Shared neural basis for experiencing the beauty of human faces and visual art: Evidence from a meta-analysis 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 of the experience of beauty, and it is controversial as to whether different forms of beauty share common neural structures. Here, we addressed this question by performing an activation likelihood estimation (ALE) meta-analysis, as well as a meta-analytic co-activation modeling (MACM) analysis, which delineated the co-activation patterns of brain regions of interest in the BrainMap database, on published neuroimaging literature of beautiful faces and beautiful visual art. We observed that the left ventromedial prefrontal cortex(vMPFC)/pregenual anterior cingulate gyrus (pgACC) was convergently activated by both beautiful visual art and beautiful faces, suggesting a common neural basis for general beauty. In addition, the beauty of faces was also associated with activity in the left ventral striatum, while the beauty of visual art was also associated with left anterior medial prefrontal cortex (aMPFC). These results indicate a shared neural basis exists for processing different forms of beauty, meanwhile, different neural mechanisms were co-existed to support the domain specific experiences of beauty.

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

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 [1], and David Hume asserted a common basis for evaluating beautiful objects [2]. This presupposition has led to many discussions regarding beauty. Other scholars (e.g., Kubovy, 2000 [3]) 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 basis of aesthetic responses to beauty via experimental approaches [(e.g. 4,5)]. In this study, we examined whether there is a common neural mechanism for beauty by employing an activation likelihood estimation (ALE)-based meta-analysis on data from previous functional magnetic resonance imaging (fMRI) studies.

What is the experience of beauty? One obstacle 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 [4]. This conceptual ambiguity hampers interdisciplinary communication [6]. Therefore, it is necessary to offer a clear operational definition of beauty first.

From the perspective of an information processing model [7,8], 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 operationalized definition of the experience of beauty avoids the confusion with other concepts related to aesthetics or pleasure. First, it distinguishes the current concept of beauty from other aesthetic experiences, because aesthetic experiences could include both positive and negative affective states [6]. Second, this operationalized definition also distinguishes beauty from general pleasure, which can be elicited by non-aesthetic stimuli, for example, food and sex [9], or moral behavior [10]. Further, the experience of beauty is different from complex emotions such as “awe”, “sublime” or “being moved”, while the experience of beauty may be accompanied by one or more of these complex emotions, these emotions are not defining features of the experience of beauty. That is, people may appreciate the beauty of an aesthetic object without having all of these complex emotions.

Most important of all, this operationalized definition of the experience of beauty gives us a specific criterion 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 use aesthetic preference as an index of beauty [11].

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 (e.g., beautiful faces vs. beautiful art; self-related vs. other-related stimuli). With this logic, cognitive neuroscientists have identified many different types of stimulus 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 [12], the left intraparietal sulcus is associated with processing both perceptually salient and socially salient stimuli [13], 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 [14].

In this sense, the common neural basis for different forms of beauty can be identified by shared brain structures activated across different forms of beauty. In fact, previous studies have suggested certain common mechanisms for the experience of beauty. Behaviorally, Reber proposed that beauty resulted from the cognitive processing fluency of the perceivers in general[15]. At the neural level, Ishizu and Zeki [16] proposed that the common beauty across modals 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, et al. [17] drew the conclusion that the insula was the common neural basis for aesthetic appraisal based on a meta-analysis of studies related to aesthetics. More interestingly, an implicit theory of common beauty held by cognitive neuroscientists suggests that beauty is equal to reward. This view has been supported by studies that used beautiful stimuli as rewarding stimuli [18-23] along with other reward-related stimuli such as money. 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 [5]). 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 common mechanisms for the experience of beauty, we cannot draw a consistent conclusion that there is a common neural basis for beauty due to three issues in the field. The first issue 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 [24,25] or the subjective response to art [26], but these two psychological processes are different from the response to beauty [2,6,27]. This heterogeneity not only makes it difficult to draw a consistent conclusion on the neural basis for the experience of beauty but also renders meta-analyses that include all these studies less relevant to the common neural basis of 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 [28] and the high false-positive rates [29,30] of single neuroimaging studies that occur due to limited sample sizes [28] or the flexibility of fMRI data processing [31]. Third, it is difficult to interpret the function of brain regions based on single fMRI studies, and reverse inference, which is prevalent among researchers, is used without methodological rigidity [32].

Current study. To explore the common neural basis of aesthetic responses to beauty, and 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-analysis 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 [(e.g. 5)], thus providing enough studies for a meta-analysis. Second, they represent two different typical categories of beauty: faces are the most representative of natural beauty in social life, the preference to which was shaped by both evolution [e.g. 33] and environment [34], 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-analysis of 38 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-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 [35,36]. Furthermore, it provides more decisive results and greater statistical power than individual studies [37]. To address the issues of reverse inference, a meta-analytic co-activation model (MACM) analysis, which could delineate the co-activated neural network for specific brain region [38] and a function characterization, which allowed us to make evidence-based inverse-inferences regarding the psychological processes [39], were conducted based on the BrainMap database.

Using these analysis methods, the current study aimed to (1) identify convergent neural activation across studies for the two forms of beauty, (2) assess the possible distinct brain regions and corresponding co-activation network 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.

Results

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) (The meta-data for current analysis is available at: https://osf.io/jf7g8/?view_only=1860fef0058b4cd29f8379de13c1d985). Figure 1 depicts the process of article selection in detail. For selected articles, see Table 1 (for more details, see Supplementary Material S6).

< Figure 1 and Table 1 here>

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

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

The conjunction results showed that a cluster located in the ventromedial frontal cortex (vMPFC) (include part of pgACC) was shared by beautiful faces and beautiful art (Table 3 and Figure 2D). The contrast analysis showed that a locus with 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).

< Insert Table 2, Table 3 and Figure 2 >

MACM analyses of the beauty of visual art. The first seed from the meta-analysis of the beauty of visual art, aMPFC, exhibited convergent co-activation with a large cluster include the precuneus, posterior cingulate cortex (PCC), midcingulate cortex (MCC). Other brain regions co-activated include the left superior frontal gyrus, the left lateral occipital cortex/angular cortex, the left temporal pole/inferior frontal cortex, the right hippocampus, the left parahippocampal gyrus, the right postcentral lobule, and the right middle temporal gyrus. Also, the neighboring regions of the seed, such as bilateral superior medial prefrontal gyrus, frontal pole and ACC, were also co-activated (see Figure 3A and Supplementary Table S1 online).

The second seed, left vMPFC/pgACC, of the beauty of visual art was also co-activated a large cluster centered at the PCC (include bilateral precuneus), Other co-activated brain regions include the middle cingulate cortex (MCC), bilateral inferior temporal gyrus/temporal pole, bilateral middle temporal gyrus, the left lateral occipital cortex/angular gyrus, left ventral striatum, bilateral superior frontal gyrus, bilateral cerebellum (crus 2). The neighboring regions of the seed such as bilateral superior medial prefrontal gyrus, the left ACC, the right olfactory cortex and the left aMPFC were also activated (see Figure 3B and Supplementary Table S2 online).

