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Research report

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

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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 and Bianchini, 2004; Dittrich et al., 1996; Sawada et al., 2003). Recently, Calvo-Merino et al. (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 et al. (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., 2001), 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, 2009b; Cross and Ticini, 2012; Ticini et al., 2015; Kirsch et al., 2016 for a review). It is worth noting, however, that the role of perceived dynamism and

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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 Umilta' et al. (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 et al. (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 et al. (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 and Gallese, 2009; Freedberg and 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 et al. (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 and 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, 1993b) 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) 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 et al. (2011) study, 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