This is a post-print version of https://link.springer.com/article/10.3758/s13415-020-00827-z, please cite the published version.

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

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Abstract

During the last two decades, cognitive neuroscientists have sought to elucidate the common neural basis of the experience of beauty. Still, empirical evidence for such common neural basis of different forms of beauty is not conclusive. To address this question, we performed an activation likelihood estimation (ALE) meta-analysis on the existing neuroimaging studies of beauty appreciation of faces and visual art by non-expert adults (49 studies, 982 participants, meta-data are available at https://osf.io/s9xds/). We observed that perceiving these two forms of beauty activated distinct brain regions: While the beauty of faces convergently activated the left ventral striatum, the beauty of visual art convergently activated the anterior medial prefrontal cortex (aMPFC). However, a conjunction analysis failed to reveal any common brain regions for the beauty of visual art and faces. The implications of these results are discussed.

Keywords: beauty; faces; visual art; functional magnetic resonance imaging (fMRI); activation likelihood estimation (ALE)

1. Introduction

The nature of beauty is a long-standing question in many disciplines. A critical issue from psychologists and neuroscientists is whether there is a common neural basis representing different forms of beauty in the brain. Researchers have attempted to investigate this issue using experimental approaches to assessing aesthetic responses to beauty while brain activities were recorded (e.g. (Aharon et al., 2001; Chatterjee & Vartanian, 2014; Pearce et al., 2016)). Almost two decades have passed. There is still no consensus on whether there is a unique brain representation specific to beauty (Conway & Rehding, 2013; Ishizu & Zeki, 2011; Skov & Nadal, 2020). Inconsistent findings across studies might suggest that there are beautify form- specific modules in the brain. The discrepant results might also reflect variations of tasks and relevant parameters used in these studies, although there might be a common beauty-representation in the brain. One way to examine these two views is to conduct meta-analysis by synthesizing the empirical neuroimaging studies in the fields. This was conducted here using activation likelihood estimation (ALE) meta-analyses by focusing on the studies examining the experience of beauty[1].

From the computational view of cognition (Marr, 1982/2010), understanding how beauty is experienced in humans may need different levels' analyses: implementational level, algorithmic-representational level, and computational level. As pointed out by Pearce et al. (2016), brain imaging studies are mainly addressing the implementation level, less on algorithmic-representational or computational levels. Thus, one way to define the common neurobiological implementation of beauty is testing the existence of overlapping brain regions when experiencing the beauty from different sources (e.g., faces or visual art rated as beautiful). This overlap-based approach has been widely-used to searching the common neural basis of different cognitive processes. For instance, recent studies reported that the right inferior parietal lobule engaged in processing spatial, temporal, and social distance (Parkinson, Liu, & Wheatley, 2014), the left intraparietal sulcus was associated with processing both perceptually salient and socially salient stimuli (Sui, Liu, Mevorach, & Humphreys, 2015), and the dorsal anterior cingulate cortex and the left anterior insula were involved in processing both psychological and physical selves (C. 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

[1] Note that the present study focused on the experience of beauty instead of a broad aesthetic experience in general. For example, viewing an ugly but famous artwork is part of aesthetic experience but may have no experience of beauty evoked (Pearce et al., 2016).

beauty. The question remains:, are there such common brain regions that convergently are activated with different forms of beauty. There are contradictory arguments to this question.

Some researchers claimed that there exists a brain region that is specific to beauty, regardless of the sources of beauty and task type (Ishizu & Zeki, 2011, 2013; Zeki, Romaya, Benincasa, & Atiyah, 2014). For instance, Ishizu and Zeki (2011) reported that the medial orbito-frontal cortex (mOFC) activated when experiencing both musical and visual beauty. The follow-up work from the same group showed that viewing mathematical formulas also activated the mOFC (Zeki et al., 2014). Based on these results, Ishizu and Zeki (2011) conclude that there is a single neural characteristic within the mOFC that is correlated with the experience of beauty. Other researchers proposed that the experience of beauty activated a network of connected brain regions instead of a single brain region; the network includes synchronized activity over the occipital, parietal, and frontal regions (Cela-Conde et al., 2013; Chatterjee & Vartanian, 2014; Vessel, Starr, & Rubin, 2012). That is, aesthetic experiences are dynamic states arising from the interactions between sensory-motor, emotion-valuation, and meaning-knowledges neural systems[2].

Furthermore, some researchers argued that different forms of beauty might be associated with common brain region(s), but the region(s) might not be specific to beauty. For example, the ventromedial prefrontal cortex (vmPFC, which includes mOFC and adjacent brain regions) is not only activated when experiencing beauty but also when processing hedonic values (Nadal et al., 2008; Pegors, Kable, Chatterjee, & Epstein, 2015; Skov, 2019; Skov & Nadal, 2018). Similarly, they proposed that the experience of beauty could not be distinguished from general pleasure (Nadal & Skov, 2018) and share the neural basis with other pleasure (Berridge & Kringelbach, 2015; Kringelbach & Berridge, 2009). Based on the qualitative comparison of meta-analyses from neuroaesthetics and reward processing, Skov (2019) argued that there may be the same underlying neural mechanisms for experiencing aesthetic objects and assessing values, such as liking for food and drinks. Although disagreeing on whether the vmPFC is beauty-specific, these researchers agree that the vmPFC is a common brain region associated with the experience of beauty.

