Title: Different contributions of visual and motor brain areas during liking judgments of same- and different-gender bodies

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Keywords: Neuroaesthetics; Extrastriate body area; Premotor cortex; embodiment; Transcranial magnetic stimulation.

Abstract

Previous neuroimaging studies have shown that body aesthetic appreciation involves the activation of both visual and motor areas, supporting a role of sensorimotor embodiment in aesthetic processing. Causative evidence, however, that neural activity in these areas is crucial for reliable aesthetic body appreciation has so far provided only for extrastriate body area (EBA), while the functional role played by premotor regions remained less clear. Here, we applied short trains of repetitive transcranial magnetic stimulation (rTMS) over bilateral dorsal premotor cortex (dPMC) and EBA during liking judgments of female and male bodies varying in weight and implied motion. We found that both dPMC and EBA are necessary for aesthetic body appreciation, but their relative contribution depends on the model's gender. While dPMC-rTMS decreased the liking judgments of same-, but not of different-gender models, EBA-rTMS increased the liking judgments of different-, but not of same-gender models. Relative contributions of motor and visual areas may reflect processing of diverse aesthetic properties, respectively implied motion vs. body form, and/or greater sensorimotor embodiment of same- vs. different-gender bodies. Results suggest that aesthetic body processing is subserved by a network of motor and visual areas, whose relative contribution may depend on the specific stimulus and task.

1. Introduction

The human body has been considered one of the maximal expressions of artistic inspirations throughout history and cultures. Nevertheless, only few neuroscientific studies have so far investigated the brain bases of perceiving and appreciating the beauty of the body (Kirsch et al., 2016). As one of the most artistic expressions, the art of dance has offered an ideal paradigm for the study of the aesthetic appreciation of another person's body in motion, seen that dance may induce emotional reactions in the observer (Chichella & Bianchini, 2004; Dittrich et al., 1996; Sawada et al., 2003). Recently, Calvo-Merino and colleagues (2008) have reported that more dynamic ballet moves were more liked by participants as compared to less dynamic ones, pointing to the role of implied motion in driving the appreciation of the beauty of the body. Importantly, the observation of preferred (i.e., more dynamic) stimuli induced a greater activation of bilateral early visual cortices as well as of right premotor cortex (PMC). In another study, Cross, Kirsch and colleagues (2011) asked participants to provide explicit ratings about the aesthetic value and the perceived reproducibility of a series of dance moves. Results showed that participants liked more those moves that they found more difficult to physically replicate. Furthermore, greater activity in bilateral occipito-temporal cortices and right inferior parietal lobule was observed when participants watched actions that they liked more but were less able to reproduce. This result is in keeping with previous findings suggesting that the extrastriate body area (EBA), an occipito-temporal area which is selectively activated by visual body processing (Downing et al., 2011), is more activated by unfamiliar/impossible than familiar body postures (e.g., contortionists or robotic actions, Cross et al., 2010, 2012). These studies offer an intriguing contribution showing that the aesthetic appreciation of dance might be associated with a mechanism of coding the degree of deviation between the observed and observer’s body/physical abilities (Cross et al., 2011). This supports the view that aesthetic experience is related to sensorimotor embodiment, namely to mapping others’ actions and sensations onto the observer’s bodily states (see also Cross et al. 2009a,b; Cross &

Ticini, 2012; Ticini et al., 2015; Kirsch, Urgesi and Cross, 2015 for a review). It is worth noting, however, that the role of perceived dynamism and embodiment processes may not be limited to the appreciation of human figures, since representational paintings with greater implied motion are preferred when they depict either human figures or landscapes (Massaro et al., 2012). Indeed, a recent EEG study by Umiltà and colleagues (2012) found suppression of the mu rhythm (indexing motor activation) during passive observation of Lucio Fontana's slashed canvases (where the action of the artist is not seen, but can readily be inferred), but not during observation of graphically modified versions of them. Furthermore, Battaglia and colleagues (2011) explored the effects of viewing the '*Michelangelo's Expulsion from Paradise'* painting on corticospinal excitability, an index of motor activation and hence motor simulation. They found that corticospinal excitability was higher during observation of the action in that painting than during observation of the real hand photographed in the same pose depicted in the painting. They argued that the results might point to the relationship between the aesthetical quality of a work and the perception of implied movement within it. In a similar vein, Di Dio and colleagues (2007) showed a greater activation of lateral occipital cortex, ventral PMC and posterior parietal cortex during the observation of Classical and Renaissance human body' sculptures that were respectful vs. non respectful of the golden section, an index of body proportion that is accepted as a normative Western representation of beauty.

All together, previous studies of perceiving the body in pieces of arts converge on the view that a crucial element of the brain response to bodily aesthetic stimuli consists of the activation of embodied mechanisms encompassing the simulation of actions, emotions and corporeal sensations (Di Dio & Gallese, 2009; Freedberg & Gallese, 2007). The correlational nature of the neuroimaging and corticospinal excitability recording techniques that were used in these studies, however, does not allow making causative inference on the functional role played by visual and motor body processing areas in the aesthetic appreciation of the body. Recently, Calvo-Merino and colleagues (2010) used repetitive Transcranial Magnetic Stimulation (rTMS) to interfere with neural activity in ventral PMC and EBA during aesthetic preference judgments of static postures of dance moves with respect to objects. Results demonstrated that EBA-rTMS blunted aesthetic judgments about body postures relative to vertex sham stimulation, thus disrupting the pattern of aesthetic preference observed for each participant in a rating session without stimulation. Conversely, ventral PMC-rTMS heightened aesthetic sensitivity, thus making the aesthetic preferences provided during the stimulation session more in line with the ratings provided without stimulation. While these findings suggest that interfering with neural activity in EBA prevents providing reliable aesthetic preferences, no systematic change in the aesthetic value of the stimuli was observed; in other words, stimuli were not systematically liked more or less after either EBA- or ventral PMC-rTMS, thus making unclear the actual contribution of visual and motor areas to the aesthetic evaluation of the body.

