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Research Report

Classical paintings may trigger pain and pleasure in the gendered brain

Beatrice de Gelder [a,b,e,*], Rebecca Watson [a], Minye Zhan [a], Matteo Diano [a,c,d], Marco Tamietto [b,c] and Maarten J. Vaessen [a]

[a] Brain and Emotion Laboratory, Department of Cognitive Neuroscience, Faculty of Psychology and Neuroscience, Maastricht University, Maastricht, the Netherlands
[b] Department of Computer Science, UCL, United Kingdom
[c] Department of Psychology, University of Torino, Italy
[d] GCS-fMRI, Koelliker Hospital, Torino, Italy
[e] Italian Academy for Advanced Studies, Columbia University, New York, United States

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ABSTRACT

The human body is the most common object of pictorial representation in western art and its representations trigger a vast range of experiences from pain to pleasure. The goal of this study was to investigate brain activity triggered by paintings of male and female body images exemplifying conditions associated with pleasure or pain. Our findings show participant-general as well as gender specific brain activity for either the pain or the pleasure conditions. Although our participants were fully aware that they were viewing artworks, the inferior parietal lobule – known for its role in the perception of emotional body images – and the somatosensory cortex related to touch were selectively active for female body paintings in all participants in the pleasure conditions. As regards gender we observed that the sight of female bodies activated the subgenual anterior cingulate cortex in males, an area known to subserve autonomic arousal. In contrast, in females the sight of the male body activated reward and control related parts of the dorsal anterior cingulate cortex. This study supports the notion that some basic evolutionary processes operate when we view body images, also when they are cultural heritage paintings far removed from daily experience.

1. Introduction

Art has been around since the dawn of mankind and the power in images endures across cultures (Freedberg, 1991; Mithen, 1996). Societies dedicate enormous financial resources and time to the creation and enjoyment of artworks. Recently, neuroscientists have launched studies of the brain basis of art perception focusing mainly on the visual arts and music. Interesting research findings cover a

* *Corresponding author*. Department of Cognitive Neuroscience, Room 3.009, Oxfordlaan 55, 6229 EV, Maastricht, the Netherlands.
E-mail address: b.degelder@maastrichtuniversity.nl (B. de Gelder).

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broad spectrum, ranging from visual analysis of artworks (Cavanagh, 2005) to findings about motor resonance created in the viewer (Freedberg & Gallese, 2007), and to inquiries into the neural basis of subjective esthetic experience (Ishizu and Zeki, 2011, 2014; Zeki, 2011). Studies using functional magnetic resonance imaging (fMRI) so far converge on medial orbitofrontal cortex, anterior cingulate and lingual gyrus as the major areas involved in visual art perception (Ishizu & Zeki, 2011). Since our study uses images of paintings we also expected those areas to play an important role here. Furthermore, as we specifically selected paintings of bodies we predicted activity in areas in temporal cortex recently associated with perception of body shape and with movement and action perception mainly in parietal, premotor and somatosensory cortices (de Gelder, 2006; de Gelder, 2016).

Beyond these general considerations, our choice of materials was also motivated by specific question about so far undiscovered markers of the biological roots of visual art perception in the brain e.g., specific markers of pleasure versus pain images or if male and female participants reacted differently to images of whole bodies. Similar to what has long been argued for the basic organization of sensory perception and cognition, art perception may have a specific neural basis with roots in the evolutionary history of the brain. Indeed, Darwin famously struggled with the role of art and settled for a close link between art and its role in sexual selection. Adopting this general perspective challenges visual art perception studies to turn to processes of emotion, motivation and reward. This link has already been addressed by various authors, for example in the pleasure/reward/appetitive component of the esthetic brain model (Chatterjee, 2013; Chatterjee & Vartanian, 2014) and the state of the art has been extensively discussed in a recent review (Kirsch, Urgesi, & Cross, 2016). Specifically, some studies using photographs have already advanced the evolutionary argument about art by looking at facial attractiveness from the perspective that physical beauty confers survival advantages (Aharon et al., 2001; Hahn & Perrett, 2014). This leads to the question whether similar preferences, possibly based on the evolutionary advantages conferred by attractiveness, can be found when whole body images are used. The specific hypothesis addressed here is whether beyond the previously reported brain areas involved in visual art perception there are neural markers of gender in brain activations as measured with functional MRI (fMRI) when people view classical paintings depicting male ("male paintings") and female bodies ("female paintings") representing either states of pleasure or of pain. Surprisingly, this hypothesis has not yet been tested with exemplars from the visual arts, specifically by using paintings that make up the bulk of the artistic environment western people are familiar with, from church decorations to daily exposure to the decoration of cookie tins.