MACM analyses of the beauty of faces. The first seed, the vMPFC/pgACC, from the meta-analysis of the beauty of faces showed convergent co-activation with a large cluster that centered at the PCC, include precuneus, MCC, and the lingual gyrus. Other co-activated brain regions included the left superior medial prefrontal gyrus, the left amygdala/hippocampus/insula, bilateral middle temporal gyrus, bilateral lateral superior occipital cortex, the right lateral superior occipital cortex, the left middle cingulate cortex, the right superior temporal gyrus. This seed also was co-activated with nearby brain structures, including the bilateral ventral striatum, bilateral hippocampus, the right amygdala, and bilateral superior medial prefrontal gyrus. (see Figure 3C and Supplementary Table S3 online).

The second seed, the left ventral striatum, from the meta-analysis of the beauty of faces showed convergent co-activation of the left vMPFC/pgACC, the thalamus, the left MCC, the right postcentral gyrus and the cerebellar vermis. The neighboring structures such as the right ventral striatum, right amygdala, left insula, and right hippocampus were also co-activated (see Figure 3D and Supplementary Table S4 online).

MACM analyses of conjunction results of both art and faces

The co-activation network of the seed, the vMPFC/pgACC, from the conjunction analysis of the beauty of visual art and faces included the precuneus/PCC, bilateral MCC, the right hippocampus/parahippocampal gyrus, the right superior lateral occipital cortex, bilateral superior/middle frontal gyrus, bilateral middle temporal gyrus, bilateral temporal pole/inferior temporal gyrus, the right superior medial prefrontal gyrus, the left fusiform gyrus, and bilateral cerebellum lobule (crus 2). Also, brain structures nearby the seed were co-activated, such as bilateral ventral striatum, left aMPFC, bilateral superior medial prefrontal gyrus, ACC, and left superior frontal gyrus (see Figure 3E and Supplementary Table S5 online).

< Figure 3 >

Functional characterization. Functional characterization according to the BrainMap meta-data was performed for all seeds derived from the meta-analysis of the beauty of art and faces and for the seed derived from the conjunction analysis of both types of beauty.

For the first seed from the ALE results of the beauty of visual art, the left aMPFC, was associated with behavioral domains (BDs) related to cognition and emotion, and the most common paradigm classes (PCs) involved were face monitor/discrimination and reward (see Figure 3A), the second seed, the vMPFC/pgACC, was associated with behavioral domain (BD) related to fear emotion, social cognition, gustation, emotion and cognition, and the most common paradigm classes were theory of mind and reward (see Figure 3B).

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

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

Discussion

The main goal of this study was to explore the commonality and specificity of the neural basis of the experiences of the beauty of visual art and faces. To this end, we performed a conjunction analysis on two individual ALE meta-analytic results and found convergent activation in the left vMPFC/pgACC was associated with both forms of beauty. Meanwhile, the individual ALE and contrast analyses showed that the left ventral striatum was more convergently activated for beautiful faces, while the aMPFC was more activated for beautiful art. These results suggest that there is a common neural basis for processing beauty in the vMPFC/pgACC along with specific neural networks for each form of beauty.

The common neural basis for visual beauty. The shared neural basis for the beauty of visual art and faces of the left vMPFC/pgACC is consistent with previous meta-analysis of art processing [40] and visual beauty[17], confirmed the notion that this part of the brain is activated by different forms of visual beauty. For example, Pegors, et al. [41] has shown that this brain region is activated when participants view both beautiful faces and beautiful places. Additionally, this brain region, with a label of the medial orbital frontal cortex (mOFC), was activated by beauty associated with both music and visual arts[16]. Together with these studies, our results suggest that this region of vMPFC/pgACC may serve as a common neural basis for processing beauty.

More specifically, the activation of the vMPFC/pgACC during experiences of beauty may reflect a pleasant affective meaning generated by the integration of abstract knowledge, personal preferences and physical information from stimuli. Firstly, with its connection between subcortical structures and other higher-level cortical structures, vMPFC/pgACC was suggested as a hub for integrating sensory information and abstract concept by linking concepts with brainstem systems to generate affective meaning [42]. Our MACM results supported this view by showing that vMPFC/pgACC was convergently co-activated with brain regions involved in both knowledge processes (inferior and middle temporal gyrus) and the sensory cortex (such as fusiform gyrus and the superior lateral occipital cortex). Our function characterization of vMPFC/pgACC was consistent with this view by showing that it involved the function of sensory (taste), social cognition (theory of mind) and reward (see Figure 3 E).

Secondly, vMPFC/pgACC is a crucial part of default mode network (DMN) [43] but also activated by a wide range of emotional and social cognitive tasks. For example, Lindquist and colleagues (2012) reported that this brain area is involved in emotional processing in general but not specifically associated with a specific basic emotion (e.g. fear, or sad). Etkin and colleagues [44] also argued that the vMPFC/ACC is involved in emotion conflict processing. Other researchers reported that the vMPFC is associated with positive effects of subjective values in decision making [45] and self-referential processing [14,46]. These results indicate that processing beauty of visual art and faces may reflect positive valence of these stimuli, and it may also relate to emotion experience during the processes by linking the external positive value of stimuli to the internal self. This latter view is consistent with a recent study showing that the activation of vMPFC during art appreciating signals the self-relevance processing and results in the individual variability in art preference [47].

Taking together, these findings supported the role of vMPFC/pgACC in integrating both abstract concept and sensory information and generating positive affective meaning about visual objects. This view is consistent with previous accounts regarding aesthetic processing in that the appreciation of beauty requires the brain network involved in process emotion [5,40]. Also, the activation of vMPFC/pgACC by beauty is in line with the implicit "common theory" of beauty among cognitive scientists, given that this part of MPFC/pgACC plays a role in processing different kinds of reward reported by previous meta-analyses [48-50]. Theoretically, the results echo David Hume's view that "there is a common basis for evaluating beautiful objects" [2].

Neural basis underlying the beauty of faces. The results showed that beautiful faces induced greater converging activation in the vMPFC/pgACC and the left ventral striatum than non-beautiful faces. While the vMPFC/pgACC was partially overlapped with the nearby brain region activated by the meta-analysis of the beauty of art, part of vMPFC and left ventral striatum showed greater activation for the beauty of faces than for the beauty of art.

These results provided support for the two-system model about perceiving beautiful faces. In this model, beautiful faces were processed by a core system to process basic features of faces and an extended system to appraise the beauty of faces [51]. Further, the extended system for beauty processing is divided into two parts: rewarding beauty and pure aesthetic beauty [51]. Our results supported this extended system for processing beauty in two ways.

First, our results provided evidence for the existence of an extended system for appraising the beauty of faces, which is consisted of interconnected brain regions: the vMPFC/pgACC and the ventral striatum. In fact, consistent with the previous anatomical study about the vMPFC network[52], our MACM analysis showed that vMPFC/pgACC and ventral striatum are co-activated with each other, forming a vMPFC-subcortical network. Accordingly, our functional characterization showed that these two brain regions were also significantly more involved with reward paradigms than with other experimental paradigms.

