men the liking judgments of opposite-gender models decreased after virtual disruption of both right and left EBA as compared to vertex stimulation. Crucially, no significant effect was found for the perceptual task, showing that left- and right-EBA rTMS did not affect weight perception. Our results provide evidence of gender difference in the hemispheric asymmetry of EBA in the esthetic processing of human bodies, with women showing stronger right hemisphere dominance in comparison with men.

Keywords: Extrastriate body area; Transcranial magnetic stimulation; body perception; esthetic judgments.

1. Introduction

The human brain is tuned to rapidly detect bodily cues from conspecifics and this perceptual categorization process is reflected in body-selective occipito-temporal regions (Hietanen & Nummenmaa, 2011). From an evolutionary perspective, the perceptual 'highway' for processing bodily cues seems to be highly beneficial for triggering sexual behaviour and subsequently guaranteeing mating and reproduction (Deaner, Khera & Platt, 2005; Grammer et al., 2003). Compatible with this view, we may expect that esthetic evaluation of the body of conspecifics plays a vital role for our survival. This raises a key question on what is relevant in the esthetic judgements of human bodies for successful mate selection and reproduction. Identification of mating partners in primates mainly relies on the visual system, with respect to other sensory modalities (Ghazanfar & Santos, 2004). However, evidence on the neural underpinning of perceiving and appreciating the beauty of the body of conspecifics has remained elusive.

Repetitive transcranial magnetic stimulation (rTMS) and neuroimaging studies have established that a specialized brain network involving the occipital and temporal cortices subserves perception of bodies in humans (Urgesi, Candidi et al., 2007; Urgesi, Calvo-Merino et al., 2007; de Gelder et al., 2010; Minnebusch & Daum, 2009; Peelen & Downing, 2007). In particular, extrastriate body area (EBA) located at the posterior inferior temporal sulcus/middle temporal gyrus (Downing et al., 2001) and the fusiform body area located at the ventro-medial temporal cortex (Peelen & Downing, 2007) display a highly selective activity for visual presentations of human bodies. These areas respond selectively to photorealistic depictions of whole human bodies or body parts, still images of human bodies or body parts extending to 'stick figures' and silhouettes, in preference to human faces, images of object parts and scenes (Downing et al., 2004; 2006; Peelen & Downing, 2007; Urgesi, Berlucchi & Aglioti, 2004).

Interestingly, recent findings have shown that visual body representations are crucially involved during esthetical appreciation of body stimuli (Freedberg & Gallese, 2007). For example, Di Dio et al. (2007) found stronger neural activity in the lateral occipital cortex for images of whole-body statues obeying the ‘Golden section’, a principle of spatial proportion traditionally felt to be beautiful, than for statues not following this principle. Cross et al. (2011) reported a greater activation of EBA during observation of the dance moves that participants rated as both more pleasing and more difficult to reproduce. Crucially, only one study used rTMS to interfere with EBA during esthetic preference judgements of static postures of dance moves (Calvo-Merino et al., 2010). The results of this study showed that rTMS interference with either left or right EBA had a detrimental effect on the consistency of participants’ esthetic judgments across multiple sessions, thus blunting esthetic judgments about body postures. The authors interpreted these results within the framework of a ‘dual-route’ model of visual body perception (Urgesi, Calvo-Merino et al., 2007), which suggests that EBA may be involved in the local processing of the details of human body parts, while other regions, including the fronto-parietal cortex and FBA may be involved in configural body processing. In this view, the results of Calvo-Merino et al. (2010) may suggest that disruption of the local processing system, housed in EBA, blunts esthetic sensitivity, while interference with the global processing system (i.e., premotor and parietal areas) tends to heighten esthetic sensitivity. Importantly, Calvo-Merino and colleagues (2010) did not find any hemispheric lateralization effect, thus proposing that both left and right EBA contributed in a similar manner to esthetic body processing. However possible gender difference effects were not explored in that study and, thus, it could not be established whether different lateralization patterns of EBA involvement in esthetic body perception occur in male and female observers.

Recent evidence suggests that the gender of the observer may influence the lateralization of EBA response to human body images. Aleong and Paus (2010) showed that healthy women exhibited greater response to human bodies in the right vs. left EBA and greater right EBA response compared with men. The right and left hemispheres may have complimentary roles in visual body representation and their relative involvement may be different in women and men. A behavioral study of Mohr and colleagues (2007) showed that unilateral presentation of self-body images in the left visual hemi-field, which projects first to the right hemisphere, resulted into an overestimation bias in women, but not in men. These findings suggest a role of right hemisphere body representation in the development and maintenance of body image distortions in women and may shed light on the neural mechanisms of eating disorders (EDs), seen that higher prevalence of this psychiatric disorder is in women than in men. Accordingly, recent findings suggest that structural and functional alteration in the EBA in EDs patients might explain the body size misjudgement in this clinical population (Suchan et al., 2010; 2013).

