Seeking the common beauty in the brain: A meta-analysis of fMRI studies of beautiful human faces and visual art

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Abstract

The existence of a common beauty is a long-standing debate in philosophy and related disciplines. In the last two decades, cognitive neuroscientists have sought to elucidate this issue by exploring the neural basis of the experience of beauty. Still, it is unclear whether different forms of beauty share a common neural structures. To address this question, we performed an activation likelihood estimation (ALE) meta-analysis on the existing neuroimaging studies of beautiful faces and beautiful visual art. We observed that perceiving two forms of beauty activated distinct brain regions: while the beauty of faces was associated with activities in the left ventral striatum, the beauty of visual art was associated with the anterior medial prefrontal cortex (aMPFC). There was no strong evidence for the common neural basis of different forms of beauty, although with a more liberal threshold, a small cluster at the left ventromedial prefrontal cortex (vMPFC) was activated by both forms of beauty. The implications of these results are discussed.

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. 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). Other scholars (e.g., Kubovy (2000)), however, have opposed this common theory by suggesting that “beauty is in the eye of the beholder,” emphasizing the role of individuals’ experiences in appreciating beautiful 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 basis of aesthetic responses to beauty via experimental approaches (e.g. (Aharon et al., 2001; Chatterjee and Vartanian, 2014; Pearce et al., 2016)). However, after two decades of study, the existence of a common neural basis for different forms of beauty is still not strongly supported (Ward, 2015). In this study, we evaluate the empirical studies by conducting an activation likelihood estimation (ALE)-based meta-analyses on functional magnetic resonance imaging (fMRI) studies that explored the neural basis of beauty.

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,

or the appreciation of art (Pearce et al., 2016). This conceptual ambiguity hampers interdisciplinary communication (Bergeron and Lopes, 2012). Therefore, it is necessary first to offer a clear operational definition of beauty.

From the perspective of an information processing model (Leder et al., 2004; Leder and 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). This operational definition of the experience of beauty avoids the confusion with other concepts in relation to aesthetics or pleasure. First, it distinguishes the experience of beauty from other aesthetic experiences, because aesthetic experiences could include both positive and negative affective states (Bergeron and Lopes, 2012). Second, this definition distinguishes the experience of beauty from the general pleasure, which can be elicited by non-aesthetic stimuli, for example, food and sex (Berridge and Kringelbach, 2013), or moral behaviors (Diessner et al., 2008). Furthermore, although the experience of beauty may be accompanied by some complex emotions (e.g., “awe”, “sublime” or “being moved”), the experience of beauty is not equal to any of these complex emotions. That is, people may appreciate the beauty of an aesthetic object without any of these complex emotions.

Most importantly, this operational definition of the experience of beauty gives us a specific criterion in empirical studies. For example, with this definition of beauty, the brain activity underlying the experience of beauty can be measured by comparing brain activity when perceiving beautiful stimuli with brain activity when perceiving non-beautiful stimuli with similar physical properties. Such method allows us to identify the brain regions that are positively correlated with beauty ratings or preference (Ramachandran and Hirstein, 1999).

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

For psychologists and neuroscientists, one approach to defining a “common mechanism” is to test whether processing different types of information (e.g., beautiful faces vs. beautiful visual art) share neural structures. For instance, recent studies have shown that spatial, temporal and social distance have common neural representations in the right inferior parietal lobule (Parkinson et al., 2014), the left intraparietal sulcus is associated with processing both perceptually salient and socially salient stimuli (Sui et al., 2015), and that the 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, a common neural basis for different forms of beauty can be identified if there are common regions activated by experiencing different forms of beauty.

In fact, previous studies have suggested that the experience of beauty has a common mechanism. Reber proposed that beauty resulted from the cognitive processing fluency of the perceivers in general (Reber et al., 2004). Ishizu and Zeki (2011) suggested that common beauty across modalities was associated with activation of the medial orbitofrontal cortex (mOFC). Based on a meta-analysis of neuroimaging studies on fMRI studies related to aesthetics, Brown et al. (2011) argued that the insula was the common neural basis for aesthetic appraisal. More interestingly, there was an implicit theory of common beauty that beauty is equal to reward, which is indicated by the fact that many studies used beautiful stimuli as rewarding stimuli (Aharon et al., 2001; Bray and O'Doherty, 2007; Cloutier et al., 2008; Lacey et al., 2011; Liang et al., 2010; Smith et al., 2014), along with other monetary reward-related stimuli. This implicit theory of common beauty was also supported by theorists in neuroaesthetics who suggested that

reward processing was an import component of aesthetic appreciation (e.g., (Chatterjee and Vartanian, 2014)).

However, we cannot conclude that there is a common neural basis for beauty due to two issues. First, the heterogeneity of fMRI studies on aesthetics makes it difficult to draw a consistent conclusion on the neural basis for the experience of beauty. Although a number of studies 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 the aesthetic judgment process (Bzdok et al., 2012; Ishizu and Zeki, 2013) or the processing of art (Mizokami et al., 2014), but these two psychological processes are different from the response to beauty (Bergeron and Lopes, 2012; Conway and Rehding, 2013; Shimamura, 2012). Second, not limited to neuroaesthetics, single neuroimaging study suffered from low statistical power (Button et al., 2013) and the high false-positive rates (Eklund et al., 2016; Wager et al., 2007) due to small sample sizes (Button et al., 2013) or the flexibility of fMRI data processing (Carp, 2012).

1.3. The current study.

To explore the common neural basis of beauty, taking into account the above concerns, we conducted an ALE meta-analysis of fMRI studies of beauty, and compared the neural activities elicited by the beauty of faces and the beauty of the 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 (e.g. Chatterjee and Vartanian (2014)), thus providing enough studies for a meta-analysis. Second, they represent two typical categories of beauty: faces are the most representative natural beauty in social life, and the preference of

human face is shaped by both evolution (e.g. Little et al. (2011)) and environment (Germine et al., 2015), while the visual arts are the most representative artificial beauty, which is reflected in the subjective aesthetic preference of human beings. Therefore, a comparison between the neural responses to these two types of beauty may provide valuable insights into the exploration of common and distinct neural bases of beauty.

We employed an ALE meta-analysis of 38 fMRI studies on the beauty of faces and the beauty of art according to our definition of beauty. The ALE meta-analysis 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 et al., 2014; Laird et al., 2011). Furthermore, it provides more decisive results and greater statistical power than individual studies (Eickhoff et al., 2016). To avoid the influence of 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.

The current study seeks to (1) identify convergent neural activation across studies for the two forms of beauty, (2) assess the distinct brain regions and corresponding co-activation network observed in face-based beauty and visual art-based beauty. Additionally, to provide evidence-based inverse-inferences regarding the function of the results of the meta-analysis, we further conducted functional characterizations based on the Brainmap database (Eickhoff et al., 2011; Fox et al., 2014; Yarkoni et al., 2011).

2. 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 Jan 2017). “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 (to increase reproducibility of the current study, the syntax used for searching strategy was added in the supplementary methods, see Supplementary information). For a 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 et al., 2016; Mende-Siedlecki et al., 2013; Vartanian and 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 contrast of current meta-analyses interested in (Lebreton et al., 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 et al., 2009a) due to the influence of expertise on aesthetic appreciation (Hekkert and 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, therefore, studies using visual art or faces as stimuli that did not report the effect of beauty or preference were excluded, also were studies that did not report the effect of faces or visual art separately were excluded; and c) studies that included a high-level baselines (i.e., beauty art > not-beautiful art or beautiful faces > non-beautiful faces), instead of low-level baselines (e.g., photos or resting state).

