

Is moral beauty different from facial beauty? Evidence from an fMRI study

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Is moral beauty different from facial beauty? Two functional magnetic resonance imaging experiments were performed to answer this question. Experiment 1 investigated the network of moral aesthetic judgments and facial aesthetic judgments. Participants performed aesthetic judgments and gender judgments on both faces and scenes containing moral acts. The conjunction analysis of the contrasts ‘facial aesthetic judgment > facial gender judgment’ and ‘scene moral aesthetic judgment > scene gender judgment’ identified the common involvement of the orbitofrontal cortex (OFC), inferior temporal gyrus and medial superior frontal gyrus, suggesting that both types of aesthetic judgments are based on the orchestration of perceptual, emotional and cognitive components. Experiment 2 examined the network of facial beauty and moral beauty during implicit perception. Participants performed a non-aesthetic judgment task on both faces (beautiful vs common) and scenes (containing morally beautiful vs neutral information). We observed that facial beauty (beautiful faces > common faces) involved both the cortical reward region OFC and the subcortical reward region putamen, whereas moral beauty (moral beauty scenes > moral neutral scenes) only involved the OFC. Moreover, compared with facial beauty, moral beauty spanned a larger-scale cortical network, indicating more advanced and complex cerebral representations characterizing moral beauty.

Keywords: facial beauty; fMRI; moral beauty; OFC; putamen

INTRODUCTION

Imagine two scenarios. In the first, you are shocked from viewing a stunning beauty. In the second, you are touched for seeing that a little boy is taking off his coat to cover an injured pigeon. These two scenes seem quite irrelevant to each other. However, they both involve the aesthetic experience of beauty: facial beauty and moral beauty.

According to aesthetic theories, a sense for beauty involves the disinterested and detached mental pleasure induced by various forms, including natural, artistic and moral beauty (Berlyne, 1971; Cupchik, 2002; Haidt *et al.*, 2004). Both natural beauty and artistic beauty are directly based on the auditory pathway and/or visual pathway. It implies that the sensory and symbolic elements of aesthetic objects conform to certain aesthetic rules (e.g. proportion, color and texture) (Berlyne, 1971; Cupchik, 2002). While audiovisual beauty combines sensory and symbolic elements, moral beauty involves complex social meanings and is therefore more complex and abstract (Haidt, 2003a,b, 2007; Keltner and Haidt, 2003; Haidt *et al.*, 2004; Diessner *et al.*, 2006; Gu, 2008; Algoe and Haidt, 2009). By definition, moral beauty is the expression of humanity, virtue and talents independent of perceivable physical forms, which is based on the understanding of social rules and involves highly developed social affects and cognitions (Haidt, 2003a,b, 2007; Keltner and Haidt, 2003; Haidt *et al.*, 2004; Diessner *et al.*, 2006; Gu, 2008; Algoe and Haidt, 2009). It is noteworthy that although moral beauty may objectively refer to the same human act as moral goodness, subjectively they are different (Haidt, 2003a,b, 2007; Keltner and Haidt, 2003). An observer can cognitively judge an act as morally

good but remain unmoved. However, when an observer perceives an act as morally beautiful, it implies that his or her emotion has been moved by the act (Haidt, 2003a,b, 2007; Keltner and Haidt, 2003). Therefore, exploring the neural mechanisms of moral beauty is of great importance not only in filling the gap in neuroaesthetics but also in establishing a bridge between moral and aesthetic areas (Greene *et al.*, 2001, 2004; Agnati *et al.*, 2007; Haidt, 2007; Chapman *et al.*, 2009; Greene and Paxton, 2009; James, 2011; Tsukiura and Cabeza, 2011; Zaidel and Nadal, 2011; Avram *et al.*, 2012).

For neuroaesthetics, previous studies have mainly focused on two aspects. The first is to identify the cortical network involved in aesthetic judgments. Aesthetic judgments refer to the evaluation process during appreciation. Irrespective of the beauty level of the stimulus, aesthetic judgments occur when people try to understand and appreciate certain aesthetic objects. Previous studies have identified the neural substrates of aesthetic processing by directly comparing the brain areas underlying aesthetic judgments vs non-aesthetic judgments. Several lines of neural evidence have converged on the consistent involvement of the ventral visual systems [V1, V2, V4 and inferior temporal gyrus (ITG)], superior frontal gyrus (SFG) and orbitofrontal cortex (OFC) in aesthetic judgments (Jacobsen *et al.*, 2006; Winston *et al.*, 2007; Avram *et al.*, 2012). The reliance on these regions is in agreement with aesthetic theories, which pose that aesthetic judgments consist of perceptual, cognitive and emotional processing (Berlyne, 1971; Cupchik, 2002). The second is to identify the cortical network involved in beauty. ‘Beauty’ refers to the particular valences of aesthetic judgments (e.g. attractive faces and appealing artwork). Thus, beauty represents a specific level of aesthetic objects. Previous research has identified the neural substrates of beauty by directly comparing beautiful vs neutral objects or by parametrically manipulating the levels of beauty. A variety of studies using painting, music, dance, sculpture and architecture have shown that ‘beauty’ is reliably correlated with activity of cortical and subcortical areas implicated in the processing of reward, especially the OFC and the striatum (including caudate, putamen and nucleus accumbens) (Blood *et al.*, 1999; Aharon *et al.*, 2001; Blood and Zatorre, 2001; Cela-Conde *et al.*, 2004; Kawabata and Zeki, 2004;