[2] We appreciate this comment from an anonymous reviewer.

In contrast to the evidence suggesting that the vmPFC/mOFC is the center of beauty in the brain, others reported different neural basis associated with the experience of beauty. For example, Silveira, Fehse, Vedder, Elvers, and Hennig-Fast (2015) found that paintings from Museum of Modern Art elicited higher involvement of right precuneus, bilateral anterior cingulate cortex (ACC), and temporoparietal junction (TPJ), but not mOFC. Moreover, Brown, Gao, Tisdelle, Eickhoff, and Liotti (2011) conducted a meta-analysis focusing on an aesthetic appraisal. They examined the overlapping brain voxels associated with aesthetic appraisals from different modalities, including visual, audition, gustation, and olfaction. They found that a common neural basis might exist in the insula, a region typically associated with reward and emotion.

No conclusive findings in the field partially reflect that much evidence comes from theoretical analysis using studies with great variability in task and data analysis. Thus, the primary aim of the current study was to conduct a meta-analysis of neuroimaging studies of beauty to examine the cross-study convergence. The meta-analytical approach will overcome the common issues of low statistical power (Button et al., 2013) and high false-positive rates (Carp, 2012; Eklund, Nichols, & Knutsson, 2016; Wager, Lindquist, & Kaplan, 2007) with a single neuroimaging study using the activation likelihood estimation (ALE) (C. Hu, Di, Li, Sui, & Peng, 2015; Wager et al., 2007). This approach is a well-developed coordinate-based meta-analysis technique which accommodates the spatial uncertainty of activation data in neuroimaging studies and allows researchers to form statistically defensible conclusions (Eickhoff et al., 2016; Fox, Lancaster, Laird, & Eickhoff, 2014; Laird et al., 2011). Note, we focused on the neuroimaging studies of the experience of visual beauty (Pearce et al., 2016). Specifically, we focused on the studies that compared the neural activities associated with the faces and visual arts (i.e., paintings, visual patterns, architectures, and dances) rated as beauty to those rated as nonbeauty. These two forms of beauty were selected because faces and visual arts represent two typical categories of beauty. Face beauty is the most representative natural beauty in social life, the preference of which is shaped by both (e.g., Little, Jones, and DeBruine (2011)) and environment (Germine et al., 2015), whereas visual art is the most representative artificial beauty that reflects the subjective aesthetic preference of human beings (Skov & Nadal, 2020). Another methodological reason for this is that these lines of research could provide enough amount of studies for meta-analysis (Müller et al., 2018). A comparison of the ALE results of fMRI studies between these two types of beauty may provide reliable and meaningful results, which could serve as a valuable start point for exploring a common neural representation of beauty.

Given that beauty is an abstract concept and difficult to define (Bergeron & Lopes, 2012; Conway & Rehding, 2013), the present meta-analysis used operational criteria for study selection. That is, we looked into the literature and checked whether a neuroimaging study not only used faces or visual art reported the neural effect of beauty but also reported the activities evoked by stimuli rated as beautiful (vs. not beautiful) or preferred (vs. not preferred). Specifically, fMRI studies reported the contrast between stimuli rated as beautiful versus stimuli rated as not beautiful, or studies in which the original authors argued that this contrast contained the neural activities related to the subjective feeling of beauty in different tasks, such as aesthetic judgement, asymmetry judgment, or passive viewing. We assumed that the meta-analysis that synthesized these existing studies independent of task type could capture the common neural basis for this subjective feeling of beauty.

The goals of the current study were to (1) identify common brain regions activated by both the experience of visual art and face beauty, (2) assess the specific brain regions activated by either the beauty of faces or the beauty of visual art. To fulfill these goals, we first conducted a systematic literature search of the neuroimaging studies on the beauty of visual art and face; we selected articles that included the brain data of experiencing beauty. Based on the data extracted from 49 selected neuroimaging studies, we conducted ALE meta-analyses for the beauty of visual art and the beauty of faces separately. Then we applied conjunction and contrast analyses to the meta-analytical results to identify the common and distinct neural basis of the beauty of visual art and faces. In addition to this primary meta-analysis, we conducted another two sets of meta-analysis to assess the effect of heterogeneity of studies – an important issue in meta-analysis, one with a restrict criterion that only focused the studies using a specific task (i.e., an explicit aesthetic judgment task), the other with a liberal criterion that included the studies regardless of stimulus domain and task type.

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 Dec 12, 2018). “Face” or “facial” were paired with “attractiveness,” “beauty” or “aesthetic” for aesthetic studies of faces; and “paintings”, “visual art”, “architecture”, or “dance” were paired with “beauty” or “aesthetic” 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 complete coverage, articles were also identified from recent meta-analyses and reviews (Boccia et al., 2016; Brown et al., 2011; Bzdok et al., 2011; Kirsch, Urgesi, & Cross, 2016; Mende-Siedlecki, Said, & Todorov, 2013; Vartanian & Skov, 2014). Additional studies were identified by searching through the reference lists of studies obtained via the initial search.

In our primary analysis, we selected studies based on the following inclusion and exclusion criteria:

(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, Jorge, Michel, Thirion, & Pessiglione, 2009).