2.2. Activation likelihood estimation.

The meta-analysis was carried out using the revised ALE algorithm, which was implemented in Matlab code, for the coordinate-based meta-analysis of neuroimaging results (Eickhoff et al., 2009; Laird et al., 2009a; Laird et al., 2009b; Turkeltaub et al., 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 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 Full-Width Half-Maximum (FWHM) of these Gaussian 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). Specifically, the number of subjects in the studies in our meta-analysis ranged from 8 ~ 87, with a median of 18, and the range of Full-Width Half-Maximum (FWHM) was from 8.5 mm ~ 10.94 mm (median: 9.5 mm).

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 analysis, a process that can be solved analytically (Eickhoff et al., 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 $p < 0.05$ (cluster-level corrected for multiple-comparison; cluster-forming threshold $p < 0.001$ at voxel level) (Eickhoff et al., 2012). All significant clusters were reported, and the volume, weighted center and locations and Z-scores at the peaks within the regions are given.

2.3. Overlap analysis and comparison of individual meta-analyses.

We used two methods to determine brain regions that were activated by both types of beauty. First, we used the conjunction analyses (Nichols et al., 2005), which used the voxel-wise minimum of each single ALE results. However, this conjunction analysis was based on corrected results and therefore has the risk of false negative and low power (Radua et al., 2012), therefore we also used uncorrected thresholds to explore the overlap between two ALE results.

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 analysis 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.

2.4 Data Visualization.

Given that there is no standard brain atlas for neuroimaging studies, we used probabilistic cytoarchitectonic maps (as implemented in SPM Anatomy Toolbox) (Eickhoff et al., 2006; Eickhoff et al., 2007; Eickhoff et al., 2005), Automated Anatomical Labeling (AAL) (Tzourio-Mazoyer et al., 2002), and the Harvard-Oxford Atlas (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Atlases) (the latter two are implemented in DPABI (Yan et

al., 2016)) to assign our resulting coordinates to anatomical structures. When the labels are not consistent, we chose the label that most specifically describes the brain structures. For visualization purposes, BrainNet Viewer (Xia et al., 2013) was used to present the meta-analytical results.

2.5 Functional characterization.

To qualify the interpretation of the function of each brain region, we conducted functional characterization 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 (Laird et al., 2011; Turner and Laird, 2012). As a first step, we searched in the BrainMap database for those experiments that featured at least one focus of activation within the current ROI (each was defined by the meta-analysis results). Then, we analyzed the behavioral domain and paradigm class metadata of the retrieved BrainMap experiments, that is, those experiments with activation of the current seed, to determine the frequency of domain relative to its likelihood across the entire database. The functional role of the ROI was thus identified by significant overrepresentation of behavioral domains and paradigm classes. For quantitative function inference, we tested whether the conditional probability of activation given a particular label [P(Activation|Task)] was significantly higher than a priori probability of activation (P(Activation)) as assessed by a binomial test ($p < .05$, FDR-corrected for multiple comparisons) (Langner et al., 2014; Nickl-Jockschat et al., 2015; Rottschy et al., 2012). Likewise, we reported the reverse inference in which the conditional probability of label given an activation of a particular brain region [P(Task

|Activation)] was tested (Langner et al., 2014; Nickl-Jockschat et al., 2015; Rottschy et al., 2012; Yarkoni et al., 2011).

3. Results

3.1. Studies included in the meta-analyses.

After applying our search strategy (see method section for more details), 38 articles were identified (15 articles for beauty in the visual arts, including 15 experiments, 84 foci, and 321 subjects; 23 articles for the beauty of faces, including 23 experiments, 127 foci, and 525 subjects). To increase the reproducibility of the current study, all the metadata for the current study is available at https://osf.io/jf7g8/?view_only=1860fef0058b4cd29f8379de13c1d985. Figure 1 depicts the process of article selection in detail (see Table 1; the article-selection process in Endnote was available online, see Supplementary methods).

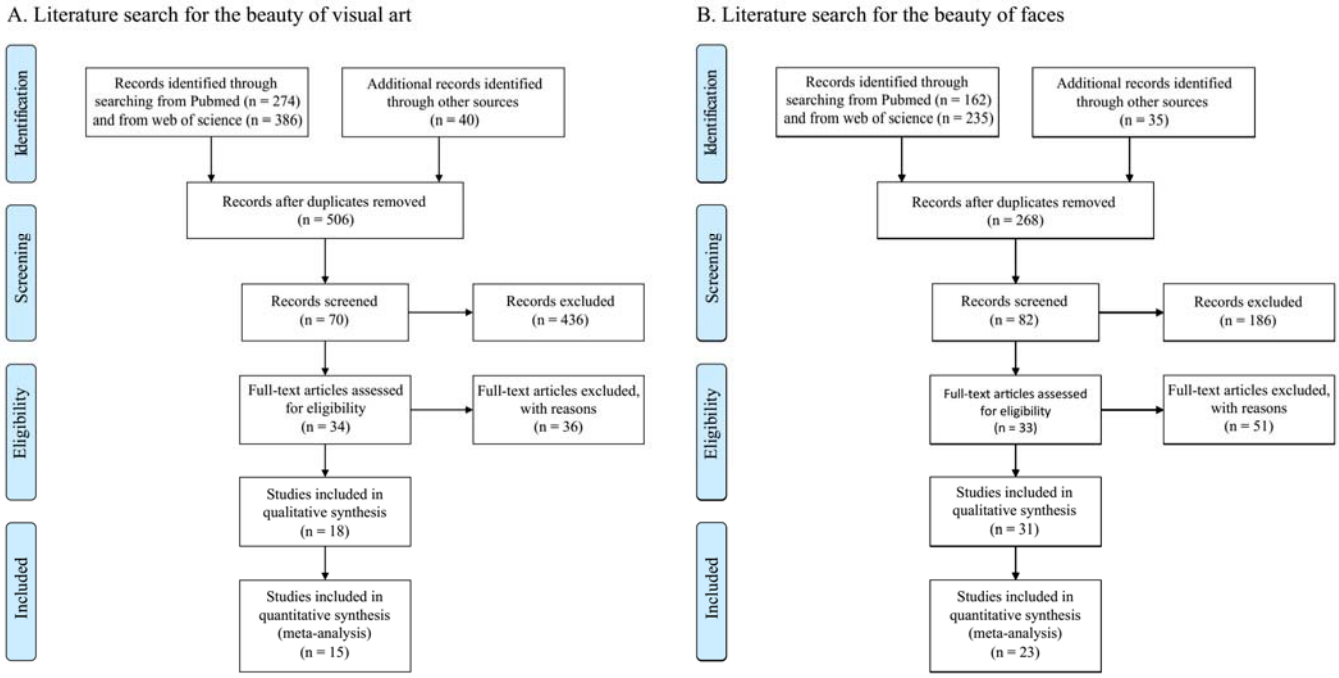

Figure 1. Flow diagram for literature search for the beauty of visual art (A) and the beauty of faces (B), as recommended by Liberati et al. (2009).

< insert Table 1>

3.2. ALE Meta-analyses of the aesthetic beauty of visual art and faces.

The ALE results of the beauty of visual art revealed that two regions were convergently activated. The first region located within the left anterior medial prefrontal cortex (aMPFC), the second region located in the left ventromedial prefrontal cortex (vMPFC), which also includes voxels in the left pregenual anterior cingulate gyrus (pgACC) and the left gyrus rectus (Table 2 and Figure 2A).

The ALE results of the beauty of faces showed that two brain regions were more convergently activated by beautiful faces than by non-beautiful faces: the first region located in the ventromedial prefrontal cortex (vMPFC) extending to the pgACC, and subcortical structures such as the ventral striatum and subcallosal cortex (Table 2 and Figure 2B).

The conjunction analysis with the minimum statistic (Nichols et al., 2005) (i.e., finding the minimum t-value across the two original ALE results voxel-wisely) showed no survival cluster. Our exploratory analysis of the overlap between two ALE results, with uncorrected thresholds and cluster size greater than 50 voxels, found the ventromedial frontal cortex (vMPFC) (include part of pgACC) was shared by both types of visual beauty at $p < 0.01$ uncorrected (results are available at https://osf.io/jf7g8/?view_only=1860fef0058b4cd29f8379de13c1d985, see Table 3 and Figure 2D). A complementary ALE analysis in which data from both beautiful faces and art were pooled together also found that vMPFC/pgACC were convergently activated (see Supplementary Information S2).

