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Original citation: Calvo-Merino, B., Urgesi, C., Orgs, G., Aglioti, S.M. & Haggard, P. (2010). Extrastriate body area underlies aesthetic evaluation of body stimuli. *EXPERIMENTAL BRAIN RESEARCH*, 204(3), pp. 447-456. doi: 10.1007/s00221-010-2283-6

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Calvo-Merino B, Urgesi C, Orgs G, Aglioti SM, Haggard P (2010) Extrastriate body area underlies
aesthetic evaluation of body stimuli. *Experimental Brain Research*. 204(3), 447-56
DOI: 10.1007/s00221-010-2283-6

Extrastriate body area underlies aesthetic evaluation of body stimuli

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Abstract

Humans appear to be the only animals to have developed the practice and culture of art. This practice presumably relies on special processing circuits within the human brain associated with a distinct subjective experience, termed aesthetic experience, and preferentially evoked by artistic stimuli. We assume that positive or negative aesthetic judgments are an important function of neuroaesthetic circuits. The localization of these circuits in the brain remains unclear, though neuroimaging studies have suggested several possible neural correlates of aesthetic preference. We applied repetitive transcranial magnetic stimulation (rTMS) over candidate brain areas to disrupt aesthetic processing while healthy volunteers made aesthetic preference judgments between pairs of dance postures, or control non-body stimuli. Based on evidence from visual body perception studies, we targeted the ventral premotor cortex (vPMC) and extrastriate body area (EBA), in the left and right hemispheres. rTMS over EBA reduced aesthetic sensitivity for body stimuli relative to rTMS over vPMC, while no such difference was found for non-body stimuli. We interpret our results within the framework of dual routes for visual body processing. rTMS over either EBA or vPMC reduced the contributions of the stimulated area to body processing, leaving processing more reliant on the unaffected route. Disruption of EBA reduces the local processing of the stimuli, and reduced observers' aesthetic sensitivity. Conversely, disruption of the global route via vPMC increased the relative contribution of the local route via EBA, and thus increased aesthetic sensitivity. In this way, we suggest a complementary contribution of both local and global routes to aesthetic processing.

Keywords

Neuroaesthetic, aesthetic perception, body perception, transcranial magnetic stimulation, extrastriate body area, premotor cortex.

Introduction

The body of a conspecific is a salient and powerful stimulus. Recent studies in both humans and other animals have shown sensory (Keysers et al., 2004; Downing et al., 2001), motor (Di Pellegrino et al., 1992, Calvo-Merino et al., 2005; 2006) and affective responses (Wicker et al., 2003) in several cortical areas triggered by viewing conspecifics. These responses are often interpreted with reference to a hypothesis of ‘the social brain’ (Frith and Frith, 2007). This view emphasises how the brain represents the behaviour and mental states of others in order to learn from them, and interact with them either competitively or co-operatively (Sebanz et al., 2005).

Here we focus on a less-studied aspect of visual processing of bodies, namely aesthetics. Artistic activity is thought to be a uniquely human behaviour (Cela-Conde et al, 2004), associated with development of specific cortical circuits. Art objects may be considered to activate brain networks that generate aesthetic experiences. However, several different views exist in the literature. Specifically, neural correlates of aesthetic experience have been proposed in reward regions of the brain (i.e. orbitofrontal cortex) (Kawabata and Zeki, 2004; Vartanian and Goel, 2004), in emotional centres such as the amygdala (Di Dio et al., 2007), in specialised visual perceptual areas (Zeki and Lamb, 1994), in dorsolateral prefrontal regions associated with higher ‘executive’ functions such as monitoring (Cela-Conde et al., 2004) and with frontomedian regions underlying social and moral judgment (Jacobsen et al., 2006) (see Nadal et al., 2008 for a comprehensive review).

Aesthetic objects are described using specific labels, including but not limited to ‘beauty’ (Jacobsen et al., 2004). In the case of performing arts such as dance, the observer’s aesthetic experience is presumably grounded in the responses of their neural sensory, motor and affective circuits to the expressive actions of the dancer’s body. Consistent with this account, viewing dance recruited a network of parietal and premotor areas in a manner dependent on the viewer’s previous sensorimotor experience (Calvo-Merino et al., 2005). Importantly, dance movements and dance postures may be judged beautiful or otherwise, quite independently of whether the dancer is judged to be personally attractive or not (Brown et al., 2005). We therefore conjectured that brain circuits specialised for representing the bodies and actions of conspecifics might also underlie aesthetic experience associated with dance.

Aesthetics has a long history in both psychology and neurology (Fechner, 1876). Psychophysical studies aimed to identify stimulus features producing positive and negative aesthetic evaluations (Fechner, 1876; McManus et al., 1985). More recent neuroscientific studies investigated neural correlates of aesthetic evaluation. These studies typically used a ‘subjectivist’ approach, presenting a wide range of stimuli, and comparing the responses for those liked, or found ‘beautiful’ to responses for those disliked, or found ‘ugly’, while acknowledging that participants differ in their evaluation of any particular stimulus. For example, Cela-Conde et al. (2004) found that liked pictures elicited stronger prefrontal cortex activations than disliked pictures. Kawabata and Zeki (2004) found stronger activation of orbitofrontal cortex for pictures found beautiful than for pictures judged ugly, and

stronger activation of sensorimotor cortex for the opposite contrast. Calvo-Merino et al. (2008) applied this approach to dance actions. They found stronger activity in occipital cortex bilaterally and in the right premotor cortex when six subjects viewed short dance passages that they reported liking in a later evaluation, compared to those they disliked. Subjectivist approaches are well-suited to small-scale studies of the neural bases of aesthetic experience, but cannot explain why particular stimuli produce particular experiences. Only one neuroaesthetic study relevant to body representation has focussed on objective stimulus properties, to our knowledge. Di Dio et al. (2007) found stronger neural activity in both occipital cortex and right anterior insula for images of statues obeying the golden section, a principle of spatial proportion traditionally felt to be beautiful than for statues not following this principle.