Our materials consisted of classical paintings of the human body chosen because they are universally seen as beautiful and recognized as artworks. We were not interested in specific bodily expressions of emotion as frequently seen in paintings but in positive versus negative displays related to pleasure and pain. Bodies pierced with arrows are a classic topic in the history of Western art but not in daily life and this guaranteed that seeing these pain and pleasure manifestations tapped in a realm of experience remote from daily life and persons. Starting from these images two sets, representing either pleasure or pain, were constructed as follows. To maximize homogeneity, paintings of the male body were selected from among representations of the San Sebastian theme, a male figure penetrated by arrows (see Fig. 1). This set represented the male pain condition. Next, to create a set of male pleasure paintings the arrows were removed by image editing. Finally, to arrive at a balanced set for each gender, we composed a set of painting with females without obvious pain elements and created a set of female paintings with the arrows taken from rom the male paintings now added to them (see Fig. 1). In order to avoid any familiarity, memory or other cognitive processes related to the stimuli, a sample of naive college students was used. While the images we used were clearly perceived as artworks we were careful to avoid asking for an esthetic judgment or to trigger an artistic reaction in the participants. Second, the images were seen as traditional masterpieces of western painting as found in major museums, but any further details were unknown to the participants. Since none of our subjects was familiar with any of the paintings and the presence/absence of the arrows in the manipulated paintings was not systematically related to the original paintings, participants did not miss the arrows in the male pictures nor did they view the addition of arrows in the female pictures as a deviation from the original.

Fig. 1 – Example of stimuli. From left to right of male painting with no arrow, male with arrow, female with no arrow, female with arrow.

2. Materials and methods

2.1. Participants

Twenty healthy participants (10 males, mean age of the whole group 25 y, range 21–29 y) participated in the study. All had normal or corrected-to-normal vision, and no history of neuropsychiatric disorders. Experimenters were acquainted with the participants and selection for participation was consistent with biographical information about gender preference. None of the participants had a previous background in art or had any special interest in painting. The experiment was approved by the Ethics committee of Maastricht University, and written informed consent was obtained from each participant beforehand. The study was conducted in accordance with the approved guidelines. Participants were screened for fMRI experimentation safety and received monetary compensation.

2.2. Materials and design

16 male and 16 female full-body classical oil painting were selected from the internet (for a full list of stimuli, see Supplementary Table 4). The theme of the male-body paintings was Saint Sebastian pierced with arrows, in either a standing or half-lying position. Female-body paintings were selected from the themes of Andromeda, Cleopatra, Danae and Venus, in standing or lying positions. Some male paintings showed the bodies bound with ropes or chains and these were modified in Photoshop CS6 (Adobe systems incorporated, USA) in order to create a more homogeneous set for four different stimulus conditions: "male bodies with arrows"; "male bodies with no arrows", "female bodies with arrows"; and "female bodies with no arrows". Firstly, as the original male body paintings all depicted bodies pierced with arrows, the arrows and blooddrops from the paintings (including those in the background) were removed to create the "male bodies with no arrows" set. Furthermore, as none of the original female body paintings showed bodies pierced with arrows, we created the "female with arrow stimuli" set by copying the arrows from the San Sebastian paintings, and adding 2–4 arrows with roughly matching painting style onto the limbs, the torso, or the neck of the female bodies, adding shadows and some blood drops accordingly. The number of arrows in the female paintings roughly matched the number in male paintings (Male: arrow on the bodies: mean = 2.64, SD = 1.28; arrow in the scene: mean = 3.29, SD = 2.20. Female: mean = 2.75, SD = .68). The faces were blurred and other faces in the background were also blurred. See Fig. 1 for illustrative examples of the modified sets. Finally, all images were then cropped to contain only the body of interest.

2.2.1. Behavioral experiments

In an offline behavioral experiment, 13 participants (10 female, mean age ± standard deviation 23 ± 6.1 years) were presented with each painting in turn, and instructed to inspect it for as long as they wanted to. Paintings were presented on a PC screen, using Presentation software (Neurobehavioural Systems, San Francisco, CA). Presentation was self paced. They pressed a key on the computer keyboard when ready to view the next stimulus. This provided a measure of the relative looking time per image. In addition an independent cohort of 12 participants rated each stimulus on perceived pain (7 point rating scale), in order to assess bias in female/male and edited/original paintings with regards to pain perception.

2.2.2. fMRI experiment

Participants were scanned using a Siemens 3T Prisma scanner (Siemens, Erlangen, Germany). Earplugs were used to attenuate scanner noise and paddings to reduce head movements. All stimuli presented during the fMRI session were projected onto a clear screen at the back of the scanner bore that participants could see using a mirror mounted on top of a head coil. Participants passively viewed the stimuli and were not instructed to perform any task. Each stimulus was presented in the center of the screen on a white background using Presentation software (Neurobehavioural Systems, San Francisco, CA). The study consisted of 4 experimental conditions: female paintings with arrows; female paintings with no arrows; male paintings with arrows; male paintings with no arrows. Stimuli were resized to 408 pixels by 547–1084 pixels and the visual angle was $19.02 \times 19.49^\circ$. Presentation was blocked, with ten blocks per condition (40 blocks in total) and 8 trials per block. The order of blocks as well as the order of the trials within each block was pseudorandomized. Within blocks, each painting was presented for 1800 msec, and the inter-trial interval was 200 msec. Time between blocks was 12000 msec.

