Shared neural basis for experiencing the beauty of human faces and visual art: Evidence from a meta-analyses of fMRI studies

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Abstract

The nature of beauty has been debated in philosophy for thousands of years. Recently, cognitive neuroscientists have sought to elucidate this issue by exploring the neural basis for the experience of beauty. However, the neural representations of beauty remain poorly understood, especially regarding whether various forms of beauty, such as the beauty of faces and the beauty of art, share a common neural basis. Here, we addressed this question by performing an activation likelihood estimation (ALE) meta-analyses, which quantitatively summarized the published neuroimaging literature of beautiful faces and beautiful visual art, and an meta-analytic connectivity modeling (MACM) analyses, which delineated the co-activation patterns of brain regions of interest in the BrainMap database. We observed that the left medial orbitofrontal cortex (mOFC) was convergently activated by both beautiful visual art and beautiful faces, suggesting a common neural basis for beauty. In addition, the beauty of faces was exclusively associated with activity in the ACC and the gyrus rectus. These results indicate a shared neural basis for processing different forms of beauty.

Keywords: beauty; faces; visual art; functional magnetic resonance imaging (fMRI); activation likelihood estimation (ALE); meta-analytic connectivity modeling (MACM)

1. Introduction

The nature of beauty is a long-standing topic in philosophy which can be traced back to the 4th century B.C.. For example, philosophers, such as Plato, suggested that there is a "common and abstract beauty" that is independent of various concrete forms of beautiful things (Allen, 1993), and David Hume asserted a common basis for evaluating beautiful objects (Shimamura, 2012). This presupposition has led to many discussions regarding beauty. Other scholars (e.g., Kubovy, 2000) have opposed this common theory by suggesting that "beauty is in the eye of the beholder," emphasizing the role of the individual's experiences in their attitudes toward different objects in different circumstances and refuting the assertion that there are common underpinnings to different evaluations of beauty. Though these debates lie within the scope of philosophy for centuries, recently modern cognitive neuroscientists and psychologists have begun to address the scientific bases of aesthetic responses to beauty via experimental approaches (Chatterjee, 2012; Chatterjee & Vartanian, 2014, 2016; Di Dio & Vittorio, 2009; Pearce et al., 2016). In this study, we examined whether there is a common neural mechanism for beauty by employing an activation likelihood estimation (ALE)-based meta-analyses on data from previous functional magnetic resonance imaging (fMRI) studies.

1.1 What is the experience of beauty?

One problem in studying the cognitive and neural mechanisms of beauty lies in conceptual ambiguity. In the neuroaesthetics literature, beauty is often confused with aesthetic experiences and art, though cognitive neuroscience of beauty is different from cognitive neuroscience of aesthetics or art (Pearce et al., 2016). This conceptual ambiguity hampers interdisciplinary

communication (Bergeron & Lopes, 2012). Therefore, it is necessary first to offer a clear operational definition of beauty.

From the perspective of an information processing model (Leder, Belke, Oeberst, & Augustin, 2004; Leder & Nadal, 2014), we define the experience of beauty as a pleasurable aesthetic experience that is the outcome of the multi-stage processing of an aesthetic object (including both art and non-art objects). In this sense, the experience of beauty includes both a cognitive component and an affective component. The cognitive component includes the mnemonic and semantic information associated with the evaluation of the object, whereas the affective component consists of pleasurable satisfaction or other positive affective states. While these two components differ conceptually, they are reciprocally linked (Leder et al., 2004).

This operationalization of the definition of the experience of beauty distinguishes it from other aesthetic experiences because aesthetic experiences include both positive and negative affective states (Bergeron & Lopes, 2012). Additionally, it gives us a specific criterion for use in empirical studies; for example, it can be used to measure the brain activity underlying the experience of beauty by comparing brain activity when perceiving beautiful stimuli with brain activity when perceiving non-beautiful stimuli with similar physical properties. Such techniques allow us to identify the brain regions that are positively correlated with beauty ratings or to determine preference as an index of beauty (Ramachandran & Hirstein, 1999).

1.2 Is there a common neural basis for the experience of beauty?

For psychologists and neuroscientists, a “common mechanism” means a shared cognitive mechanism or neural basis during the processing of different types of information. For example, in the low-level vision system, all visual information shares the same pathway from the retina to

the V1 cortex. Using similar logic, cognitive neuroscientists have identified many different types of stimuli that share a common neural mechanism. For instance, recent studies have shown that spatial, temporal and social distance have common neural representations in the right inferior parietal lobule (Parkinson, Liu, & Wheatley, 2014), the left intraparietal sulcus is associated with processing both perceptually salient and socially salient stimuli (Sui, Liu, Mevorach, & Humphreys, 2015), and that mental processing of the psychological and physical selves shares a common neural basis in the dorsal anterior cingulate cortex and the left anterior insula (Hu et al., 2016).

In this sense, the common neural basis for different forms of beauty can be identified by the shared brain regions activated by different forms of beauty. In fact, previous studies have suggested a common neural basis for the experience of beauty. Behaviorally, Reber proposed that beauty resulted from the cognitive processing fluency of the perceivers (Reber, 2012; Reber, Schwarz, & Winkielman, 2004). At the neural level, Ishizu and Zeki (2011) proposed that beauty was associated with activation of the medial orbitofrontal cortex (mOFC) by comparing the neural activation of individuals when listening to music and viewing visual art, and Brown, Gao, Tisdelle, Eickhoff, and Liotti (2011) drew the conclusion that the insula was the common neural basis for aesthetic appraisal based on a meta-analyses of studies related to aesthetics. More interestingly, an implicit theory of common beauty held by cognitive neuroscientists claims that beauty is equal to reward. This view has been supported by studies that used beautiful stimuli as rewarding stimuli (Aharon et al., 2001; Bray & O'Doherty, 2007; Cloutier, Heatherton, Whalen, & Kelley, 2008; Lacey et al., 2011; Liang, Zebrowitz, & Zhang, 2010; Smith, Clithero, Boltuck, & Huettel, 2014) along with other monetary reward-related stimuli. This implicit theory of common beauty was partially confirmed by theorists in neuroaesthetics who found that reward

processing was an import component of aesthetic appreciation (e.g., Chatterjee and Vartanian, 2014). However, to date, it lacks of direct evidence showing that reward is the common mechanism for different forms of beauty.

Even if some studies have advocated a common mechanism for the experience of beauty, we cannot draw a conclusion that there is a common neural basis for beauty due to three issues in the field. First is the heterogeneity of fMRI studies on aesthetics. While a number of studies have utilized beautiful stimuli or visual art, many of these focused on other psychological processes during aesthetic appreciation instead of the neural response to beauty. For example, some researchers studied aesthetic judgment (Bzdok et al., 2012; Ishizu & Zeki, 2013) or the subjective response to art (Mizokami et al., 2014), but these two psychological processes are different from the response to beauty (Bergeron & Lopes, 2012; Conway & Rehding, 2013; Shimamura, 2012). The heterogeneity of fMRI studies in aesthetics makes it difficult to draw a consistent conclusion on the neural basis for the experience of beauty and also renders meta-analyses that include these studies irrelevant to the common neural basis for the experience of beauty.

The second issue, which is not limited to neuroaesthetics but also applies to other fields of neuroimaging, is the low statistical power (Button et al., 2013) and the high false-positive rates (Eklund, Nichols, & Knutsson, 2016; Wager, Lindquist, & Kaplan, 2007) of single neuroimaging studies that occur due to limited sample sizes (Button et al., 2013) or the flexibility of fMRI data processing (Carp, 2012). Third, it is difficult to interpret the function of brain regions based on fMRI studies, and reverse inference is usually used without methodological rigidity (Poldrack, 2006).

1.3 Current study

To explore the common neural basis of aesthetic responses to beauty, taking into account the above concerns, we proposed an approach that compares the neural activation of the experience of beauty driven by different kinds of beautiful objects with the ALE meta-analyses method, focusing on human faces and visual art.