Second, our results provided evidence that the interconnected beauty appraisal system consists of two dissociable components: the left ventral striatum for processing the rewarding value of beautiful faces and the vMPFC/pgACC for processing the aesthetic value of beautiful faces. Our MACM results found that the vMPFC/pgACC co-activated with a wide range of brain structures and showed a variety of functions, while the left ventral striatum was specifically involved with reward. As mentioned before, vMPFC/pgACC, which was activated by both faces and art, also participated many other social cognitive and emotional functions, suggesting its role in processing the abstract aesthetic value of beautiful faces. On the other hand, the ventral striatum, was more likely to be associated with rewards, especially primary reward [48], suggesting its role in processing the rewarding beauty when perceiving beautiful faces.

It is noteworthy that our meta-analysis did not show greater activation of the fusiform face areas or other sensory cortical areas for beautiful faces than for non-beautiful faces, which is inconsistent with previous studies [53,54]. Also, other researchers reported that there is a strong degree of shared preference for faces [55,56], indicating that the beautiful faces and not-beautiful faces do have different physical features. Hence this discrepancy whether sensory processing contributes to beauty remains to be assessed in future studies.

In short, the meta-analysis results reported here confirmed previous work suggesting that facial beauty involves both reward beauty and aesthetic beauty [51,57-59], which are associated with the ventral striatum and vMPFC/pgACC, respectively.

Neural basis underlying the beauty of visual art. Regarding the beauty of visual art, the meta-analysis of fMRI studies showed a convergent activation in the left aMPFC and vMPFC/pgACC. These two brain structures are also co-activated in other functional tasks, as shown by the

MACM analysis. In line with a previous theoretic framework, (e.g., Chatterjee and Vartanian, 2014 [5]; Leder and Nadal, 2014 [7]), the current results may provide evidence of the involvement of brain regions responsible for emotion and knowledge-meaning processing when appreciating the beauty of visual art.

The involvement of vMPFC/pgACC, which was partially shared with the beauty of faces, confirmed the affective meaning generating in processing the beauty of visual art. As we mentioned above, this brain region may serve as a hub for processing the affective value of external stimuli by referencing to self, which was consistent with previous work that has demonstrated that the value of art is represented in the vMPFC [16,18,60-64].

The activation of aMPFC may reflect the role of abstract knowledge in processing art. Our MACM analysis showed that aMPFC were co-activated with a wide range of cortical and subcortical structures, including superior frontal gyrus, PCC, and hippocampus. Also, the previous meta-analysis of fMRI studies found that aMPFC participated in autobiographic memory [65] [66] and secondary reward (i.e., money) [48]. Together, these results suggest that aMPFC maybe play a role of processing abstract knowledge when perceiving the beauty of visual art.

It should be noted that our meta-analysis results failed to show any brain region in the sensory-motor network, which seems to contradict previous theories [5,7,40]. However, the results do not contradict these studies because the current study focused on the neural response to 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-analysis results reflected the aesthetic beauty of visual art, not art processing in general.

Hemispheric differences in processing beauty. Regarding the hemispheric differences, it seemed that the peak location of both face and visual art beauty appeared in the left hemisphere, consistent with a popular view that "art is processed by the left brain" among layperson. However, this hemispheric asymmetry is not real. In fact, most of these cluster located near the midline of the brain, and the MACM results demonstrated symmetric co-activations in the two hemispheres. The present results, along with the previous meta-analysis on appreciating of visual art [40], suggest that the visual beauty is processed by both hemispheres.

Methodological considerations. Several limitations of the results 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 [67]. Second, coordinate-based meta-analysis approaches of neuroimaging studies, ALE is a representative one, use the "averaged" likelihood in common volumetric space [29], thus may 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 s different studies. Third, the meta-analysis was based on the available literature and may have been affected by potential publication bias disfavoring null results [68], which also need further evidence from specified experiments.

Given these considerations, further experimental data are needed to test novel hypotheses. For example, to study the neural basis specific to beauty, we selected only studies that compared beautiful stimuli with baselines that have similar physical features as the experimental condition. However, as we mentioned above, the differences in physical features probably exist. Therefore, future experiments are needed to further explore this possibility. Another example is concerning the individual difference in beauty processing: if vMPFC/pgACC plays a vital role in processing beauty, it is possible that individual differences in the vmPFC/pgACC or its connectivity could contribute to individual differences in aesthetic preference or sensitivity, yet more data are needed to test this hypothesis.

Conclusion

Convergent findings across fMRI studies on the beauty of visual art and faces were analyzed using ALE meta-analysis and MACM analysis. We observed a convergent activation in left vMPFC/pgACC for both visual art and faces, suggesting that the beauty of visual art and the beauty of faces are supported by a common neural substrate. Additionally, we observed distinct neural specificities for beautiful visual art and faces. These results support the view that beauty has both stimuli-dependent and stimuli-independent neural underpinnings.

Methods

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 (for the details of the searching strategy, see Supplementary

Material S6). For a complete coverage, articles were also identified from recent meta-analyses and reviews [17,40,69-72]. 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 [73].

(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 [74].

(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 [62] due to the influence of expertise on aesthetic appreciation [75].

(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).

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 [76-79]. 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 [76]. 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 [80]. 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 [81]. 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) [81]. All significant clusters were reported, and the volume, weighted center and locations and Z-scores at the peaks within the regions are given.

Conjunctions and comparison of individual meta-analyses. Conjunction analyses identify voxels where a significant effect is present in all separate analyses. To explore the common neural basis for the beauty of both visual art and faces, we used liberal threshold when using the minimum statistic [82]. More specifically, we first used 'imcalc' function in SMP8 for the Z-maps produced by ALE results, then, thresholded the conjunction map at $p < 0.01$ (uncorrected) level, with cluster size more than 50 voxels. 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 [38,83]. 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 and thresholded with a probability of more than 95% for true differences.

Data visualization. Given that there is no standard brain atlas for neuroimaging studies, we used probabilistic cytoarchitectonic maps (as implemented in SPM Anatomy Toolbox) [84-86], Automated Anatomical Labeling (AAL) [87] and the Harvard-Oxford Atlas (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Atlases) (both are implemented in DPABI [88]) to assign our resulting coordinates to anatomical structures. When the labels are not consistent between atlases, we chose the label that most specifically describe the brain structures. For visualization purposes, BrainNet Viewer [89] was used to present the meta-analytical results.

Meta-analytic co-activation model. To analyze functional connectivity of regions engaged in the beauty of visual art and faces, we conducted a MACM analysis. 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 analysis first identifies all the experiments in a database that activated the seed region and then employs a quantitative meta-analysis 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 [90,91].

More specifically, we used the results of the ALE meta-analysis of the beauty of visual art and the beauty of faces as seeds to find experiments that reported those seeds in the BrainMap database [35,78] (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 analysis of beauty of visual art, the left aMPFC resulted in 86 experiments (with 1283 subjects, 1251 foci); for the second cluster, the left vMPFC/pgACC, resulted in 106 experiments (with 1701 subjects, 1338 foci). For the beauty of faces, the seed in the vMPFC/pgACC resulted in 253 experiments (with 4119 subjects, 3184 foci), while the left ventral striatum resulted in 122 experiments (with 2154 subjects, 1557 foci). For the vmPFC/pgACC from the conjunction analysis, 117 experiments (with 1923 subjects, 1480 foci) were found. After extracting 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 [92].