2.2.3. MRI parameters and functional data processing

High-resolution anatomical [T1-weighted, flip angle (FA) = 9°, TR = 2250, TE = 2.6 msec, 192 slices, field of view (FoV) = 256 mm, isotropic voxel resolution of $1 \times 1 \times 1$ mm^3] and whole-brain functional images [T2*-weighted echo-planar imaging: TR = 2000, TE = 30 msec, 35 contiguous slices, slice thickness = 3 mm, voxel resolution = $3 \times 3 \times 3$ mm^3] were obtained. FMRI data were processed using BrainVoyager QX (Brain Innovation, Maastricht, The Netherlands). Preprocessing included slice acquisition time correction, temporal high-pass filtering, rigid-body transformation of data to the first acquired image to correct for motion, and spatial smoothing with a 4 mm FWHM Gaussian kernel. Functional data were co-registered to anatomical data per subject, and further transformed to Talairach space.

2.2.4. Activation data analysis

BOLD time courses of 16 sec individual blocks were regressed onto a pre-specified model in a conventional GLM. Separate predictors were implemented for the four different conditions. We then computed a group statistical map, calculated by using a random-effects (RFX) model, restricting this by using a mask to exclude non-brain matter voxels. Further to this, we computed the following t-contrasts: Female paintings versus Male paintings; Paintings with no arrows versus Paintings with arrows; Female paintings with no arrows versus Female paintings with arrows; Male paintings with no arrows versus Male paintings with arrows. We also computed these contrasts at the group level for female and male participants separately.

The statistical thresholding and multiple-comparison correction was performed in a two-step procedure. First, a single voxel threshold of $p = .01$ (uncorrected) was used for initial statistical maps. Next, a whole-brain correction criterion was calculated by estimating a false-positive rate for each cluster. This was established with the BrainVoyager plugin *Cluster-level statistical threshold estimator*, by means of Monte-Carlo simulation (1000 iterations). The minimum cluster size threshold obtained from simulation was applied to the statistical maps, corresponding to a cluster-level false positive rate (α) of 5%. Cluster size is reported in number of anatomical voxels. We also reported the averaged effect size of the voxels in each cluster, by computing Cohen's d (mean difference between conditions/pooled standard deviation across conditions).

3. Results

3.1. Behavioral data

To assess whether the male paintings with the arrows removed still carried some connotation of pain, an independent cohort of 12 participants rated each stimulus on perceived pain (7 point rating scale), with the aim to be able to exclude any bias in female/male and edited/original paintings with regards to pain perception. The difference in pain ratings for arrows versus no arrows was very large for both male and female paintings (male: 4.7 *vs* 1.8, $p < .001$; female: 5.9 *vs* 1.6, $p < .001$). Male bodies with no arrows (edited) versus female painting without arrows (originals) were rated only slightly higher on pain (paired sample *t*-test: 2.0 *vs* 1.7, $p < .04$).

Average looking times were calculated for each participant and each painting condition (Female with no arrow, female with arrow, male with no arrow, male with arrow) and submitted to a 2 × 2 (painting gender, arrow presence) repeated measures ANOVA. We observed a significant main effect of painting gender [F (1,15) = 6.194, $p = .03$] and arrow presence [F (1,15) = 22.24, $p < .0001$], but no significant interaction between the two factors. Inspection of the main effects showed that all participants generally spent longer looking at female paintings than male paintings (5.45 sec *vs* 5.27 sec), and longer at the paintings with arrows than those without (5.79 sec *vs* 4.93 sec). As we shall see, this pattern is not reflected in the brain activation data.

3.2. fMRI results

The fMRI analyses were performed separately for all participants, and for two subgroups within our sample (male and female participants).

3.2.1. All participants

The contrast of *female* versus *male paintings* showed activity in the right inferior parietal lobule, bilateral lingual gyrus and left precentral gyrus. Only one cluster in the left superior temporal gyrus showed a stronger response to male versus female paintings, see Fig. 2.

Next, within this contrast, the contrast of *arrows* versus *no arrows* influences some activations differently. Paintings with no arrows, compared to those with arrows, elicited activity in the bilateral middle frontal gyrus, left middle frontal gyrus and the left precuneus see Fig. 3.

Next, for all participants we see that female paintings with no arrows versus those with arrows showed activations in the bilateral superior frontal gyrus, bilateral medial superior frontal gyrus, bilateral cuneus, left precuneus and left postcentral gyrus. No regions showed more activity for female paintings with arrows versus no arrows. Finally, the contrast of male paintings with no arrows versus male paintings with arrows triggered heightened responses in the cuneus and cingulate gyrus whereas the reverse contrast showed activity in the left middle occipital gyrus. Similarly, when we look at contrasts as a function of the gender of the paintings and the role of the arrows, we see that female paintings with no arrows versus male painting with no arrows revealed increased activation in middle frontal gyrus, fusiform gyrus, bi-lateral precentral gyrus, bilateral middle occipital gyrus, bilateral lingual gyrus and the right superior parietal lobule, see Fig. 4. For a complete overview of all participants results, see Supplementary Table 1.