To our knowledge, no studies have so far investigated the causative role of visual brain regions in the esthetic appreciation of the body of same- vs. opposite-gender individuals. Crucially, it is unknown whether the differences in the functional lateralization of body perception in men and women may extend into appreciating the beauty of the body of conspecifics. Thus, we sought to investigate: a) the active contribution of right (rEBA) and left EBA (lEBA) on esthetic vs. perceptual judgments of human bodies; b) the potential differences between men and women in the hemispheric asymmetry of EBA during perceiving and appreciating the beauty of the body. To answer these questions, we applied brief trains of rTMS (10 Hz, 500 ms) over lEBA and rEBA to investigate their relative role in perceptual and esthetic body processing. Stimulation of the vertex served as control condition. **In keeping with a previous study of Calvo-Merino et al. (2008) which first**

reported that only 'liking–disliking' may be a fundamental dimension of aesthetic experience, with more clear and consistent neural correlates, we focused on the subjective esthetic dimension of like–dislike judgments rather than on the objective dimension of beautiful-non-beautiful ratings (Calvo-Merino et al. 2010; Cross et al., 2011; Cattaneo et al., 2013). Furthermore, we extended previous Neuroesthetic works by using systematic variations of virtual body' size which have shown group-average aesthetic evaluations in a previous experiment of our research group (Cazzato, Siega, & Urgesi, 2012; Mele, Cazzato, & Urgesi, 2013). This group average of all subjects' liking ratings revealed a preference for more thinner and dynamic stimuli. Finally, a recent fMRI study of Holliday and colleagues (2011) showed that EBA can be modulated by artificially produced body-shaped stimuli with varying weight. Thus, in the same way, we considered group-consensus on a body dimension (weight) which is specifically related to EBA activity rather than relying on the personal esthetic judgements of each individual (Calvo-Merino et al., 2008, 2010; Cross et al., 2011; Cattaneo et al., 2013).

We asked female and male healthy volunteers to judge how much they liked the body of opposite- and same-gender conspecifics (virtual avatars) rendered in different body figures. Moreover, in a further task, volunteers were required to express weight judgments about the virtual models, thus allowing us to compare the effects of rEBA and lEBA on esthetic (liking) and perceptual (weight) judgments of human bodies. According to Aleong and Paus (2010), we anticipated a greater right hemisphere dominance of EBA involvement in both perceptual and esthetic judgments of human bodies among women than among men. Furthermore, we controlled for the relationship between the hemispheric lateralization of EBA and variations of participants' body mass index (BMI). BMI is a measure of human body weight based on individual's weight and height (Kg/m^2). Several studies have suggested that the BMI of an individual is an important factor in how both men and women perceive physical attractiveness (Tovée et al., 2000; George et al., 2003). Furthermore, since higher BMI values are observed in men than women, considering this confounding variable is crucial when testing gender differences in body perception. Aleong and Paus (2010) reported that men and women with higher BMI showed reduced hemispheric asymmetry in the response of EBA. Given these findings, we controlled that any gender differences in the hemispheric lateralization of esthetic body perception was due to differences in the BMI of men and women or was independent from it. **Finally, we controlled if the hemispheric lateralization of EBA was related to gender differences in body dissatisfaction, internalization of Western ideals and personality dimensions associated with EDs.**