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

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

(4) Studies investigated the beauty appreciation of visual art or faces. Given that we are interested in the experience of beauty, we only included studies that reported the effect of beauty, i.e., the contrast between stimuli that was rated as beautiful versus stimuli that was rated as not beautiful. We further derived three sub-criteria for this standard: 4a), studies using visual art or art-like stimuli or faces as stimuli; 4b), 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 studies did not report the effect of faces or visual art separately were excluded; and 4c), studies reported the effect of beauty by contrast the stimuli rated as beautiful to a high-level baseline (i.e., stimuli that have similar physical properties, e.g., luminance, visual complexity, but not rated as beautiful or not preferred by the participants), instead of low-level baselines (e.g., fixation or blank screen), so that the contrast included were specific to effect of beauty, instead of a combined effect of beauty and visual properties.

Coordinates of the peak activations of brain regions, which serves as our principal measures, were extracted from each article by searching the contrast of interest from both the main text and supplementary materials. For each experiment, only one contrast's coordinate data was extracted. Beside the coordinates data, we also reported the number of valid participants, mean age or range of age, number of male participants, modality (fMRI or PET), stimuli, tasks, and the contrast from which the data were entered our meta-analyses (see Table 1).

2.2. Data analysis.

In addition to the primary analysis that used the above-mentioned four criteria, we also conducted two supplementary analyses. The first meta-analysis tested whether increasing the homogeneity of the included studies would result in better convergence among the included studies. To do this, a meta-analysis only included the studies using a specific task (i.e., an explicit aesthetic judgment task) from the primary meta-analysis. In contrast, another meta-analysis examined whether increasing the number of included studies would result in a better convergence because of greater statistical power. However, the liberal criterion might also increase the heterogeneity of studies for meta-analysis instead. If this is true, we would expect weaker results in this meta-analysis with liberal criteria compared to the primary analysis (see Supplementary Material). In this liberal meta-analysis, we selected studies without applying the sub-criteria 4b and 4c.

2.3. Activation likelihood estimation.

The revised ALE algorithm, which was implemented in Matlab code, for the coordinate-based meta-analysis of neuroimaging results (Eickhoff et al., 2009; Laird, Eickhoff, et al., 2009; Laird, Lancaster, & Fox, 2009; Turkeltaub, Eden, Jones, & Zeffiro, 2002). This algorithm aims to identify areas that exhibit a convergence of reported coordinates across experiments that is higher than expected under a random spatial association. The key idea behind ALE is to treat the reported foci not as single points but rather as centers for 3D Gaussian probability distributions that capture the spatial uncertainty associated with each focus. The 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 6 ~ 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 location of the brain. To distinguish 'true' convergence among studies from random convergence (i.e., noise), we compared ALE scores 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, Bzdok, Laird, Kurth, & Fox, 2012). The p-value of the "true" ALE was then given by the proportion of equal or higher values obtained under the null-distribution. The resulting non-parametric *p*-values were then thresholded at the $p < 0.05$ (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. Contrast and conjunction analysis of individual meta-analyses.

To explore the distinct and common neural basis for two forms of beauty, we further conducted contrast and conjunction analyses based on the 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. The conjunction analyses used the voxel-wise minimum of each single ALE results, i.e., finding the minimum z-value across the two thresholded ALE results voxel-wisely (Nichols, Brett, Andersson, Wager, & Poline, 2005).

2.4 Data Visualization.

Given that there is no golden-standard atlas for neuroimaging studies, we used probabilistic cytoarchitectonic maps (as implemented in SPM Anatomy Toolbox, the third version) (Amunts et al., 2013; Eickhoff, Heim, Zilles, & Amunts, 2006; Eickhoff et al., 2007; Eickhoff et al., 2005) to assign our resulting coordinates to anatomical structures. For visualization purposes, BrainNet Viewer (Xia, Wang, & He, 2013) was used.

3. Results

3.1. Studies included in the meta-analyses

Our primary analysis identified 49 articles. 20 articles for the beauty of visual arts, including 20 independent samples, 107 foci, and 295 subjects; 29 articles using attractive faces, including 29 independent sample, 183 foci, and 687 subjects. All the code for search literature, endnote files for selecting articles, and metadata for the current study are available at https://osf.io/s9xds/. See Figure 1 for the process of article selection in detail, and Table 1 for the information of selected articles.