These two types of beauty were selected for two reasons. First, they are the two most intensively studied beautiful stimuli in laboratory settings (Chatterjee & Vartanian, 2014, 2016; Etcoff, 2011), thus providing enough studies for a meta-analyses. Second, they represent two different typical categories of beauty: faces are the most representative of natural beauty in social life, reflecting the evolutionary preferences of human beings (Langlois, et al., 2000; Little, Jones, & DeBruine, 2011; Rhodes, 2006, but see Germine, et al., 2015), while the visual arts are the most representative of artificial beauty, which is reflected in the subjective aesthetic preference of human beings. Therefore, a comparison between the aesthetic responses to these two types of beauty in available studies can provide valuable insight into the exploration of common and distinct neural bases of beauty.

We employed an ALE meta-analyses of 36 fMRI studies on the beauty of faces and the beauty of art according to our definition of beauty. Specifically, to avoid the negative influence caused by the heterogeneity of different studies, we included only studies that compared beautiful visual art/faces with non-beautiful visual art/faces or that were positively correlated to beauty ratings/preferences, therefore addressing the issues of confusion between different psychological processes. Additionally, the ALE meta-analyses method provides a quantitative measure of cross-study consistency that accommodates the spatial uncertainty of activation data

and allows statistically defensible conclusions to be formed (Fox, Lancaster, Laird, & Eickhoff, 2014; Laird et al., 2011). Furthermore, it provides more decisive results and greater statistical power than individual studies (Eickhoff et al., 2016). To address the issues of reverse inference and ignorance of the network, a meta-analytic co-activation model (MACM) analyses was conducted based on the BrainMap database. The MACM analyses allowed us to make evidence-based inverse-inferences regarding the psychological processes based on the activation of brain structures (Eickhoff et al., 2011; Laird, Eickhoff, Li, et al., 2009; Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011).

Using these analyses methods, the current study aimed to (1) identify convergent neural activation across studies for the two forms of beauty, (2) assess the distinct activation patterns observed in face-based beauty and visual art-based beauty and (3) provide a data-driven interpretation for the functional role of each brain structure using MACM.

2. Materials and methods

2.1. Literature search and study selection

Articles included in the present meta-analyses were identified based on a systematic literature search using specific terms in PubMed and the Web of Science (up to March 2016). “Face” or “facial” was paired with “attractiveness,” “beauty” or “aesthetic” for aesthetic studies of faces; and “paintings” or “visual art” were searched for aesthetic studies of visual art. All terms were each combined (“AND”) with “functional magnetic resonance imaging or fMRI” or “Positron emission tomography or PET” to identify relevant functional neuroimaging studies. For more complete coverage, articles were also identified from recent meta-analyses and reviews (Boccia et al., 2016; Brown et al., 2011; Bzdok et al., 2011; Kirsch, Urgesi, & Cross, 2016;

Mende-Siedlecki, Said, & Todorov, 2013; Vartanian & Skov, 2014). Additional studies were identified by searching through the reference lists of studies obtained via the initial search. The inclusion criteria for articles were as follows:

(1) Only studies reporting whole-brain analyses were included, while studies based on partial coverage or employing only region-of-interest analyses were excluded. One study was included after the author provided the whole brain analyses with the interested contrast of current meta-analyses (Lebreton, Jorge, Michel, Thirion, & Pessiglione, 2009).

(2) Articles reporting results as coordinates in a standard reference frame (Talairach and Tournoux or MNI). To address problems induced by different coordinates used across the studies, coordinates originally published in the Talairach space were converted to the MNI space using the Lancaster transformation (Lancaster et al., 2007).

(3) Only studies with non-expert young and middle-aged adults (18-50 years old) were included; studies that included art experts were excluded if they did not report results for non-experts separately (Kirk, Skov, Christensen, & Nygaard, 2009) due to the influence of expertise on aesthetic appreciation (Hekkert & Wieringen, 1996).

(4) According to our operationalization of beauty, only studies reporting the effect of beauty or the preference of faces and visual art were included. Criteria for these studies consisted of the following rules: a) studies using visual art or faces as stimuli, b) studies reporting the effect of beauty or the subjective preference for visual art or faces separately and directly and c) studies that included a baseline that also corresponded to visual art or faces. Therefore, studies using visual art or faces as stimuli that did not report the effect of beauty or preference were excluded [for visual art (Boccia et al., 2015; Cupchik, Vartanian, Crawley, & Mikulis, 2009; Di Dio,

Canessa, Cappa, & Rizzolatti, 2011; Fairhall & Ishai, 2008; Huang, Bridge, Kemp, & Parker, 2011; Ishizu & Zeki, 2013; Lutz et al., 2013; Mizokami et al., 2014; Silveira et al., 2012; Wiesmann & Ishai, 2010); for faces (Bzdok et al., 2012; Funayama et al., 2012; Kedia, Mussweiler, Mullins, & Linden, 2014; Nakamura et al., 1998; Turk et al., 2004; Ueno et al., 2014)]. Additionally, studies that did not report the effect of faces or visual art separately were excluded (Kawabata & Zeki, 2008; Tsukiura & Cabeza, 2011). Studies using low-level stimuli as baseline were also excluded (Silveira et al., 2014).

After applying these criteria, 36 articles were included (14 articles for beauty in the visual arts, including 14 experiments, 98 foci and 304 subjects; 22 articles for the beauty of faces, including 22 experiments, 132 foci and 478 subjects). Figure 1 depicts the process of article selection in detail. For selected articles, see Table 1.

< Figure 1 and Table 1 here>

2.2. ALE methodology

2.2.1. Activation likelihood estimation

The meta-analyses was carried out using the revised ALE algorithm, which was implemented in MATLAB code, for the coordinate-based meta-analyses of neuroimaging results (Eickhoff et al., 2009; Laird, Eickhoff, Kurth, et al., 2009; Laird, Lancaster, & Fox, 2009; Turkeltaub, Eden, Jones, & Zeffiro, 2002). This algorithm aims to identify areas that exhibit a convergence of reported coordinates across experiments that is higher than expected under a random spatial association. The key idea behind ALE is to treat the reported foci not as single points but rather as centers for 3D Gaussian probability distributions that capture the spatial uncertainty associated with each focus. The width of these uncertainty functions was determined

based on empirical data on the between-subject variance by the number of examined subjects per study, accommodating the notion that larger sample sizes should provide more reliable approximations of the "true" activation effect and should therefore be modeled by "smaller" Gaussian distributions (Eickhoff et al., 2009).

The probabilities of all foci reported in a given experiment were then combined for each voxel, resulting in a modeled activation (MA) map (Turkeltaub et al., 2012). Taking the union across these MA maps yielded voxel-wise ALE scores that described the convergence of the results across experiments at each particular location of the brain. To distinguish 'true' convergence among studies from random convergence (i.e., noise), ALE scores were compared to an empirical null distribution reflecting a random spatial association among experiments. Here, a random-effects inference was invoked, focusing on the inference on the above-chance convergence among studies rather than the clustering of foci within a particular study. Computationally, deriving this null-hypothesis involved sampling a voxel at random from each of the MA maps and taking the union of these values in the same manner as performed for the (spatially contingent) voxels in the true analyses, a process that can be solved analytically (Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012). The p-value of the "true" ALE was then given by the proportion of equal or higher values obtained under the null-distribution. The resulting non-parametric p-values were then thresholded at the cluster level $p < 0.05$ (Eickhoff et al., 2012), with 10,000 threshold permutations for $p < 0.001$. All significant clusters were reported, and the volume, weighted center and locations and Z-scores at the peaks within the regions are given.

2.2.2. Conjunctions and comparison of individual meta-analyses

Conjunction analyses identify voxels where a significant effect is present in all separate analyses. The conservative minimum statistic (Nichols, Brett, Andersson, Wager, & Poline, 2005) was used, which is equivalent to identifying the intersection between cluster-level corrected results (Caspers, Zilles, Laird, & Eickhoff, 2010; Schilbach et al., 2012). Differences between conditions were tested by first performing separate ALE analyses for each condition and computing the voxel-wise difference between the ensuing ALE maps. All experiments contributing to either analyses were then pooled and randomly divided into two groups of the same size as the two original sets of experiments reflecting the contrasted ALE analyses (Eickhoff et al., 2011; Rottschy et al., 2012). The ALE scores for these two randomly assembled groups were calculated, and the differences between the ALE scores were recorded for each voxel in the brain. Repeating this process 25,000 times then yielded a null-distribution of differences in ALE scores between the two conditions. The "true" difference in the ALE scores was then tested against this voxel-wise null-distribution of label-exchangeability and thresholded at a probability of $p > 95\%$ for true differences.