The contrast analysis further showed that a locus within the left vMPFC and a locus within the left ventral striatum were more frequently activated by beautiful faces than by beautiful art, while there were two small clusters were more activated by beautiful visual art than by beautiful faces: one cluster located in the aMPFC and the other in the posterior of vMPFC (Table 3 and Figure 2C).

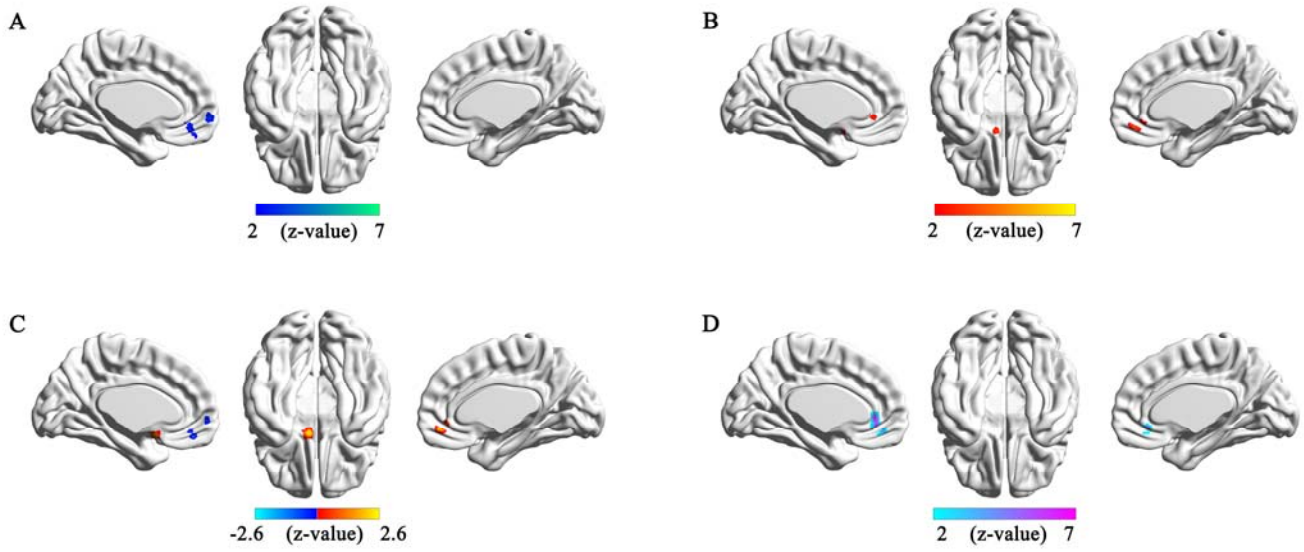

Figure 2. Results of the ALE meta-analysis and the contrast and conjunction analysis. (A) Brain regions convergently activated more for beautiful visual art than for non-beautiful visual art; (B) brain regions convergently activated more for beautiful faces than for non-beautiful faces; (C) the results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

< Insert Table 2, Table 3 >

3.3 Functional characterization.

The functional characterization based on BrainMap databased showed that the ROI from the ALE results of the beauty of visual art, the left aMPFC, was associated with behavioral domains (BDs) related to emotion and cognition, the most common paradigm classes (PCs) involved were reward and face monitor/discrimination (see Figure 3A). As for the vMPFC/pgACC, it was also associated with the behavioral domains (BD) related to emotion, cognition, as well as other domains such as social cognition, gustation, and fear processing. Similarly, this region involved in the reward paradigms as well as theory of mind (see Figure 3B).

For the ROIs from the meta-analysis of the beauty of faces, the first seed, which includes vMPFC/pgACC, was related to emotion, cognition, social cognition, fear emotion and gustation and was involved in reward and taste paradigms (see Figure 3C). The second seed from the meta-analysis of the beauty of faces, which includes the ventral striatum, was related to the behavioral domains of emotion and cognition and was only involved in the reward paradigms (see Figure 3D).

For the vMPFC/pgACC regions that possibly shared by both beautiful faces and beautiful visual art, the related behavioral domains were emotion, cognition, social cognition and gustation, and this region involved the reward, theory of mind, and taste (see Figure 3E).

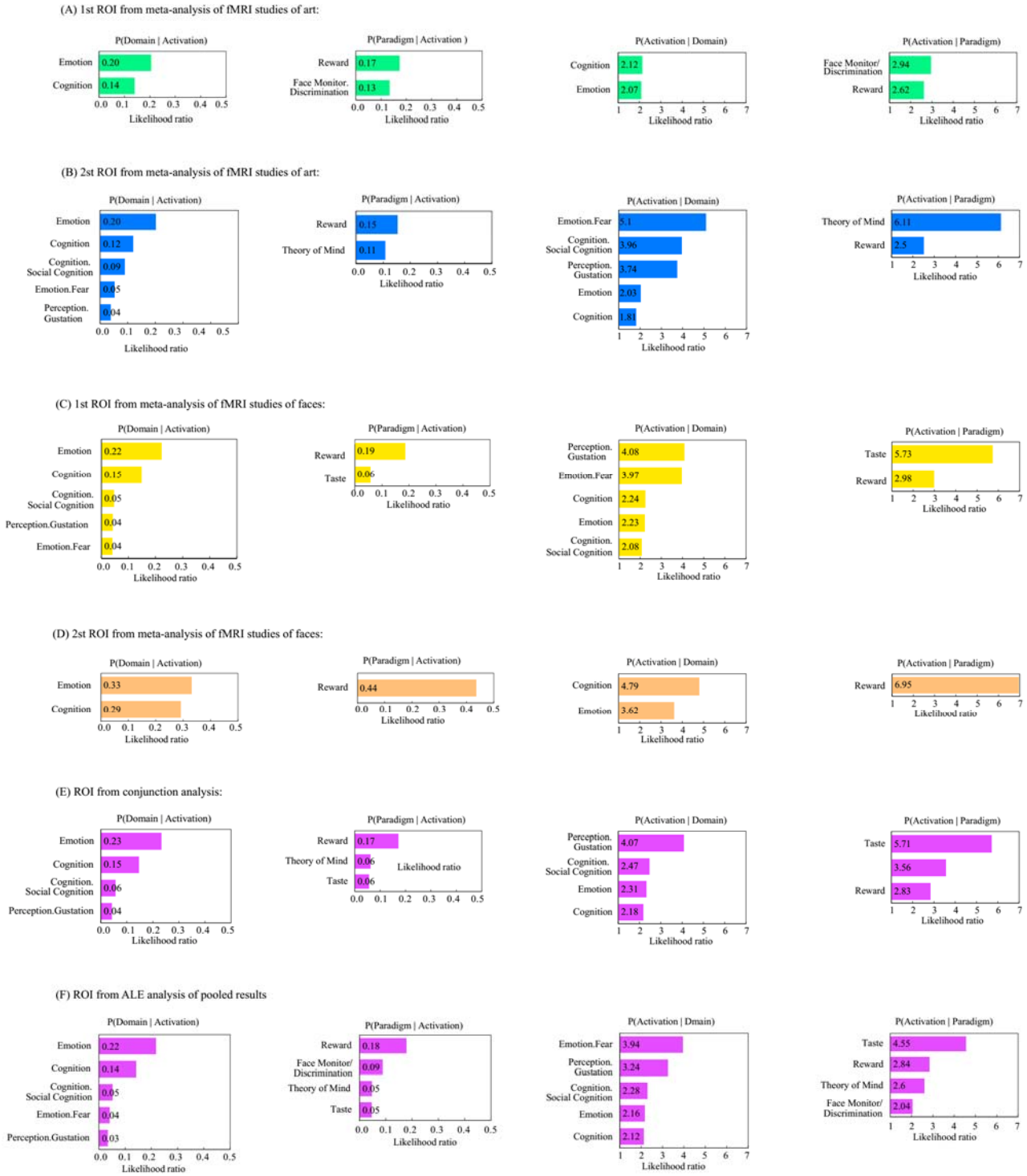

Figure 3. Functional characterization of brain regions from meta-analytic results, showing the reverse and forward inference of behavioral domain and paradigm class of each ROI. (A) The

left aMPFC from the meta-analysis of the beauty of visual art; (B) the left vMPFC/pgACC from the meta-analysis of the beauty of visual art; (C) the vMPFC/pgACC from the meta-analysis of the beauty of faces; (D) the left ventral striatum from the meta-analysis of the beauty of faces; (E) the left vMPFC/pgACC from conjunction analysis of ALE results of beauty of art and faces.