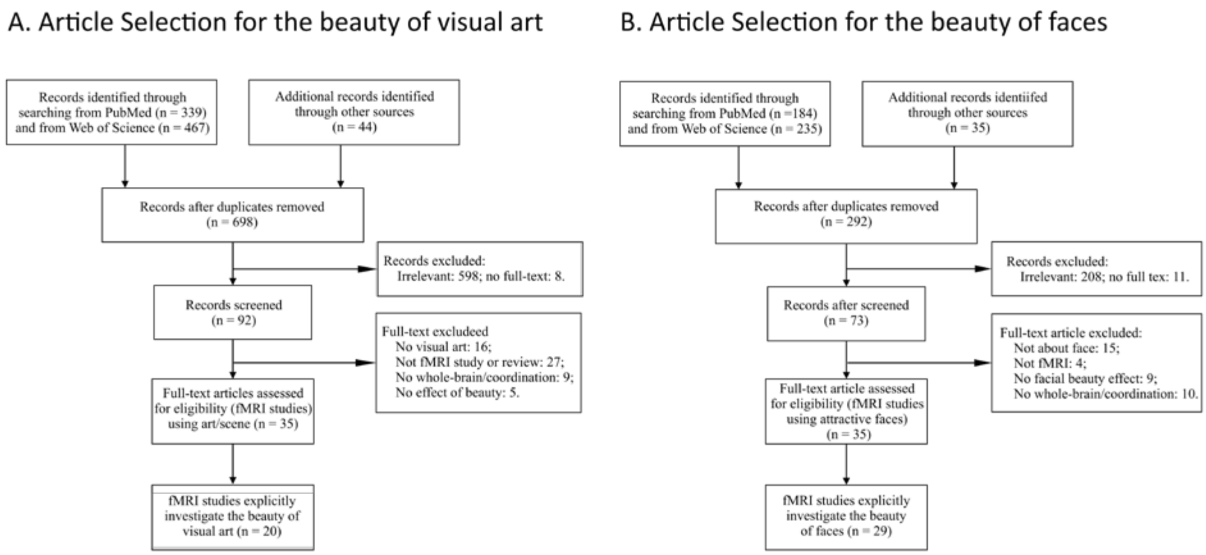

Figure 1. Flow diagram for literature search for the beauty of visual art (A) and the beauty of faces (B), adapted from Liberati et al. (2009).

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

Articles	Model	Subjects (Male)	Mean age	Stimuli	Task	selected contrast
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
Calvo-Merino et al (2008)	fMRI	6 (6M)	26	dance videos	observation	higher ‘like’ score > lower score
Cross et al (2011) *	fMRI	22 (13M)	24.8	dance videos	liking/ability judgment	movement > still position
Cupchik et al (2009) *	fMRI	16 (8M)	NA	paintings	pragmatic/aesthetic viewing	aesthetic > pragmatic viewing
Di Dio et al (2016) *	fMRI	19 (8M)	27.16	paintings	observation; aesthetic or movement judgment	paintings > baseline in aesthetic judgment
Di Dio et al (2011) a *	fMRI	32 (16M)	19-30	sculpture & human body	observation; aesthetic judgment	canonical sculpture > real human body in aesthetics judgment
Di Dio et al (2011) b *	fMRI	24 (12M)	19-30	sculpture & human body	observation; aesthetic judgment	canonical sculpture > real human body in aesthetics judgment
Di Dio, et al. (2007)	fMRI	14 (8 M)	24.5	sculpture	observation	beautiful > not beautiful
Fairhall and Ishai (2008) *	fMRI	12 (7M)	25	paintings	familiarity judgment	paintings > scrambled paintings
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
Huang et al (2011) *	fMRI	14 (8M)	20-27	portrait paintings	observation	authentic cue > copy cue
Ishizu and Zeki (2011) #	fMRI	21 (9 M)	27.5	paintings	beauty ratings	beautiful > (indifferent + ugly)
Ishizu and Zeki (2013) *	fMRI	21 (11M)	28.8	paintings	aesthetic/brightness judgment	aesthetic > brightness judgment
Jacobs, et al. (2012) #	fMRI	18 (10 M)	20-39	visual textures	beauty judgment	beautiful > ugly

Jacobsen et al (2006) #	fMRI	15 (6M)	25.4	visual pattern	aesthetic/symmetry judgment	beautiful > not-beautiful judgment
Kawabata and Zeki (2004) #	fMRI	10 (5 M)	20~31	paintings	beauty ratings	beautiful > neutral
Kesner et al. (2018) *	fMRI	24 (13M)	30	portraits	gaze direction	painterly style > linear portraits
Kirk (2008) *	fMRI	15 (9M)	24.4	photos	aesthetic ratings	correlated with aesthetics ratings
Kirk, Skov, Hulme, Christensen & Zeki. (2009) #	fMRI	14 (9 M)	26.3	paintings	aesthetic rating	correlation with aesthetics ratings
Lacey et al. (2011)	fMRI	8 (4 M)	23.1	paintings	animacy rating	correlated with beauty
Lebreton et al. (2009)	fMRI	20 (10 M)	22.0	paintings	pleasantness ratings	correlated with pleasantness
Lutz et al. (2013) *	fMRI	20 (10M)	35	artworks	attractive judgment	artworks > photos
Miura et al. (2010)*	fMRI	49 (38M)	19-29	dance videos	observation	Human > smooth robotic dance
Mizokami et al. (2014)*	fMRI	39 (NA)	27.5	paintings	aesthetic judgment	paintings > photos
Silveira, Fehse, et al. (2015) #	fMRI	17 (8M)	37.0	paintings	aesthetic judgment	positive > negative aesthetic judgment
Silveira et al. (2012) *	fMRI	15 (7M)	26	paintings	affected or not	naturalistic > surrealistic
Silveira, Gutyrchik, et al. (2015) *	fMRI	15 (7M)	26.5	paintings	emotional involvement	naturalistic > surrealistic
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
Vartanian, Navarrete et al (2013) #	fMRI	18 (6M)	23.4	architectural space	beauty/approach-avoidance judgment	parametrically correlated with beauty ratings
Vessel et al. (2012) #	fMRI	16 (11 M)	27.6	visual arts	recommendation	most recommended > least recommended
Wiesmann and Ishai (2010) *	fMRI	12 (7M)	24	paintings	object recognition	paintings > scrambled