2.2.3. Data visualization

The resulting areas were anatomically labeled by referencing probabilistic cytoarchitectonic maps of the human brain (Eickhoff, Heim, Zilles, & Amunts, 2006; Eickhoff et al., 2007; Eickhoff et al., 2005). For visualization purposes, BrainNet Viewer (Xia, Wang, & He, 2013) was used to present the meta-analytical results.

2.3. Meta-analytic co-activation model

To analyze functional connectivity of regions engaged in the beauty of visual art and faces, we conducted an MACM analyses. This approach to functional connectivity assesses which

brain regions are co-activated above chance with a particular seed region in functional neuroimaging experiments. The MACM analyses first identifies all the experiments in a database that activated the seed region and then employs a quantitative meta-analyses to test for convergence across the foci reported in these experiments. As the experiments are selected by activation in the seed, the highest convergence is observed in the seed region itself. Significant convergence of reported foci in the other brain regions, however, indicates consistent co-activation, i.e., functional connectivity with the seed (Eickhoff et al., 2010; Robinson, Laird, Glahn, Lovallo, & Fox, 2010).

More specifically, we used the results of the ALE meta-analyses of the beauty of visual art and the beauty of faces as seeds to find experiments that reported those seeds in the BrainMap database (Laird et al., 2011; Laird, Eickhoff, Kurth, et al., 2009) (http://www.brainmap.org). It is noteworthy that we used studies that reported group analyses of functional mapping experiments of healthy subjects in the BrainMap database. Regarding the seed from the ALE analyses of beauty of visual art, the left mOFC resulted in 76 experiments (with 1141 subjects, 1157 foci). For the beauty of faces, the seed in the mOFC/ACC/gyrus rectus resulted in 308 experiments (with 5081 subjects, 3667 foci), while the left gyrus rectus resulted in 151 experiments (with 2457 subjects, 1867 foci). For the mOFC from the conjunction analyses, 69 experiments (with 1058 subjects, 1037 foci) were found. After exacting these experiments, the ALE meta-analyses were conducted to find the co-activation network for each seed. In addition, to correct for potential over-representation of activation in the networks of interest in the literature, the specific co-activation likelihood estimation (SCALE) approach to MACM was used (Langner, Rottschy, Laird, Fox, & Eickhoff, 2014).

2.4. Functional decoding

To qualify the interpretation of the function of each brain region, we conducted functional decoding to obtain meaningful reverse inference (Poldrack, 2011). The functional characterization of the beauty of art and the beauty of faces was based on the "Behavioral Domain (BD)" and "Paradigm Class (PC)" meta-data categories, which are available for each neuroimaging experiment included in the BrainMap database. Behavioral domains included the main categories of cognition, action, perception, emotion and interoception; their related sub-categories; and paradigm classes to categorize the specific task employed (Laird et al., 2011; Turner & Laird, 2012).

As a first step, we determined the individual functional profile of the beauty-of-art-derived cluster and two beauty-of-faces clusters using forward and reverse inference approaches. The forward inference is the probability of observing activity in a brain region given knowledge of the psychological process, whereas reverse inference is the probability of a psychological process being presented given knowledge of activation in a particular brain region. In the forward inference approach, a cluster's functional profile was determined by identifying taxonomic labels, for which the probability of finding activation in the respective cluster was significantly higher than the overall chance (across the entire database) of finding activation in that particular cluster. Significance was established using a binomial test ($p < 0.05$, corrected for multiple comparisons using Bonferroni's method; Langner et al., 2014; Nickl-Jockschat, Janouschek, Eickhoff, & Rottschy, 2015; Rottschy et al., 2012). That is, we tested whether the conditional probability of activation given a particular label [P (Activation|Task)] was higher than the baseline probability of activation of the region in question per se [P (Activation)]. In the reverse inference approach, a cluster's functional profile was determined by identifying the most

likely behavioral domains and paradigm classes given activation in a particular cluster. This likelihood P (Task|Activation) can be derived from P (Activation|Task) and from P (Task) and P (Activation) using Bayes rule. Significance (at $p < 0.05$, corrected for multiple comparisons using Bonferroni's method) was then assessed using chi-square tests.

3. Results

3.1 Meta-analyses

The ALE results of the aesthetic beauty of visual art revealed that left mOFC was more convergently activated by beautiful visual art than non-beautiful visual art (Table 2 and Figure 2A).

The ALE results of the beauty of faces showed that the mOFC/ACC/gyrus rectus and the left gyrus rectus were more activated by beautiful faces than by non-beautiful faces (Table 2 and Figure 2B).

The conjunction results showed that the left mOFC was shared by beautiful faces and beautiful art (Table 3 and Figure 2C). The contrast results showed that the mOFC /ACC and the left gyrus rectus were more frequently activated by beautiful faces than by beautiful art, while there was a small cluster within the mOFC that was more activated by beautiful visual art than by beautiful faces (Table 3 and Figure 2D).

< Table 2 and Figure 2 here >

3.2. MACM analyses

3.2.1. MACM analyses of the beauty of visual art

The left mOFC from the meta-analyses of the beauty of visual art exhibited convergent co-activation of the left superior medial gyrus, the left precuneus/posterior cingulate cortex (PCC) / midcingulate cortex (MCC), the left superior frontal gyrus, the middle occipital/temporal gyrus, the right hippocampus, the left parahippocampal gyrus and the right cerebellum (see Table 4 and Figure 3A).

< Table 4 >

3.2.2 MACM analyses of the beauty of faces

The seed of the mOFC /ACC/gyrus rectus from the meta-analyses of the beauty of faces showed convergent co-activation of nearby brain structures, including the bilateral caudate nucleus, the right parahippocampal, the left superior frontal gyrus, the right hippocampus, the left superior medial gyrus and the right olfactory cortex. Additionally, a large cluster that included the PCC/MCC and the left calcarine sulcus was co-activated by this seed. Other brain regions included the left angular gyrus/middle occipital gyrus, the bilateral middle temporal gyrus, the left middle occipital gyrus, the left superior frontal gyrus, the left parahippocampal gyrus and the left IFG (see Figure 3B).

< Table 5 >

The seed of the left gyrus rectus from the meta-analyses of the beauty of faces showed convergent co-activation of the bilateral gyrus rectus, the left mOFC, the right postcentral gyrus and the cerebellar vermis (see Figure 3C).

< Table 6 >

3.2.3 **MACM analyses of contrast and conjunction results of both art and faces**

The co-activation network of the mOFC from the conjunction analyses of the beauty of visual art and faces included the left precuneus/PCC/calcarine gyrus, the left superior frontal gyrus, the left middle frontal gyrus, the left middle occipital gyrus, the left temporal gyrus and the right cerebellum lobule (see Table 7 and Figure 3D).

< Table 7 and Figure 3 >

3.3 Functional characterization

Functional characterization according to the BrainMap meta-data was performed for all seeds derived from the meta-analyses of the beauty of art and faces and for the seed derived from the conjunction analyses of both types of beauty. The FDR-corrected ($p < 0.05$) results are reported here. For the seeds from the ALE results of the beauty of visual art, the left mOFC was associated with behavioral domains (BDs) related to cognition and emotion. The most common paradigm classes (PCs) were face monitor/discrimination and reward (see Figure 4A). For seed from the meta-analyses of the beauty of faces, the mOFC /ACC/gyrus rectus was related to emotion (especially fear), cognition, interoception (thirst, sexuality) and perception of gustation and was involved in taste and reward paradigms (see Figure 4B). The left gyrus rectus was related to the behavioral domain of cognition and emotion and was involved in only the reward paradigms (see Figure 4C). For the mOFC, which is shared by both beautiful faces and beautiful visual art, the related BDs were cognition and emotion, and this region involved the reward paradigm (see Figure 4D).