Importantly, however, both subjectivist and objectivist neuroimaging studies have the weakness of being correlational. Activations that correlate with ‘beauty’ or liking could be purely epiphenomenal, and may not indicate the neural circuits that actually underlie aesthetic experience. Intervention studies, in contrast, can reveal brain areas or circuits actively involved in aesthetic evaluation. Here, following the principle of perceptual selectivity (Zeki and Lamb, 1994), we investigated whether body-sensitive areas also contribute to aesthetic experience of dance perception. We recently (Urgesi et al., 2007) proposed a dual-route model of visual body perception, by identifying two brain areas involved in visual body perception using repetitive transcranial magnetic stimulation (rTMS). We suggested that the extrastriate body area (EBA) (an occipital area specialised for bodies (Downing et al., 2001) houses a local representation of body parts, while the ventral premotor cortex (vPMC) houses a configural representation of complete body postures. Specifically, we found impaired perception of body postures presented either upright or inverted (suggesting an analytical or local way of processing bodies) following EBA rTMS, while rTMS over the left premotor cortex impaired perception of upright but not inverted bodies (suggesting a global or configural type of processing) (Reed and Farah, 1995; Reed et al., 2003). In normal function, these two routes presumably provide complementary information which is combined to produce a single body percept. Here, we investigated the contributions of these two routes to aesthetic evaluation of body postures, by comparing the effects of EBA rTMS and vPMC rTMS with sham rTMS in an aesthetic preference task.

Methods

Subjects

Sixteen subjects (8 women), aged 20-25 years (mean, 21.7 years), participated in the experiment. Two further participants were recruited but not included because they could not be tested in all conditions because of discomfort associated with the stimulation of the premotor sites. Participants had no previous experience with dance performance, or with any of the body postures used in the experiment. A standard handedness inventory (Briggs and Nebes, 1975) revealed that one participant was left-handed, while the remaining 15 participants were right-handed. The procedures were approved by the ethics committee of the Fondazione Santa Lucia (Rome, Italy) and were in accordance with the ethical

standards of the 1964 Declaration of Helsinki. None of the participants had neurological, psychiatric, or other medical problems or any contraindication for rTMS (Wassermann, 1998).

Stimuli

Body posture stimuli were the same as those used in a previous perceptual study (Urgesi et al., 2007). Briefly, they showed a single male dancer in frontal view, in postures taken from classical ballet, and some hybrid postures generated by recombining the upper or lower limb positions from classical ballet and other dance styles. To investigate whether any effects of rTMS on aesthetic evaluation were specific to body perception, as opposed to non-specific factors such as the discomfort associated with rTMS at particular scalp locations, we also presented scrambled non-body stimuli. These were created by pixellating the original body images into a 4x4 pixel array, and swapping two arbitrarily selected quadrants of the picture to remove information about limb posture. The resulting scrambled images resembled abstract patterns, rather than bodies. A similar technique was previously used to separate visual processing of biological motion from non-biological motion (Orgs et al., 2008). Sixteen pairs of body stimuli were used in the experiment, together with the 16 pairs of scrambled non-body images derived from them (Figure 1 and Table 1 Supplementary Material).

Trial structure

On each trial, a pair of pictures was shown. The pair consisted of two body stimuli or the two scrambled stimuli derived from them. Each pair was presented twice in a single block, with the second presentation containing the same stimuli in the reverse order of the first presentation. Each image was therefore judged 10 times across the entire experiment. Each participant was tested in a single experimental session lasting 2 h. Participants completed a 32 trial practice block before proceeding to the experimental blocks. During the experimental session two blocks of 32 trials were presented for each stimulation site. For each participant, each of the four stimulation conditions and sham condition was repeated twice according to a counterbalanced sequence. Each trial began with presentation of a fixation point. After 500 ms, this was replaced by the first image for 100 ms, followed by a binary visual noise mask for 500 ms. Then, the second image was presented for 100 ms, followed by a further mask. Finally, a visual prompt “Which do you prefer: the first or the second?” (‘Quale ti piace di più: il primo o il secondo?’), asked subjects to indicate which of the two pictures they preferred, by an unspeeded keypress response of the right index and middle fingers respectively (Figure 1).

In addition, at the end of the experiment, each participant viewed each stimulus, body or scrambled body, alone on the screen in random order, and used a visual analogue scale (VAS) to rate how much they liked it (ranging from 0 ‘I do not like it at all’ to 100 ‘I like it very very much’).