Functional characterization. To qualify the interpretation of the function of each brain region, we conducted functional characterization to obtain meaningful reverse inference [93]. 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 [35,94]. As a first step, we searched in the BrainMap database for those experiments that featured at least one focus of activation within the current seed (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 seed 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) [83,92,95].

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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

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Figure Legends

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. [96].

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.

Figure 3. Meta-analytic co-activation modeling (MACM) results and functional characterization for brain regions from meta-analytic results. (A) The MACM results and functional characterization for the left aMPFC from the meta-analysis of the beauty of visual art; (B) The MACM results and functional characterization for the left vMPFC/pgACC from the meta-analysis of the beauty of visual art; (C) the MACM results and functional characterization for the vMPFC/pgACC from the meta-analysis of the beauty of faces; (D) the MACM results and functional characterization for the left ventral striatum from the meta-analysis of the beauty of faces; (E) the MACM results and functional characterization for the left vMPFC/pgACC shared by beauty of art and faces. Note: the activation of bilateral cerebellum (crus 2) are not shown in figure 3B to consistently present images.

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 [60]	fMRI	24(13 M)	25	paintings	pleasantness rating	correlation with pleasantness
Boccia, et al., 2015 [97]	fMRI	20(11 M)	25.45	Paintings	esthetic judgment	like > dislike
Di Dio, et al., 2007 [98]	fMRI	14(8 M)	24.5	sculpture	observation	beautiful > not beautiful
Flexas, et al., 2014 [99]	fMRI	24(12 M)	23.5	paintings	beautiful or not	beautiful > not beautiful
Harvey, et al., 2010 [100]	fMRI	87(NA)	NA	paintings	preference ratings	correlation with preference
Ishizu, et al., 2011 [16]	fMRI	21(9 M)	27.5	paintings	beauty ratings	beautiful > (indifferent + ugly)
Jacobs, et al, 2012 [101]	fMRI	18(10 M)	20-39	visual textures	beauty judgment	beautiful > ugly
Kawabata et al., 2004 [61]	fMRI	10(5 M)	20~31	paintings	beauty ratings	beautiful > neutral
Kirk et al., 2009 [102]	fMRI	14(9 M)	26.3	paintings	aesthetic rating	correlation with aesthetics ratings
Lacey, et al., 2011 [22]	fMRI	8 (4 M)	23.1	paintings	animacy rating	correlated with beauty

Lebreton, et al., 2009 [73]	fMRI	20 (10 M)	22.0	paintings	pleasantness ratings	correlated with pleasantness
Silveira, et al., 2015 [103]	fMRI	17 (8M)	37.0	paintings	aesthetic judgment	positive > negative aesthetic judgment
Thakral, et al., 2012 [104]	fMRI	16 (NA)	NA	paintings	pleasant judgment	correlated with aesthetic ratings
Vartanian et al., 2004 [105]	fMRI	12(4 M)	28	paintings	preference rating	correlated with preference
Vessel, et al., 2012 [106]	fMRI	16(11 M)	27.6	visual arts	recommendation	most recommended > least recommended
Aharon et al., 2001 [18]	fMRI	10(10 M)	25.2	faces	observation	beauty > average
Bray et al., 2007 [19]	fMRI	25(12 M)	20.8	faces	location discrimination	attractive > unattractive faces
Cartmell et al., 2014 [107]	fMRI	16(7 M)	20	faces	Partner Selection	attractive > unattractive faces
Chatterjee et al., 2009 [53]	fMRI	13(6 M)	22.6	faces	beauty ratings	correlation with beauty ratings
					identity ratings	correlation with beauty ratings
Cloutier et al., 2008 [20]	fMRI	48(24 M)	21.7	faces	attractiveness judgment	increase with attractiveness
Cooper et al., 2012 [108]	fMRI	39(20 M)	21.44	faces	attractiveness rating	positively related to attractiveness
Iaria et a., 2008 [54]	fMRI	11(5 M)	24.09	faces	attractiveness rating	attractive > unattractive faces

Ito et al., 2015 [109]	fMRI	28(14 M)	21.6	faces	passive viewing	preferred > non-preferred
					choosing task	preferred > non-preferred
Kim et al., 2007 [110]	fMRI	25(13 M)	20-45	faces	ratings	correlation with attractiveness (exclude preference)
Kocsor et al., 2013 [111]	fMRI	16(8 M)	25	faces	face discrimination	attractive > unattractive faces
Liang et al., 2010 [21]	fMRI	17(8 M)	26.5	faces	passive viewing	linear correlated with attractiveness
McGlone et al., 2013 [112]	fMRI	16(0 M)	23	faces	attractiveness rating	attractive faces > unattractive faces
O'Doherty et al., 2003 [113]	fMRI	25(13 M)	23.8	faces	gender judgment	high > low attractiveness
Pegors et al., 2015 [41]	fMRI	28(14 M)	22.5	faces	attractiveness rating	correlated with face attractiveness
Shen et al., 2016 [114]	fMRI	36 (19M)	23.57	faces	attractiveness rating	linear correlated with attractiveness
Smith et al., 2010 [115]	fMRI	23(23 M)	21.8	faces	passive viewing	attractive faces > unattractive faces
Smith et al., 2014 [23]	fMRI	16(16 M)	23	faces	attractiveness rating	linear increase with attractiveness ratings
Tsukiura et al., 2011a [116]	fMRI	20(0 M)	23.4	faces	attractiveness rating	linear increase with facial attractiveness

Vartanian et al., 2013 [117]	fMRI	29(14 M)	25.1	faces	attractiveness rating	correlated with attractiveness
Wang et al., 2015b [118]	fMRI	22(10 M)	21	faces	gender judgment	beautiful face > common face
Winston et al., 2007 [119]	fMRI	15(15 M)	25.5	face	attractiveness judgment	effect of attractiveness
Yu et al., 2013 [120]	fMRI	18(9 M)	21	faces	attractiveness judgment	attractive faces > unattractive faces
Zhai et al., 2010 [121]	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