< insert Figure 4>

4. Discussion

The main goal of this study was to explore the commonality and specificity of the neural basis of the experiences of beauty of visual art and faces. To this end, we performed a conjunction analyses on two individual ALE meta-analytic results and found convergent activation in the left anterior region of the mOFC associated with the two forms of beauty. In addition, the individual ALE and contrast analyses showed that the mOFC and the left gyrus rectus were more convergently activated for beautiful faces, while a small cluster of the left mOFC was activated for beautiful art. These results suggest that there is a common neural basis for processing beauty in the mOFC along with specific neural networks for each form of beauty.

4.1. The mOFC is a common neural basis for visual beauty

The shared neural basis for the beauty of visual art and faces of the left mOFC was in line with previous research that has shown that the mOFC is activated when participants view both beautiful faces and beautiful places (Pegors, Kable, Chatterjee, & Epstein, 2014). Additionally, this result was consistent with the finding that the mOFC is activated by beauty associated with both music and visual arts (Ishizu & Zeki, 2011). Together with these studies, our results suggest that the mOFC may serve as a common neural basis for processing beauty.

The mOFC is located in the medial and anterior region of the orbital cortex, which is phylogenetically more recent than the posterior region of the orbital cortex (Öngür & Price, 2000) and is responsible for processing more complex and abstract information (Badre & D'Esposito, 2009). The activation of the mOFC during experiences of beauty may reflect a positive affective meaning generated by the integration of abstract knowledge, personal

preferences and physical information from stimuli. This notion was supported by three lines of evidence below.

First, the activation of the mOFC reflected the high-level processing during aesthetic tasks. In our study setting, we strictly selected contrasts that compared beautiful art/face stimuli with non-beautiful art/face stimuli that had similar physical features. Therefore, our results indicated that the remaining brain areas were more activated by high-level processes, i.e., the experience of beauty, rather than simply the processing of the stimuli's physical features.

Second, the activation of the mOFC by beauty was similar to the neural mechanism of processing the secondary, abstract reward. Previous meta-analyses of fMRI studies have shown that secondary rewards (e.g., money) activate the anterior portion of the orbitofrontal cortex (Sescousse, Caldú, Segura, & Dreher, 2013), while primary rewards or subjective pleasantness convergently activate limbic circuitry, such as the insula and the amygdala (Berridge & Kringelbach, 2015; Sescousse et al., 2013). This was also supported by our functional decoding results, which revealed that the mOFC was primarily involved with reward paradigms.

Third, the activation of the mOFC may reflect the integration of both abstract knowledge and personal preference. Previous studies have shown that the mOFC is activated by the pure value of stimuli and by subjective preference (Plassmann, O'Doherty, Shiv, & Rangel, 2008) and abstract knowledge (Kumaran, Summerfield, Hassabis, & Maguire, 2009), suggesting that it links concepts with brainstem systems to generate affective meaning (Roy, Shohamy, & Wager, 2012). Our MACM results showed that the mOFC was convergently co-activated with brain regions involved in both knowledge processes and the sensory cortex (see Figure 6 C),

supporting its role in integrating both high-level and low-level information and generating affective meaning.

In summary, our meta-analyses suggests that the activation of the mOFC reflects a generation of positive affective meaning by integrating information from stimuli, abstract knowledge and personal preferences. This view is consistent with previous accounts regarding aesthetic processing in that the appreciation of beauty requires sensory-motor networks, knowledge-meaning networks and emotion-evaluation networks (Boccia et al., 2016; Chatterjee & Vartanian, 2014), with an emphasis on the common role of the mOFC in generating positive affective meaning. Additionally, the data support the implicit "common theory" of beauty among cognitive scientists. More importantly, these results suggest that aesthetic beauty is similar to secondary and abstract rewards instead of primary rewards. Theoretically, the results echo David Hume's view that "there is a common basis for evaluating beautiful objects" (Shimamura, 2012).

4.2. Distinct neural networks for the beauty of faces and visual art

The meta-analyses performed in the present study also revealed distinct neural networks for the beauty of faces and visual art, which provide additional clues for understanding the specificity of processing the beauty of faces and the beauty of art.

4.2.1. Neural networks underlying the beauty of faces

The results showed that beautiful faces induced greater converging activation in the mOFC/ACC/gyrus rectus and the left gyrus rectus than non-beautiful faces, and these two parts of the brain also showed greater activation for the beauty of faces than for the beauty of art.

To perceive facial beauty, previous theoretical accounts have suggested a two-system model, including a core system to process basic features of faces and an extended system to appraise the beauty of faces (Senior, 2003). Moreover, the extended system for beauty processing is further divided into two parts: rewarding beauty and pure aesthetic beauty (Senior, 2003). The results in the present study support this extended system model in two ways.

First, the results provided evidence for the existence of an extended system for appraising the beauty of faces. More specifically, this extended system consisted of interconnected brain regions in the vmPFC: the mOFC/ACC/gyrus rectus and the left gyrus rectus. In fact, these brain regions formed a medial network of the vmPFC (Öngür & Price, 2000), which played a crucial role in the evaluation of social information (e.g., self-related information, Hu et al., 2016; Sui, 2016). In addition, the functional decoding analyses showed that based on the BrainMap database, the mOFC and the gyrus rectus were more associated with studies belonging to cognition and the emotion behavioral domain; these two brain regions were also significantly more involved with reward paradigms than with other experimental paradigms. Additionally, recent studies have shown that the medial part of the vmPFC is involved in reward and bottom-up-driven, approach/avoidance-modulation and evaluation-related processing (Bzdok et al., 2013). This area is also related to other functions, including punishment (O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001), pain (Winston, Vlaev, Seymour, Chater, & Dolan, 2014), moral judgment (Greene, Sommerville, Nystrom, Darley, & Cohen, 2001; Moll, de Oliveira-Souza, Bramati, & Grafman, 2002), self-referential processing (Hu et al., 2016; Northoff et al., 2006; Sui, Rotshtein, & Humphreys, 2013) and the default mode network (Biswal, Yetkin, Haughton, & Hyde, 1995; Di, Gohel, Kim, & Biswal, 2013).

Second, the results provide evidence that the extended beauty appraisal system consists of two dissociable components: a network for processing the primary rewarding value of beautiful faces and a network for processing the aesthetic value of beautiful faces. As mentioned before, part of the mOFC, which is responsible for generating positive affective meaning, was activated by both faces and art, while the posterior part of the mOFC and the gyrus rectus were more likely to be associated with primary rewards, such as sexuality and desire. Our MACM results provide additional evidence for the dissociated roles of these two brain regions; while the mOFC shared the processing of both the beauty of art and secondary reward, the gyrus rectus was more linked to primary reward and sexual desire.

It is noteworthy that our meta-analyses did not show greater activation of the fusiform face areas or other sensory cortical areas for beautiful faces than for non-beautiful faces, as previous studies have reported (Chatterjee, Thomas, Smith, & Aguirre, 2009; Iaria, Fox, Waite, Aharon, & Barton, 2008). This inconsistency may be resulted from the fact that we strictly selected contrast in the present study (i.e., the comparison between beautiful faces and non-beautiful faces) and consequently eliminated the low-level processing of facial features.

In short, the meta-analyses results reported here confirm previous work suggesting that facial beauty involves both primary reward beauty and secondary aesthetic beauty (Franklin Jr & Adams Jr, 2009; Hahn & Perrett, 2014; Kranz & Ishai, 2006; Senior, 2003), which are associated with the gyrus rectus and the anterior part of the mOFC, respectively.

4.2.2. Neural networks underlying the beauty of visual art

Regarding the beauty of visual art, the meta-analyses of fMRI studies showed a convergent activation in the left mOFC. The results were in line with a previous theoretic framework that

aesthetic experiences emerge from interactions among sensory-motor, emotion and higher cognitive processes (e.g., Chatterjee and Vartanian, 2014; Leder and Nadal, 2014), confirming the role of the emotion-evaluation network in processing the aesthetic beauty of visual art.