3.2.2. Female participants

First we report the contrasts as a function of the gender depicted in the paintings. The contrast of female versus male paintings showed activity in the right lingual gyrus, right middle occipital gyrus, right lingual gyrus and left middle temporal gyrus and the left superior parietal lobule. No clusters showed a stronger response to male versus female paintings. A detailed look inside this contrast shows that female versus male paintings in the no arrow condition shows activity in right middle temporal gyrus and middle occipital gyrus. The same contrast in the arrows condition showed activation in right lingual gyrus.

When we consider the overall contrast between no arrows versus arrows, activation shows up in the right precentral gyrus and cingulate gyrus, and left lingual gyrus. In more detail, the contrast of female paintings with no arrows versus female paintings with arrows showed activations in the right fusiform gyrus and medial frontal gyrus, left cuneus and postcentral gyrus. No region showed more activity in female paintings with arrows. The contrast of male paintings with no arrows versus male paintings with arrows evoked heightened responses in the right precentral gyrus, inferior frontal gyrus and bilateral anterior/mid cingulate gyrus (see Fig. 5), whereas the reverse contrast showed activity in the left middle occipital gyrus. For a complete overview of the female only participants results, see Supplementary Table 2.

3.2.3. Male participants

The contrast of female versus male paintings showed activity in the right middle frontal gyrus, right middle occipital gyrus, right precuneus, and left inferior occipital gyrus, left inferior parietal lobule and left inferior temporal gyrus. No clusters showed a stronger response to male versus female paintings. In the sub-analysis we see that paintings with no arrows

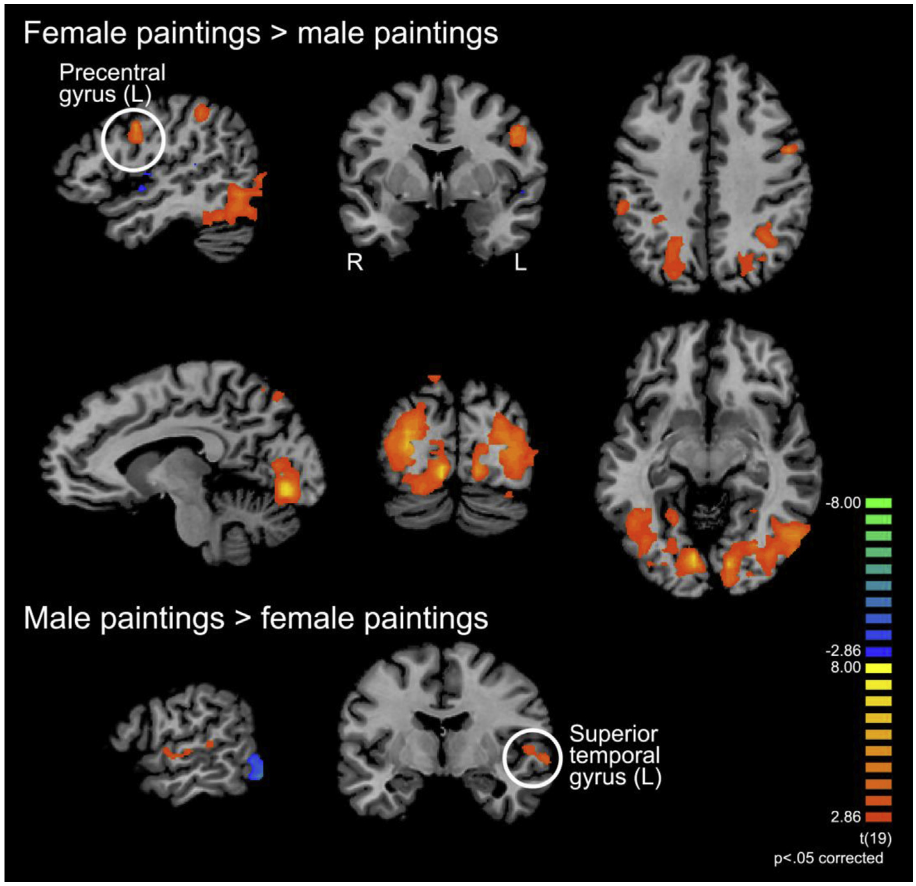

Fig. 2 – Main results of the gender in paintings contrast (alpha = .05, initial *p* = .01, cluster size corrected, minimal cluster size = 891 voxels). Top panel: increased activation for the female versus male condition. Four significant clusters: peaks in the right inferior parietal lobule, the left precentral gyrus and the bilateral lingual gyrus. Bottom panel: increased activation for the male versus female condition. One significant cluster: peak in the left superior temporal gyrus. Blue colors indicate negative t-values.