How disruption of body processing affects the embodied aesthetic experience of watching moving bodies may depend on the specific aesthetic properties of the performer’s body that are used in the aesthetic evaluation. Important aesthetic properties of the human body are those related to mate selection and sexual behaviour (Grammer et al., 2003; Ticini et al., 2015). In particular, symmetry and consistency of movements (Escós et al., 1995; Hampson & Kimura, 1988) and distribution and overall amount of body fat as also measured by waist-to-hip ratio (WHR) (Fan et al., 2004; Singh, 1993a,b) may signal attractiveness, youthfulness, health and reproductive potential. Therefore, quality of implied or actual motion and body weight may both influence the aesthetic appreciation of the body and the relative impact of these properties may vary when judging the aesthetic value of same- or different-gender bodies (Cazzato et al., 2012). Research on how the neural underpinnings of body aesthetic appreciation are shaped by the correspondence between the observer and model’s gender, however, is scant. In a recent study (Cazzato et al., 2014), we used rTMS to test the role of EBA in the judgments of the aesthetic value (“liking”) of male and female body stimuli varying in size and in implied motion. Results showed that, in both male and female observers, EBA-rTMS affected the liking judgments of only different-gender models, suggesting that neural activity of EBA is necessary for processing those aesthetic properties that are used to appreciate the body of individuals of the other gender. No study, however, has so far tested whether motor body representation may play different roles for the aesthetic appreciation of same- and different-gender bodies. While both Calvo-Merino et al. (2010)'s and Cazzato et al. (2014)'s studies supported a necessary role of EBA in aesthetic body appreciation, to our best knowledge, no study has so far provided causative evidence for the role of motor areas with these regards, thus weakening the importance of sensorimotor embodiment in perceiving and appreciating the beauty of same- and different-gender bodies. In fact, Calvo-Merino et al. (2010) reported that interfering with neural activity in the ventral PMC heightened, rather than blunting aesthetic sensitivity.

On the basis of the above state of the art, here we set out to investigate the contributions of visual and motor body representations to aesthetic evaluation of human body stimuli. We compared the effects of EBA and dorsal premotor cortex (dPMC) rTMS with the effects of vertex stimulation during an aesthetic body appreciation task. dPMC was chosen on the basis of Cross and colleagues' study (2011), which reported that this brain region was more active when observers judged how much they liked a dancer's body in motion as compared to judging the aesthetic value of a dancer's body standing still. In different groups of participants, these areas were stimulated on the left or right hemisphere. Following previous studies (Calvo-Merino et al., 2008; 2010; Cross et al., 2011; Cazzato et al., 2014), we focused on the aesthetic dimension of like–dislike ratings rather than on the objective dimension of beautiful vs. non-beautiful ratings (Augustin et al., 2012; Jacobsen et al., 2004; Knoop et al., 2016). Furthermore, to rule out the possibility that rTMS may induce a simple bias either towards preferring (or not preferring) the first image of a pair of stimuli by using a forced-choice aesthetic preference task (Calvo-Merino et al., 2010), we asked participants for explicit aesthetic ratings of how much they liked each stimulus. In addition, while previous aesthetic studies have focused on only one dimension of body aesthetic preference, presenting for examples pictures of the same model while performing different dance moves (Calvo-Merino et al., 2010), in keeping with the Cazzato et al. (2014)'s study, here we included stimuli with systematic variations of body size and body motion, which have a specific, common aesthetic value for a group of individuals, with a preference for thinner and more dynamic stimuli (Cazzato et al., 2012; Mele et al., 2013). Furthermore, rather than asking participants to separately rate the aesthetic value of the model's body or of the body posture (Cazzato et al., 2012), here, we allowed participants to rely on both body form and body action cues in their aesthetic ratings of all stimuli. We capitalized on the idea that, while in informing the aesthetic appreciation judgments, the extent of implied motion and body size should be processed by dPMC and EBA respectively, this would not necessarily determine that dPMC-rTMS should be selectively interferring with the aesthetic judgments of implied motion stimuli. In fact, it should reduce the influence of implied motion on the aesthetic appreciation of all stimuli, with predicted effects for both static and implied motion stimuli. In keeping with this idea, Cattaneo et al (2015b) have recently shown that stimulation of V5, which is involved in processing object motion, interfered with the perception of the sense of motion and with the liking judgments of paintings with various levels of implied motion. Importantly, in the present study, we compared the effects of EBA- and dPMC-rTMS on judgments of models of the same as or of the other gender than that of the observer, thus expanding previous neuroaesthetic works, which instead focused on changes in limb position of a single male dancer (Calvo-Merino et al., 2010), thus possibly masking any effects due to the model's gender.

In keeping with previous rTMS studies showing the relative roles of EBA in processing body form (Candidi et al., 2008; Urgesi, Candidi et al., 2007) and of dPMC in processing body actions (Makris & Urgesi, 2015), we expected that neural activity EBA should inform the aesthetic attribution system of the variations of body size (i.e., being more or less round), while neural activity in dPMC should inform on the variations of implied motion (i.e., displaying more or less implied motion postures) presented in each stimulus. However, the relative contribution of the two areas should vary according to the model's gender. Based on previous findings (Cazzato et al., 2014), we expected that EBA-rTMS should modulate the aesthetic preference of different-, but not same-gender bodies. No specific hypothesis regarding the direction of the effects of dPMC could be made on the basis of previous studies, although the embodiment perspective on body aesthetic perception (Cross & Ticini, 2012; Ticini et al., 2015) would claim that the involvement of dPMC should be greater for those bodies that are more similar to the observer (i.e., same-gender models). Thus, our study design allowed us to disentangle the causative role of both occipital and premotor cortices in the aesthetic evaluation of same- or different-gender bodies in a sample of young healthy participants.