TMS

For each participant, the resting motor threshold for the first dorsal interosseous muscle of the right hand was determined. Surface Ag/AgCl electrodes were placed in a belly–tendon montage. An electromyographic signal was amplified at a gain of 1000 by a Digitimer (Hertfordshire, UK) D360 amplifier, bandpass filtered (20 Hz to 2.5 kHz), and digitized (sampling rate, 5 kHz) by means of a

CED Power 1401 controlled with Spike 2 software (Cambridge Electronic Design, Cambridge, UK). The resting motor threshold, defined as the lowest intensity able to evoke 5 of 10 motor-evoked potentials with an amplitude of at least 50 μ V, was determined by holding the stimulation coil over the optimal contralateral scalp position.

rTMS was applied by connecting two Magstim Model 200 stimulators with Bistim module (The Magstim Company, Carmarthenshire, Wales, UK,) with a 70 mm figure-eight stimulation coil (Magstim polyurethane-coated coil) in separate blocked conditions, with each subject having a different random block order. For sham stimulation, the coil was placed over the vertex and oriented perpendicular to the scalp, with the border of one wing placed against the head. This ensured that no magnetic stimulation reached the brain during sham stimulation and controlled for noise and the sensation of the coil against the head. The same stimulation intensity and timing were used for magnetic and sham stimulation. In the experimental conditions, the coil was held over PMC or EBA of the left or right hemisphere, with the handle pointing posteriorly. These areas were located on each participant's scalp with the SofTaxic Navigator system (EMS, Bologna, Italy). Coordinates in Talairach space (Talairach and Tournoux, 1988) were automatically estimated by the SofTaxic Navigator from a magnetic resonance imaging-constructed stereotaxic template. These were vPMC, corresponding to Brodmann's area 44 in the pars opercularis of the inferior frontal gyrus (LH (x -57, y 11, z 22), RH (x 57, y 11, z 22)) and EBA, 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)). Participants wore a tightly fitting bathing cap on which the stimulation points of the scalp were marked.

During stimulation of the four sites, 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. The contours of the handle and of the coil placed over each stimulation site were marked on the bathing cap to check continuously the position of the coil with respect to the marks and its orientation in the axial plane.

The same pulse delay and stimulation intensity was used for the four stimulation sites and for sham stimulation. Stimulation intensity was 120% of the resting motor threshold for both pulses. This ranged from 42% to 66% (mean, 52 %) of the maximum stimulator output. A train of 2 rTMS pulses was delivered, at 150 and 250 ms after the onset of the first image. Pulses were timed to interfere with the cortical processing of the first image.

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 a blink response was observed in most participants as a result of stimulation. Blinking would not prevent the

participants from seeing the stimuli because the rTMS trains were presented 50 ms after the offset of the first stimulus and 300 ms before the onset of the second stimulus.

Results

The data consist of aesthetic preference judgements for each of the 16 body posture pairs and their non-body scrambled derivatives. The data were analysed following a 'subjectivist' design (Calvo-Merino et al., 2008). We first used each participant's VAS judgements of each image to predict which of the two images presented in each trial would be preferred. (See Table 1, Supplementary Material, for a detailed presentation of stimuli and mean preference scores at VAS). For example, for scores of 69 for image 1, and scores of 57 for image 2, we would predict that this specific participant would choose image 1 in the forced-choice preference task. This procedure was repeated for each pair, for each participant. The VAS judgements therefore allowed us to predict which stimulus each individual subject would prefer in each pair, under the null hypothesis of no rTMS effect on aesthetic judgement. We determined the percentage of trials in each condition in which the subject's response was different from that predicted by their VAS judgements. This gave a measure of the change of aesthetic preference caused by rTMS. Any preference judgement trials involving two images having identical VAS judgements were discarded (12.5% body trials in 3 subjects, 12.5% scrambled trials in 3 subjects, and 6.25% scrambled trials in another subject). Note that a given level of change from VAS predictions could be caused by either an increase in preference for the stimulus rated lower in the VAS, or a decrease of the higher-rated stimulus, or both. That is, our measure of change from VAS predictions was not simply a measure of aesthetic bias (decreased or increased liking) due to rTMS, but a measure of decreased or increased aesthetic sensitivity, corresponding to larger and smaller departures of preference judgements from VAS predictions respectively.

The change index during sham stimulation was significantly different from 0 for both the body (mean, 34.56%; SD, 15.23%; $t_{16} = 9.07$, $P < 0.001$) and the scrambled stimuli (mean, 38.53%; SD, 8.38%; $t_{16} = 18.29$, $P < 0.001$), but there was no difference between the two stimulus types ($t_{16} = -1.02$, $P = 0.325$). This indicates that in about one third of the sham trials the subjects' preferences were not predictable from the VAS judgements. This discrepancy may be due to noise, due to some natural functional variation in aesthetic evaluations, or due to different task demands of VAS and preference judgements. By the same token, roughly two thirds of all aesthetic evaluations showed agreement between VAS and preference judgements in our sham condition, implying some consistency of aesthetic judgement. Finally, to control for the substantial interindividual differences in the extent of this agreement between VAS and preference judgements, we expressed the aesthetic preference change in each experimental rTMS condition as a percentage of each subject's aesthetic preference change index during sham stimulation, by calculating the ratio between the change index for each rTMS condition and the sham. Values of percentage modulation above 100% mean that the preference judgements depart from the VAS predictions more in the rTMS condition than at sham, while values below 100% indicate the opposite. Thus a high score on this percentage modulation of change index

indicates a loss of normal aesthetic sensitivity established by the VAS. The percentage modulation in the change index for each experimental condition of our design is shown in Table 1.