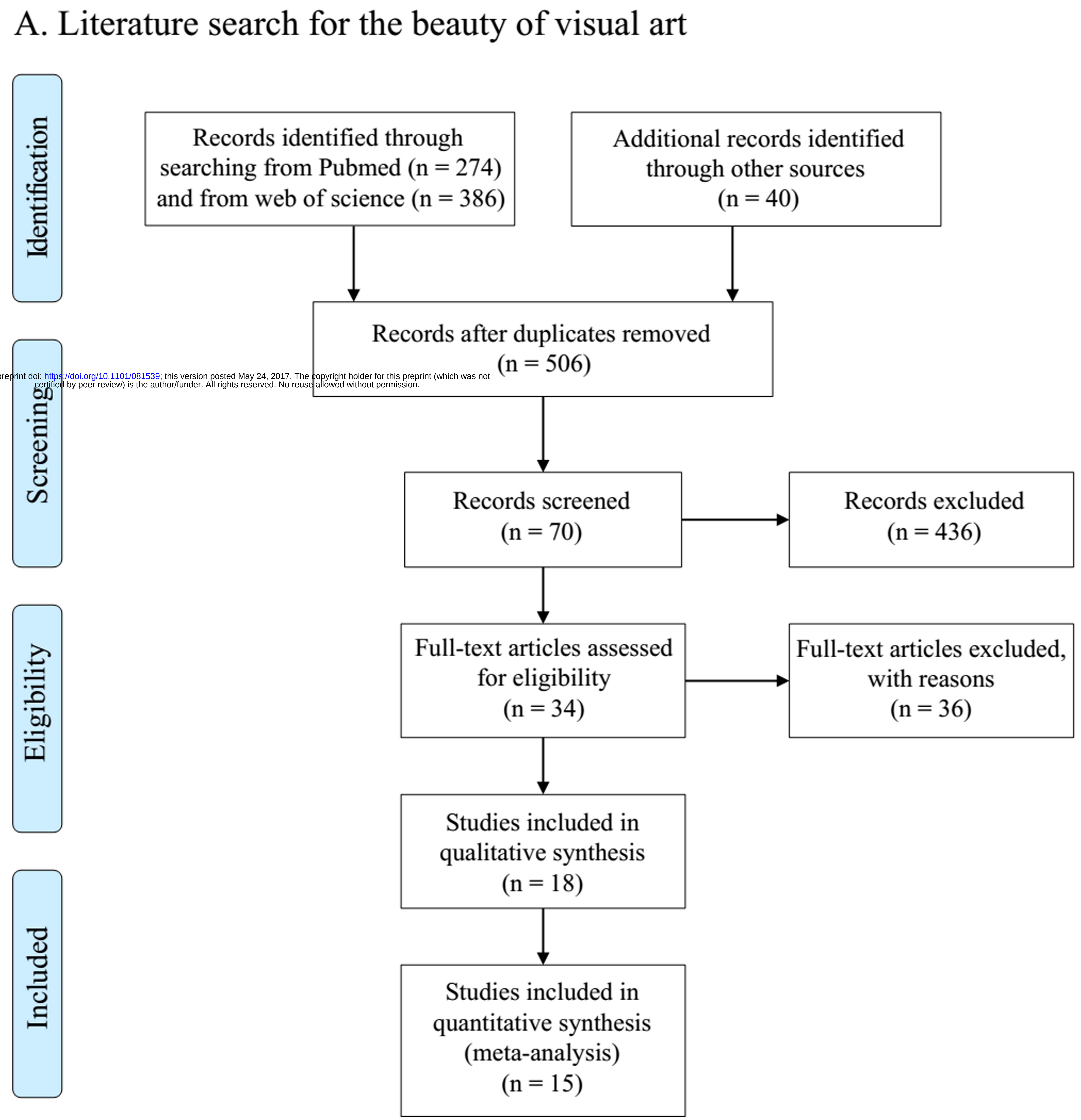
Cluster	Volume (voxels)	Weighted center x	Weighted center y	Weighted center z	Maximum Z-value	Center for maximum Z-value x	Center for maximum Z-value y	Center for maximum Z-value z	Macroanatomical location
beautiful > non-beautiful visual art									
1	101	-7	60	-2	4.06	-4	60	-2	L aMPFC
2	96	-5	42	-13	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	L 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; ACC = anterior cingulate gyrus.

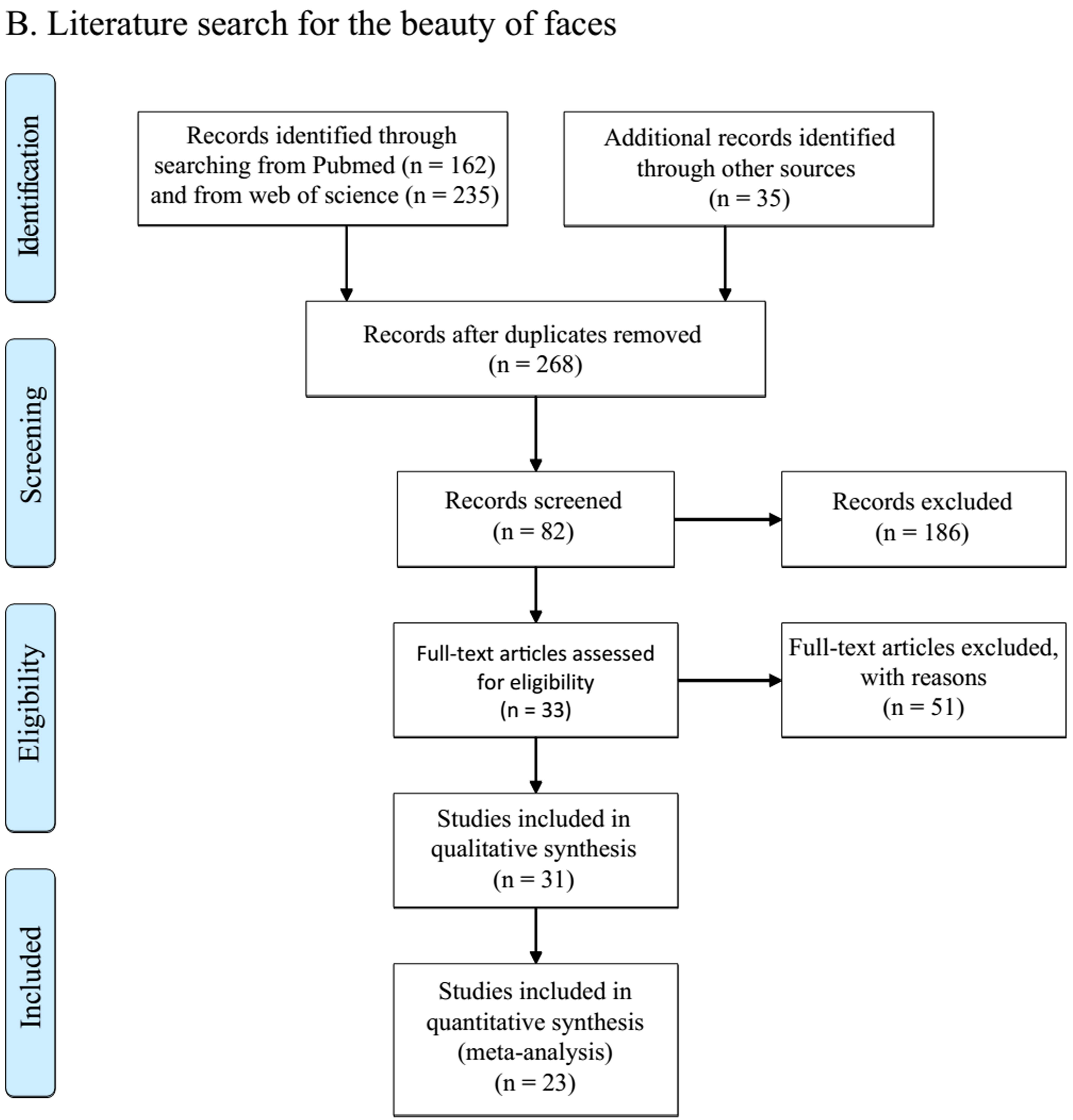
Table 3. Contrast and conjunction analyses of the meta-analysis results for the beauty of visual art and faces