Previous studies have suggested that processing art involves multiple brain systems, ranging from sensory-motor networks, knowledge-meaning networks and emotion-evaluation networks (Chatterjee & Vartanian, 2014). Similarly, Leder, et al. proposed a model for aesthetic experiences in which sensory, memory, evaluative and affective processes were all involved (Leder et al., 2004; Leder & Nadal, 2014). These comprehensive views of aesthetic experience gain support from a recent fMRI meta-analyses of visual art (Boccia et al., 2016). Our meta-analyses results, which showed that the mOFC was convergently activated, confirmed the role of the emotion-evaluation network in processing the beauty of visual art. The mOFC was co-activated with emotion/reward-related brain structures such as the precuneus and the left caudate nucleus. In addition, functional decoding based on the BrainMap database showed that this part of the brain was more related to fMRI studies that evaluated cognition and emotion behavioral domains. The most often involved paradigm classes (PCs) were reward and face monitor/discrimination. These results are consistent with previous work that has demonstrated that the value of art is represented in the vmPFC (Abitbol et al., 2015; Aharon et al., 2001; Bohrn, Altmann, Lubrich, Menninghaus, & Jacobs, 2013; Ishizu & Zeki, 2011; Kawabata & Zeki, 2004; Kirk et al., 2009; Park, Jin, Chung, & Jeong, 2012).

It should be noted that our meta-analyses results failed to show any brain regions in the sensory-motor network, which seems to contradict previous theories (Boccia et al., 2016; Chatterjee & Vartanian, 2014; Leder & Nadal, 2014). However, the results do not contradict

these studies because the current study focused on the neural response of the beauty of visual art rather than how visual art is processed in the brain per se. Based on the goal of this study, only the contrasts between beautiful visual art and non-beautiful art (e.g., beautiful art > not beautiful art) were selected, and studies that were focused on the comparison between visual art and other visual stimuli (e.g., scenes of people) were excluded. Hence, the meta-analyses results reflected the aesthetic beauty of visual art, not art processing in general.

4.3 Methodological considerations

Several limitations of the results should be addressed. First, it is worth noting that the meta-analyses was based on the available literature and may have been affected by potential publication bias disfavoring null results (Jennings & Horn, 2012).

Moreover, we selected only studies that compared beautiful stimuli with high-level baselines; theoretically, this helps eliminate the influence of low-level processing. However, processing beautiful visual art or attractive faces is a multi-stage process, and dissociating these interweaving processes is very difficult (Leder et al., 2004); therefore, the fMRI studies may not be able to effectively distinguish the aesthetic experience from other processes in aesthetic appreciation. Future studies should consider how to more clearly separate different processes.

In addition, because the ALE meta-analyses approach was based on the reported peak activations, a large part of the spatial information was discarded. Image-based meta-analyses overcome this issue, but they require the full statistic image data of all eligible experiments, which are seldom available. Moreover, the results derived from this method are in good agreement with coordinate-based meta-analyses approaches (Salimi-Khorshidi, Smith, Keltner, Wager, & Nichols, 2009). This suggests that coordinate-based meta-analyses algorithms, such as

ALE, are currently the most comprehensive approach for summarizing neuroimaging findings in a particular field.

Given that the ALE meta-analyses was based on previous studies, which are not specific to testing a novel hypothesis, further experimental data are needed to confirm the conclusion in our analyses. For instance, if the anterior mOFC was the common neural basis for beauty, it may suggest that individual differences in the mOFC or its connectivity could contribute to individual differences in aesthetic preference or sensitivity. However, this hypothesis should be tested in the future.

5. Conclusion

Convergent findings across fMRI studies on the beauty of visual art and faces were analyzed using ALE meta-analyses and MACM analyses. We observed a maximum convergence in the left mOFC across all the analyses, suggesting that the beauty of visual art and the beauty of faces are supported by a common neural substrate. Additionally, we observed distinct neural networks for beautiful visual art and faces. These results support the view that beauty has both stimuli-dependent and stimuli-independent neural underpinnings.

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Figure Legends

Figure 1. Article selection process for the beauty of visual art (left) and the beauty of faces (right), as recommended by Liberati et al. (2009).

Figure 2. Results of the ALE meta-analyses and the contrast and conjunction analyses. (A) Brain regions convergently activated more for beautiful visual art than for non-beautiful visual art; (B) brain regions convergently activated more for beautiful faces than for non-beautiful faces; (C) the results of the contrast and conjunction analyses between the ALE results of beautiful faces and beautiful visual art; negative values indicate greater activation for visual art than for faces, and positive values indicate greater activation for faces than for visual art; (D) brain regions shared by both beautiful art and beautiful faces.

Figure 3. (A) The MACM results for the left mOFC from the meta-analyses of the beauty of visual art; (B) the MACM results for the mOFC/ACC/gyrus rectus from the meta-analyses of the beauty of faces; (C) the MACM results for the left gyrus rectus from the meta-analyses of the beauty of faces; (D) the MACM results for the left mOFC shared by beauty of art and faces.

Figure 4. (A) Functional decoding of the left mOFC from the meta-analyses of the beauty of art; (B) functional decoding of the mOFC/ACC/gyrus rectus from the meta-analyses of the beauty of faces; (C) functional decoding of the left gyrus rectus from the meta-analyses of the beauty of faces; (D) functional decoding of the mOFC shared by beautiful faces and beautiful art.

Tables

Table 1. Overview of the studies and contrasts included in the present meta-analyses

Articles	Model	Subjects (Male)	Mean age	Stimuli	Task	Reported analyses
Abitbol, et al., 2015	fMRI	24(13 M)	25	paintings	pleasantness rating	correlation with pleasantness
Boccia, et al., 2015	fMRI	20(11 M)	25.45	Paintings	esthetic judgment	like > dislike
Di Dio, et al., 2007	fMRI	14(8 M)	24.5	sculpture	observation	beautiful > not beautiful
Flexas, et al., 2014	fMRI	24(12 M)	23.5	paintings	beautiful or not	beautiful > not beautiful
Harvey, et al., 2010	fMRI	87(NA)	NA	paintings	preference ratings	correlation with preference
Ishizu, et al., 2011	fMRI	21(9 M)	27.5	paintings	beauty ratings	beautiful > (indifferent + ugly)
Jaccobs, et al, 2012	fMRI	18(10 M)	20-39	visual textures	beauty judgment	beautiful > ugly
Kawabata et al., 2004	fMRI	10(5 M)	20~31	paintings	beauty ratings	beautiful > neutral
Kirk et al., 2009	fMRI	14(9 M)	26.3	paintings	aesthetic rating	correlation with aesthetics ratings
Lacey, et al., 2011	fMRI	8 (4 M)	23.1	paintings	animacy rating	correlated with beauty

Lebreton, et al., 2009	fMRI	20(10 M)	22.0	paintings	pleasantness ratings	correlated with pleasantness
Thakral, et al., 2012	fMRI	16 (NA)		paintings	pleasant judgment	correlated with aesthetic ratings
Vartanian et al., 2004	fMRI	12(4 M)	28	paintings	preference rating	correlated with preference
Vessel, et al., 2012	fMRI	16(11 M)	27.6	visual arts	recommendation	most recommended > least recommended
Aharon et al., 2001	fMRI	10(10 M)	25.2	faces	observation	beauty > average
Bray et al., 2007	fMRI	25(12 M)	20.8	faces	location discrimination	attractive > unattractive faces
Cartmell et al., 2014	fMRI	16(7 M)	20	faces	Partner Selection	attractive > unattractive faces
Chatterjee et al., 2009	fMRI	13(6 M)	22.6	faces	beauty ratings	correlation with beauty ratings
					identity ratings	correlation with beauty ratings
Cloutier et al., 2008	fMRI	48(24 M)	21.7	faces	attractive judgment	increase with attractiveness
Cooper et al., 2012	fMRI	39(20 M)	21.44	faces	attractiveness ratings	positively related to attractiveness
Iaria et a., 2008	fMRI	11(5 M)	24.09	faces	attractiveness ratings	attractive > unattractive faces
Ito et al., 2015	fMRI	28(14 M)	21.6	faces	passive viewing	preferred > non-preferred