We next considered how rTMS at each site might modulate aesthetic preference changes relative to sham stimulation. Disrupting the neural circuits involved in aesthetic evaluation might have any of several effects. It might cause an overall bias in preference for the image presented immediately before rTMS, either increasing or decreasing the probability of the image being preferred. However, every image was presented precisely once just before rTMS, and was compared to other images that would presumably be affected by rTMS in the same way. Therefore, our pairwise preference judgements should be unaffected overall by a rTMS-induced bias in aesthetic evaluation. Alternatively, rTMS might cause a change in aesthetic sensitivity, either reducing or enhancing aesthetic judgement. Reduced aesthetic sensitivity would imply that images that received higher VAS judgements would be less likely to be preferred following rTMS than their high VAS ratings would predict, while images that received lower VAS judgements would be more likely to be preferred following rTMS. That is, reduced sensitivity would make aesthetic preference judgements depart more frequently from what VAS ratings of each stimulus would predict. Enhanced sensitivity would produce the converse pattern. Thus, the precise pattern of aesthetic preference modulation at each rTMS site may reveal its role in aesthetic evaluation.

The percentage modulations of aesthetic preference change were subjected to a 3-way repeated measures ANOVA with factors of rTMS site (EBA, vPMC), hemisphere (Left, Right) and image type (Body, Scrambled). These data are shown in Table 1. The main effects of rTMS site and image type were non significant (all $F_{s,15} < 1$). The main effect of hemisphere showed a trend for left hemisphere stimulation to decrease the relation between aesthetic preference judgement and VAS, relative to its value at sham, but for right hemisphere stimulation to increase the strength of this relation ($F_{1,15} = 3.74$, $P = 0.072$; mean (\pm s.e.m.): left: $104.69\% \pm 3.5\%$ of sham, right: $96.92\% \pm 3.51\%$ of sham). The two-way interaction of hemisphere with rTMS site and image type were not significant (all $F_{s,15} < 1$). However, a significant interaction between rTMS site and image type was found ($F_{1,15} = 5.76$, $P = 0.03$; Figure 3). Duncan post-hoc tests showed that the interaction was explained by preference judgements for body stimuli departing more strongly from VAS predictions after EBA stimulation than after vPMC stimulation (means (\pm s.e.m.) EBA: $107.47\% \pm 8.18\%$ of sham, vPMC: $95.3\% \pm 4.56\%$ of sham; $P = 0.042$). No difference was obtained between EBA and vPMC stimulation conditions on the aesthetic judgement changes for scrambled stimuli (means (\pm s.e.m.) EBA: $97.67\% \pm 4.31\%$ of sham, vPMC: $102.77\% \pm 4.9\%$ of sham; $P = 0.33$). No other pair-wise comparisons were significant (all $P_s > 0.08$), and none of these conditions were significantly different from 100 (all $P_s > 0.1$).

In summary, EBA rTMS blunted aesthetic judgements about body postures relative to vPMC rTMS, making the aesthetic preference performance of each subject less predictable from his/her VAS judgements. Of the potential effects of rTMS on aesthetic judgement described above, this corresponds to a change in aesthetic sensitivity. The non significant three-way interaction between rTMS site,

hemisphere and image type ($F_{1,15} < 1$) shows that rTMS of both left and right EBA disrupted body aesthetic judgements relative to the ipsilateral vPMC.

Discussion

We applied brief trains of rTMS over each hemisphere to two brain areas selective for different aspects of visual body processing (EBA, vPMC), to investigate the neural mechanisms of aesthetic of body perception. For each participant, we classified each presented image in a pair according to its individual VAS aesthetic judgment, and whether or not it received higher or lower scores with respect to the other image in the pair. We used this index to predict each individual subject's responses to each pair of stimuli presented to them. The analysis of the modulations of aesthetic preferences showed that body aesthetic judgements in the VAS had a reduced role in predicting preference choices following stimulation of EBA, as compared to stimulation of the ipsilateral vPMC. That is, EBA stimulation tended to blunt aesthetic sensitivity (reduce congruency with VAS aesthetic scores) and vPMC stimulation tended to enhance it (increase congruency with VAS aesthetic scores). No similar changes were observed during aesthetic judgement of the scrambled control stimuli, and no other interactions or main effects were significant. This result allows us to conclude that different routes within the two-route model of body processing (Urgesi et al., 2007) play a complementary role on aesthetic perception. In this way, rTMS over EBA blunted aesthetic responding to body postures, relative to the effect in the opposite direction to rTMS over vPMC, and in contrast to the pattern of results for control non-body images. Our results suggest that the EBA and vPMC may be two complementary components of the aesthetic perception network for bodies.

It is important to remember that our study used a 'subjectivist' rather than an 'objectivist' design. We do not claim that rTMS altered the evaluation of all images, but only that each subject's idiosyncratic pattern of aesthetic evaluation for body postures was attenuated after stimulation over EBA and enhanced after stimulation over vPMC, while no similar effect was found for stimulation following presentation of non-body stimuli. Moreover, no differences between bodies and non-body stimuli were found in the sham condition. Although our data does not allow any general claim about what stimuli produce particular aesthetic experiences, it allows us to identify the regions that necessarily participate in the neural processes that underlie each individual's aesthetic evaluations of body stimuli.

To our knowledge, this is the first interventive, as opposed to correlative, study of aesthetic evaluation, and the first neuroaesthetic study of visual perception of static body postures. Moreover the pattern of results rules out some possible artefactual explanations. rTMS did not induce any simple bias either towards preferring or not preferring the first image of the pair, so the results cannot be explained in terms of general rTMS-induced discomfort, or discomfort confined to particular stimulation sites. In addition, we found no main effect of stimulus type, nor any interaction between stimulus type and preference at sham. This suggests that body and scrambled stimuli were balanced, and were both equally amenable to aesthetic evaluation.