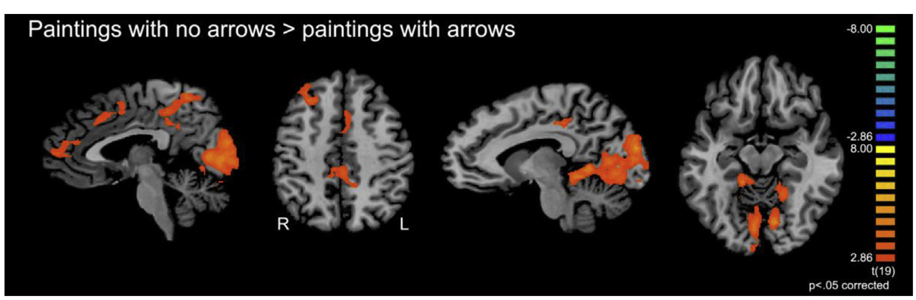

Fig. 3 – Results for the arrows contrasts (alpha = .05, initial *p* = .01, cluster size corrected, minimal cluster size = 810 voxels). Increased activations for the no arrow versus arrow condition. Significant clusters in the right medial frontal gyrus; cuneus; and left precuneus, medial frontal gyrus (two distinct clusters) and middle frontal gyrus.

versus arrows elicited activity in the cuneus, left anterior cingulate and thalamus.

When we consider the overall contrast between no arrows versus arrows, the paintings with no arrows yield increased activation in cuneus, left anterior cingulate and left thalamus. The contrast of female paintings with no arrows versus female paintings with arrows showed activations in the right lingual gyrus and left anterior cingulate and thalamus. The sub-contrast of female paintings with no arrow versus arrows activated right lingual gyrus and the left anterior cingulate. Left anterior cingulate was also seen for female paintings with arrows versus no arrows, see Fig. 5. No activity was seen in the

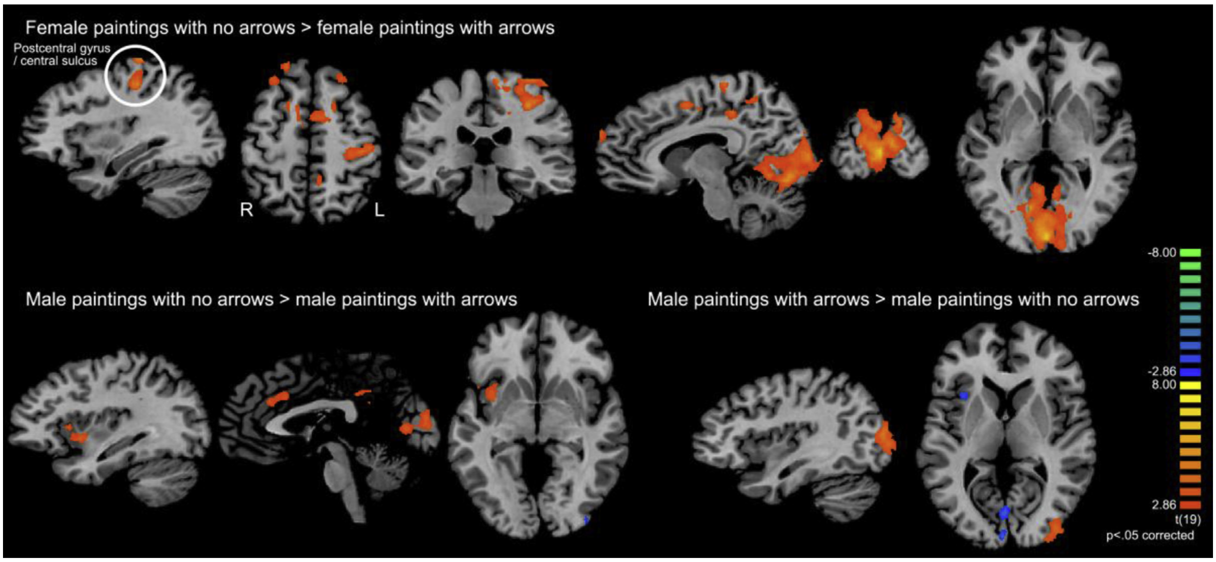

Fig. 4 – Gender and arrow contrast results (alpha = .05, initial *p* = .01, cluster size corrected). Top panel: increased activations for the female-no arrow versus female-arrow conditions (minimal cluster size = 675 voxels). Significant clusters were found in the bilateral superior frontal gyrus, bilateral medial frontal gyrus, cuneus, and left precuneus (2 distinct clusters), postcentral gyrus/central sulcus and superior frontal gyrus. Bottom left panel: increased activations for the male-no arrow versus male-arrow conditions (minimal cluster size = 648 voxels). Four significant clusters in the claustrum/insula, cuneus and cingulate gyrus (two distinct clusters). Bottom right panel: increased activations for the male-arrow versus male-no arrow conditions (minimal cluster size = 648 voxels). One significant cluster in the middle occipital gyrus. Color coding as in Figs. 2 and 3.