4. Discussion

The current study sets out to explore the common and form-specific neural basis of the beauty of the visual art and faces. The results showed that different forms of beauty activated different brain regions: the left ventral striatum was more convergently activated by beautiful faces, while the aMPFC was more activated by beautiful visual art. Also, the results showed weak evidence for the common neural basis for processing beauty in the vMPFC/pgACC.

4.1. Is there a common neural basis for visual beauty?

The existence of the common beauty is pursued by researchers from different disciplines. The current study attempt to find the common neural basis of experiencing beauty by conducting a conjunction analysis of the ALE meta-analysis of fMRI studies. To find the “pure” beauty process in the human brain, we distinguished the experience of beauty from other related but different processes, such as art appreciation (Pearce et al., 2016).

The conjunction analysis from our meta-analysis, however, didn’t find any surviving clusters. Using liberal threshold, we found that a small cluster of vMPFC/pgACC were activated in both tasks. This fact makes it’s hard to interpret the current results. On the one hand, the un-corrected results should be treated with great caution because of the possible false positivity (Eklund et al., 2016); on the other hand, the vMPFC/pgACC as the candidate for common neural basis is consistent with previous studies. This brain region is a hub for integrating sensory information

and abstract concepts to generate affective meaning (Etkin et al., 2006; Roy et al., 2012), especially positive emotions, such as safety (Haaker et al., 2013; Kalisch et al., 2006). A previous meta-analysis on the valuation system has shown that the vMPFC was engaged in the evaluation of the positive valence but not the negative valence (Bartra et al., 2013). As both beautiful faces and beautiful visual art are positive stimuli, it is possible that vMPFC might serve as a hub for processing the beauty in both forms. Indeed, previous theoretical work in neuroaesthetics has proposed the MPFC, which is important for emotion processing, plays an important role in processing the experience of beauty (Chatterjee and Vartanian, 2014).

The contrast between strong theoretical interest on but weak empirical evidence for the common neural basis for beauty calls for more critical studies. One possible approach to address this issue is adapting more powerful, multi-variable analysis to decode the pattern of different forms of beauty (e.g., (Woo et al., 2017)). Also, as science is accumulative, further studies can be integrated into the current meta-analysis to update the results. To facilitate this process, we opened the meta-data of this meta-analysis (see Method section), the future work can easily be integrated to update the knowledge about the common neural basis of beauty.

4.2. Neural basis underlying the beauty of faces.

The ALE results showed that beautiful faces induced greater activation in the vMPFC/pgACC and the left ventral striatum than non-beautiful faces. These results suggest that the vMPFC-subcortical rewarding system is engaged in processing the beauty of faces. Previous studies have shown that these two brain regions play a critical role in processing reward (Haber and Knutson, 2010; Liu et al., 2011; Vincent et al., 1993). Our functional characterization of these two brain regions also confirmed that these two brain structures are both involved in

reward paradigms. These findings are consistent with the view that the evaluating the rewarding value is crucial for appreciating the facial beauty (Chatterjee and Vartanian, 2014; Hahn and Perrett, 2014).

However, the role of the vMPFC/pgACC and the ventral striatum might differ when processing the rewarding value of facial beauty. While the vMPFC/pgACC is coactivated with a wide range of brain structures and involved in multiple higher-level functions (de la Vega et al., 2016; Roy et al., 2012), the function of the ventral striatum mainly engaged in reward processing (Haber and Knutson, 2010; Liu et al., 2011), especially primary reward (Sescousse et al., 2013). Therefore, it is possible the facial beauty is appreciated through a **ventral** pathway: the ventral striatum may primarily respond to the rewarding value of faces, the reward signal, along with other information, was then integrated in the vMPFC to generate positive affections. Further studies are needed to further dissociate these two different processes in appreciating the beauty of faces.

4.3. Neural basis underlying the beauty of visual art.

Regarding the beauty of visual art, the meta-analysis of fMRI studies showed convergent activations in the left aMPFC and the vMPFC/pgACC. These two clusters located in relative dorsal and ventral part of MPFC, suggest that they may play different roles in processing the beauty of visual art.

The aMPFC in our study is located in the dorsal MPFC, which is more engaged in high-level, top-down processing (Bzdok et al., 2013), such as episodic memory, decision-making, and social cognition (de la Vega et al., 2016). Previous studies also showed that this brain structure is also activated during positive evaluation (Bartra et al., 2013) and secondary reward (Sescousse et al.,

2013). Our functional characterization also suggests that this part of the brain engaged in both emotional and cognitive domain. We speculate that the aMPFC, when appreciating visual art, links more abstract beauty to reward, similar to that of secondary reward.

The vMPFC/pgACC, on the other hand, is coactivated with a wide range of brain structures and involved in multiple functions, especially positive affective (de la Vega et al., 2016; Roy et al., 2012), as suggested by our functional characterization of this brain region. It is possible that the beauty of art was appreciated through a **dorsal** pathway: the secondary reward meaning was appraised in the aMPFC, and this signal was then integrated in vMPFC to generate the positive aesthetic affection. However, we should be cautious that the activation pattern of the beauty of visual art probably different from the activation pattern of the beauty of faces, which might suggest different functions.

4.4. Role of the sensory cortex and hemispheric differences in processing beauty.

It is noteworthy that in both our meta-analysis about the beauty of faces and beauty of visual art, we did not found greater activations in the sensory regions. For the facial beauty, we didn't found the fusiform face areas or other sensory cortical areas for beautiful faces than for non-beautiful faces; for the visual arts, we didn't observe activation of the sensory-motor network. These results seem to contradict with previous theories about facial beauty (Chatterjee et al., 2009; Iaria et al., 2008) and art appreciating (Boccia et al., 2016; Chatterjee and Vartanian, 2014; Leder and Nadal, 2014).

One possible explanation is that the current meta-analysis only included the contrast between beautiful vs. non-beautiful stimuli, therefore eliminating the effect of physical feature and showed purer neural activities for beauty. If this is the case, the current study provided

evidence that even eliminating the difference in physical features, the beauty of faces and visual arts showed different neural representations in the high-level processing.

However, that doesn't mean that physical features are not important in the process of beauty appreciating. Actually, the sensory network is necessary for processing the beauty of faces and visual art (Chatterjee and Vartanian, 2014). Also, the shared standard for beautiful faces (Hönekopp, 2006; Leder et al., 2016) suggests that physical features are crucial for beauty. Hence future studies are needed to further examine the contribution of sensory processing to the beauty appreciation.

Regarding the hemisphere differences, it seems that peak locations of both face and art beauty appear in the left hemisphere, contradict with a popular view that "the right brain is related to imagination, (art) creativity and emotions" among layperson (Corballis, 1999). However, this hemispheric asymmetry is not real. In fact, most of these clusters located near the midline of the brain. The present results, along with the previous meta-analysis on appreciating of visual art (Boccia et al., 2016), suggest that the visual beauty is processed by both hemispheres.