2. Materials and methods

2.1 Participants

A total of 24 students (12 women, range: 19-31 years; 12 men, range: 21-31 years) from the University of Udine participated in the experiment in return for course credits. Participants were naïve as to the purposes of the experiment and information about the experimental hypothesis was provided only after the experimental tests were completed. All subjects but one man were right-handed as ascertained by means of a Standard Handedness Inventory (Briggs & Nebes, 1975). They were native Italian speakers of Caucasian race; all participants reported heterosexual orientation. All reported normal or corrected to normal vision, all were in good health, free of psychotropic or vasoactive medication, with no past history of psychiatric or neurological disease and with no contraindication to rTMS (Rossi et al., 2009). To further detect subclinical body image and eating disorders, at the end of the experiment, participants filled four questionnaires: 1) the Eating Disorder Inventory-2 (EDI-2, 11 scales; Garner, Olmstead, & Polivy, 1983) to investigate the psychological and behavioral characteristics associated with ED; 2) the Body Attitude Test (BAT-20, 4 scales; Probst et al., 1995) to measure the individual's subjective body experience and attitudes towards one's own body; 3) the Body Shape Questionnaire (BSQ-34, 1 scale; Cooper et al., 1987) to assess the degree of body dissatisfaction and 4) the Sociocultural Attitudes Toward Appearance Questionnaire-3 (SATAQ-3; 4 scales; Stefanile et al., 2011) to measure multiple aspects of societal influence as the degree of mass media internalization of the models. Furthermore, we estimated participants' BMI from self-report measures of weight (Kg) and height (cm). The participants' demographics and self-report questionnaire scores as a function of gender are reported in Table 1. Independent sample t-test indicated that BMI was significantly higher in men than in women. However, the two groups were matched for age and self-report standard clinical scales with the exception of the internalization-athlete SATAQ-3 subscale, indicating that men compared to women had a stronger internalization of media influences related to the achievement of an athletic physique. Participants gave their written informed consent and the procedures were approved by the ethics committee of the Scientific Institute (IRCCS) 'E. Medea' and were in accordance with the ethical standards of the 1964 Declaration of Helsinki.

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2.2 Stimuli

Participants were presented with a series of virtual human models that were taken from previous studies of our group (Cazzato et al., 2012; Mele et al., 2013). These were two females and two males (Alyson, Sydney, James and Torno) previously selected from a database of six-dimensional adult body stimuli, created by means of Poser Pro 2010 (e-frontier, Santa Cruz, CA). The models were pictured standing against a grey background and wearing identical underwear black clothing. Photorealistic textures were applied and the images rendered with global illumination. In order to avoid the influence of facial features, the pictures were imported into Adobe Photoshop 7.0 (Adobe System Inc. CA; http://www.adobe.com) and a circle region around the face was

scrambled. Each model was rendered in four different postures viewed from a frontal or three-quarter perspective. Furthermore, the widths of the bodies were progressively increased or decreased to create moderate to extreme levels of round and thin figures. These body stimuli were previously evaluated by a large number of participants that were required to express weight and liking judgments of each stimulus (Cazzato et al., 2012). The results of this study showed a parametric correspondence between the intended manipulation of body weight and the perceptual judgments of participants who rated the stimuli as varying from extremely thin to extremely round. Furthermore, participants expressed higher liking judgments for thin than round body stimuli.

2.3 Tasks Procedure

The experiment was created with E-Prime software (version 2.0, Psychology Software Tools, Inc., Pittsburgh, PA) and it consisted initially of the requests for the participants' demographic details, followed by brief written task instructions and, finally, by the rating scale trials. Each trial started with the appearance of a black central fixation cross presented on a grey light background. After 500 ms, an image depicting a male or female model appeared for 150 ms at the centre of the screen subtending a visual angle of approximately 12° × 10°. Then, the stimulus was replaced by a visual noise mask for 500 ms. Tachistoscopic presentation of the stimulus was used to avoid recursive exploration of its details and to ensure, on the one hand, that the responses were based on initial perception of the stimulus and, on the other, that short trains of rTMS could have maximal interference effects with its visual processing. In two different blocks, a visual prompt 'How much do you like the model?' (*Quanto ti piace il modello?* in Italian), for the esthetic task, or 'How round is the model?' (*Quanto ritieni che il modello sia grasso?*), for the perceptual task, appeared on the top of the screen. The question was presented along with a vertical, 10-cm VAS ranging from 'I like it very much' (*Mi piace molto*; score = 100) to 'I do not like it at all' (*Non mi piace per* *niente*, score = 0) for the esthetic task and from 'very round' (M*olto grasso*, score = 100) to 'not round at all' (*Per nulla grasso*, score = 0) for the perceptual task (see Figure 1). The up- and down-ward position of the anchor words of the VAS was balanced across participants and was always presented for each question. Each participant was tested in a single experimental session lasting about 2 hours. Participants completed two 4-trial practice blocks, respectively one for the esthetic and the other for the perceptual task, before proceeding to the experimental blocks. During the experimental session, two blocks of 32 trials each were presented for each stimulation site (lEBA, rEBA, vertex): one block required the esthetic task and one the perceptual task. The order of task and stimulation site was counterbalanced across participants. Each stimulus was presented once in a single block, with random presentation of male and female models, round and thin figures rendered in different postures. No time limit was fixed for the response, but participants were required to express their ratings as quickly as possible. Each participant provided a total of 192 VAS ratings.