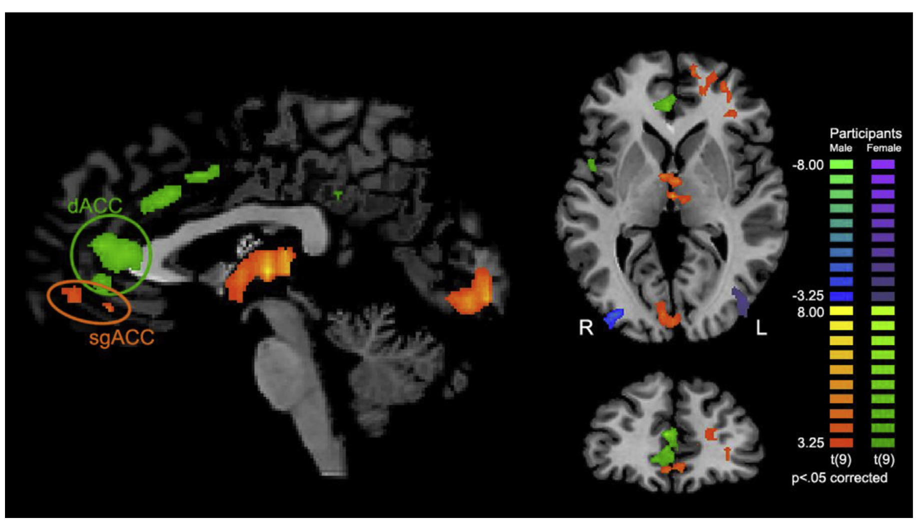

Fig. 5 – Gender of participant effects (alpha = .05, initial *p* = .01, cluster size corrected, for both maps minimal cluster size = 567 voxels). The ACC clusters found for the female paintings with no versus with arrows, for male participants in the sgACC (orange) and male paintings with no versus with arrows for female participants in the dACC (green).

contrast of male paintings with no arrows versus male paintings with arrows and vice versa. For a complete overview of the male participants results, see Supplementary Table 3.

4. Discussion

Our goal was to investigate the brain basis of viewing images derived from classical paintings of male and female bodies representing pain or pleasure and also to answer the question of gender specific brain activation patterns in participants with no knowledge or expertise in this domain. Our novel results show important and significant activity in brain areas other than those recently associated either with perception of the body, with beauty and/or with reward that have mainly been found in parietal, primary motor and somatosensory cortices (Kirsch et al., 2016). Furthermore, our results indicate a specific pattern of gender specificity suggesting that the preferential pattern seen here for male and female body perception may reflect an evolutionary basis. We discuss these results in more detail, first looking at the overall contrast for all participants between the presence or absence of arrows and then contrasts between the genders of the images in the paintings.

Overall we see that all participants showed more activation for the no arrows than for the arrow condition suggesting that viewing pictures that may be related to pleasure constitutes a stronger trigger than those that may be related to pain. First, commenting on the negative finding concerning the pain condition, this asymmetry between results for pain and pleasure may be related to the fact that we used historical paintings and that such art images of pain do not or much less trigger the kind of empathy for pain responses that have been found for example, when naturalistic photos or needles are used (Bufalari, Aprile, Avenanti, Di Russo, & Aglioti, 2007). Furthermore, we note that in most of those studies participants watched images of a face or an object being touched. This may have triggered a more active involvement of the participant possibly triggering motor resonance with the sight of the action performed while in our design there is no direct reference to a painful action on another person. Importantly, besides posterior visual areas (cuneus and precuneus), the contrast no arrows-arrows activated the medial prefrontal gyrus (mPFC) bilaterally. The former are generally considered as visual areas although the precuneus has also been related to social processes (Bzdok et al., 2016) and is related to the fantasy content of visual materials (Rikandi et al., 2016). Activation of the mFPC is consistent with findings that the mPFC figures prominently in explanations of processes that have an affective component; furthermore, the medial orbitofrontal cortex and the ventromedial prefrontal cortex are activated when people judge objects to be beautiful (Cattaneo et al., 2013; Ishizu & Zeki, 2011; Jacobs, Renken, & Cornelissen, 2012; Jacobsen, Schubotz, Höfel, & Cramon, 2006; Kawabata & Zeki, 2004). Interestingly, the main activation in this contrast can be related to the pleasure/reward/appetitive component in the model by Chatterjee (Chatterjee & Vartanian, 2014). The PFC is rich in sex hormone receptors, and has one of the highest concentration of oestrogen receptors in the human brain (Lansdell, 1964; McEwen & Milner, 2017). It is worth noting that contrary to what one might expect there was no increased activation triggered by the arrow condition in a number of areas related to pain perception (Hu & Iannetti, 2016; Price, 2000). This finding contrasts with the behavioral results showing that looking times are overall longer for images with than without arrows. This suggests that the presence of the arrows was clearly consciously noticed by the participants but did not trigger a brain reaction indicating pain related activity.

The female versus male paintings contrast for all participants reveals inferior parietal, left precentral and bilateral lingual gyrus activity, areas that correspond to the sensorimotor component of the esthetic experience (Chatterjee & Vartanian, 2014). Inferior parietal lobule (IPL) activity was reported in a number of studies using body expressions (Borgomaneri, Gazzola, & Avenanti, 2015; de Borst & de Gelder, 2016; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004) and is causally related to processing emotional body expressions (Engelen, de Graaf, Sack, & de Gelder, 2015). In this context it is interesting to note that these activations do not show in the contrasts by participant gender, except for IPL activation in the male participant group as discussed below.