Zhang et al. (2016) #	fMRI	16 (9M)	22.2	pictograph	aesthetic judgment	beautiful > ugly pictograph
Zhang et al. (2017) #	fMRI	19 (7M)	21.7	visual symbols	aesthetic judgment	beautiful > ugly pictograph
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/ identity ratings	correlation with beauty ratings
Chien, et al. (2016)	fMRI	32 (16 M)	25.1	faces	faces as reward cue	main effect of attractiveness
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
Funayama et al. (2012)	fMRI	42 (21M)	18-24	faces	choose one face from two	chosen for partners > control
Iaria et al. (2008) #	fMRI	11 (5 M)	24.09	faces	attractiveness rating	attractive > unattractive faces
T. Ito et al. (2014)	fMRI	12 (4M)	19.2	generated faces	social preference rating	chosen > unchosen
A. Ito et al. (2015)	fMRI	28 (14 M)	21.6	faces	passive viewing	preferred > non-preferred
A. Ito et al. (2016)*	fMRI	32 (16M)	21.3	faces	pleasantness rating	correlated with pleasantness
Kedia, et al. (2014)*	fMRI	25 (0M)	23.46	female faces	beauty judgement	beauty > distance judgment
Kim, et al. (2007) #	fMRI	25 (13 M)	20-45	faces	ratings	correlated 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	correlated with attractiveness
Martín-Loeches, et al. (2014) #	fMRI	20 (10M)	21.3	faces	beauty judgment	beautiful > neutral faces
McGlone et al. (2013) #	fMRI	16 (0 M)	23	faces	attractiveness rating	attractive > unattractive faces

Nakamura et al. (1998) *	PET	6 (6M)	19-25	face	attractiveness rating	attractiveness > emotion judgment
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	correlated with attractiveness
Silveira et al (2014) a*	fMRI	16 (16M)	24.13	female faces	ratings	attractive opposite-sex faces > dot
Silveira et al (2014) b*	fMRI	16 (0M)	24.64	male faces	ratings	attractive opposite-sex faces > dot
Smith et al. (2010)	fMRI	23 (23 M)	21.8	faces	passive viewing	attractive > unattractive faces
Smith et al. (2014) [#]	fMRI	16 (16 M)	23	faces	attractiveness rating	linear increase with attractiveness
Tsukiura and Cabeza (2011) [#]	fMRI	20 (0 M)	23.4	faces	attractiveness rating	linear increase with attractiveness
Turk et al (2004) *	fMRI	18 (9M)	22	faces	partner choice	date partner > face choosing task
Ueda et al (2016)	fMRI	36 (36M)	25	female faces	partner preference	attractive > unattractive
Ueno et al. (2014) [#]	fMRI	28 (14M)	20.7	female faces	attractiveness rating	correlated with attractiveness
Vartanian, Goel, Lam, Fisher & Granic, 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, Zhou, and Zhou (2013) [#]	fMRI	18 (9 M)	21	faces	attractiveness judgment	attractive faces > unattractive faces
Zaki et al (2011) [*]	fMRI	14 (14M)	21.8	faces	attractiveness rating	peer rating high > peer rating low
Zhai, Zhang, and Su (2010) [#]	fMRI	18 (10 M)	20.8	faces	attractiveness judgment	attractive > unattractive faces

* Included in supplementary analysis 1 with a liberal standard; [#] Included in supplementary analysis 2, a more conservative analysis. see Method for details.

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

Our primary analyses revealed that the frontal pole was convergently activated by the beauty of visual art. This brain region was also labeled as the anterior medial prefrontal cortex (aMPFC) in the literature (Table 3 and Figure 2A). The ALE results of the beauty of faces showed that two brain regions were more convergently activated: the first region located in the ventromedial prefrontal cortex (vmPFC) extending to the pgACC; while the second region includes subcortical structures such as the ventral striatum and subcallosal cortex (Table 3 and Figure 2B).

Critically, the conjunction analysis found no survival cluster (see supplementary results for the additional exploration of the results). The contrast analysis further revealed that a locus within the pgACC and a locus within the left ventral striatum were more frequently activated by beautiful faces than by beautiful art, while there the left frontal pole was more activated by visual art rated as beautiful than by faces rated as beautiful (Table 4 and Figure 2C).

3.1. Results for the meta-analyses with conservative inclusion standards

The first supplementary meta-analysis with more conservative inclusion standards (both explicit beauty judgment and beauty vs. non-beauty contrast) resulted 11 studies for visual art (54 foci, 192 subject) and 16 studies for faces (97 foci, 383 subject). The analysis of the beauty of visual art did find any survival clusters. The analysis of beautiful faces resulted in one brain regions as in primary analysis: the pgACC (see Table 4). These results suggested that there was not convergent activation for the experience of beauty across studies used explicit beauty judgment task. Interestingly, meta-analysis with liberal inclusion standards (Supplementary Analysis 1) also did not show survived clusters for the beauty of visual art, but found similar results as in primary analysis for the beauty of faces: both vmPFC (extending to the pgACC) and the ventral striatum (extending to subcallosal cortex) were convergently activated (see Table S2 in Supplementary Materials).