2. Results

The preliminary 3-way ANOVA (gender*size*implied motion) on the VAS scores for the liking judgment at baseline showed that participants preferred slimmer rather than fat models (63.22 ± 2.14 mm vs. 30.30 ± 1.52 mm; $F_{(1,35)}=136.903$, $p < 0.001$, $\eta_p^2 = 0.796$). Furthermore, participants preferred more dynamic than static models (50.06 ± 1.63 mm vs. 43.46 ± 1.44 mm; $F_{(1,35)}=12.226$, $p = 0.001$, $\eta_p^2 = 0.259$). Most importantly, the 2-way interaction between gender and size resulted significant [$F_{(1,35)}=15.607$, $p < 0.001$, $\eta_p^2 = 0.308$]. Duncan's post-hoc comparisons revealed that while same-gender models were preferred over opposite-gender models when they were depicted in the slim figures (65.25 ± 2.74 mm vs. 61.19 ± 3.1 mm; $p = 0.033$), they were liked less than opposite-gender models when they were depicted in the round figures (27.23 ± 1.9 mm vs. 33.37 ± 2.31 mm; $p = 0.002$). Thus, the way in which the perceived body weight affected aesthetic appreciation was different for same and different gender models. Moreover, the 2-way interaction between size and implied motion resulted significant [$F_{(1,35)} = 6.498$, $p = 0.015$, $\eta_p^2 = 0.157$]. Post-hoc comparisons revealed that dynamic posture were always preferred as compared to static postures when rendered in both fat (34.82 ± 2.01 mm vs. 25.77 ± 1.36 mm; $p < 0.001$) and slim figures (65.3 ± 2.51 mm vs. 61.14 ± 2.48 mm; $p = 0.004$); however, the effect of implied motion was greater for round than slim figures (ΔRound = 9.05; ΔSlim = 4.16, $t_{(35)} = 2.549$; $p = 0.015$). The 3-way interaction of gender*size*implied motion was not significant [$F_{(1,35)}=0.541$, $p = 0.467$, $\eta_p^2 = 0.015$], thus suggesting that the interaction between body size and implied motion was comparable for the two genders. Finally, no other main effects or interactions were significant [$F<2.217$, $p>0.145$].

The ANOVA on the normalized VAS judgments (see Fig. 1) revealed significant main effect of site [$F_{(2,68)} = 5.614$; $p = 0.006$; $\eta_p^2 = 0.142$], which was further qualified by a significant interaction between site and model's gender [$F_{(2,68)} = 6.466$; $p = 0.003$; $\eta_p^2 = 0.16$]. Post-hoc pair-wise comparisons showed that participants decreased their liking judgments of same-gender model bodies after dPMC-rTMS (85.67 ± 5.69%) as compared to both vertex- (105.15 ± 4.28%, $p < 0.001$) and EBA-rTMS (102.92 ± 6.04%, $p = 0.002$), which in turn did not differ ($p = 0.665$). Conversely, for different-gender model bodies, participants increased their liking judgments after EBA-rTMS (114.69 ± 5.16%) as compared to both vertex- (96.74 ± 3.41%, $p = 0.002$) and dPMC-rTMS (101.53 ± 5.13%, $p = 0.02$), which in turn did not differ ($p = 0.352$). Furthermore, dPMC-rTMS reduced more the liking judgments of same- than of different-gender model bodies ($p = 0.004$), while EBA-rTMS increased more the liking judgments of different- than of same-gender model bodies ($p = 0.032$). No difference between same- and different-gender models was obtained after vertex stimulation ($p = 0.138$). No other main effects or two-way interactions were significant (all Fs < 2.18; $p > 0.149$; $\eta_p^2 < 0.06$), nor was significant the three-way interaction between stimulation side, stimulation site and model's gender [$F_{(2,68)} < 1$; $\eta_p^2 = 0.025$], suggesting comparable effects of left and right hemisphere areas. Finally, the correlational analysis revealed that the rTMS effects were not predicted by participants' BMI or by any psychological measures (all $-0.25 < r$s < 0.317, $p > 0.06$).

Please insert Figure 1 near here

3. Discussion

The present study investigated whether and how applying brief trains of rTMS over left and right EBA and dPMC modulates the aesthetic appreciation of human body stimuli. Previous neuroimaging studies have shown that the aesthetic appreciation of bodies involves the activation of both visual and motor areas (Calvo-Merino et al., 2008; Cross et al., 2011). Causative evidence, however, that neural activity in these areas is crucial for reliable aesthetic body appreciation has so far provided only for EBA (Calvo-Merino et al., 2010; Cazzato et al., 2014), while the role of premotor regions has remained supported only by correlational evidence in neuroimaging studies or by the finding of heightened aesthetic sensitivity after rTMS over ventral PMC (Calvo-Merino et al., 2010). Here, we directly compared the effects of rTMS interference with neural activity of EBA and dPMC in the aesthetic appreciation of human body figures varying in size and implied motion. The results of the baseline liking rating of the stimuli confirmed previous findings (Cazzato et al., 2012) that body size and implied motion interact in influencing the aesthetic appreciation of human bodies and may play a different role for the appreciation of same- or different-gender bodies. Importantly, we found that both motor and visual areas are necessary for reliable aesthetic appreciation of body stimuli, but the specific contribution of visual and motor representations is different according to whether the observer is processing the body of same- or different-gender models. In particular, while rTMS of dPMC decreased the liking judgments of same-, but not of different-gender models, rTMS interference with EBA increased the liking judgments of different-, but not of same-gender models.