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2.4 TMS

Each subject's resting motor threshold (rMT) was determined by placing the TMS coil over primary motor cortex and was defined by the minimum single pulse intensity required to produce a visible twitch on more than 5 of 10 consecutive trials in the hand contralateral to the site of stimulation. rTMS was administered with 70-mm figure-of-eight stimulation coil (Magstim Double 70mm Air Film Coil), connected to a Magstim SuperRapid2 Stimulator (The Magstim Company, Carmarthenshire, Wales), producing a magnetic field up to 0.8 T at the coil surface. Although there is no clear relation between the intensities needed to stimulate the motor and visual cortices, we set the stimulation intensity on the basis of the rMT since this is considered as a safety way to reduce the possible discomfort and adverse effects of rTMS (Rossi et al., 2009) and the diffusion of neural alteration to distant sites

(Speer et al., 2003). Thus, we decided to estimate rMT on the safe side by recording from the dominant hand (with left hemisphere stimulation in most participants), which was expected to provide lower and more reliable rMT values as compared to non-dominant hand muscles. The rMT values ranged from 45% to 60% (53.17 ± 1.7%) of the maximum stimulator output in women and from 45% to 60% (51.25 ± 1.44%) in men, with no significant differences between the two groups [$t_{(22)} = 0.86$, $p = 0.4$]. In the experimental conditions, stimulation intensity was 110% of the rMT. The target areas were located on each participant's scalp with the SofTaxic Navigator system (EMS, Bologna, Italy). Coordinates in Talairach space (Talairach & Tournoux, 1988) were automatically estimated by the SofTaxic Navigator from a magnetic resonance imaging-constructed stereotaxic template. EBA coordinates were corresponding to Brodmann's area 37 in the posterior part of the middle temporal gyrus (lEBA: x =-52, y = -72, z = 4; rEBA: x = 52, y = -72, z = 4) and were taken from a previous rTMS study on the role of EBA in visual esthetic body perception (Calvo-Merino et al., 2010) (See Figure 2). As a control site, the vertex was stimulated with the induced current running from posterior to anterior along the interhemispheric fissure (x = 0, y = -44, z = 69).

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During stimulation, the coil was held using a coil holder and was kept tangential to the scalp, with the handle pointing backward and, for EBA stimulation, at a ± 45° angle from the axial axis of the participants' head. A train of five 10 Hz rTMS pulses was delivered, starting at 150 ms after the onset of the image. The rTMS pulses were timed to interfere with the cortical processing of the image (see Urgesi, Berlucchi, & Aglioti, 2004; Urgesi, Candidi et al., 2007; Urgesi, Calvo-Merino et al., 2007). The same pulse delay and stimulation intensity was used for the three stimulation sites. During stimulation, participants wore commercial earplugs to protect their hearing. None of the participants reported limb muscle twitches or phosphenes due to rTMS, suggesting that we did not inadvertently allow stimulation to spread to either primary motor or visual cortex. Stimulation occasionally induced peripheral activation of facial muscles, and some jaw movements or blink responses were observed in most participants as a result of stimulation. Since the rTMS trains were presented 50 ms after the offset of the stimulus, blinking would not prevent the participants from seeing it.

2.5 Data handling

Statistical analyses were run with STATISTICA 8.0 (StatSoft Inc, Tulsa, Oklahoma). The mean VAS score (in mm) for each cell of the design (16 trials per cell) were calculated for each stimulation condition for each participant. To control for the residual effects of BMI and internalization-athlete SATAQ-3 subscale differences between women and men, we entered liking and weight VAS scores in a full-factor 4-way 2×2×3×2 analysis of covariance (ANCOVA) design, with the between-subjects factor observer's gender (women, men) and task (esthetic, perceptual), rTMS site (lEBA, rEBA, vertex), and model's gender (same, opposite) as within-subject variables; the individual observer's BMI and internalization-athlete SATAQ-3 subscale were added as covariates since the two groups were different on these variables. The source of all significant repeated-measure ANOVA interactions was analyzed using the Duncan post-hoc test. A significance threshold of $p < 0.05$ was set for all effects. Effect sizes were estimated using the partial eta square measure (η_p^2). All data are reported as Mean (*M*) and Standard Error of the Mean (*s.e.m.*). **Furthermore, Pearson correlation coefficients were computed to investigate the relationship between the absolute values of a laterality index (LI) for males and females [LI = (abs(rEBA – vertex))- (abs(lEBA – vertex))] of the effects of EBA stimulation relative to esthetic and perceptual judgments of human body and observer's BMI and standard clinical scales. The Pearson's r coefficient between the individual absolute LI values of esthetic and perceptual judgments and scores on the clinical scales were calculated with Bonferroni correction procedure to control for multiple correlations (22 correlations).**