4.5. Methodological considerations.

Several limitations of the present study should be addressed. First, the current meta-analysis methods were based on the reported peak activations, a large part of the spatial information was discarded. However, this limitation can be alleviated by the fact that the results derived from imaged-based meta-analysis are in good agreement with coordinate-based meta-analysis approaches (Salimi-Khorshidi et al., 2009). Second, coordinate-based meta-analysis approaches of neuroimaging studies, ALE is a representative one, use the "averaged" likelihood in common

volumetric space (Wager et al., 2007), thus it might lead to false positives of convergent activation in adjacent regions across studies. Therefore, it should be cautious when forming a conclusion for common activations across different studies. Third, the meta-analysis was based on the available literature and may have been affected by potential publication bias disfavoring null results (Jennings and Horn, 2012), which also need further evidence from specified experiments.

Given these considerations, further experimental data are needed to test the common neural basis of beauty using more robust methods. For instance, using multivoxel analysis to find the same activation pattern cross-task.

In sum, our meta-analytic results showed distinct neural specificities for beautiful visual art and faces, while the evidence for the common neural basis of beauty is not strong. These results suggest more studies are needed to further test the common beauty theory.

References

Abitbol, R., Lebreton, M., Hollard, G., Richmond, B.J., Bouret, S., Pessiglione, M., 2015. Neural mechanisms underlying contextual dependency of subjective values: converging evidence from monkeys and humans. J Neurosci 35, 2308-2320.

Aharon, I., Etcoff, N., Ariely, D., Chabris, C.F., O'Connor, E., Breiter, H.C., 2001. Beautiful Faces Have Variable Reward Value: fMRI and Behavioral Evidence. Neuron 32, 537-551.

Allen, R.E., 1993. The Dialogues of Plato, Volume 2: The Symposium. Yale University Press, New Haven.

Bartra, O., McGuire, J.T., Kable, J.W., 2013. The valuation system: A coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. NeuroImage 76, 412-427.

Bergeron, V., Lopes, D.M., 2012. Aesthetic theory and aesthetic science, in: Shimamura, A.P., Palmer, S.E. (Eds.), Aesthetic science: Connecting minds, brains, and experience. Oxford University Press, New York, US, pp. 61-79.

Berridge, K.C., Kringelbach, M.L., 2013. Neuroscience of affect: brain mechanisms of pleasure and displeasure. Curr Opin Neurobiol 23, 294-303.

Boccia, M., Barbetti, S., Piccardi, L., Guariglia, C., Ferlazzo, F., Giannini, A.M., Zaidel, D.W., 2016. Where does brain neural activation in aesthetic responses to visual art occur? Meta-analytic evidence from neuroimaging studies. Neurosci Biobehav Rev 60, 65-71.

Boccia, M., Nemmi, F., Tizzani, E., Guariglia, C., Ferlazzo, F., Galati, G., Giannini, A.M., 2015. Do you like Arcimboldo's? Esthetic appreciation modulates brain activity in solving perceptual ambiguity. Behavioural Brain Research 278, 147-154.

Bray, S., O'Doherty, J., 2007. Neural Coding of Reward-Prediction Error Signals During Classical Conditioning With Attractive Faces. Journal of Neurophysiology 97, 3036-3045.

Brown, S., Gao, X., Tisdelle, L., Eickhoff, S.B., Liotti, M., 2011. Naturalizing aesthetics: Brain areas for aesthetic appraisal across sensory modalities. NeuroImage 58, 250-258.

Button, K.S., Ioannidis, J.P.A., Mokrysz, C., Nosek, B.A., Flint, J., Robinson, E.S.J., Munafo, M.R., 2013. Power failure: why small sample size undermines the reliability of neuroscience. Nat Rev Neurosci 14, 365-376.

Bzdok, D., Langner, R., Caspers, S., Kurth, F., Habel, U., Zilles, K., Laird, A., Eickhoff, S.B., 2011. ALE meta-analysis on facial judgments of trustworthiness and attractiveness. Brain Struct Func 215, 209-223.

Bzdok, D., Langner, R., Hoffstaedter, F., Turetsky, B.I., Zilles, K., Eickhoff, S.B., 2012. The modular neuroarchitecture of social judgments on faces. Cereb Cortex 22, 951-961.

Bzdok, D., Langner, R., Schilbach, L., Engemann, D.A., Laird, A.R., Fox, P.T., Eickhoff, S., 2013. Segregation of the human medial prefrontal cortex in social cognition. Front Hum Neurosci 7.

Carp, J., 2012. The secret lives of experiments: Methods reporting in the fMRI literature. NeuroImage 63, 289-300.

Cartmell, S.C.D., Chun, M.M., Vickery, T.J., 2014. Neural antecedents of social decision-making in a partner choice task. Soc Cogn Affect Neurosci 9, 1722-1729.

Chatterjee, A., Thomas, A., Smith, S.E., Aguirre, G.K., 2009. The neural response to facial attractiveness. Neuropsychology 23, 135-143.

Chatterjee, A., Vartanian, O., 2014. Neuroaesthetics. Trends Cogn Sci 18, 370-375.

Cloutier, J., Heatherton, T.F., Whalen, P.J., Kelley, W.M., 2008. Are Attractive People Rewarding? Sex Differences in the Neural Substrates of Facial Attractiveness. J Cogn Neurosci 20, 941-951.

Conway, B.R., Rehding, A., 2013. Neuroaesthetics and the Trouble with Beauty. PLoS Biol 11, e1001504.

Cooper, J.C., Dunne, S., Furey, T., O'Doherty, J.P., 2012. Dorsomedial Prefrontal Cortex Mediates Rapid Evaluations Predicting the Outcome of Romantic Interactions. J Neurosci 32, 15647-15656.

Corballis, M.C., 1999. Are we in our right minds, in: Sala, S.D. (Ed.), Mind myths. John Wiley & Sons, Chichester, UK, pp. 26-42.

de la Vega, A., Chang, L.J., Banich, M.T., Wager, T.D., Yarkoni, T., 2016. Large-Scale Meta-Analysis of Human Medial Frontal Cortex Reveals Tripartite Functional Organization. J Neurosci 36, 6553-6562.

Di Dio, C., Macaluso, E., Rizzolatti, G., 2007. The Golden Beauty: Brain Response to Classical and Renaissance Sculptures. PLoS One 2, e1201.

Diessner, R., Solom, R.D., Frost, N.K., Parsons, L., Davidson, J., 2008. Engagement With Beauty: Appreciating Natural, Artistic, and Moral Beauty. J Psychol 142, 303-332.

Eickhoff, S.B., Bzdok, D., Laird, A.R., Kurth, F., Fox, P.T., 2012. Activation likelihood estimation meta-analysis revisited. Neuroimage 59, 2349-2361.

Eickhoff, S.B., Bzdok, D., Laird, A.R., Roski, C., Caspers, S., Zilles, K., Fox, P.T., 2011. Co-activation patterns distinguish cortical modules, their connectivity and functional differentiation. NeuroImage 57, 938-949.

Eickhoff, S.B., Heim, S., Zilles, K., Amunts, K., 2006. Testing anatomically specified hypotheses in functional imaging using cytoarchitectonic maps. NeuroImage 32, 570-582.

Eickhoff, S.B., Laird, A.R., Grefkes, C., Wang, L.E., Zilles, K., Fox, P.T., 2009. Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: A random-effects approach based on empirical estimates of spatial uncertainty. Hum Brain Mapp 30, 2907-2926.

Eickhoff, S.B., Nichols, T.E., Laird, A.R., Hoffstaedter, F., Amunts, K., Fox, P.T., Bzdok, D., Eickhoff, C.R., 2016. Behavior, Sensitivity, and power of activation likelihood estimation characterized by massive empirical simulation. NeuroImage 137, 70-85.