Cluster	Volume (voxels)	Weighted center			Maximum Z-value	Center for maximum Z-value			Macroanatomical location
		x	y	z		x	y	z	
beauty of visual art > beauty of faces									
	9	-7	44	-14	1.96	-8	44	-14	L vMPFC /pgACC
	8	-10	58	-2	1.91	-8	56	-4	L aMPFC
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
					2.24	-6	12	-16	L subcallosal cortex
beauty of faces ∩ beauty of visual art*									
1	96	-1	39	-7	3.23	-2	42	-12	L pgACC/vMPFC
					3.11	4	36	-10	R pgACC/vMPFC
					3.00	-4	42	-8	L pgACC/vMPFC
					2.96	-4	38	-6	L pgACC/vMPFC

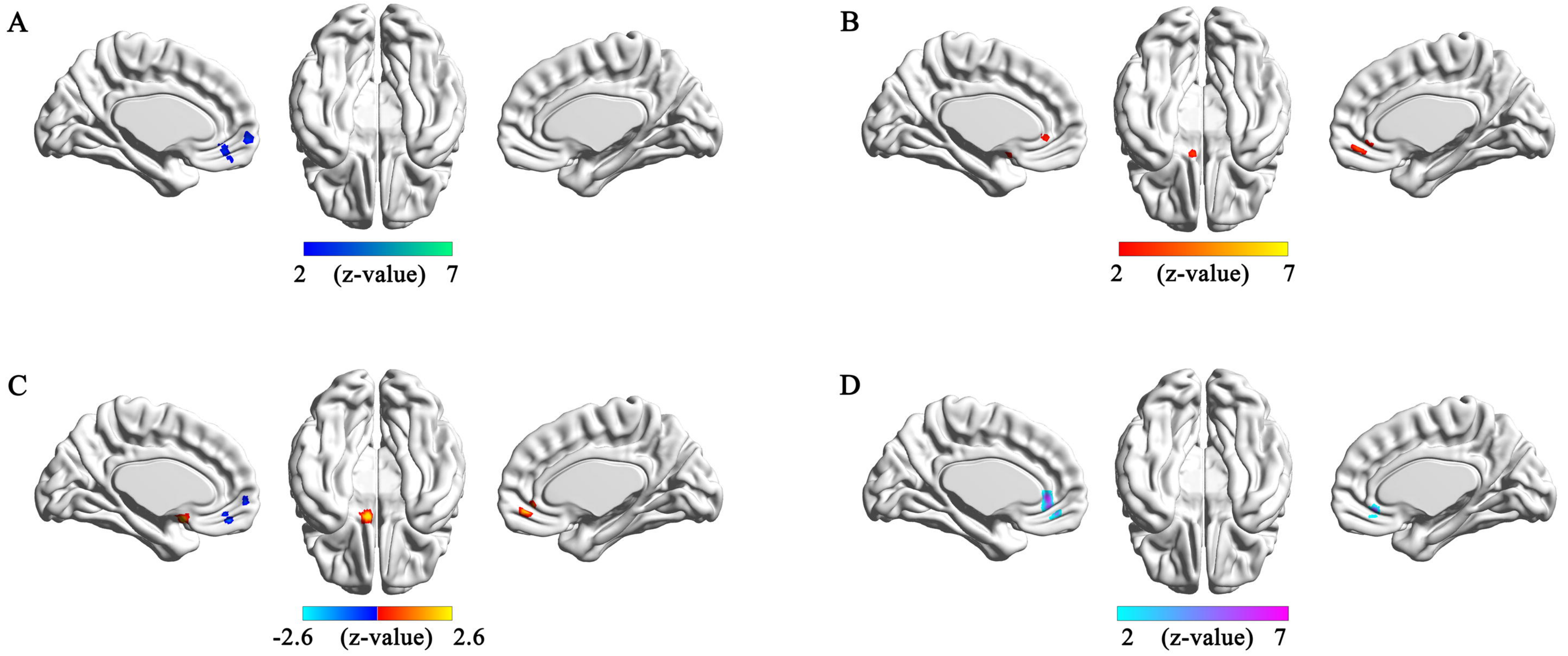
All peaks were assigned to the most probable brain area using the SPM Anatomy Toolbox, Harvard-Oxford Atlas, and AAL. * indicates that these voxels are significant at $p < 0.01$ (uncorrected). aMPFC = anterior ventromedial prefrontal cortex; vMPFC = ventral ventromedial prefrontal cortex; pgACC = pregenual anterior cingulate gyrus.



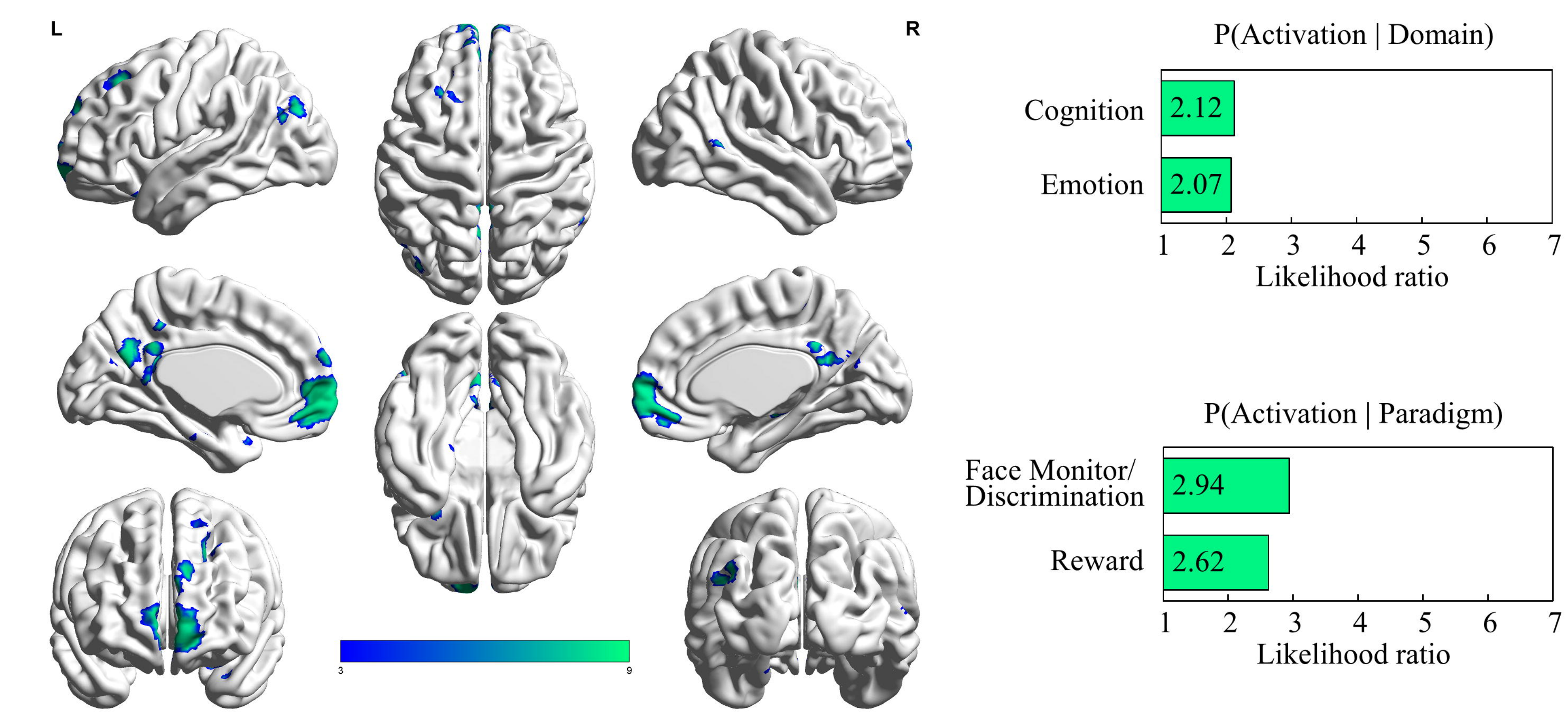
A. Literature search for the beauty of visual art
Identification
Screening
Eligibility
Included
Records identified through searching from Pubmed (n = 274) and from web of science (n = 386)
Additional records identified through other sources (n = 40)
Records after duplicates removed (n = 506)
Records screened (n = 70)
Records excluded (n = 436)
Full-text articles assessed for eligibility (n = 34)
Full-text articles excluded, with reasons (n = 36)
Studies included in qualitative synthesis (n = 18)
Studies included in quantitative synthesis (meta-analysis) (n = 15)