3. Results

After controlling for the observers' BMI and SATAQ-3 internalization-athlete subscale scores as covariates [all $Fs_{(1,21)}$<1], the ANCOVA on the VAS judgments revealed a significant 2-way interaction between observer's gender and model's gender [$F_{(1,20)} = 6.808$; $p = 0.017$; $\eta_p^2 = 0.254$], a significant 3-way interaction observer's gender × model's gender × rTMS site [$F_{(2,40)} = 5.737$; $p = 0.006$; $\eta_p^2 = 0.223$], further qualified by a significant interaction between all the three repeated-measure variables and the between-subjects factor (observer's gender × model's gender × rTMS site × task: [$F_{(2,40)} = 4,176$; $p = 0.023$; $\eta_p^2 = 0.173$]). Since the VAS judgments were largely different for the two tasks, to better spot the effects of this high-level interaction, we run two separate 3-way repeated-measure analysis of variance (ANOVA) for the esthetic and perceptual tasks, separately.

3.1 Esthetic Task

The ANOVA on the esthetic judgments revealed a significant 2-way interaction of model's gender × rTMS site [$F_{(2,44)} = 4.009$; $p = 0.025$; $\eta_p^2 = 0.154$], further qualified by a significant 3-way interaction of observer's gender × rTMS site × model's gender [$F_{(2,44)} = 5.361$; $p = 0.008$; $\eta_p^2 = 0.196$]. Duncan post-hoc comparison showed that, during vertex stimulation, both women and men gave higher liking VAS judgments to opposite- than to same-gender models (all $ps < 0.021$). Crucially, in women rEBA-rTMS increased the liking judgments of opposite-gender models (51.23 ± 2.24) as compared to both vertex (47.22 ± 2.58; $p = 0.019$) and lEBA stimulation (45.36 ± 2.37; $p = 0.001$). No effect was found for same-gender models (all $p > 0.493$). Conversely, in men the liking judgments of opposite-gender models decreased after virtual disruption of both rEBA (41.53 ± 2.24) and lEBA (44.04 ± 2.37) as compared to vertex stimulation (48.02 ± 2.58; and $p < 0.001$ $p = 0.024$ respectively for rEBA and lEBA; See Figure 3**A**). No difference was found between rEBA and lEBA conditions for opposite-gender models ($p = 0.17$); nor did we find any difference between the three stimulation conditions for same-gender models (all *ps* > 0.05). In sum, the results suggest a selective interference of rEBA stimulation with the esthetic judgments of opposite-gender models in women, while in men both rEBA and lEBA stimulations affected the esthetic judgments of opposite-gender models. Thus, we found in women but not in men a strong right-hemisphere lateralization of the active role of EBA in esthetic judgments. These effects were specific for the esthetic judgments of opposite-gender models, as no interferential effects were observed after rEBA or lEBA-rTMS for same-gender models. **No significant correlation was found between LI and Observers' BMI and self-report clinical scale (women: $-0.573 < rs < 0.617$; *ps-corr* > 0.719; men: $-0.449 < rs < 0.514$; *ps-corr* > 1), thus suggesting that increased right hemisphere dominance in women than in men, relatively to the esthetic preference of opposite- and same-gender models is not associated with observers' BMI or body image concerns.**

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3.2 Perceptual Task

The ANOVA on weight judgments revealed that only the 2-way interaction of observer's gender × model's gender was highly significant [$F_{(1,22)} = 12.863$; $p = 0.002$; $\eta_p^2 = 0.369$]. Duncan post-hoc comparisons demonstrated that, while women gave higher weight VAS scores to same- than to opposite-gender models (47.66 ± 2.35 vs. 43.1 ± 2.58, $p = 0.014$), men judged as rounder opposite- than same-gender models (50.40 ± 2.58 vs. 46.7 ± 2.35, $p = 0.042$). This effect reflects that the female models were considered rounder by both male and female observers. Crucially, rTMS over lEBA and rEBA did not affect the VAS weight judgments of opposite- or same-gender virtual model bodies, as demonstrated by the non-significant 3-way interaction of observer's gender × model's gender × rTMS site: $F_{(2,44)} = 1.080$; $p = 0.348$; $\eta_p^2 = 0.047$ (Figure **3B**). No other effects resulted significant (all *F*s < 1.9, $p > 0.176$, $\eta_p^2 < 0.07$). **No significant correlation was found between the LI of perceptual**

judgments of same- and opposite-gender model and Observers' BMI and self-report clinical scale nor in women (-0.449<rs<0.514; *ps-corr* > 1) neither in men (-0.608<rs<0.546; *ps-corr* > 0.791).