Eickhoff, S.B., Paus, T., Caspers, S., Grosbras, M.-H., Evans, A.C., Zilles, K., Amunts, K., 2007. Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. NeuroImage 36, 511-521.

Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. NeuroImage 25, 1325-1335.

Eklund, A., Nichols, T.E., Knutsson, H., 2016. Cluster failure: Why fMRI inferences for spatial extent have inflated false-positive rates. Proc Natl Acad Sci USA 113, 7900-7905.

Etkin, A., Egner, T., Peraza, D.M., Kandel, E.R., Hirsch, J., 2006. Resolving Emotional Conflict: A Role for the Rostral Anterior Cingulate Cortex in Modulating Activity in the Amygdala. Neuron 51, 871-882.

Flexas, A., Rossello, J., de Miguel, P., Nadal, M., Munar, E., 2014. Cognitive control and unusual decisions about beauty: an fMRI study. Front Hum Neurosci 8, 520.

Fox, P.T., Lancaster, J.L., Laird, A.R., Eickhoff, S.B., 2014. Meta-analysis in human neuroimaging: computational modeling of large-scale databases. Annu Rev Neurosci 37, 409–434.

Germine, L., Russell, R., Bronstad, P.M., Blokland, Gabriëlla A.M., Smoller, Jordan W., Kwok, H., Anthony, Samuel E., Nakayama, K., Rhodes, G., Wilmer, Jeremy B., 2015. Individual Aesthetic Preferences for Faces Are Shaped Mostly by Environments, Not Genes. Curr Biol 25, 2684-2689.

Haaker, J., Gaburro, S., Sah, A., Gartmann, N., Lonsdorf, T.B., Meier, K., Singewald, N., Pape, H.-C., Morellini, F., Kalisch, R., 2013. Single dose of l-dopa makes extinction memories context-independent and prevents the return of fear. Proc Natl Acad Sci USA 110, E2428-E2436.

Haber, S.N., Knutson, B., 2010. The Reward Circuit: Linking Primate Anatomy and Human Imaging. Neuropsychopharmacology 35, 4-26.

Hahn, A.C., Perrett, D.I., 2014. Neural and behavioral responses to attractiveness in adult and infant faces. Neurosci Biobehav Rev 46, Part 4, 591-603.

Harvey, A.H., Kirk, U., Denfield, G.H., Montague, P.R., 2010. Monetary Favors and Their Influence on Neural Responses and Revealed Preference. J Neurosci 30, 9597-9602.

Hekkert, P., Wieringen, P.C.W.V., 1996. Beauty in the Eye of Expert and Nonexpert Beholders: A Study in the Appraisal of Art. Am J Psychol 109, 389-407.

Hönekopp, J., 2006. Once more: Is beauty in the eye of the beholder? Relative contributions of private and shared taste to judgments of facial attractiveness. J Exp Psychol Hum Percept Perform 32, 199-209.

Hu, C., Di, X., Eickhoff, S.B., Zhang, M., Peng, K., Guo, H., Sui, J., 2016. Distinct and common aspects of physical and psychological self-representation in the brain: A meta-analysis of self-bias in facial and self-referential judgements. Neurosci Biobehav Rev 61, 197–207.

Iaria, G., Fox, C.J., Waite, C.T., Aharon, I., Barton, J.J.S., 2008. The contribution of the fusiform gyrus and superior temporal sulcus in processing facial attractiveness: Neuropsychological and neuroimaging evidence. Neuroscience 155, 409-422.

Ishizu, T., Zeki, S., 2011. Toward A Brain-Based Theory of Beauty. PLoS ONE 6, e21852.

Ishizu, T., Zeki, S., 2013. The brain's specialized systems for aesthetic and perceptual judgment. Eur J Neurosci 37, 1413-1420.

Ito, A., Abe, N., Kawachi, Y., Kawasaki, I., Ueno, A., Yoshida, K., Sakai, S., Matsue, Y., Fujii, T., 2015. Distinct neural correlates of the preference-related valuation of supraliminally and subliminally presented faces. Hum Brain Mapp 36, 2865-2877.

Jacobs, R.H.A.H., Renken, R., Cornelissen, F.W., 2012. Neural Correlates of Visual Aesthetics – Beauty as the Coalescence of Stimulus and Internal State. PLoS One 7, e31248.

Jennings, R., Horn, J., 2012. Publication bias in neuroimaging research: Implications for meta-analyses. Neuroinformatics 10, 67-80.

Kalisch, R., Korenfeld, E., Stephan, K.E., Weiskopf, N., Seymour, B., Dolan, R.J., 2006. Context-Dependent Human Extinction Memory Is Mediated by a Ventromedial Prefrontal and Hippocampal Network. J Neurosci 26, 9503-9511.

Kawabata, H., Zeki, S., 2004. Neural Correlates of Beauty. Journal of Neurophysiology 91, 1699-1705.

Kim, H., Adolphs, R., O'Doherty, J.P., Shimojo, S., 2007. Temporal isolation of neural processes underlying face preference decisions. Proc Natl Acad Sci USA 104, 18253-18258.

Kirk, U., Skov, M., Christensen, M.S., Nygaard, N., 2009a. Brain correlates of aesthetic expertise: A parametric fMRI study. Brain Cogn 69, 306-315.

Kirk, U., Skov, M., Hulme, O., Christensen, M.S., Zeki, S., 2009b. Modulation of aesthetic value by semantic context: An fMRI study. NeuroImage 44, 1125-1132.

Kirsch, L.P., Urgesi, C., Cross, E.S., 2016. The Shaping and Reshaping of the Aesthetic Brain: Emerging Perspectives on the Neurobiology of Embodied Aesthetics. Neurosci Biobehav Rev 62, 56-68.

Kocsor, F., Feldmann, A., Bereczkei, T., Kállai, J., 2013. Assessing facial attractiveness: individual decisions and evolutionary constraints. Socioaffective Neuroscience & Psychology 3, 21432.

Kubovy, M., 2000. Visual aesthetics, in: Kazdin, A.E. (Ed.), Encyclopedia of psychology. Oxford University Press, New York, pp. 188-193.

Lacey, S., Hagtvedt, H., Patrick, V.M., Anderson, A., Stilla, R., Deshpande, G., Hu, X., Sato, J.R., Reddy, S., Sathian, K., 2011. Art for reward's sake: Visual art recruits the ventral striatum. NeuroImage 55, 420-433.

Laird, A.R., Eickhoff, S., Fox, P.M., Uecker, A., Ray, K., Saenz, J., McKay, D.R., Bzdok, D., Laird, R., Robinson, J., Turner, J., Turkeltaub, P.E., Lancaster, J.L., Fox, P.T., 2011. The BrainMap strategy for standardization, sharing, and meta-analysis of neuroimaging data. BMC Res Notes 4, 349.

Laird, A.R., Eickhoff, S.B., Kurth, F., Fox, P.M., Uecker, A.M., Turner, J.A., Robinson, J.L., Lancaster, J.L., Fox, P.T., 2009a. ALE meta-analysis workflows via the BrainMap database: progress towards a probabilistic functional brain atlas. Front Neuroinform 3, 23.

Laird, A.R., Lancaster, J.L., Fox, P.T., 2009b. Lost in localization? The focus is meta-analysis. NeuroImage 48, 18-20.

Lancaster, J.L., Tordesillas-Gutiérrez, D., Martinez, M., Salinas, F., Evans, A., Zilles, K., Mazziotta, J.C., Fox, P.T., 2007. Bias between MNI and Talairach coordinates analyzed using the ICBM-152 brain template. Hum Brain Mapp 28, 1194-1205.

Langner, R., Rottschy, C., Laird, A.R., Fox, P.T., Eickhoff, S.B., 2014. Meta-analytic connectivity modeling revisited: Controlling for activation base rates. NeuroImage 99, 559-570.