The double dissociation between effects on same- or different-gender models induced, respectively, by the stimulation of EBA and dPMC rules out that the results can be explained by non-specific effects of rTMS *per se* or by different levels of complexity or motivational values associated to the tasks of judging the bodies of same- vs. different-gender models, because in all these cases no difference between task and/or stimulation site should be obtained. Rather, indeed, these results suggest that the type of body processing in EBA or dPMC influences differently the aesthetic appreciation of same- and different-gender models.

Two possible, non-mutually exclusive interpretations of the findings can be proposed. On the one hand, the dissociation between the EBA and dPMC involvement may derive from the greater potential for embodying same- versus different-gender model's bodies. On the other, it may reflect the different importance of body form and implied motion cues in driving the aesthetic appreciation of same- and different-gender models, respectively.

Previous studies have shown that watching the moving body of other individuals implies mapping their motor, sensory and emotional states onto the observer's bodily states and that this shared representation is one of the source of body aesthetic appreciation (for review, see Cross & Ticini, 2012; Ticini et al., 2015; Freedberg & Gallese 2007). The extension of this shared representation is dependent upon the commonalities of action (i.e., motor repertoire; Calvo-Merino et al., 2005; 2006; Aglioti et al., 2008; Makris & Urgesi, 2015) and form (i.e., ethnicity; Müller et al. 2011; Avenanti et al., 2010) parameters between the observed and the observer's body. Furthermore, the extent to which the observed dance moves overlap with the observer's motor repertoire (i.e., perceived reproducibility) also affects their aesthetic appreciation (Cross et al., 2011). It is arguable that sensorimotor embodiment and, hence, involvement of dPMC, is stronger for same- than different-gender models. Therefore, disruption of sensorimotor embodiment of same-gender models following dPMC-rTMS caused a decrease of liking judgments, supporting the role of sensorimotor embodiment in aesthetic body perception (Calvo-Merino et al., 2008).

Conversely, the bodies of different-gender models may be less easy to be simulated and their aesthetic appreciation may rely more on visual processing in EBA. Accordingly, previous studies have shown greater brain responses to different- than to same-gender bodies involving in particular those electro- (Hietanen & Nummenmaa, 2011) or magneto-encephalographic (Costa et al., 2003) components related to perceptual processing of the stimuli in the occipito-temporal cortex.

Importantly, interferential rTMS over left and right EBA increased, rather than decreasing, the liking judgments of different-gender bodies. While this result supports that visual body processing in EBA influences aesthetic body perception (Calvo-Merino et al., 2008; 2010; Cross et al., 2011), it does not support the view that EBA is actively involved in attributing an aesthetic value to the body of other individuals. Notably, a similar increase of liking ratings after stimulation of EBA was obtained in the sample of young women tested by Cazzato et al. (2014) and it was interpreted in the framework of a 'dual-route model' of visual body perception (Urgesi 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 fusiform body area, may be involved in configural body processing. In this view, interference with local body processing in EBA might favour configural body processing in the fronto-parietal cortex, including dPMC, thus leading to greater sensorimotor embodiment and increased aesthetic value attributed to different-gender bodies.

The modulation of the involvement of EBA and dPMC in aesthetic body appreciation according to the gender of the model may also be referred to the different types of body cues that are processed in these areas and that may have different weight for judging the aesthetic value of same- and different-gender bodies. Previous neuroimaging (Downing et al., 2006; Jastorff & Orban, 2009; Sugiura et al., 2006; Cross et al., 2010; Grossmann et al., 2013), brain stimulation (Urgesi, Candidi, et al., 2007; Candidi et al., 2008) and brain-lesion (Moro et al., 2008) studies have shown that body representations in extrastriate and premotor areas play complementing roles for visual processing of body form and body actions, respectively. For example, a study of Urgesi, Candidi et al. (2007) showed that rTMS over EBA impaired performance on a match-to-sample form task but not on a similar task requiring the discrimination of implied motion from the same static body images. It is worth noting that exactly the same stimuli were used for both tasks, thus suggesting that the different roles of extrastriate and premotor areas in processing body forms and body actions arise from the implicit task demands (i.e., whether the stimuli can be differentiated by form or action cues) rather than from the stimulus features per se (i.e., whether the posture implies more or less motion). Furthermore, EBA activity is sensitive to subtle variation of human body size and shape in healthy individuals (Aleong & Paus, 2010) and its structural (Suchan et al., 2010) and neurofunctional alteration (Vocks et al., 2010) is associated with body image disturbance, such us body size overestimation and negative body evaluation in patients with EDs (Uher et al., 2005). Conversely, it has been largely demonstrated that PMC is part of a mirror-like system that matches action observation and execution (Binkofski & Buccino, 2006; Cross et al., 2011; Calvo-Merino et al., 2008). In fact, rTMS over PMC impairs visual discrimination of static (Urgesi et al., 2007) and dynamic displays of moving body parts (Pobric & Hamilton, 2006), suggesting that motor representations are necessary for visual discrimination of others' actions (Avevanti et al., 2013; Urgesi et al., 2014). Furthermore, activity of dPMc while watching dance is influenced by the motor expertise of the observer (Calvo-Merino et al., 2005, 2006) and is associated with the greater aesthetic appreciation of larger displacements of the dancer's limbs (Calvo-Merino et al., 2008). Taken together, the results of the above mentioned studies suggest that while EBA crucially contributes to processing of the size and shape of human bodies, PMC is involved in perceiving the actions implied by the observed body. Here, we show that such perceptual processing of body form and body actions in EBA and dPMC, respectively, is also *necessary* for their aesthetic appreciation.