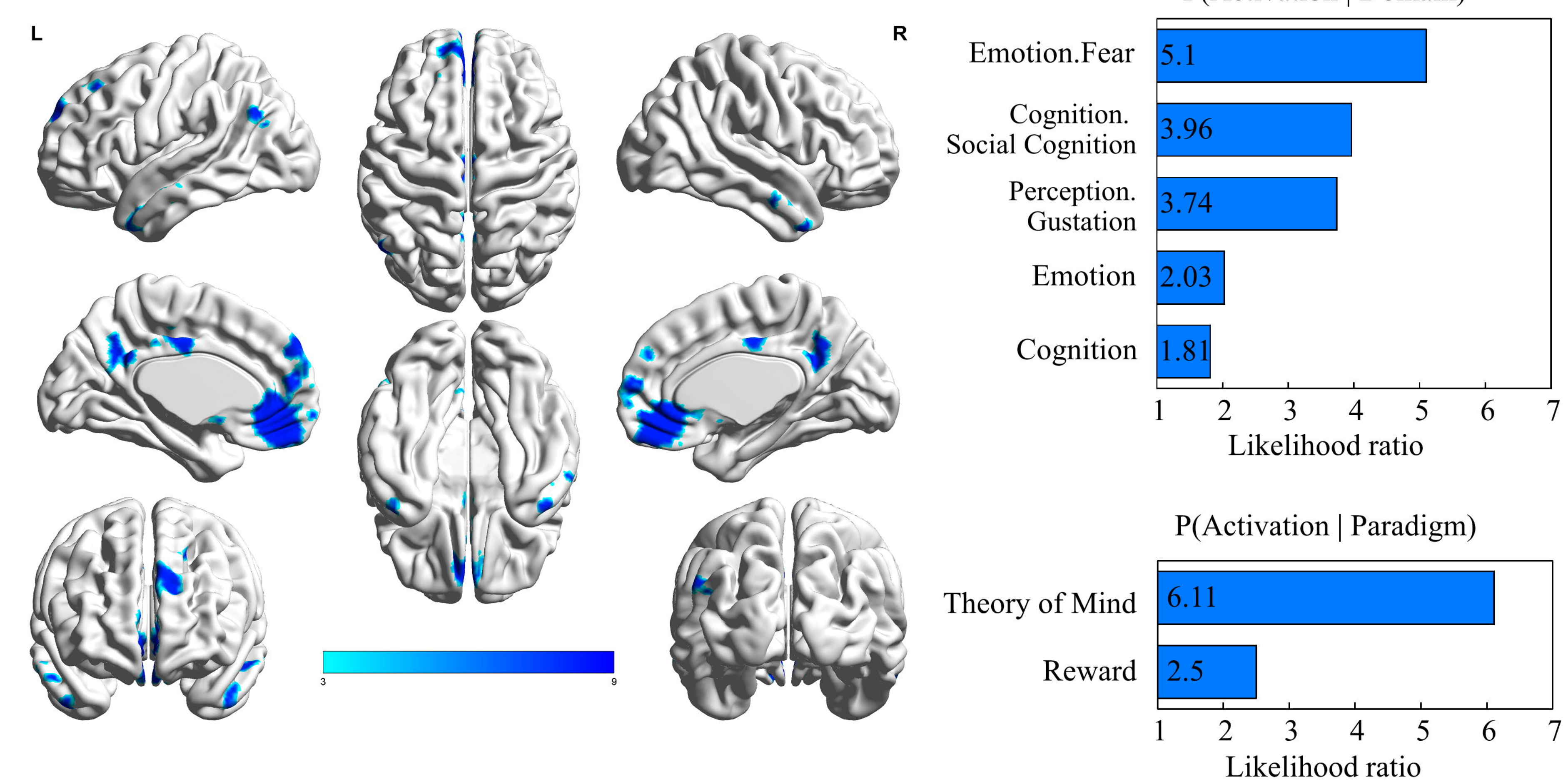
B. Literature search for the beauty of faces
Identification
Screening
Eligibility
Included
Records identified through searching from Pubmed (n = 162) and from web of science (n = 235)
Additional records identified through other sources (n = 35)
Records after duplicates removed (n = 268)
Records screened (n = 82)
Records excluded (n = 186)
Full-text articles assessed for eligibility (n = 33)
Full-text articles excluded, with reasons (n = 51)
Studies included in qualitative synthesis (n = 31)
Studies included in quantitative synthesis (meta-analysis) (n = 23)