					choosing task	preferred > non-preferred
Kim et al., 2007	fMRI	25(13 M)	20-45	faces	ratings	correlation with attractiveness (exclude preference)
Kocsor et al., 2013	fMRI	16(8 M)	25	faces	face discrimination	attractive > unattractive faces
Liang et al., 2010	fMRI	17(8 M)	26.5	faces	passive viewing	linear correlated with attractiveness
McGlone et al., 2013	fMRI	16(0 M)	23	faces	attractiveness rating	attractive faces > unattractive faces
O'Doherty et al., 2003	fMRI	25(13 M)	23.8	faces	gender judgment	high > low attractiveness
Pegors et al., 2014	fMRI	28(14 M)	22.5	faces	attractive ratings	correlated with face attractiveness
Smith et al., 2010	fMRI	23(23 M)	21.8	faces	passive view	attractive faces > unattractive faces
Smith et al., 2014	fMRI	16(16 M)	23	faces	attractiveness rating	linear increase with attractiveness ratings
Tsukiura et al., 2011a	fMRI	20(0 M)	23.4	faces	attractive ratings	linear increase with facial attractiveness
Vartanian et al., 2013	fMRI	29(14 M)	25.1	faces	attractiveness rating	correlated with attractiveness
Wang et al., 2014b	fMRI	22(10 M)	21	faces	gender judgment	beautiful face > common face

Winston et al., 2007	fMRI	15(15 M)	25.5	face	attractive & age judgment	effect of attractiveness
Yu et al., 2013	fMRI	18(9 M)	21	faces	attractive judgment	attractive faces > unattractive faces
Zhai et al., 2010	fMRI	18(10 M)	20.8	faces	attractive judgment	attractive faces > unattractive faces

Table 2. The results of the meta-analyses for beautiful visual art and beautiful faces

Cluster	Volume (voxels)	Weighted center			Maximum Z-value	Center for maximum Z-value			Macroanatomical location
		x	y	z		x	y	z	
beautiful > non-beautiful visual art									
1		-6	60	-2	4.02	-4	60	-2	L mOFC
beautiful > non-beautiful faces									
1	421	0	42	-2	6.59	0	48	-8	mOFC
					4.22	-2	36	2	L ACC
					3.93	2	36	10	R ACC
					3.37	-4	36	-16	L rectal gyrus
2		-9	13	-9	4.96	-10	16	-6	L rectal gyrus
					4.09	-8	10	-16	L rectal gyrus

All peaks were assigned to the most probable brain area using the SPM Anatomy Toolbox.

Table 3. Contrast and conjunction analyses of the meta-analyses results for the beauty of visual art and faces

Cluster	Volume (voxels)	Weighted center			Maximum Z-value	Center for maximum Z-value			Macroanatomical location
		x	y	z		x	y	z	
beauty of visual art > beauty of faces									
1	11	-9	58	2	1.96	-8	58	-4	L mOFC
beauty of faces > beauty of visual art									
1	143	2	41	0	2.6	2	44	-2	R mOFC
					2.49	4	40	2	R mOFC
					2.24	6	36	6	R ACC
					2.02	0	36	6	ACC
2	25	-6	9	-14	2.29	-4	8	-14	L rectal gyrus
beauty of faces ∩ beauty of visual art									
1	71	-5	59	-2	4.02	-4	60	-2	L mOFC

All peaks were assigned to the most probable brain area using the SPM Anatomy Toolbox.

Table 4. The results of MACM for the left mOFC

Cluster	Volume (voxels)	Weighted center			Maximum Z-value	Center for maximum Z-value			Macroanatomical location
		x	y	z		x	y	z	
1	2176	-2	59	0	8.36	-2	58	-2	L mOFC
					8.16	-2	62	24	L superior medial gyrus
2	763	-4	-53	23	8.17	-6	-60	22	L precuneus
					8.16	-8	-56	18	L precuneus
					8.16	-6	-46	28	L PCC
					8.16	2	-44	32	N/A
					8.16	-6	-54	10	L calcarine gyrus
					8.15	-2	-32	26	N/A
					8.15	-6	-40	44	L MCC
					3.35	-10	-52	6	L linual gyrus
3	283	-20	30	47	8.16	-16	34	44	L superior frontal gyrus
					8.16	-24	28	48	L middle frontal gyrus
					8.15	-16	20	54	L superior frontal gyrus
					8.14	-22	24	54	L middle frontal gyrus
					3.35	-20	22	56	L middle frontal gyrus
4	154	-43	-75	30	8.16	-40	-78	32	L middle occipital gyrus
					8.15	-48	-68	28	L middle temporal gyrus

					8.15	-44	-72	26	L middle temporal gyrus
					8.15	-52	-66	26	L middle temporal gyrus
5	89	30	-23	-13	8.16	28	-22	-12	R hippocampus
6	64	-12	55	32	8.16	-10	54	32	L superior medial gyrus
7	64	-24	-18	-25	8.15	-24	-18	-22	L parahippocampal gyrus
					3.35	-24	-12	-26	L parahippocampal gyrus
					3.16	-20	-26	-22	L parahippocampal gyrus
8	51	7	-57	-38	8.15	6	-56	-36	R cerebellum Lobule IX
					3.35	6	-60	-40	R cerebellum Lobule IX

All peaks were assigned to the most probable brain area using the SPM Anatomy Toolbox.

Table 5. The results of MACM for the mOFC/ACC/rectal gyrus

Cluster	Volume (voxels)	Weighted center			Maximum Z-value	Center for maximum Z-value			Macroanatomical location
		x	y	z		x	y	z	
1	7117	1	37	-2	8.47	0	50	-6	L mOFC
					8.25	-10	8	-6	L caudate nucleus
					8.24	24	-6	-20	R parahippocampal gyrus
					8.22	10	8	-4	R caudate nucleus
					8.21	-4	54	14	L superior medial gyrus

					8.19	38	-8	-10	N/A
					8.19	26	-20	-14	R hippocampus
					8.17	4	2	-10	N/A
					8.17	-14	54	28	L superior frontal gyrus
					8.17	-20	62	10	L superior frontal gyrus
					8.16	4	22	2	R olfactory cortex
2	2811	0	-49	29	8.24	0	-52	32	L PCC
					8.22	-6	-56	22	L precuneus
					8.21	2	-62	22	N/A
					8.20	-10	-60	14	L calcarine gyrus
					8.20	-2	-38	38	L PCC
					8.20	6	-50	18	R precuneus
					8.19	0	-16	40	L MCC
					8.17	12	-56	10	R linual gyrus
					8.17	-14	-50	0	L linual gyrus
					8.16	14	-50	0	R linual gyrus
					8.15	-6	-46	-50	L MCC
3	787	-21	35	45	8.2	-22	32	44	L superior frontal gyrus
					3.35	-4	50	44	L superior medial gyrus
4	210	-45	-74	31	8.2	-44	-76	32	L angular gyrus
					3.35	-50	-64	32	L angular gyrus
5	180	55	-3	-27	8.18	56	-4	-22	R middle temporal gyrus

					3.16	48	2	-38	R inferior temporal gyrus
6	180	-21	-17	-21	8.22	-22	-16	-20	N/A
					8.20	-22	-8	-24	L parahippocampal gyrus
7	79	-36	10	-12	8.2	-36	12	-10	L IFG
8	79	-56	-10	-21	8.18	-54	-8	-20	L middle temporal gyrus
					3.35	-58	-6	-22	L middle temporal gyrus
9	60	49	-71	29	8.17	48	-72	30	R middle occipital gyrus

All peaks were assigned to the most probable brain area using the SPM Anatomy Toolbox.