Lebreton, M., Jorge, S., Michel, V., Thirion, B., Pessiglione, M., 2009. An Automatic Valuation System in the Human Brain: Evidence from Functional Neuroimaging. Neuron 64, 431-439.

Leder, H., Belke, B., Oeberst, A., Augustin, D., 2004. A model of aesthetic appreciation and aesthetic judgments. Brit J Psychol 95, 489-508.

Leder, H., Goller, J., Rigotti, T., Forster, M., 2016. Private and Shared Taste in Art and Face Appreciation. Front Hum Neurosci 10.

Leder, H., Nadal, M., 2014. Ten years of a model of aesthetic appreciation and aesthetic judgments : The aesthetic episode – Developments and challenges in empirical aesthetics. Brit J Psychol 105, 443-464.

Liang, X., Zebrowitz, L.A., Zhang, Y., 2010. Neural activation in the “reward circuit” shows a nonlinear response to facial attractiveness. Soc Neurosci 5, 320-334.

Liberati, A., Altman, D.G., Tetzlaff, J., Mulrow, C., Gøtzsche, P.C., Ioannidis, J.P.A., Clarke, M., Devereaux, P.J., Kleijnen, J., Moher, D., 2009. The PRISMA Statement for Reporting Systematic Reviews and Meta-Analyses of Studies That Evaluate Health Care Interventions: Explanation and Elaboration. PLoS Med 6, e1000100.

Little, A.C., Jones, B.C., DeBruine, L.M., 2011. Facial attractiveness: evolutionary based research. Philos T Roy Soc B 366, 1638-1659.

Liu, X., Hairston, J., Schrier, M., Fan, J., 2011. Common and distinct networks underlying reward valence and processing stages: A meta-analysis of functional neuroimaging studies. Neuroscience & Biobehavioral Reviews 35, 1219-1236.

McGlone, F., Österbauer, R.A., Demattè, M., Spence, C., 2013. The crossmodal influence of odor hedonics on facial attractiveness: Behavioural and fMRI measures, in: Signorelli, F., Chirchiglia, D. (Eds.), Functional Brain Mapping and the Endeavor to Understand the Working Brain. InTech.

Mende-Siedlecki, P., Said, C.P., Todorov, A., 2013. The social evaluation of faces: a meta-analysis of functional neuroimaging studies. Soc Cogn Affect Neurosci 8, 285-299.

Mizokami, Y., Terao, T., Hatano, K., Hoaki, N., Kohno, K., Araki, Y., Kodama, K., Makino, M., Izumi, T., Shimomura, T., Fujiki, M., Kochiyama, T., 2014. Difference in brain activations during appreciating paintings and photographic analogs. Front Hum Neurosci 8, 478.

Nichols, T.E., Brett, M., Andersson, J., Wager, T., Poline, J.-B., 2005. Valid conjunction inference with the minimum statistic. NeuroImage 25, 653-660.

Nickl-Jockschat, T., Janouschek, H., Eickhoff, S.B., Rottschy, C., 2015. Lack of meta-analytic evidence for an impact of COMT Val158Met genotype on brain activation during working memory tasks. Biol Psychiatry 78, e43-46.

O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D.M., Dolan, R.J., 2003. Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. Neuropsychologia 41, 147-155.

Parkinson, C., Liu, S., Wheatley, T., 2014. A Common Cortical Metric for Spatial, Temporal, and Social Distance. J Neurosci 34, 1979-1987.

Pearce, M.T., Zaidel, D.W., Vartanian, O., Skov, M., Leder, H., Chatterjee, A., Nadal, M., 2016. Neuroaesthetics: The Cognitive Neuroscience of Aesthetic Experience. Perspectives on Psychological Science 11, 265-279.

Pegors, T.K., Kable, J.W., Chatterjee, A., Epstein, R.A., 2015. Common and Unique Representations in pFC for Face and Place Attractiveness. J Cogn Neurosci 27, 959-973.

Poldrack, R.A., 2011. Inferring Mental States from Neuroimaging Data: From Reverse Inference to Large-Scale Decoding. Neuron 72, 692-697.

Radua, J., Mataix-Cols, D., Phillips, M.L., El-Hage, W., Kronhaus, D.M., Cardoner, N., Surguladze, S., 2012. A new meta-analytic method for neuroimaging studies that combines reported peak coordinates and statistical parametric maps. European Psychiatry 27, 605-611.

Ramachandran, V.S., Hirstein, W., 1999. The science of art: a neurological theory of aesthetic experience. Journal of Consciousness Studies 6, 15-51.

Reber, R., Schwarz, N., Winkielman, P., 2004. Processing Fluency and Aesthetic Pleasure: Is Beauty in the Perceiver's Processing Experience? Pers Soc Psychol Rev 8, 364-382.

Rottschy, C., Langner, R., Dogan, I., Reetz, K., Laird, A.R., Schulz, J.B., Fox, P.T., Eickhoff, S.B., 2012. Modelling neural correlates of working memory: A coordinate-based meta-analysis. NeuroImage 60, 830-846.

Roy, M., Shohamy, D., Wager, T.D., 2012. Ventromedial prefrontal-subcortical systems and the generation of affective meaning. Trends Cogn Sci 16, 147-156.

Salimi-Khorshidi, G., Smith, S.M., Keltner, J.R., Wager, T.D., Nichols, T.E., 2009. Meta-analysis of neuroimaging data: A comparison of image-based and coordinate-based pooling of studies. NeuroImage 45, 810-823.

Sescousse, G., Caldú, X., Segura, B., Dreher, J.-C., 2013. Processing of primary and secondary rewards: A quantitative meta-analysis and review of human functional neuroimaging studies. Neurosci Biobehav Rev 37, 681-696.

Shen, H., Chau, D.K., Su, J., Zeng, L.L., Jiang, W., He, J., Fan, J., Hu, D., 2016. Brain responses to facial attractiveness induced by facial proportions: evidence from an fMRI study. Scientific reports 6, 35905.

Shimamura, A.P., 2012. Toward a Science of Aesthetics in: Shimamura, A.P., Palmer, S.E. (Eds.), Aesthetic Science: Connecting Minds, Brains, and Experiences. Oxford University Press, Oxford, pp. 3-28.

Silveira, S., Fehse, K., Vedder, A., Elvers, K., Hennig-Fast, K., 2015. Is it the picture or is it the frame? An fMRI study on the neurobiology of framing effects. Front Hum Neurosci 9, 528.

Smith, D.V., Clithero, J.A., Boltuck, S.E., Huettel, S.A., 2014. Functional connectivity with ventromedial prefrontal cortex reflects subjective value for social rewards. Soc Cogn Affect Neurosci 9, 2017-2025.

Smith, D.V., Hayden, B.Y., Truong, T.K., Song, A.W., Platt, M.L., Huettel, S.A., 2010. Distinct value signals in anterior and posterior ventromedial prefrontal cortex. J Neurosci 30, 2490-2495.

Sui, J., Liu, M., Mevorach, C., Humphreys, G.W., 2015. The Salient Self: The Left Intraparietal Sulcus Responds to Social as Well as Perceptual-Salience After Self-Association. Cerebral cortex (New York, N.Y. : 1991) 25, 1060-1068.

Thakral, P.P., Moo, L.R., Slotnick, S.D., 2012. A neural mechanism for aesthetic experience. NeuroReport 23, 310-313.

Tsukiura, T., Cabeza, R., 2011. Remembering beauty: Roles of orbitofrontal and hippocampal regions in successful memory encoding of attractive faces. NeuroImage 54, 653-660.

Turkeltaub, P.E., Eden, G.F., Jones, K.M., Zeffiro, T.A., 2002. Meta-analysis of the functional neuroanatomy of single-word reading: method and validation. Neuroimage 16, 765-780.