4. Discussion

The present study used rTMS to investigate the contribution given to the esthetic appreciation of human bodies by processing in EBA, a region that is well-known to be involved in selective aspects of visual body processing. Crucially, we compared the degree of hemispheric lateralization of EBA in the esthetic and perceptual judgments of human bodies in male and female observers. We also controlled that any gender difference in the hemispheric lateralization of the contribution of EBA to perception and esthetic appreciation of body stimuli might be related to the observers' BMI, which is known to be higher in men than in women, **together with personality dimensions associated with EDs.**

At baseline, both women and men expressed higher liking VAS scores for opposite- than same-gender models, thus showing esthetic preference for the body of opposite-gender conspecifics. This is not surprising, since a basic evolutionary problem is how to choose a partner and the body plays a vital role in 'mate selection'. Relative to this, considerable evidence has been accumulated supporting the notion that both facial and bodily physical attractiveness are 'health certifications' and thus represent honest signals of phenotypic and genetic quality (Grammer et al., 2003). From this perspective, the esthetic evaluation of human body, and in particular of the body of individuals of the opposite gender (in heterosexual individuals), has a particular importance for our survival, being strictly connected with reproductive behavior (Cela-Conde et al., 2009; Dixson, A., Dixson, B., & Anderson, 2005). Accordingly, previous studies have shown greater brain responses to opposite than same-gender bodies involving in particular those electro- (Hietanen &

Nummenmaa, 2011) or magneto-encephalographic (Costa, Brawn, & Birbaumer, 2003) components related to perceptual processing of the stimuli in the occipito-temporal cortex. Nevertheless, what is relevant here is that, for both male and female observers, the modulation of esthetic preferences by interferential stimulation over right and left EBA was selective for the body of opposite- vs. same-gender bodies, but yielded different effects in men and in women. In fact, we found that in women virtual disruption of rEBA selectively increased the liking judgments of opposite-gender models, as compared to both vertex and lEBA stimulation. A different pattern was obtained in men; indeed, their liking judgments of opposite-gender models decreased after stimulation of both rEBA and lEBA as compared to vertex. These effects were obtained after controlling for any between-gender differences in BMI and internalization of athletic ideals, which showed different distributions in the two groups. **Furthermore, no relation was observed between the absolute value of LI and the individual level of body dissatisfaction and internalization of Western ideals. This suggests that the increased right hemisphere dominance we found in women is not associated with observers' BMI or body image concerns. This might be due to the fact that the range of observers' BMI and self-report measures in our female and male samples was not enough to disclose any relevant effects of BMI, body dissatisfaction (BD) and other standard clinical scales. At any rate,** results provide causative evidence of gender differences in the hemispheric asymmetry of EBA in the esthetic appreciation of human bodies, with a strong right hemisphere lateralization in women but not in men. Overall, the presence of such right hemisphere asymmetry in women seems to be in agreement with a large number of previous behavioral and neuroimaging studies (Smeets & Kosslyn, 2001). For example, a study of Mohr and colleagues (2007) reported that unilateral presentation of self body image in the left visual hemi-field, which is projected first to the right hemisphere, resulted into an overestimation bias in women, but not in men. This suggests a role of right hemisphere areas in body image distortion in women. In keeping with this suggestion, neuroimaging studies have documented that women with EDs as compared to healthy women show reduced activation of the occipito-temporal cortex, especially in the right hemisphere (Seeger et al., 2002; Uher et al., 2005). Of greatest important, Aleong and Paus (2010) offered evidence that the lateralization of the neural response to human body perception is influenced by the gender of the observers. They found that women showed a greater response to human bodies in rEBA than in lEBA; furthermore, women had greater rEBA response compared with men. However, none of the studies mentioned above examined possible gender differences in the hemispheric lateralization of perceiving and appreciating the beauty of the body. To our knowledge, this is the first causative evidence that the neural underpinnings of the esthetic appreciation of human bodies have different degree of hemispheric asymmetry in women and men, with women showing stronger right hemisphere lateralization.