Interestingly, studies on facial attractiveness have not so far shown the gender-based interaction reported in the present study (Chatterjee at al., 2009; Vartanian et al., 2013). For example, Roye and colleagues (2008) compared the ERP activation during the judgments of male and female faces, and, while they didn't find any difference for the 400-480 ms negativity component, they reported an earlier negativity (280-400 ms) for male faces only and a late positivity (400-580 ms) that was higher for female faces. This suggests that male and female faces were processed with different temporal patterns. Similar results have been recently reported for the perception of male and female bodies (Muñoz & Martín-Loeches, 2015). Unfortunately, these studies did not take into account the gender of the observer, thus leaving open the question of whether the different temporal profile of the ERP responses for male and female faces was influenced by the gender of the observer.

In a recent study of Ferrari and colleagues (2015) male and female participants were required to evaluate the attractiveness of same- or opposite-gender faces before and after tDCS over the dorsolateral prefrontal cortex (DLPFC). The authors found that anodal tDCS in the right but not in the left DLPFC increased the perceived attractiveness of the faces, irrespective of the faces' and observers' gender. This is in contrast with our current and recent study (Cazzato et al. 2014, but see also Cela-Conde et al. 2009 for aesthetic ratings of paintings and photographs; Aleong and Paus, 2010 for visual body processing in men and women) where we found a different modulation of the aesthetic judgments of same- and opposite-gender bodies after stimulation of dPMC and/or EBA. All in all, these studies provide contrasting evidence on the involvement of different patterns of neural activity during the aesthetic processing of faces and bodies according to the observer and model's gender. Differences in the aesthetic judgments required from the participants (e.g., liking, symmetry, or beauty), use of different perceptual cues and processing strategies for faces and bodies, as well as difficulties in detecting between-gender differences with small sample size might explain such discrepancy and warrant further research into this interesting topic.

Another relevant finding of this study is that no difference was obtained between the effects of left and right hemisphere stimulations, for either EBA or dPMC. Previous studies have reported contrasting findings on the hemispheric lateralization of aesthetic body perception. To give some examples, Calvo-Merino et al. (2008) reported bilateral early visual regions but only right PMC responses when participants watched movements they rated as likable. Furthermore, Di Dio, Macaluso and Rizzolatti (2007) reported left sensorimotor cortex brain response correlating with explicit subjective judgments of ugliness. Finally, Calvo-Merino and colleagues (2010) found a general trend for left hemisphere rTMS to decrease the aesthetic sensitivity but non-significant effects of hemisphere. Thus, the author concluded that both hemispheres equally contribute to the perceptual analysis underlying aesthetic evaluation. Finally, Cazzato et al. (2014) reported different lateralization of EBA-rTMS effects in men and women, thus suggesting that gender might influence the lateralization of human body perception. The present results are in keeping with a bilateral involvement of visual areas in body aesthetic perception and extend it to motor body representations in the dPMC.

The effects of EBA and dPMC stimulation on the aesthetic experience of body stimuli may reflect their involvement in the affective components of aesthetic experience (attributing an hedonic value) or in the coding of those perceptual features that drive aesthetic experience.

Indeed, one possible interpretation of our findings is that stimulation of dPMC or EBA interfered with aesthetic processing because it blurred the perception of the implied motion or body form conveyed in the pictures rather than altering the observer’s aesthetic system. On the one hand, this interpretation is in keeping with the TMS study of Cattaneo et al. (2015b), which showed that V5-TMS significantly decreased the perceived sense of motion and, thus, it also significantly reduced the liking of abstract (but not representational) paintings. On the other hand, Cattaneo et al. (2015a) showed that rTMS of lateral occipital cortex altered the liking judgments of representational paintings, but not their perceived clearness, suggesting that the role of perceptual areas in aesthetic experience may go beyond simply providing perceptual information. Similarly, we have previously shown that EBA-rTMS altered the aesthetic judgments of human bodies, but not the perceptual estimation of body weight, thus pointing to a genuine role of this area in aesthetic experience and not only perception of body size (Cazzato et al., 2014). This is also in keeping with the different activation of the PMC during the aesthetic appreciation of rhythm as compared to temporal perceptual judgments (e.g., Kornysheva, von Anshelm-Schiffer & Schubotz, 2011).

In sum, perceptual, motor, and affective components of aesthetic experience can be mapped into different nodes of a complex neural network, and their different contributions to aesthetic experience may vary depending on the gender of the body being appreciated. However, it remains to be demonstrated how specific is this involvement for aesthetic experience vs. general perceptual processing (see e.g., Kirsch, Urgesi, Cross, 2015 for further discussion of this issue).

3.1 Limitations and Conclusions

Even though this study provides evidence concerning the causative role of lateral-occipital and premotor cortices in the aesthetic perception of human virtual stimuli, it also has limitations.