Table 6. The results of MACM for the left rectal gyrus

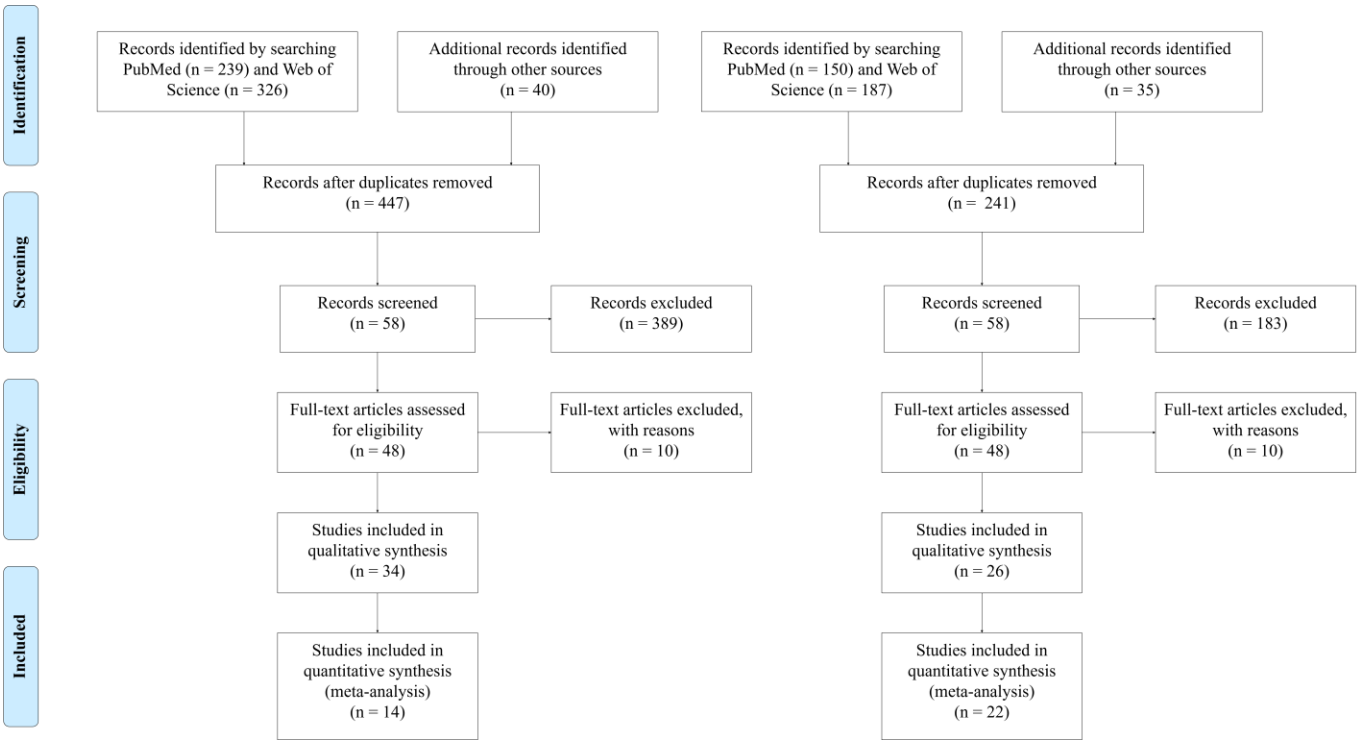
Cluster	Volume (voxels)	Weighted center			Maximum Z-value	Center for maximum Z-value			Macroanatomical location
		x	y	z		x	y	z	
1	3291	0	12	-8	8.49	-10	12	-6	L rectal gyrus
					8.33	12	12	-6	N/A
					3.35	10	-4	-18	N/A
2	299	1	43	-5	8.18	2	48	-10	R rectal gyrus
					8.17	0	42	-4	L mOFC
					8.15	-12	44	0	L mOFC
					3.35	0	48	-16	L rectal gyrus
3	180	2	-8	10	8.19	2	-10	10	N/A
4	92	2	-49	-33	8.17	2	-48	-32	Cerebellar vermis(10)
5	73	13	-7	-38	8.13	16	-6	-36	N/A
					3.35	12	-14	-38	N/A
6	61	12	-19	-10	8.17	10	-20	-10	N/A
7	51	60	-20	47	8.16	58	-20	46	R postcentral gyrus

All peaks were assigned to the most probable brain area using the SPM Anatomy Toolbox.

Table 7. The results of MACM for the left mOFC shared by beautiful art and faces

Cluster	Volume (voxels)	Weighted center			Maximum Z-value	Center for maximum Z-value			Macroanatomical location
		x	y	z		x	y	z	
1	2015	-2	59	0	8.36	-2	58	-2	L mOFC
					8.16	-2	62	24	L superior medial gyrus
2	628	-4	-56	20	8.17	-6	-60	24	L precuneus
					8.16	-6	-46	28	L PCC
					8.16	-6	-54	10	L calcarine gyrus
					8.15	-6	-46	18	L PCC
					3.35	-4	-42	18	L PCC
3	262	-21	32	45	8.16	-16	34	44	L superior frontal gyrus
					8.16	-24	28	48	L middle frontal gyrus
					8.14	-22	26	52	L superior frontal gyrus
4	196	-43	-74	29	8.16	-40	-78	32	L middle occipital gyrus
					8.15	-48	-68	28	L middle temporal gyrus
					3.35	-48	-72	20	L middle temporal gyrus
					3.16	-52	-66	26	L middle temporal gyrus
5	58	8	-57	-38	8.15	6	-56	-36	R cerebellum lobule IX

All peaks were assigned to the most probable brain area using the SPM Anatomy Toolbox.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Screening
Eligibility
Included
Records identified by searching PubMed (n = 239) and Web of Science (n = 326)
Additional records identified through other sources (n = 40)
Records after duplicates removed (n = 447)
Records screened (n = 58)
Records excluded (n = 389)
Full-text articles assessed for eligibility (n = 48)
Full-text articles excluded, with reasons (n = 10)
Studies included in qualitative synthesis (n = 34)
Studies included in quantitative synthesis (meta-analysis) (n = 14)
Records identified by searching PubMed (n = 150) and Web of Science (n = 187)
Additional records identified through other sources (n = 35)
Records after duplicates removed (n = 241)
Records screened (n = 58)
Records excluded (n = 183)
Full-text articles assessed for eligibility (n = 48)
Full-text articles excluded, with reasons (n = 10)
Studies included in qualitative synthesis (n = 26)
Studies included in quantitative synthesis (meta-analysis) (n = 22)

Figure 1.

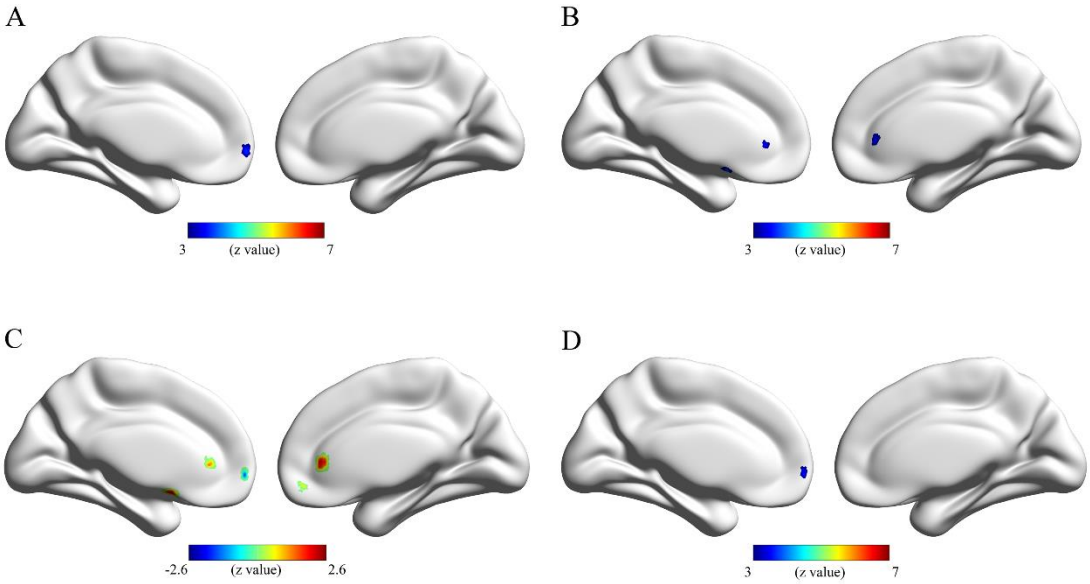
A
3
(z value)
7
B
3
(z value)
7
C
-2.6
(z value)
2.6
D
3
(z value)
7

Figure 2.