Turkeltaub, P.E., Eickhoff, S.B., Laird, A.R., Fox, M., Wiener, M., Fox, P., 2012. Minimizing within-experiment and within-group effects in activation likelihood estimation meta-analyses. Hum Brain Mapp 33, 1-13.

Turner, J., Laird, A., 2012. The Cognitive Paradigm Ontology: Design and Application. Neuroinformatics 10, 57-66.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., Joliot, M., 2002. Automated Anatomical Labeling of Activations in SPM Using a Macroscopic Anatomical Parcellation of the MNI MRI Single-Subject Brain. NeuroImage 15, 273-289.

Vartanian, O., Goel, V., 2004. Neuroanatomical correlates of aesthetic preference for paintings. NeuroReport 15, 893-897.

Vartanian, O., Goel, V., Lam, E., Fisher, M., Granic, J., 2013. Middle temporal gyrus encodes individual differences in perceived facial attractiveness. Psychology of Aesthetics, Creativity, and the Arts 7, 38-47.

Vartanian, O., Skov, M., 2014. Neural correlates of viewing paintings: Evidence from a quantitative meta-analysis of functional magnetic resonance imaging data. Brain Cogn 87, 52-56.

Vessel, E.A., Starr, G.G., Rubin, N., 2012. The Brain on Art: Intense Aesthetic Experience Activates the Default Mode Network. Front Hum Neurosci 6.

Vincent, S., Khan, Y., Benes, F., 1993. Cellular distribution of dopamine D1 and D2 receptors in rat medial prefrontal cortex. J Neurosci 13, 2551-2564.

Wager, T.D., Lindquist, M., Kaplan, L., 2007. Meta-analysis of functional neuroimaging data: current and future directions. Soc Cogn Affect Neurosci 2, 150-158.

Wang, T., Mo, L., Mo, C., Tan, L.H., Cant, J.S., Zhong, L., Cupchik, G., 2015. Is Moral Beauty Different from Facial Beauty? Evidence from an fMRI Study. Soc Cogn Affect Neurosci 10, 814-823.

Ward, C., 2015. Beauty: 4 big questions. Nature 526, S17-S17.

Winston, J.S., O'Doherty, J., Kilner, J.M., Perrett, D.I., Dolan, R.J., 2007. Brain systems for assessing facial attractiveness. Neuropsychologia 45, 195-206.

Woo, C.-W., Schmidt, L., Krishnan, A., Jepma, M., Roy, M., Lindquist, M.A., Atlas, L.Y., Wager, T.D., 2017. Quantifying cerebral contributions to pain beyond nociception. Nature Communications 8, 14211.

Xia, M., Wang, J., He, Y., 2013. BrainNet Viewer: A Network Visualization Tool for Human Brain Connectomics. PLoS ONE 8, e68910.

Yan, C.-G., Wang, X.-D., Zuo, X.-N., Zang, Y.-F., 2016. DPABI: Data Processing & Analysis for (Resting-State) Brain Imaging. Neuroinformatics 14, 339-351.

Yarkoni, T., Poldrack, R.A., Nichols, T.E., Van Essen, D.C., Wager, T.D., 2011. Large-scale automated synthesis of human functional neuroimaging data. Nat Meth 8, 665-670.

Yu, H., Zhou, Z., Zhou, X., 2013. The amygdalostriatal and corticostriatal effective connectivity in anticipation and evaluation of facial attractiveness. Brain Cogn 82, 291-300.

Zhai, H., Zhang, W., Su, J., 2010. Functional MRI of the perception of facial attractiveness. Scientia Sinica Vitae 40, 551-560.

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Author Contributions

C-P. H., K.P. designed the study. C-P.H. and S.E. performed the statistical analyses. C-P. H., Y.H., J.S analyzed the findings and wrote the manuscript. All authors reviewed the manuscript.

Additional Information

Competing financial interests: The authors declare no competing financial interests.

Tables

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

Articles	Model	Subjects (Male)	Mean age	Stimuli	Task	Reported analysis
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 and Zeki (2011)	fMRI	21(9 M)	27.5	paintings	beauty ratings	beautiful > (indifferent + ugly)
Jacobs et al. (2012)	fMRI	18(10 M)	20-39	visual textures	beauty judgment	beautiful > ugly
Kawabata and Zeki (2004)	fMRI	10(5 M)	20~31	paintings	beauty ratings	beautiful > neutral
Kirk et al. (2009b)	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
Silveira et al. (2015)	fMRI	17 (8M)	37.0	paintings	aesthetic judgment	positive > negative aesthetic judgment
Thakral et al. (2012)	fMRI	16 (NA)	NA	paintings	pleasant judgment	correlated with aesthetic ratings
Vartanian and Goel (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 and O'Doherty (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	attractiveness judgment	increase with attractiveness
Cooper et al. (2012)	fMRI	39(20 M)	21.44	faces	attractiveness rating	positively related to attractiveness
Iaria et al. (2008)	fMRI	11(5 M)	24.09	faces	attractiveness rating	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. (2015)	fMRI	28(14 M)	22.5	faces	attractiveness rating	correlated with face attractiveness
Shen et al. (2016)	fMRI	36 (19M)	23.57	faces	attractiveness rating	linear correlated with attractiveness
Smith et al. (2010)	fMRI	23(23 M)	21.8	faces	passive viewing	attractive faces > unattractive faces
Smith et al. (2014)	fMRI	16(16 M)	23	faces	attractiveness rating	linear increase with attractiveness ratings
Tsukiura and Cabeza (2011)	fMRI	20(0 M)	23.4	faces	attractiveness rating	linear increase with facial attractiveness

Vartanian et al. (2013)	fMRI	29(14 M)	25.1	faces	attractiveness rating	correlated with attractiveness
Wang et al. (2015)	fMRI	22(10 M)	21	faces	gender judgment	beautiful face > common face
Winston et al. (2007)	fMRI	15(15 M)	25.5	face	attractiveness judgment	effect of attractiveness
Yu et al. (2013)	fMRI	18(9 M)	21	faces	attractiveness judgment	attractive faces > unattractive faces
Zhai et al. (2010)	fMRI	18(10 M)	20.8	faces	attractiveness 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	101	-7	60	-2	4.06	-4	60	-2	L aMPFC
2	96	-5	42	-13	3.89	-6	40	-10	L vMPFC/pgACC
					3.73	-4	44	-16	L gyrus rectus
beautiful > non-beautiful faces									
1	309	1	44	-6	6.57	0	48	-8	vMPFC
					4.11	-2	36	-2	ACC
2	91	-9	11	-11	4.13	-10	14	-6	L ventral striatum
					4.07	-8	10	-16	subcallosal cortex

All peaks were assigned to the most probable brain area using the SPM Anatomy Toolbox, Harvard-Oxford Atlas, and AAL. aMPFC = anterior ventromedial prefrontal cortex; vMPFC = ventral ventromedial prefrontal cortex; pgACC = pregenual anterior cingulate gyrus.

Table 3. Contrast and conjunction analyses of the meta-analysis 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	
the beauty of visual art > beauty of faces									
1	9	-7	44	-14	1.96	-8	44	-14	L vMPFC /pgACC
2	8	-10	58	-2	1.91	-8	56	-4	L aMPFC
the beauty of faces > beauty of visual art									
1	74	3	46	-6	2.57	6	46	-4	R pgACC/vMPFC
2	47	-8	9	-15	2.30	-6	6	-16	L ventral striatum
beautiful stimuli ∩ non-beautiful stimuli (conjunction analysis at p < 0.01 uncorrected)									
1	93	-1	39	-7	3.23	-2	42	-12	L pgACC/vMPFC

All peaks were assigned to the most probable brain area using the SPM Anatomy Toolbox, Harvard-Oxford Atlas, and AAL. aMPFC = anterior ventromedial prefrontal cortex; vMPFC = ventral ventromedial prefrontal cortex; pgACC = pregenual anterior cingulate gyrus.