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

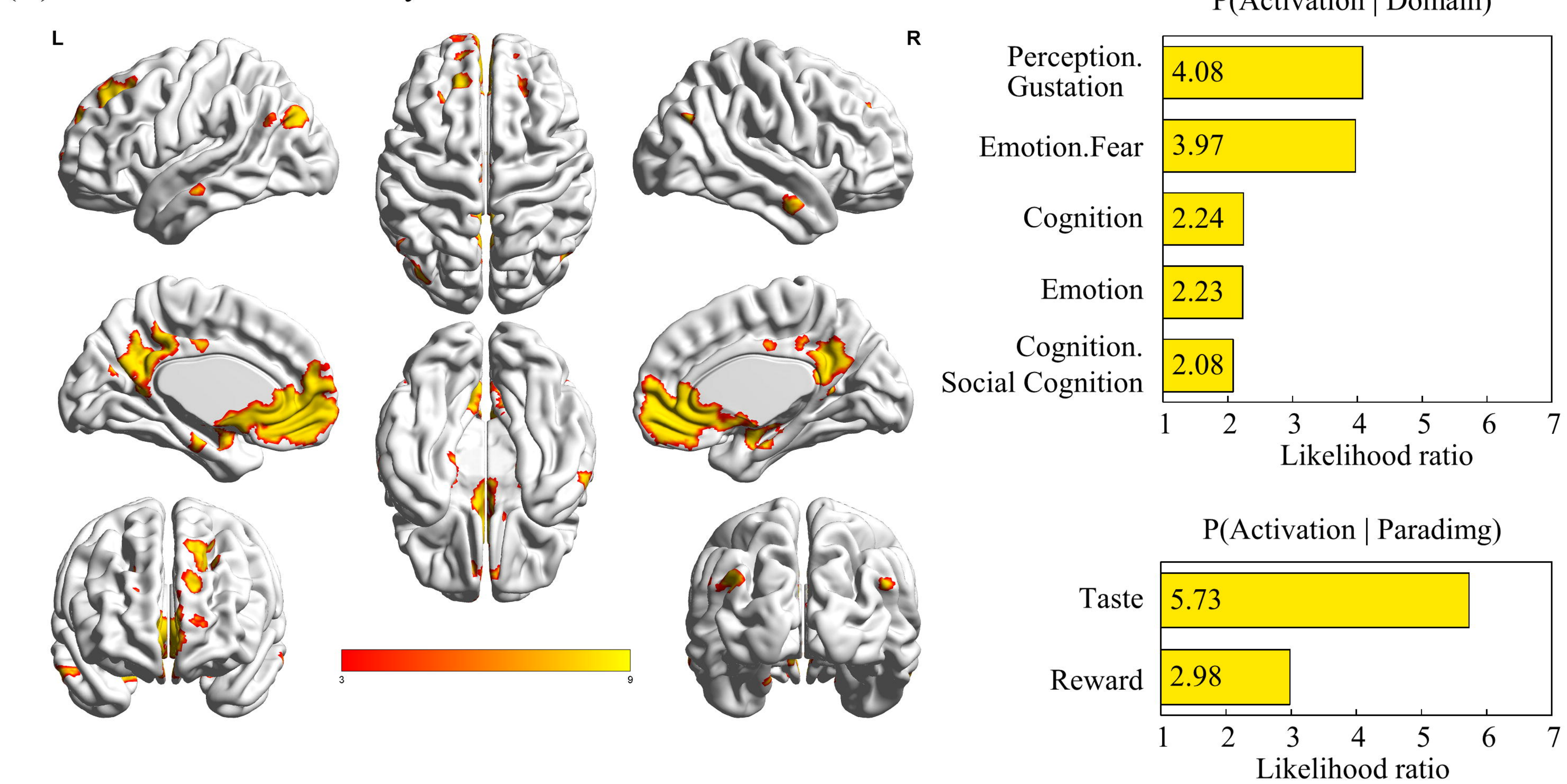
(A) 1st ROI from meta-analysis of fMRI studies of art:



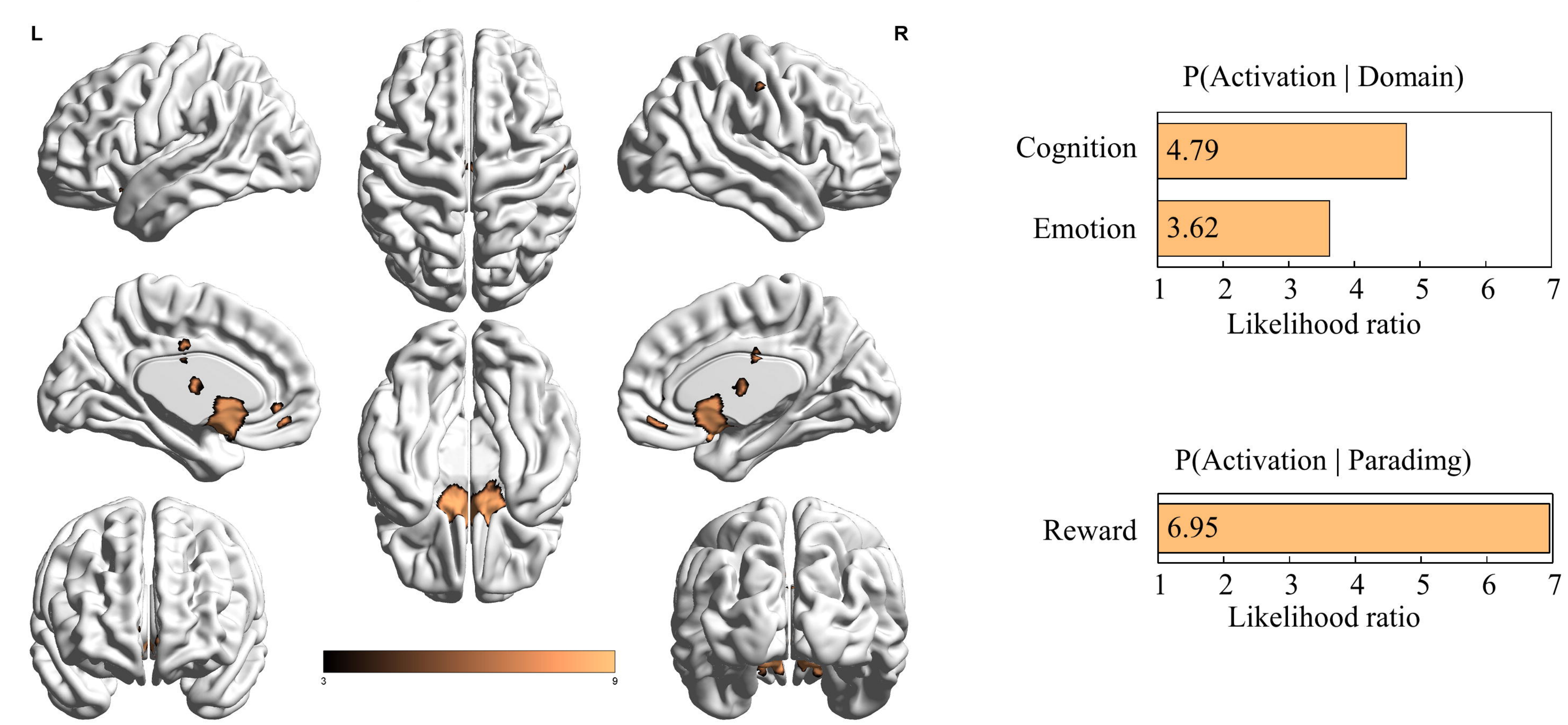
(B) 2nd ROI from meta-analysis of fMRI studies of art:



(C) 1st ROI from meta-analysis of fMRI studies of face:



(D) 2nd ROI from meta-analysis of fMRI studies of face:



(E) ROI from conjunction analysis