First of all, we only focused on the subjective "liking" dimension and our findings cannot shed light on other important dimensions (e.g., complexity, interest, tension, and powerfulness) that account for the complexity of aesthetic experience (Berlyne, 1974). Furthermore, semantic analyses of the terms that people use to label aesthetic appreciation of different types of visual objects, including clothes and faces (Jacobsen et al., 2004; Augustin et al., 2012), music (Istok et al., 2009) and different literary genres (Knoop et al., 2016) have shown that the dimensions of beautifulness and ugliness were dominant across several domains. Nevertheless, other dimensions were relevant in specific domains, for example interestingness and suspensefulness in literature (Knoop et al., 2016). While similar semantic analyses are lacking in the domain of body aesthetics, the "liking" dimension has been widely used in neuroscientific study of the appreciation of the human body, for example in dance, (Kirsch et al., 2015; Cross and Ticini, 2012) and it has been associated to the processing of essential kinematics aspects of the movements, such as speed, and movement direction, at both behavioural and brain levels (Calvo-Merino et al., 2008; Cross et al., 2011). Furthermore, in our previous study (Cazzato et al. 2012) we directly compared different types of judgments on the stimuli used here (liking, beauty, and attractiveness ratings), and found largely overlapping modulations by size and implied motion. Still the question remains as to whether the involvement of visual and motor cortices is sensitive to different dimensions of aesthetic experience.

A further limitation of this study is that we did not directly manipulate (e.g., by presenting variations of body size while keeping implied motion constant and the other way round) how participants used implied motion or body forms cues in providing the liking judgements of same- and different-gender bodies. Similarly, we could not directly test whether the involvement of the dPMC or EBA was influenced by the amount of implied motion or the body size of the stimuli. Further studies using task analysis and functional specification of body aesthetic appreciation similarly to what has been done with the perception of rhythm excerpts (Kornysheva, von Anshelm-Schiffer & Schubotz, 2011; Kornysheva, von Cramon, Jacobsen & Schubotz, 2010) are needed to finally disentangle the specific role of these areas in aesthetic appreciation of bodies.

Although our participants had self-report BMI within the normal range and no significant correlations were found between BMI and the rTMS effects, we cannot exclude that the relative importance of body weight in judging same- or different-gender bodies may vary as a function of the observer's BMI. Furthermore, the design of our study had not enough power to analyze and detect gender differences in the pattern of results, but it is possible that the relative contribution of left and right hemisphere areas in the aesthetic appreciation of same and different-gender bodies may vary also according to the gender of the observer (Cazzato et al., 2014; Aleong & Paus, 2010). Further studies are needed to proof the role of gender into the hemispheric lateralization of aesthetic body processing. This may be especially important if we consider our results in light of the large incidence of EDs among women. Still, we cannot ascertain whether the participants' aesthetic judgments were driven by systematic differences in focusing attention to specific parts of same- or different-gender bodies (Abbassi et al., 2009). By using eye-tracker technique, future studies may disentangle whether different oculomotor patterns for same- and different-gender bodies may explain the different involvement of visual and motor areas in aesthetic body perception. Finally, it is worth noting that, while the different preference granted to different- versus same-gender bodies at baseline cannot explain the site selectivity of the rTMS effects, this difference may be called into consideration in explaining the direction of the rTMS alterations after stimulation of the two areas. For example, stimulation of EBA may be more likely to interfere with preferred stimuli categories, while stimulation of dPMC with less liked stimuli. However, different appreciation of different- vs.

same-gender models is an intrinsic feature of an individual's preference system that needs to be taken in consideration when studying body aesthetic appreciation.

To conclude, our study provides evidence for the different roles of visual and motor representations of the human body to its aesthetic appreciation. We found that 'virtual lesion' of left and right EBA selectively affected the liking judgments of different-gender models, while 'virtual lesion' of left and right dPMC affected the liking judgments of same-gender models. The relative involvement of visual and motor areas in the aesthetic appreciation of same- or different-gender bodies may reflect the use of diverse aesthetic properties, respectively body forms or implied motion cues, and/or the relative similarity between the observer's and observed body structure which may facilitate the use of shared representations for same- but not for different-gender bodies, for which only a visual representation can be used. In both cases, the present study is in keeping with the existence of a distributed network in which EBA and dPMC regions play complementary roles in aesthetic processing of the body and their individual contributions influence the final aesthetic judgment. Future research may be advanced by focusing on understanding the functional connectivity among the components of this distributed network of visual and motor areas for aesthetic body perception.

4. Experimental Procedure

4.1 Participants

Thirty-eight students from the University of Udine participated in the experiment in return for course credits. According to a random assignment procedure, 19 participants (10 female - 9 male) underwent right cerebral hemisphere stimulation and the other 19 (10 female – 9 male) left cerebral hemisphere stimulation. 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 participants but two females 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 a 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. Moreover, participants completed a series of self-report standard clinical scales, namely the Body Shape Questionnaire (BSQ-34, Cooper et al., 1987), the Eating Disorder Inventory (EDI-2, Garner, 1991), the Body Attitude Test (BAT-20, Probst et al., 1995) and the Sociocultural Attitudes towards appearance questionnaire (SATAQ-3, Thompson et al., 2004; Stefanile et al., 2011). This allowed us to ensure that no participant showed positive symptoms of Eating Disorders (EDs) or of body image disturbance. Furthermore, we estimated participants' body mass index (BMI) from self-report measures of weight and height. Two female participants, one per each hemisphere stimulation group, could not be tested in all conditions because of discomfort associated with the stimulation of the premotor sites and were not further considered for the analyses. Therefore, for the final analyses we retained a sample of 36 participants, 18 in each hemisphere stimulation group. The demographics and clinical variables of the participants in the two hemisphere stimulation groups are reported in Table 1. Independent sample t-test indicated that the two groups were matched for age, handedness, weight, high, BMI and clinical measures with the exception of the maturity fear EDI-2 subscale, which showed that left hemisphere group had stronger maturity fear than the right hemisphere group. All 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.

Please Insert Table 1 about here

4.2 Stimuli

Participants were presented with a series of virtual human models. 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).