Nevertheless, we found that virtual disruption of EBA with respect to vertex yielded different effects on the esthetic judgments of the body of opposite-gender models in men and women. In fact, while in women we observed an increase of the liking judgments of male models, in men we observed a decrease in the liking judgments of female models. The source of this differential modulation might reside in the specific cognitive and anatomic organization of the neural network for esthetic body perception in male and female observers or in the specific features of the model body under evaluation. Indeed, since we found effects of EBA stimulation for only opposite gender models in both gender groups, the relative effects of the observers' esthetic appreciation system or of the intrinsic features of male and female body stimuli cannot be disentangled. Furthermore, since we did not include a non-body control condition in our design, we cannot rule out that the same lateralization of esthetic appreciation system is found when men and women evaluate other objects. It is worth noting, however, that previous studies have consistently demonstrated the selectivity of EBA activity for body stimuli with respect to non-corporeal objects and even faces (Peelen & Downing, 2007; Urgesi, Candidi et al., 2007). Furthermore, since Calvo-Merino et al. (2010) showed that EBA-rTMS affects the esthetic appreciation of human bodies but not of other objects, it is unlikely that we could expect any effects for non-corporeal objects. Finally, our effects were selective for opposite-gender models and did not extend to the esthetic judgments provided for the body of same-gender models, pointing to a high degree of selectivity of the effects of EBA-rTMS on esthetic judgments for opposite-gender models. Thus, the effects we found in the present study seem to be selective for human bodies, especially for those of opposite-gender models, and other areas in the extrastriate or higher-level cortex may be involved in the esthetic evaluation of non-corporeal objects.

Whichever is the source of the gender differences in the effects of EBA stimulation, it is very plausible that the esthetic appreciation of opposite-gender models in women and men relied on different perceptual cues and on the use of different processing strategies. Previous studies have shown that men and women show comparable esthetic preference for the same features of either male or female bodies, valuing especially thinness (Brown & Slaughter, 2011; Cornelissen et al., 2009) and movement quality (Grammer et al., 2003; McCarty et al., 2013) as important markers of attractiveness. However, using eye-movement recording during observation of whole body pictures, other studies (Nummenmaa et al., 2012; Smith et al., 2007) have shown important differences in the specific body parts that men and women use when they evaluate opposite-gender models. In particular, both women and men tend to spend more time looking at the body of opposite- than same-gender models; however, women tend to concentrate fixations onto the head area of male models, while men tend to fixate onto the bust and buttocks areas of female bodies, in keeping with the notion that the bust–waist ratio may provide a useful cue to reproductive potential and thus influence attractiveness judgments of female bodies (Jasienska et al., 2004). Furthermore, electroencephalographic recording (Hietanen & Nummenmaa, 2011) showed that the amplitude of the N170 component, which is particularly sensitive to visual presentations of human faces and bodies, was increased when men observed female vs. male bodies, whereas no effect was obtained when men observed female vs. male faces; in contrast, no difference was found between male and female stimuli, either bodies or faces, in women. These gender-specific patterns of eye movements and neural responses to human bodies suggest the use of different perceptual cues for the esthetic ratings of opposite gender models in men and women, with greater reliance on body form cues in men than in women. Indeed, while uncovering the body of opposite-gender models strongly increased the affective and attractiveness ratings of men, a much less increment was obtained in women during observation of nude vs. clothed male bodies (Costa et al., 2003). Since EBA is specifically involved in processing the form of non-facial body parts (Peelen & Downing, 2007; Urgesi et al., 2004), its alteration following rTMS may reduce the impact of body form cues on the esthetic appreciation given by men to female bodies and, therefore, reduce their final esthetic appreciation. In contrast, the same alteration in women might reduce the impact of body form processing in judging the esthetic appearance of male bodies, thus leading to an overall increase of esthetic judgments based on other cues (e.g., body implied motion).

A further, non-mutually exclusive interpretation of the findings is that the esthetic VAS judgments of opposite- gender model bodies in men and women rely at different extent onto configural vs. local processing of human bodies. **Accordingly, it is interesting to note that a recent neuroimaging study of Cela-Conde and colleagues (2009) reported bilateral parietal activity in women but a lateralized activation to the right hemisphere in men, when participants judged artistic paintings or natural objects as beautiful. These gender-related differences in the neural activation of the parietal lobe point out**

different spatial processing strategies for beauty appreciation in the two genders. Furthermore, as discussed by the authors, different strategies used by men and women in assessing aesthetic preference may reflect differences in the strategies associated with the division of labor between our male and female hunter-gatherer hominid ancestors. Thus, the study shows that even today women relay on global and local features, whereas men preferably use local features in beauty appreciation of artistic paintings or natural objects. Indeed, the less attention given by women to single parts of male bodies might reflect that they value more the whole body configuration in driving esthetic appreciation, thus relying more on configural processing. In contrast, the attention given by men to single parts of female bodies (especially bust and buttocks) might reflect that they value more the appearance of single body parts and rely more on local than configural processing during esthetic body appreciation. Since EBA seems to be specifically involved in local processing of human body parts (Urgesi, Candidi et al., 2007; Taylor, Wiggett, & Downing, 2007), interferential stimulation applied over it might favor configural body processing, increasing or decreasing, respectively, the esthetic value attributed to opposite-gender stimuli by women and men. Interestingly, women diagnosed with anorexia nervosa, for whom a distorted body image is a diagnostic criterion, not only show significant alterations in their attractiveness ratings of other women's bodies with respect to healthy controls (Tovée et al., 2000), but also show altered patterns of eye movements when they judge body size and attractiveness (George et al., 2011) and deficits of configural versus local processing of human bodies (Urgesi et al., 2013). Although these interpretations are highly speculative and we do not have clear data to explain the differential direction of EBA stimulation in men and women, these previous studies showed clear gender-differences in the esthetic appreciation of human bodies and such differences might be related, on the one hand, to stronger right lateralization of body selective areas in women than men and, on the other hand, to differential contribution of visual body representation to the esthetic value attributed by women and men to opposite-gender bodies. An important challenge for future research will be to clarify the cognitive processes and neural underpinnings of these gender differences in esthetic body appreciation.