To conclude the discussion of the two major contrasts, our results are consistent with the results of a meta-analysis of studies on visual aesthetics (Ishizu & Zeki, 2014; Vartanian & Skov, 2014; Zeki, 2011) in revealing a role for lingual gyrus, middle occipital gyrus, inferior and superior temporal gyri and precuneus. Yet beyond that, there appears to be a major role for areas that have not come into the foreground in previous studies but that seem to have a clear significance here. These are mPFC, IPL and somatosensory cortex and their importance comes more to the foreground in the specific sub-contrasts.

We next consider the gender specificity in the no arrows condition for all participants. When looking more in detail at the female versus male images in the no arrows versus arrows contrast only, we see again a strong bilateral mPFC activity. This area is related to reward as well as to encoding beauty (Kawabata & Zeki, 2004). Higher activity for female no arrow suggests that female bodies have higher reward value independently of the gender of the observer. Another aspect revealed in this sub-contrast is the activation of somatosensory cortex. Recent studies have shown that somatosensory cortex is reactive to not only external stimulation such as being touched as well as to mental imagery of touching (de Borst & de Gelder, 2016), but also to the sight of body parts in situations of non-informative vision or visual enhancement of touch. Seeing a hand can enhance tactile acuity in the hand, even when tactile stimulation is not visible. Under normal conditions, touch observation activates the SI below the threshold for perceptual awareness (Blakemore, Bristow, Bird, Frith, & Ward, 2005). Vision of the body may act at an early stage in stimulus elaboration and perception, allowing an anticipatory tuning of the neural circuits in primary somatosensory cortex that underlie tactile acuity (Fiorio & Haggard, 2005). Note, this effect is obtained for all participants underscoring that it is specific for this type of stimulus. A speculative interpretation may be that female bodies convey to the brain of the observer a tactile experience, in line with studies on touch showing thalamus with primary somatosensory cortex connectivity (de Borst & de Gelder, 2016; Ellingsen et al., 2014; Gazzola et al., 2012).

Last, we discuss the relation between the gender of the participants and the paintings. The most intriguing aspect of our results is in the combined effects of gender of the participant and gender of the stimuli. Interestingly, gender-specific effects of stimulus type are found in one specific area, the anterior cingulate cortex (ACC). Here the effects are more specifically located in two different subsections of the ACC and appear to follow the dorsal-ventral division and functions of the ACC. Female participants show greater activation to male images in dorsal ACC (dACC) and male viewers more to female paintings in subgenual ACC (sgACC).

First, brain activations of female participants looking at male paintings revealed increased activation in the dACC. The dACC is thought to play a crucial role in the development of human cognitive control and guiding behavior (Rushworth, Buckley, Behrens, Walton, & Bannerman, 2007). It is associated with attention modulation, competition monitoring, complex motor control, motivation, novelty, error detection, and the modulation of reward-based decision making [for review, see (Shenhav, Botvinick, & Cohen, 2013)]. Meta-analyses of the neuroimaging literature have confirmed that the dACC plays a central role in control-demanding tasks (Nee, Kastner, & Brown, 2011; Niendam et al., 2012; Ridderinkhof, Nieuwenhuis, & Braver, 2007; Shackman et al., 2011). The role of dACC may be that of monitoring (Botvinick, 2007; Botvinick et al., 2001, 2004). Second, when male participants look at female paintings the pattern of activations reveals a different, equally specific activation, this time in sgACC. Interestingly, this area is often reported in relation to emotion and arousal. It has long been recognized that the sgACC contributes to autonomic control and the sgACC is densely interconnected with structures that play a central role in visceromotor control, such as the hypothalamus [for a review see (Critchley, 2005)]. Moreover, the sgACC has strong connections with ventromedial and posterior orbitofrontal regions and is therefore ideally positioned to play a role in emotion, memory, and regulating internal states (Joyce & Barbas, 2018). The sgACC may contribute to positive affect by sustaining arousal in anticipation of positive emotional events (Rudebeck et al., 2014). The sgACC is densely connected with mesolimbic pathways that facilitate the release of oxytocin (Skuse & Gallagher, 2009) – a neuropeptide which bolsters interpersonal trust and cooperation (Zak, Kurzban, & Matzner, 2004) – and also sends direct projections to subcortical areas that control autonomic responses (Freedman & Cassell, 1994). Lesions in this area result in blunted responses to emotionally meaningful stimuli (Damasio, Everitt, & Bishop, 1996). Other studies have contrasted the different roles of sgACC and the dACC based on anatomical connectivity: a pre-genual region strongly connected to medial prefrontal and anterior midcingulate cortex and a subgenual region with strongest connections to nucleus accumbens, amygdala, hypothalamus, and orbitofrontal cortex (Johansen-Berg et al., 2008). Interestingly, the connections between mPFC and amygdala have recently been viewed as targets for understanding the role of internalizing and psychopathology (Marusak et al., 2016).