Two-route model of body processing

It has been suggested that aesthetic judgements are made in frontal regions (Jacobsen et al., 2006) that evaluate information provided by earlier stages of visual processing streams. By applying rTMS to two regions of the network that contribute differently to body perception (EBA and vPMC for local and configural processing, respectively; Urgesi et al., 2007), we could investigate how these two regions contribute to aesthetic perception. Here, we show a reduction of aesthetic sensitivity for body stimuli following EBA stimulation relative to vPMC stimulation, while no such effect was found for non-body stimuli. This result suggests that the early perceptual analytical processing of body form by EBA contributes to the final aesthetic evaluation of body stimuli. Configural processing in vPMC may also contribute to aesthetic evaluation, but intervention here produced a less conclusive effect (Figure 4). In this way, both EBA and vPMC play a role in aesthetic processing, and information from both paths is integrated in a final body percept to be evaluated in frontal decision making regions. However, our results show that their individual contributions influence final aesthetic judgment in a different manner.

Psychology has widely investigated the role of global configurations on aesthetics, from artworks (McManus et al., 1985) to simple geometrical shapes (i.e. the golden ratio, Livio, 2002) and complex biological configurations such as faces (Abbas and Duchaine, 2008). In painting, global configurations are suggested to underlie high aesthetic quality (Vartanian et al 2005). Therefore, it may seem surprising that the local processing of the EBA, rather than the global configural processing of the vPMC, seems to underlie strong aesthetic sensitivity in our study. However, modifying the balance or composition of a painting does not necessarily change its aesthetic value, suggesting that its value is not only in the structural configuration but also in the local content (Shaw 1962). Therefore, both local and global components may play a role for aesthetic judgements. The present study employed a forced-choice of aesthetic judgments, between two meaningless body postures that had different leg and arm positions. In this way, participants' attention might have been driven to the detail of the body parts rather than to the global configuration. In this way, purely local changes could be crucial for aesthetic values of these particular stimuli. Accordingly, disruption of the configural path would enhance local processing and therefore facilitate aesthetic sensitivity. Further studies should explore if driving attention to configural features of visual stimuli might change the direction of this effect between both body processing paths.

The present results also extend our view of these two body processing regions. Previous studies identified roles of EBA and vPMC in perception of body parts and whole-body configurations respectively (Downing et al., 2001; Taylor, Wiggett and Downing, 2007; Urgesi et al., 2007). EBA has been traditionally considered merely an early category-selective region for the visual processing of static images of the human body and not to pictures of other stimulus categories such as objects (e.g. a chair, a spoon) (Downing et al., 2001, Moro et al., 2008, Urgesi et al., 2004; Peen and Downing 2005). However many recent studies suggest EBA relation with more cognitive functions and frontal sensorimotor regions (Astafiev et al., 2004; Helmich et al., 2007; David et al., 2007). Recent studies have shown functional connectivity of EBA with higher cortical areas such as the PMC and posterior

parietal cortex (PPC) during different cognitive tasks, such as mental hand rotation (Helmich et al., 2007) or self-other attribution (David et al., 2007). In general, these studies showed functional interactions between EBA and PMC and PPC, and extend EBA basic body perception function to one more integrative and dynamic that may include visual integration, spatial attention, and sensorimotor signals involved in the representation of the observer's body (David et al., 2007). The present study supports the idea of further and more extensive roles of EBA within the body perception circuit. We propose its contribution to a particularly human way of seeing such as aesthetic perception.

Multiple visual areas for aesthetic processing

While we did not test low-level perceptual processing of these stimuli directly, the pattern of our results makes it unlikely that blunting of aesthetic sensitivity was simply due to participants failing to see the stimuli following stimulation over EBA regions. First, reports of rTMS-induced visual masking are confined to disruption of early visual areas (Kammer, 1999). Secondary visual areas such as EBA, which is situated in the posterior part of the inferior temporal sulcus, are not classical loci for TMS-induced masking. Second, a purely low-level perceptual effect would apply equally to both types of stimuli presented in the experiment (bodies and scrambled bodies). However our pattern of results suggests that rTMS over EBA and PMC disrupted aesthetic processing only for body stimuli, in contrast to non-body scrambled stimuli.

In general, an initial perceptual analysis is inevitable during the aesthetic processing of visual stimuli. Most psychological work on aesthetic has focussed on investigating what perceptual features related to artworks are generally preferred by the observer (Berlyne, 1974; Zeki, 1999; Leder, 2004). Most designs vary only one perceptual feature at a time (i.e. complexity, contrast, colour, symmetry, balance) and evaluate how people tend to prefer one stimulus over another. Occipital visual processing areas are supposed to be involved at this level. In the present study, we have not sought for particular stimulus feature that are more or less preferred. Rather, we show that the early analytical visual processing of body stimuli has a significant role in the later aesthetic evaluation. This type of result strengthens the role of multiple perceptual regions in aesthetic perception (Zeki and Lamb, 1994).