Crucially, we found that left and rEBA-rTMS did not interfere with weight VAS judgments of opposite- or same-gender virtual model bodies, suggesting that the effects of EBA-rTMS on the esthetic appreciation of opposite-gender bodies could not be explained by changes in perceived weight. This finding, however, might appear in contrast with previous studies showing that EBA-rTMS impairs visual body discrimination (Urgesi et al., 2004; Urgesi, Candidi et al., 2007; Urgesi, Calvo-Merino et al., 2007; Pitcher et al., 2009). However, EBA-rTMS seems to affect selectively the local processing of body parts details, as shown, for example, by the finding that it interferes with matching inverted bodies, which can be discriminated only using local processing, but not with matching upright whole body figures, which can be discriminated using also configural processing (Urgesi, Candidi et al., 2007). Furthermore, Taylor and colleagues (2007) proposed that, while EBA is biased toward the representation of individual body parts, other regions such as the FBA may show greater selectivity in detecting changes of larger portions of the human body. It is worth noting that participants in our study were required to judge the weight of whole body models, detecting larger scale rather than individual body parts size variations. Thus, visual processing for estimating body weight could rely more on configural than local body processing. In keeping with this view, a recent study by Hummel et al. (2012) found significant neural adaptation to specific body size and shape in FBA but not in EBA.

In summary, our results provide first evidence of gender differences in the hemispheric asymmetry of EBA in the esthetic processing of human bodies, with women showing stronger right hemisphere dominance than men. These results have potentially relevant implications for the understanding of the neural underpinning of visual body perception as well as for understanding and treatment of body image disorders in EDs patients. Indeed, the results suggest that cognitive neuroscience studies urge to take into account important gender differences in the neural organization of visual body perception when trying to investigate how early visual processing of human bodies might contribute to higher-level affective and social behaviours. Furthermore, the more lateralized representation of body esthetic in women than in men might be related to explain the greater incidence of EDs among women. Finally, the results might be useful for designing psychotherapeutic interventions for EDs patients using body exposure (Vocks, S., Busch et al., 2010; Vocks, Schulte et al., 2010), highlighting the importance of considering lateralized presentations of body stimuli to the left visual hemifield in women (Mohr et al., 2007).

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Figure and Table Captions

Table 1: Table 1: Mean and Standard Error of Mean (S.E.M., in brackets) of demographic variables and self-report questionnaire scores for male and female participants. The data of the two gender groups were compared by means of independent sample *t*-test (two-tailed). Notes: BMI, Body Mass Index; EDI-2, Eating Disorder Inventory-2; BSQ, Body Shape Questionnaire; BAT, Body Attitude Test; SATAQ-3, Sociocultural attitudes toward appearance questionnaire.

Figure 1: Time course and example stimuli for the esthetic and weight Visual Analogue Scale (VAS) judgment tasks.

Figure 2: Stimulation sites plotted on the coronal view of a standard brain. According to Mean Talairach coordinates system, the coordinates of extrastriate body area (EBA) corresponded to Brodmann's area 37 in the posterior part of the Middle temporal gyrus (left EBA (x = -52, y = -72, z = 4); right EBA (x = 52, y = -72, z = 4)). As control site, the vertex was stimulated with the induced current running from posterior to anterior along the interhemispheric fissure (x = 0, y = -44, z = 69).

Figure 3: Effects of repetitive transcranial magnetic stimulation (rTMS) on liking **(A) and on weight subjective ratings (B)** of human models as a function of observers' gender (women, men), rTMS site (lEBA, rEBA, vertex) and models' gender (same, opposite). Notes: Left EBA, lEBA; right EBA, rEBA. Error bars indicate standard errors of the mean; * $p < 0.05$.