4. Discussion

The present study was set out to test the convergent neural basis of experiencing the beauty of visual art and faces. The results did not reveal any overlapped brain regions linked to the two forms of visual beauty, but each of which was associated with distinct brain regions.. The VMPFC/frontal pole was activated when experiencing visual art compared to face beauty, while the left ventral striatum and vmPFC/pgACC activated face beauty contrasting to visual art.

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

Previous fMRI studies on beauty suggested the vmPFC/mOFC was involved in processing different forms of beauty (Ishizu & Zeki, 2011, 2013; Nadal et al., 2008; Pegors et al., 2015; Skov, 2019; Skov & Nadal, 2018; Zeki et al., 2014). It has also been reported that the vmPFC serves as a hub for subjective values (Etkin, Egner, Peraza, Kandel, & Hirsch, 2006; Levy & Glimcher, 2012; Roy, Shohamy, & Wager, 2012), positive signals (Bartra, McGuire, & Kable, 2013; Kalisch et al., 2006), and self-referential processes (C. Hu et al., 2016; Northoff et al., 2006). By synthesizing the available neuroimaging studies that examined the beauty of faces and visual art, the present meta-analysis did not find a convergent result between the neural activations elicited by these two forms of beauty. Moreover, this null result was robust even by increasing the homogeneity of the included studies. Given the strong statistical power of meta-analysis and its capacity to address the cross-study variance, the present results suggest that the common neural basis of beauty may not exist (also see Supplementary Materials).

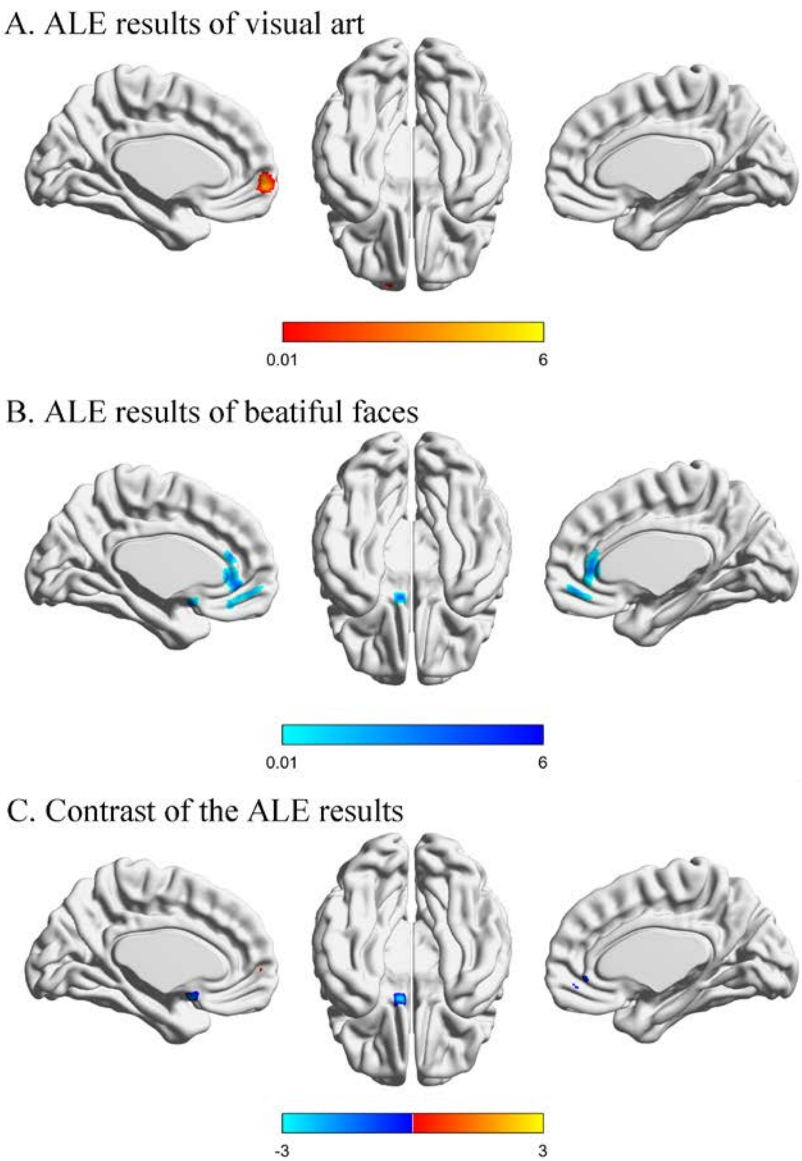

Figure 2. Results of the ALE meta-analysis and the contrast analysis. (A) Brain regions convergently activated more for visual art rated as beautiful than for visual art rated as not beautiful; (B) brain regions convergently activated more for faces rated as beautiful than for faces rated as not beautiful; (C) the results of the contrast analysis between the ALE results of visual art rated as beautiful and faces rated as beautiful; positive values (red) indicate greater activation for the beauty of visual art than for faces, and negative values (blue) indicate greater activation for the beauty of faces than for visual art.