Hemispheric lateralisation of aesthetic processing

The lack of hemisphere effects suggests that both hemispheres contributed in a similar manner to aesthetic processing. This is consistent with other rTMS studies investigating other aspects of body processing such as form and action discrimination, on the right and left EBA and PMC, where no modulation by hemisphere stimulated was found (Urgesi et al., 2007). Although previous studies of body perception reported stronger activation of the right EBA (Downing et al., 2001) for body parts, most reported activations are clearly bilateral (Chan et al., 2004; Peelen and Downing 2007). A recent meta-analysis and review of premotor cortex activation in action observation reported no convincing lateralisation (Morin and Grèzes, 2008). Moreover, lateralization in aesthetic processing has not been clearly addressed. The few published neuroaesthetic studies using visual stimuli have not achieved

consensus on the lateralisation of aesthetic responses. For example, two fMRI studies report left sensorimotor cortex activations associated with explicit subjective judgements of ugliness (Di Dio et al., 2007; Kawabata and Zeki, 2004). In contrast, Calvo-Merino et al.'s (2008) participants first viewed dance movements, and later gave them aesthetic evaluations in a separate session. They found that right, but not left, PMC activity correlated with aesthetic evaluation. Although we observed a general trend for left hemisphere rTMS to decrease the aesthetic sensitivity in the present study, no significant hemisphere effect or interaction were found. We therefore suggest that both hemispheres contribute to the perceptual analysis necessary for aesthetic evaluation in EBA in relation to the processing of the ipsilateral PMC.

Interpretative and methodological issues

Several previous neuroaesthetic studies identified neural correlates of positive and negative aesthetic judgements, by comparing activation for stimuli found beautiful and those judged ugly. Such studies cannot identify the neural processes of aesthetic evaluation and discrimination, since the evaluation process presumably occurs whether its output is positive or negative. In contrast, the pattern of our data suggests that rTMS impaired the aesthetic sensitivity necessary to perform an aesthetic evaluation judgement itself (whether this is positive or negative). These results imply loss of aesthetic sensitivity or aesthetic discrimination, rather than simple bias towards positive or negative evaluations. In general, we suggest that neuroaesthetic studies should distinguish the process of aesthetic evaluation from the stimulus properties that cause specific evaluation outputs on the one hand, and from the subjective experiences associated with specific evaluation outputs on the other. We know of only one other neuroscientific study focussing on aesthetic processing, as opposed to aesthetic evaluation. Jacobsen et al. (2006) contrasted activation during aesthetic judgement with activations during symmetry judgements of the same stimuli. However, this study faces the same criticism as other correlative fMRI designs. The activation could reflect an epiphenomenal correlate of aesthetic processing, rather than aesthetic processing. For example, making aesthetic judgements may be more engaging and arousing than making symmetry judgements, which could explain the greater activation in attentional and limbic regions of cortex. Future studies might combine our TMS approach to aesthetic processing with the approach taken by Jacobsen et al (2006). A study applying TMS to target areas during both aesthetic and non-aesthetic control judgements about the same stimuli might distinguish brain areas contributing to visual perception in general, from those contributing to aesthetic processing in particular.

Finally, we consider some methodological issues. First, the results obtained here are partial rather than total. rTMS over EBA reduced aesthetic sensitivity to body postures, relative to rTMS stimulation over PMC, and in contrast to non-body stimuli. However EBA rTMS but did not entirely abolish aesthetic evaluation. This could reflect the relatively mild rTMS intervention that we applied. Alternatively, the aesthetic preferences expressed in our study may be quite subtle, since they are caused by changes in limb position of a single male dancer. More extreme aesthetic variations, between different dancers, or different dance forms, might produce stronger results. Second, our study

cannot clarify what body postures, if any, involve absolute beauty, due to its subjectivist approach. We recorded each person's individual evaluation of each stimulus, without assuming that evaluations generalise across people. These results cannot therefore be used for 'neuromarketing' (McClure et al., 2004), or predicting the aesthetic impact of an object on the population in general. Instead, subjectivist designs focus on identifying the neural correlates of aesthetic processing. Third, our study cannot reveal why a subject prefers a particular stimulus on any particular trial, because we recorded preferences but not the reasons underlying preferences. Preference judgements have the merit of face validity (Samuelson, 1938). They also have the great advantage of not requiring any explicit definition of 'beauty', either in the instructions given to the participant, or in the interpretation of results. Rather, each individual's preference judgements are taken to reveal their personal yet implicit concept of beauty. However, preference judgements are not very informative about which aspects of a stimulus lead subjects to like or dislike it. Future studies might combine a large-scale psychometric approach to identify specific stimulus features associated with specific aesthetic evaluations, and then translate these to quantitative neuroscientific studies.

Acknowledgements

We are grateful to Deborah Bull, Tom Sapsford, Mavin Khoo and Matteo Candidi for advice and assistance. This work was supported by grants from the Economics and Social Science Research Council (ESRC - PTA-026-27-1587), City University London Fellowship, and Ramon y Cajal Fellowship to BC-M, a research fellowship of the German Academic Exchange Service (DAAD) to GO, grants from the IRCCS "E. Medea" (Ricerca Corrente 2009, Italian Ministry of Health) to CU, a BBSRC project grant, Leverhulme Trust project grant and Leverhulme Trust Major Research Fellowship to PH, a BBSRC-ISIS grant to PH and SMA, and the Ministero Italiano Università e Ricerca, Italy, University of Rome "La Sapienza" and the IRCCS Fondazione Santa Lucia to SMA.

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Table 1. Mean (s.e.m) normalized aesthetic preference changes in each experimental condition of the ANOVA design. Factors are: image type (Body, Scrambled), hemisphere stimulated (Left, Right) and rTMS stimulation site (EBA, vPMC).