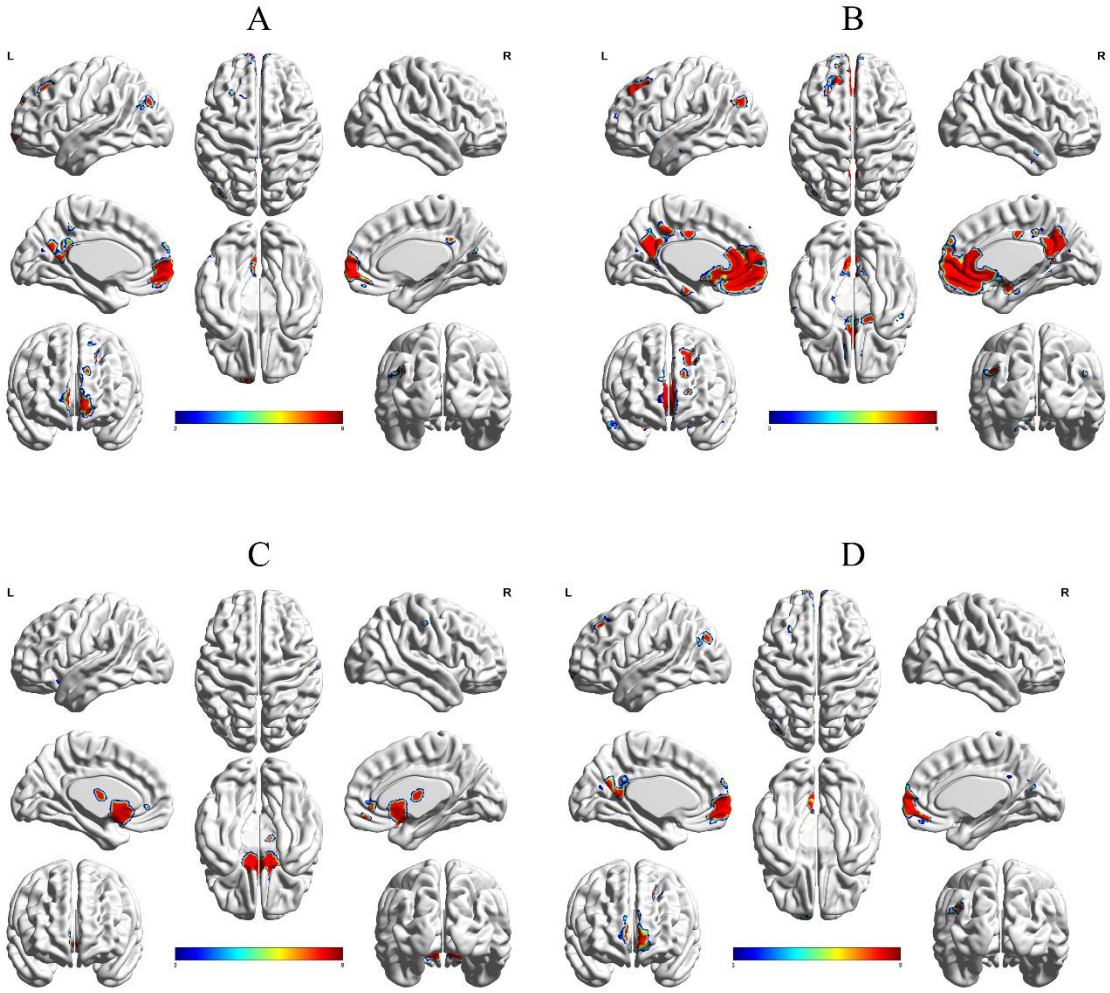

Figure 3.

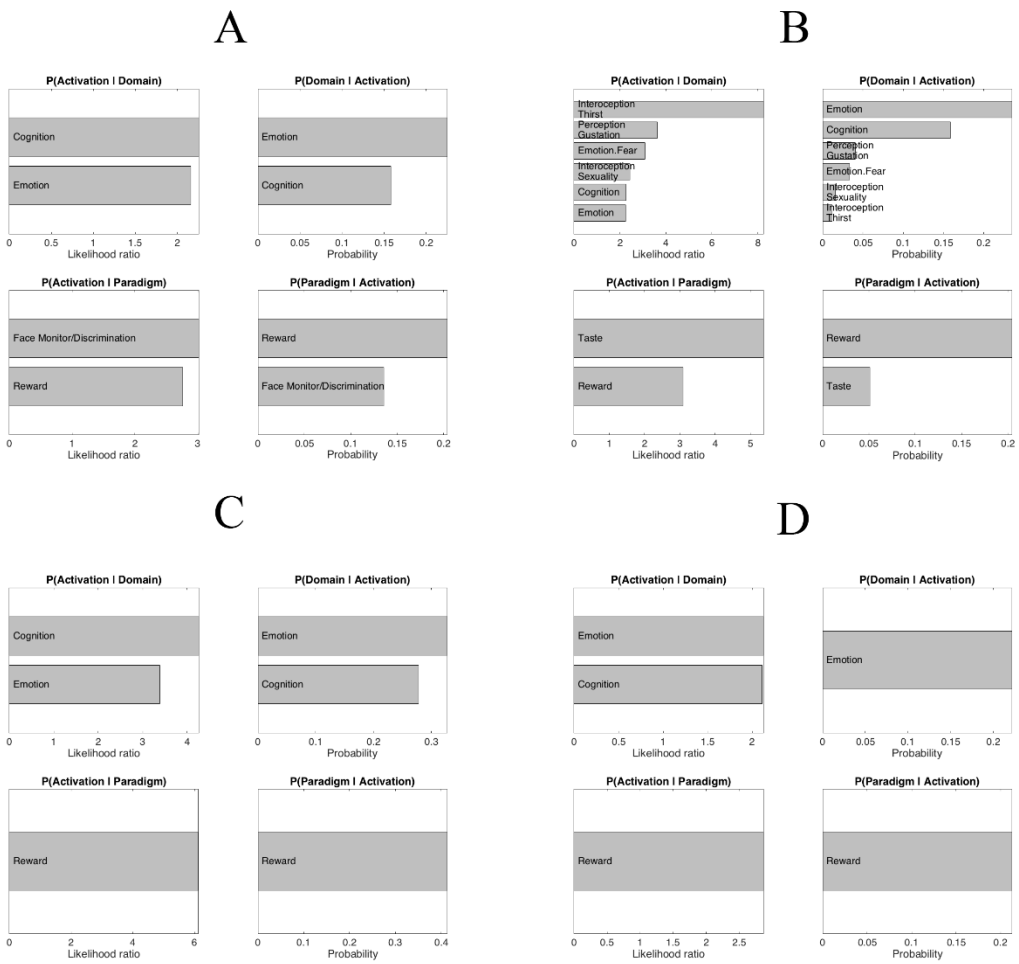
A
P(Activation | Domain)
Cognition
Emotion
Likelihood ratio
P(Domain | Activation)
Emotion
Cognition
Probability
P(Activation | Paradigm)
Face Monitor/Discrimination
Reward
Likelihood ratio
P(Paradigm | Activation)
Reward
Face Monitor/Discrimination
Probability
B
P(Activation | Domain)
Interoception
Thirst
Perception
Gustation
Emotion.Fear
Interoception
Sexuality
Cognition
Emotion
Likelihood ratio
P(Domain | Activation)
Emotion
Cognition
Perception
Gustation
Emotion.Fear
Interoception
Sexuality
Interoception
Thirst
Probability
P(Activation | Paradigm)
Taste
Reward
Likelihood ratio
P(Paradigm | Activation)
Reward
Taste
Probability
C
P(Activation | Domain)
Cognition
Emotion
Likelihood ratio
P(Domain | Activation)
Emotion
Cognition
Probability
P(Activation | Paradigm)
Reward
Likelihood ratio
P(Paradigm | Activation)
Reward
Probability
D
P(Activation | Domain)
Emotion
Cognition
Likelihood ratio
P(Domain | Activation)
Emotion
Probability
P(Activation | Paradigm)
Reward
Likelihood ratio
P(Paradigm | Activation)
Reward
Probability

Figure 4.