Each model was rendered in two static and two dynamic postures taken from a frontal or three-quarter view. Furthermore, the apparent weight of the bodies were set each of four different levels applying naturalistic settings available in the rendering software to create moderate to extreme levels of round and thin figures (4 levels: extremely-round, moderate-round, moderate-thin and extremely-thin). Thus, in total there were 4 models (2 males and 2 females) rendered in 4 different postures and in 4 different body size figures, for a total of 64 stimuli (32 males and 32 females) (see Fig. 2). The body stimuli were taken from a previous study (Cazzato et al., 2012) in which we asked a large number of participants to judge the weight and other perceptual and affective dimensions of each stimulus. 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, we found that aesthetic judgments were influenced by body size and implied motion, with a preference for thinner and more dynamic stimuli (see Cazzato et al., 2012, for details). Thus, the manipulation of both size and implied motion ensured creating a large variation of aesthetic judgments that could be manipulated by stimulation of both body form and body action areas. 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. Finally, 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.

Please insert Figure 2 near here

4.3 Trial Structure

During the experiment, participants seated in a dimly light room 57 cm away from a 19-inches CRT monitor (resolution of 1027*768 pixels, refresh frequency at 60 Hz). The experiment was created with E-Prime software (version 1.1, 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, then, by the rating scale trials. Each trial started with the appearance of a black central fixation cross-presented on a light grey background. After 500 ms, an image depicting the model appeared for 150 ms on the center of the screen subtending a visual angle of approximately 12.58° × 11.11°. Then, the stimulus was replaced by a visual-noise mask for 500 ms. Finally, a visual prompt ‘How much do you like the model?’ (‘Quanto ti piace il modello?’ in Italian) appeared on the top of the screen and above a vertical, 100-mm (252 pixels) VAS ranging from "I like it very much" (Mi piace molto, in Italian; score = 100) to "I do not like it at all" (Non mi piace per nulla, in Italian; score = 0) (see Fig. 3). The up- and down-ward position of the anchor words of the VAS scale was balanced across participants. After response was provided and recorded, an inter-trial interval of 4 sec was allowed before proceeding to the next trial in order to ensure that the repetition frequency of the rTMS trains in a block was lower than 0.2 Hz, thus reducing the possibility of carry-over effects of rTMS at the end of the stimulation session (Chen et al., 1997). Furthermore, participants were given a short break (about 5 minutes) between each block in order to allow for positioning of the stimulation coil. Each participant was tested in a single experimental session lasting about 2 hours. Participants completed a 4 trial practice block before proceeding to the experimental blocks.

During the experimental session, a block of 64 trials was presented for each stimulation site (EBA, dPMC and vertex), with random presentation of male and female model stimuli. Therefore, each participant provided a total of 192 VAS ratings during rTMS stimulation. Block order was balanced according to a Latin square procedure. Each stimulus was presented once in a single block. No time limit was fixed for the response, but participants were required to express their ratings as quickly as possible. Furthermore, at the end of the experimental session, all stimuli were again presented asking for the aesthetic VAS evaluation in order to establish individual baseline levels of how much participants liked the stimuli. The procedure for the baseline session was as in the main experiment, but stimuli were presented in free-viewing conditions to ensure full evaluation of their different aspects (see also Calvo-Merino et al., 2010 for a similar procedure).

Please insert Figure 3 near here

4.4 Transcranial Magnetic Stimulation

rTMS was administered with the Magstim Rapid (The Magstim Company, Carmarthenshire, Wales, UK) using a 70-mm figure-of-eight air-cooled coil. 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. As control site, the vertex was stimulated with the induced current running from posterior to anterior along the interhemispheric fissure. In the experimental conditions, the coil was held over dPMC or EBA of the left (LH) or right hemisphere (RH) with the handle pointing posteriorly. These areas were located on each participant's scalp with the SofTaxic Navigator system (EMS, Bologna, Italy). Skull landmarks (nasion, inion, and two preauricular points) and 60 points providing a uniform representation of the scalp were digitized by means of a Polaris Vicra optical tracking system (Northern Digital, Inc., Waterloo, Ontario, Canada). The SofTaxic Otpic system allowed us to automatically estimate the coordinates in standard space from an MRI-constructed stereotaxic template template and to monitor online the position of the coil focus over the target positions during stimulation.

Premotor cortices coordinates were chosen on the basis of Cross and colleagues' study (2011) and specifically from a main contrast showing which brain regions were more active when observing a dancer's body in motion compared to viewing a dancer's body standing still; following this study, we targeted dPMC located close to Brodmann's area 6 in the precentral gyrus (LH: (*x* -50, *y* -1, *z* 44); RH: (*x* 50, *y* -1, *z* 44)). EBA coordinates (LH: (*x* -52, *y* -72, *z* 4); RH: (*x* 52, *y* -72, *z* 4)) were taken from previous rTMS studies on body aesthetic perception (Calvo-Merino et al., 2010; Cazzato et al., 2014) and corresponded to Brodmann's area 37 in the posterior part of the middle temporal gyrus (See Fig. 4). Mean coordinates of the stimulation sites were in Talairach space (Talairach & Tournoux, 1988).