	Left Hemisphere rTMS		Right Hemisphere rTMS	
	Body	Scrambled	Body	Scrambled
EBA	113.67% (11.86)	101.47% (5.36)	101.28% (5.66)	93.86% (7.73)
vPMC	99.27% (7.18)	104.34% (5.96)	91.34% (6.35)	101.2% (6.49)

Figure 1. Time course and example stimuli for aesthetic preference judgements between pairs of body postures (left) and pairs of non-body stimuli (right).

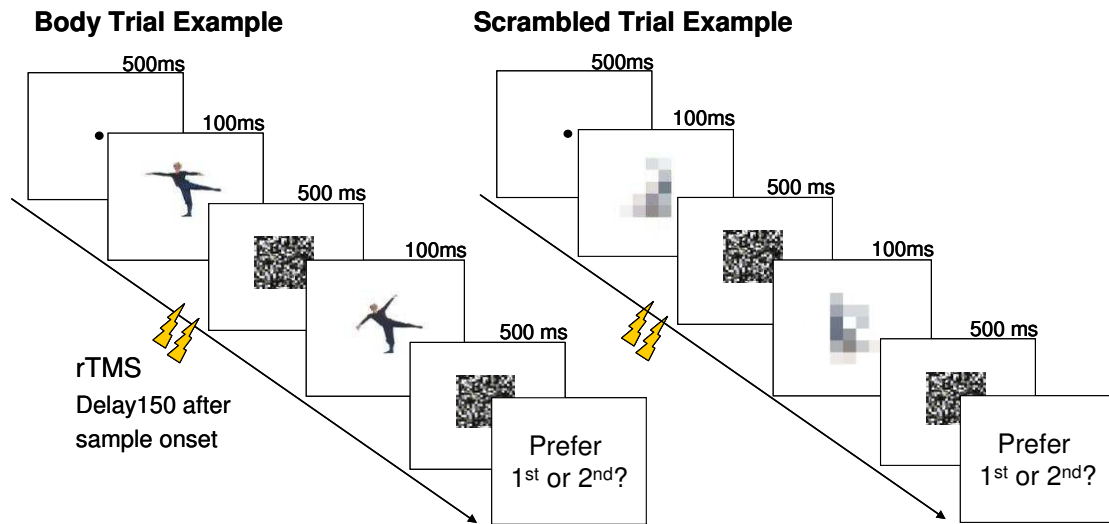


Figure 2. Stimulation sites plotted on the lateral views of a standard brain. Mean Talairach coordinates of the stimulation sites were as follows: vPMC, corresponding to Brodmann's area 44 in the pars opercularis of the inferior frontal gyrus (LH: (x -57, y 11, z 22), RH (x 57, y 11, z 22) and EBA, corresponding to Brodmann's area 37 in the posterior part of the lateral occipitotemporal (LH: x -52, y -72, z 4 ; RH x 52, y -72, z 4). L: Left Hemisphere, R: right hemisphere.

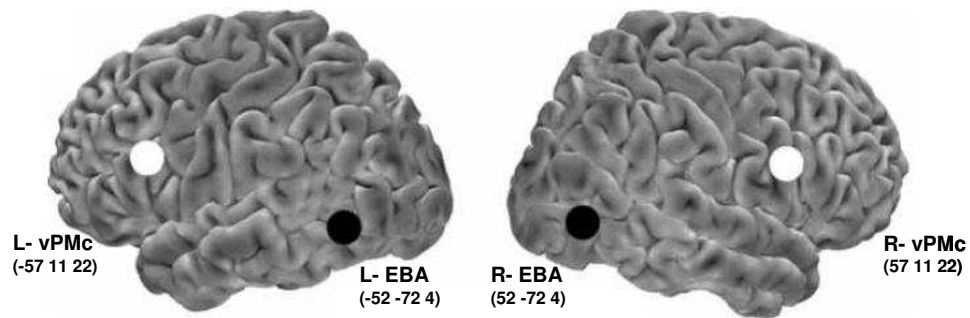


Figure 3. Effects of rTMS on normalized aesthetic preference judgements as a function of image type and rTMS site (EBA, vPMC). Results are shown averaged over left and right hemispheres stimulation (see text). Error bars indicate standard errors over participants. *: $P < 0.05$.