Previous studies have used paintings as a means to probe the neural basis of beauty perception and findings have highlighted a multicomponent system consisting of emotion-valuation, sensorimotor and knowledge–meaning (Chatterjee & Vartanian, 2014). Our findings about specific gender related effects are consistent with that literature but also extend and modify it significantly. Concerning the emotion-valuation and the appetitive component, we find that the mPFC activation is specific for female stimuli independent of the gender of the participants. The sensorimotor component, IPL and motor activation are each equally stimulus gender-specific.

Furthermore, our results represent an important step forward in understanding gender specific processes in artistic experience. Previous studies looking at gender effects in body perception have mainly focused on brain activation to neutral bodies in EBA and reported right lateralization in women (Aleong & Paus, 2010) including when an esthetic/liking of natural body appearance was measured (Cazzato, Mele, & Urgesi, 2014). When emotional whole body expressions were studied gender/stimulus specific effects were found for male participants viewing male anger expressions (Kret, Pichon, Grèzes, & de Gelder, 2011).

We considered various alternatives for adding control conditions to the current design but considered that the disadvantages would largely outweigh the advantages. One possibility was to create a similar stimulus set consisting of realistic photographs. There are compelling arguments against this. First, we wanted specifically to compare how male and female paintings are viewed, not how paintings versus realistic photographs were processed. Our question was not whether paintings trigger a different experience than photorealistic images, but about the neural basis of viewing male or female body paintings showing pain versus pleasure. Second, the difference between a painting and a photorealistic image involves many more aspects besides the body representation itself. To illustrate, a previous study successfully compared a painting and a photorealistic image of a hand, in order to compare the effects on motor output of observation of an action in a painting (Battaglia, Lisanby, & Freedberg, 2011). The results show that observing an action in a painting increases cortical-spinal excitability but observation of the photograph did have a lesser effect. The authors argue that the effect obtained in the painting must be due to the artist's skill in creating the movement illusion. Complementary or different explanations must be considered though, including for example that in the case of the arm representation in the painting, participants were familiar with the whole painting even if for the comparison photo or painting only the arm gesture of the painting was shown. Furthermore, if one were to look for a photo image set comparable to the paintings, one quickly realizes that a whole range of other processes are involved in viewing photos versus paintings. We might have consulted specialized image bases to find this, but the socio-cultural context of viewing Renaissance paintings is rather different from that of viewing erotic or pornographic images. In other words, comparing paintings to photographs introduces major confounds that in our view render impossible any conclusion one may draw because vision is not just an object-focused and object-constrained process, but objects bring with them all the daily life experiences and semantic associations. Presenting an actor in a way that is comparable to the San Sebastian paintings would undoubtedly have resulted in confounds due to social and cultural factors. For example, paintings showing male and female bodies in arrangements including arrows like the San Sebastian paintings belong to the mainstream representations in the history of Western art. But photorealistic images with the same physical content are not part of the visual materials that the average viewer is exposed to on a daily basis. Our study and its results cannot be compared therefore with studies that have used mainstream images of faces and bodies and obtained attractiveness ratings [reviewed in (Kirsch et al., 2016; Vartanian & Skov, 2014)]. While we wanted to investigate the biological basis of a gender specific neural preference when people view paintings of bodies, our goal was not to argue for continuity between the experience of paintings and that of photorealistic body images.

The observation of gender specificity in the neural basis of viewing paintings stands on its own independent of other equally interesting findings about face and body attractiveness of real life images. This raises interesting questions about the continuity between esthetic experience of natural images and that of art works. In support of our interpretation that we measured aspects of aesthetic preference we note that certain areas associated in the literature with attractiveness have their activation level going up with reported attractiveness (Kirsch et al., 2016) do not emerge in our study of body paintings. For example, EBA does not show increased activation either in the group or in the gender specific analysis. Such increase is found for example when the stimuli are images of dance movements (Cross, Kirsch, Ticini, & Schütz-Bosbach, 2011). In the same vein, we did not observe activation in Insula as found in studies using an explicit rating task (Kirsch et al., 2016) and for conscious body perception (Tamietto et al., 2015).

In conclusion, our results show important and significant activity in brain areas beyond those recently associated with perception of the body, of subjective liking and of the experience of beauty in visual arts in general. What is common to both genders when viewing the female body are the IPL and somatosensory cortex. While our participants were fully aware that they were viewing artworks, the brain mobilizes IPL, known for its role in perception of emotional body images (de Gelder, 2016) and for its relation to embodiment (Gallese & Cuccio, 2014). Similarly, we note somatosensory cortex activation associated with the sight of the female body, consistent with findings on emotions and tactile experience. On the other hand, the most specific finding concerning the role of gender is that the sight of female bodies activates in males an area known to sustain autonomic arousal. However, in females the sight of the male body activates reward and control related part of the dACC. Taken together, the general and the gender specific activities provide support for the notion that basic bodily experience processes operate when we view body images, regardless of the fact that they are artifacts.

Author contribution

BdG, RW, MV and MT wrote the manuscript, BdG, RW, MD, MV prepared the figures, BdG, RW designed the experiment, RW, MZ, MD ran the experiments and analyzed the data.

Conflicts of interest

The authors have no competing financial interests.

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Supplementary data

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