316

Table 3. The results of the meta-analyses for visual art and faces rated as beautiful

Cluster	Volume (voxels)	Weighted center			Maximum Z-value	Center for maximum Z-value			Macroanatomical location
		x	y	z		x	y	z	
visual art rated as beautiful > rated as not beautiful									
1	149	-12	62	-2	4.33	-12	62	-2	Frontal pole
					3.97	-4	60	-2	Frontal pole/paracingulate gyrus
					3.97	-6	60	-2	Frontal pole/paracingulate gyrus
faces rated as beautiful > rated as not beautiful									
1	393	0	48	-6	5.56	0	48	-6	Paracingulate gyrus/Frontal medial cortex
					4	-2	36	2	Anterior cingulate gyrus
					3.7	2	36	10	Anterior cingulate gyrus
					3.2	-4	36	-16	Frontal medial cortex/paracingulate gyrus
2	121	-10	16	-6	4.69	-10	16	-6	Left accumbens/Left caudate
					3.84	-8	10	-16	Subcallosal cortex
					3.84	-8	10	-14	Subcallosal cortex/left accumbens

All peaks were assigned to the most probable brain area using the SPM Anatomy Toolbox v3

Table 3. Contrast and conjunction analyses of the meta-analysis results

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	30	-12	58	2	1.98	-12	58	2	Frontal pole/paracingulate gyrus
the beauty of faces > beauty of visual art									
1	48	4	46	-2	2.23	4	46	-2	Paracingulate gyrus/ anterior cingulate gyrus

2	45	-6	6	-16	2.78	6	6	-16	L Accumbens/subcallosal cortex
the beauty of visual art ∩beauty of faces									
	No cluster survived								

All peaks were assigned to the most probable brain area using the SPM Anatomy Toolbox v3.

Table 4. The results of the meta-analysis with conservative inclusive standards

Cluster	Volume (voxels)	Weighted center			Maximum Z-value	Center for maximum Z-value			Macroanatomical location
		x	y	z		x	y	z	
visual art rated as beautiful > as not beautiful *(No cluster survived)*									
faces rated as beautiful > as not beautiful									
1	93	-2	36	2	4.26	-2	36	2	Anterior cingulate gyrus

One might argue that our meta-analysis based on loose-defined operationalization criteria (including studies using different tasks) led to the high heterogeneity of studies. And this heterogeneity resulted in the null result of conjunction analysis. However, the argument was not supported by the meta-analysis using the conservative inclusive criteria, which failed to show convergent results. Although the additional meta-analysis, which had a small number of studies, might suffer from low statistical power, in contrast to the convergent results in the primary analysis, it suggests that heterogeneity was less important than the number of studies in the current analysis. These results indicated that the primary analysis, with a relatively large number of studies, at least detected some shared mental processes associated with the experience of beauty. Otherwise, if the studies with different tasks evoked different mental processes (i.e., increased heterogeneity), the primary meta-analysis should have found less convergent results than the meta-analysis with conservative criteria.

Understanding a common mechanism of experience beauty is of great interest in both empirical aesthetics but also in aesthetics in general because of the long-last debate about the center of beauty. Previous theories in neuroaesthetics suggest a common neural basis representing beauty in the brain (Ishizu & Zeki, 2011, 2013; Nadal et al., 2008; Pegors et al., 2015; Skov, 2019; Skov & Nadal, 2018; Zeki et al., 2014). However, this view was not supported by the present meta-analyses.

The discrepancy between the strong theoretical prediction of a common neural basis for beauty and lack of empirical evidence calls for more rigorous studies. Recently, the field of cognitive neuroscience has been challenged for its reproducibility (Botvinik-Nezer et al., accepted; C.-P. Hu, Jiang, Jeffrey, & Zuo, 2018; Poldrack et al., 2017). Small sample size (which results in low statistical power) (Button et al., 2013), flexibility in data analysis (Botvinik-Nezer et al., accepted; Carp, 2012), and errors in implementing software (Eklund et al., 2016), accompanied by publication bias (Jennings & Horn, 2012), all threatened the reliability and reproducibility of the field (C.-P. Hu et al., 2018; Poldrack et al., 2017). Direct replication, albeit very few, found that pessimistic results (Boekel et al., 2015). To better test the common neural basis of beauty, researchers need to adopt new practices that have been recommended recently, including the standard reporting, preregistration, and large sample size (Munafò 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 have opened the meta-data of this meta-analysis (see Method section). Future works can easily be integrated to update the knowledge about the common neural basis of beauty.

4.2. Unique neural basis underlying the beauty of faces and visual art.

The ALE results of face beauty demonstrated that experiencing face beauty induced greater activation in the vmPFC/pgACC and the left ventral striatum than when faces rated as not beautiful. In contrast, the ALE results of the beauty of visual art showed convergent activations in the left frontal pole/aMPFC related to visual art rated as not beautiful. The result was consistent with previous studies demonstrating that the vmPFC-subcortical rewarding system is engaged in processing the beauty of faces (Chatterjee & Vartanian, 2014; Hahn & Perrett, 2014). On the other hand, the vmPFC/pgACC and the ventral striatum play different roles in cognition. For example, the vmPFC/pgACC is activated with a wide range of brain structures when involved in multiple higher-level functions (e.g., (de la Vega, Chang, Banich, Wager, & Yarkoni, 2016; Roy et al., 2012)). It has consistently been reported that the ventral striatum is engaged in reward processing (Haber & Knutson, 2010; Liu, Hairston, Schrier, & Fan, 2011), especially primary reward (Sescousse, Caldú, Segura, & Dreher, 2013). Therefore, it is possible the facial beauty is appreciated through a ventral pathway: the ventral striatum primarily responds to the rewarding value of faces, the reward signal, along with other information, and then integrated into the vmPFC to generate positive affections.