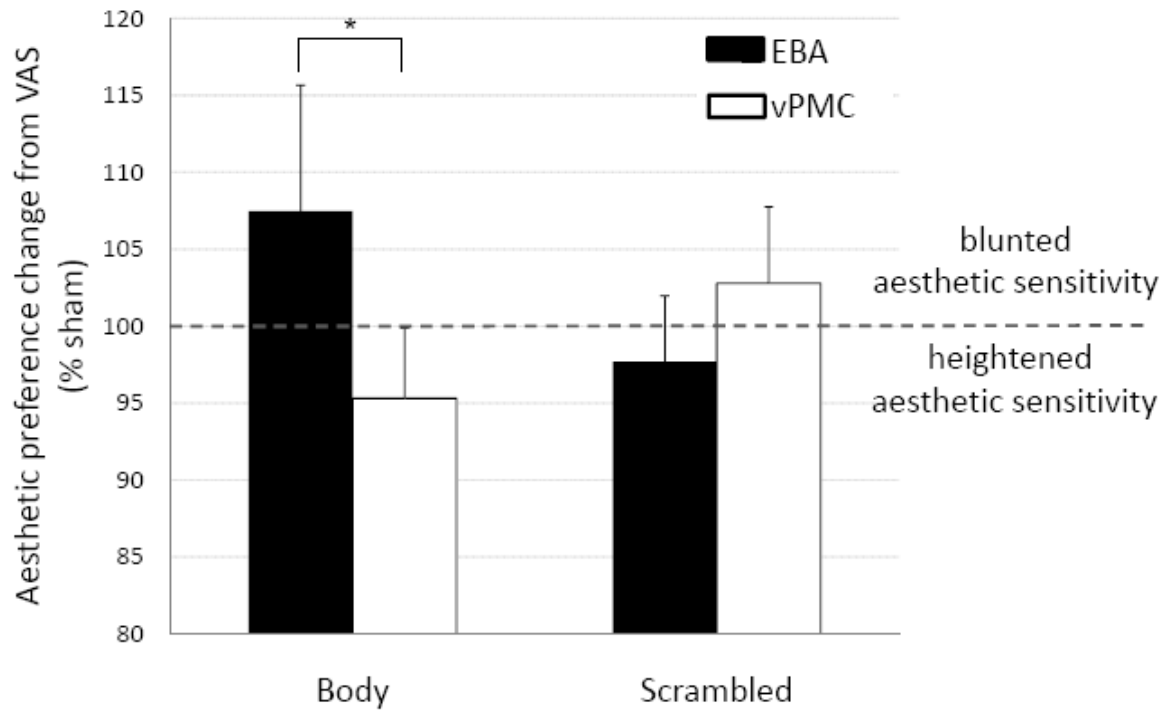
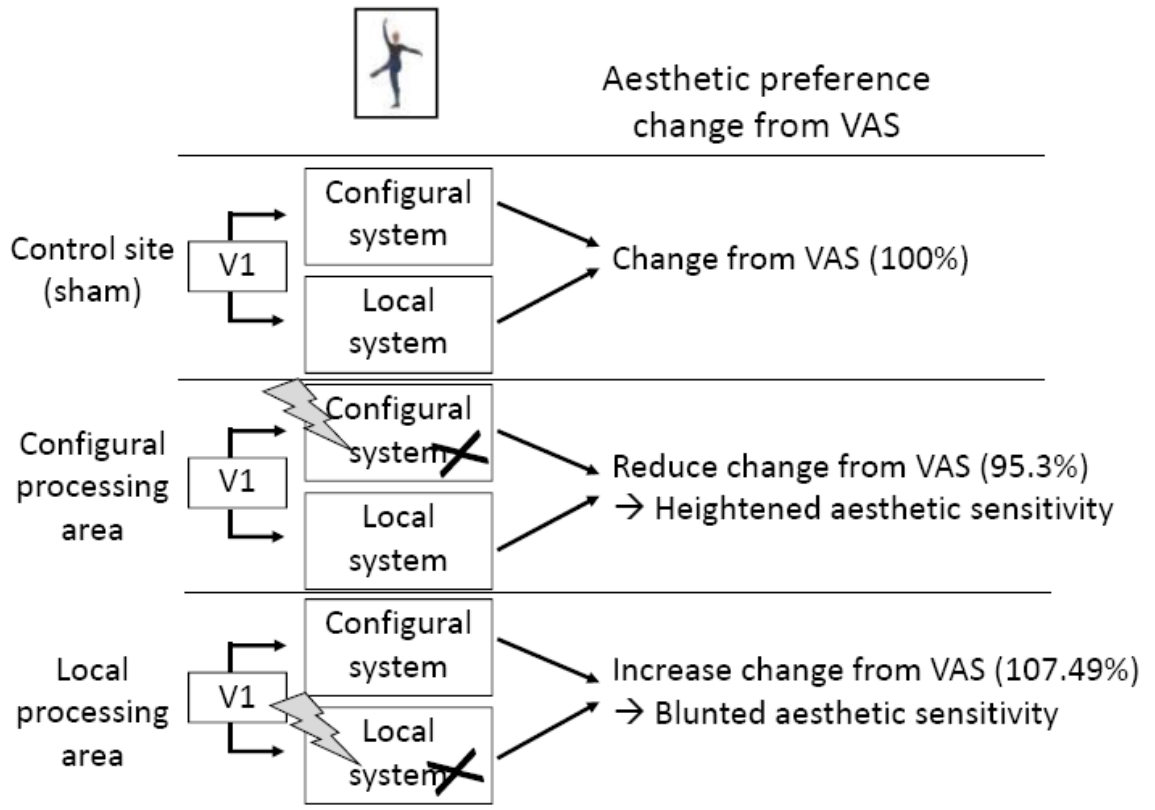


































































Figure 4. Aesthetic processing in the two-route body model.



Supplementary Material:

Table 1: Body and non-body (scrambled) stimuli and mean visual analogue scale ratings across participants (VAS) ranging from 0 ‘I do not like it at all’ to 100 ‘I like it very very much’).

Body Stimuli		Body Stimuli		Body Scrambled		Body Scrambled	
	68.4		60.2		50.7		55.4
	54.2		56.8		51.3		38.8
	61.3		49.5		54.1		49.3
	57.6		57.5		49.8		43.8
	70.3		59.4		48.3		53.8
	58.0		44.2		51.2		49.2
	54.4		61.2		55.7		53.8
	69.2		28.0		57.0		52.8
	58.0		62.5		50.6		50.3
	56.1		44.1		41.8		44.8
	59.3		45.2		45.5		46.4
	66.0		48.0		56.1		48.1
	56.8		43.0		38.2		48.8
	42.8		55.1		41.2		53.4
	44.8		48.7		47.1		57.1
	68.0		44.2		55.5		52.3