Please insert Figure 4 near here

The coil was held by hand tangential to the scalp, with the handle pointing backward and medially at a 45° angle from the middle sagittal axis of the participants' head for the four active stimulation sites and pointing backward for the control stimulation of the vertex. The same pulse delay and stimulation intensity was used for the four stimulation sites and for vertex stimulation. Stimulation intensity was 110% of the rMT for the dominant hand. 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). The rMT values ranged from 47% to 70% (54.61 ± 1.48) of the maximum stimulator output in the right hemisphere group and from 40% to 65% (52.33 ± 1.72%) in left hemisphere group, with no significant differences between the two groups [$t_{(1,34)} = 1$, $p = 0.32$]. In each trial, 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 Candidi et al., 2008; Urgesi et al., 2004; Urgesi, Candidi et al., 2007; Urgesi, Calvo-Merino et al., 2007), whereas long-lasting after-effects are unlikely (Chen et al., 1997; Rossi et al., 2009). 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 at the offset of the stimulus, blinking would not prevent the participants from seeing the stimuli. Finally, while we cannot exclude that the peripheral effects of rTMS might have affected the perception of the mask, which was simultaneously on, this should not influence the site- and gender-specificity of EBA- and PMC-rTMS as compared to vertex rTMS.

4.5 Data handling

Statistical analyses were run with Stat Soft STATISTICA 8.0 (StatSoft Inc, Tulsa, Oklahoma). The study design had a between-subjects factor (right or left hemisphere stimulation group) and 6 repeated-measures cells produced by the factorial combination of 3 stimulation sites (dPMC, EBA, vertex) and 2 model's gender (male, female). While variations of the posture's implied motion and model's body size were used to manipulate the aesthetic value of the stimulus set, they were not part of our design because we hypothesized that the specific role of EBA and dPMC should arise from the relative use of body form or body action cues in attributing an aesthetic value to same- or different-gender bodies, rather than from the relative degree of body size or amount of implied motion (see Urgesi, Candidi et al., 2007 and Candidi et al., 2008 for a similar approach to studying the relative role of EBA and PMC in body form and action perception according to task demands rather than stimulus features). The VAS ratings provided for all trials were converted to metrical scale by dividing by 2.52 (i.e., a hundredth of the VAS length in pixels) the number of pixels between the point where the participants positioned the mouse and the VAS starting point. Then, the mean VAS scores (in mm) for each cell of the design (32 trials per cell: 2 models * 4 postures * 4 weights) were calculated for each stimulation condition for each participant. Preliminary analyses of the raw VAS scores showed that both male and female participants preferred the different-gender models. Thus, for each participant, we coded male and female model stimuli according to their correspondence to the participant's gender (i.e., same- vs. different-gender models). To explore how body size and implied motion influenced the aesthetic appreciation of same- and different-gender bodies, we performed a preliminary 2×2×2 repeated-measure ANOVA with model's gender (same, different), body size (round, slim) and implied motion (implied motion, still) as within-subjects variable on the raw VAS scores for the liking judgment provided at the end of the experimental session while no rTMS was applied (baseline session).

To reduce the impact of interindividual and between-gender differences in the absolute scale values used to evaluate the stimuli, the VAS judgments during the rTMS session were normalized [(VAS rTMS site/VAS baseline)*100] on the judgments provided by each participant on the same stimulus in the baseline session. The use of such a procedure allowed us to scale the estimation of the rTMS effects to the individual baseline VAS judgments and to compare the effects of EBA- and dPMC-rTMS on same- vs. different-gender bodies as compared to a neutral, vertex stimulation condition. The normalized VAS values (expressed as % of the baseline VAS judgments) were entered into a 2×3×2 mixed-model ANOVA, with the between-subjects factor stimulation side and rTMS site and model's gender (same, different) as within-subjects variables. The source of all significant interactions was analyzed using the Duncan's post-hoc correction for multiple comparisons. 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.*). Finally, to explore whether the amount of the rTMS effects obtained in the main analysis were correlated to participants' BMI and to their scores at standard clinical scales of personality dimensions associated to EDs, we calculated a measure of the change of aesthetic judgments (CEJ) as the difference between the normalized VAS values for the active rTMS sites and those during vertex stimulation. Higher CEJ values correspond to a greater change in aesthetic judgment, with positive values indicating an increase and negative values a decrease after active vs. vertex rTMS. Pearson correlations were calculated separately for same- and different-gender stimuli. A significance threshold of $p < 0.05$ was set for all statistical tests.

Acknowledgments: This work was supported by grants from Italian Ministry of Health (Progetto Giovani Ricercatori GR-2008-1137139), Italian Ministry of University and Research (Bando Futuro in Ricerca 2012, Prot. no. RBFR12F0BD) and IRCCS “E. Medea” (Ricerca Corrente 2014, Italian Ministry of Health) to C.U. We are grateful to Francesca Masiello for assistance with data collection.

All of the co-authors of this paper have no financial or other conflicts of interest

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Figure legends

Figure 1: Effects of rTMS on mean Liking subjective rating (expressed as % of the baseline VAS judgments) of human models as a function of stimulation sites (dPMC, EBA, vertex) and model's gender (same, different). Results are shown collapsing right and left cerebral hemispheres group, as no difference was obtained between the two groups. *Error bars* indicate standard errors mean over participants * $p < 0.05$

Figure 2: Examples of female and male stimuli used in the experiment. All four models (2 males and 2 females) were presented in the four body size variations and displaying the four postures.

Figure 3: Time course and example stimuli for the aesthetic Visual Analogue Scale (VAS) judgment task.

Figure 4: Stimulation sites plotted on the sagittal views of a standard brain. According to Talairach coordinates system, dorsal premotor cortices (dPMC) were located close to Brodmann's area 6 in the precentral gyrus (LH (x -50, y -1, z 44); RH (x 50, y -1, z 44)). EBA regions were instead corresponding to Brodmann's area 37 in the posterior part of the middle temporal gyrus (LH (x -52, y -72, z 4); RH (x 52, y -72, z 4)). *LH*, Left Hemisphere; *RH*, Right hemisphere.