In contrast, the frontal pole/aMPFC convergently activated in appreciating the beauty of visual art is more engaged in high-level, top-down processing. Previous studies have shown that it involves in episodic memory, decision-making, and social cognition (de la Vega et al., 2016) such as positive evaluation (Bartra et al., 2013) and secondary reward (Sescousse et al., 2013). We speculated that the aMPFC, when appreciating visual art, links more abstract beauty to reward, like that of secondary reward.

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

We did not find activations in the sensory regions in meta-analyses of either the beauty of faces or the beauty of visual art. For the facial beauty, no significant activations in either the fusiform face areas or other sensory cortical areas were observed when rating faces as beautiful contrasting to rating faces as not beautiful. Likewise, there was no activation of the sensory-motor network observed when experiencing the beauty of visual art. 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 & Vartanian, 2014; Leder & Nadal, 2014).

One possibility to these results is that current meta-analyses exclusively included the contrasts between beautiful vs. non-beautiful stimuli with similar perceptual features (high-level baselines, see Method section), therefore eliminating the effect of the physical feature processing on the experience of visual beauty. If this is the case, the present results indicated that the beauty of faces and visual arts showed different neural representations at high-level processing.

Notably, our results do not suggest that physical features are less important in beauty appreciating. Actually, the sensory network is necessary for processing the beauty of faces and visual art (Chatterjee & Vartanian, 2014). Also, the shared standard for faces rated as beautiful (Hönekopp, 2006; Leder, Goller, Rigotti, & Forster, 2016) suggests that physical features are crucial for experiencing visual beauty. Hence future studies are needed to examine the contribution of sensory processing to beauty appreciation.

Regarding the hemisphere differences, it seems that peak locations in experiencing both face and art beauty appear in the left hemisphere, contradicting the view that the right brain is dominated for imagination, creativity, and emotions (see, Bromberger et al., 2011). However, our meta-analytic results did not reveal hemispheric asymmetry: most clusters were near the midline of the brain. The present results, together with the previous meta-analysis on appreciating visual art (Boccia et al., 2016), suggest that the visual beauty is processed by both hemispheres.

4.4. Further considerations.

Based on the available research in the literature, the current meta-analysis attempted to examine whether there is a common beauty of faces and visual art in the brain and whether albeit each category of beauty had its convergent brain regions. One limitation of the current meta-analysis is that the analyses were based on the reported peak activations, which may have two disadvantages. First, a large part of the spatial information from the original study was discarded. However, this limitation can be alleviated by the fact that the results derived from image-based meta-analysis are in good agreement with coordinate-based meta-analysis approaches (Salimi-Khorshidi, Smith, Keltner, Wager, & Nichols, 2009). Second, studies that did not report any activations for the contrast of interest were not included in the current analyses. Indeed, there are studies used the beauty appreciation task but did not report results of beautiful-non-beautiful contrast (Kampe, Frith, Dolan, & Frith, 2001), therefore they couldn't be included in our meta-analysis. However, this selection bias, if exists, together with potential publication bias in neuroimaging studies (Jennings & Horn, 2012), may result in inflated false positive. This inflated false positive rate is not a concern for the current meta-analysis because no positive results for the conjunction analysis were observed in the present study. A related issue is that coordinate-based meta-analysis approaches of neuroimaging studies, like ALE, use the averaged likelihood in common volumetric space (Wager et al., 2007); it might lead to false positives of convergent activation in adjacent regions across studies. However, this is not a concern in the current meta-analysis given our negative results.

The meta-analyses inherently include many seems trivial but important choices that bring extra flexibility in research practices. For example, the standard for inclusion may not be clear for a few papers, and results from more than one contrast are qualified with the inclusion standard. In these cases, the final choice might be arbitrary. Studies have shown that flexibility in research practice can inflate the false positive rate (Botvinik-Nezer et al., accepted; Carp, 2012; Simmons, Nelson, & Simonsohn, 2011). It might also be true for meta-analysis. To alleviate this limitation (Schönbrodt, Maier, Heene, & Zehetleitner, 2015), we adopted an open and transparent practice and uploaded the article selection process (as recorded in Endnote® X8, Clarivate Analytics, Philadelphia, USA) and meta-data (see https://osf.io/s9xds/).

4.5. Conclusion.

Our meta-analytic results revealed distinct neural specificities for visual art and face beauty, but lack of evidence for the common neural basis of visual beauty. This negative result suggests that the available data did not support the notion of the existence of a common brain for process different forms of beauty. To support such a common neural basis for beauty, more rigorous studies are needed.

Acknowledgments

This work was supported by the Economic and Social Research Council (UK, ES/K013424/1) and by the National Natural Science Foundation of China (Project 31371017, and 31471001). SBE acknowledges funding by the the National Institute of Mental Health (R01-MH074457) and the European Union’s Horizon 2020 Research and Innovation Programme under Grant Agreement No.945539 (HBP SGA3). We thank Dr. Steven Brown for helpful comments on the previous versions of this manuscript.

Author Contributions

H. C-P., K.P. designed the study. H.C-P. and S.E. performed the statistical analyses. H.C-P. , 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.

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