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Vartanian and Goel, 2004; Menon and Levitin, 2005; Calvo-Merino *et al.*, 2008; Chatterjee *et al.*, 2009; Cupchik *et al.*, 2009; Di Dio *et al.*, 2011; Ishizu and Zeki, 2011; Vessel *et al.*, 2012).

However, in contrast to the abundant insights gained in these studies, the focus of which has been confined to audiovisual beauty, little is known about the neural correlates of moral beauty. Does the neural mechanism of moral beauty involve more complex and advanced networks than other beauty forms because of its more abstract and complicated social meaning-based nature? Two functional magnetic resonance imaging (fMRI) experiments were conducted to answer this question. Facial beauty was chosen as a comparison, as it is the most typical form of audiovisual beauty. Experiment 1 sought to characterize the network of facial aesthetic judgments and moral aesthetic judgments. We used an aesthetic judgment task and a relatively unrelated gender judgment task as a baseline condition (Jacobsen *et al.*, 2006; Winston *et al.*, 2007; Avram *et al.*, 2012). Hence, the network of facial aesthetic judgments was identified by the contrast of 'facial aesthetic judgment > facial gender judgment', whereas the network of moral aesthetic judgments was identified by the contrast of 'scene moral aesthetic judgment > scene gender judgment'. That is, Experiment 1 focused on the difference between tasks (aesthetic *vs* non-aesthetic). Experiment 2 examined the network of facial beauty and moral beauty during implicit perception. Participants performed a non-aesthetic judgment task on both scenes containing morally beautiful or neutral information, and beautiful faces or common faces. The neural substrates of facial beauty were identified by the contrast of 'beautiful faces > common faces', whereas the neural substrates of moral beauty were identified by the contrast of 'moral beauty scenes > moral neutral scenes'. That is, Experiment 2 focused on the difference between stimuli (beautiful *vs* common or neutral). Besides, as no aesthetic task was involved, we could examine whether people could appreciate beauty (moral or facial) automatically and implicitly. Based on previous findings, we hypothesized that the moral aesthetic judgments might rely on similar neural substrates with facial aesthetic judgments, but that moral beauty will involve more complex brain networks related to social cognition.

EXPERIMENT 1

Experiment 1 investigated the network of facial aesthetic judgments and moral aesthetic judgments.

Materials and methods

Participants

Twenty-eight (mean age = 22 years, range, 18–25 years; 14 females) healthy, right-handed college students with no history of psychiatric and neurological disorders were recruited as participants. All participants were assessed to ensure normal or corrected to normal vision. Informed consent was obtained from all participants before the experiment according to the requirements of the Ethics Committee of Department of Psychology, South China Normal University.

Stimuli

During the scan, participants viewed two types of stimuli, facial photos for facial beauty and scene drawings for moral beauty. For facial stimuli, 72 photographs of greyscale photographs of non-famous Asian human faces (with only neutral facial expressions) were selected from the photographic databases of South China Normal University and Beijing Normal University, and rated by an independent group of 48 participants on a 7-point scale, forming two equal-sized sets: 'beautiful' faces (5.07 ± 0.27) and 'common' faces (3.09 ± 0.18) (see Figure 1). Each set consisted of 18 male and 18 female faces. Facial photographs were digitized at 600 dpi in 8 bit greyscale, spatially downsized and cropped to fit in an oval 'window' sized 350×470 pixels. The scene

drawings were 72 black-and-white drawings, in which the behaviours of cartoon characters in everyday life scenes were described. In the same pilot study, the 48 participants rated 360 candidate drawings based on the degree of moral beauty conveyed in these pictures (e.g. altruistic behaviour), which yielded 36 'moral beauty' scenes (5.67 ± 0.70) and 36 'moral neutral' scenes (4.22 ± 0.42) (see Figure 1). In both stimulus sets, the main characters in half the drawings were male. Scene drawings were cropped to fit in a square 'window' sized 589×500 pixels.

Task

During the scan, participants performed the aesthetic judgment task and the gender judgment task on both stimulus types. In the face aesthetic (FA) judgment task, participants were instructed to judge whether the face was beautiful or common. In the scene moral aesthetic (SA) judgment task, participants were instructed to judge whether the scene drawing was morally beautiful or neutral. In the face gender (FG) task, participants were instructed to judge whether the face was male or female. In the scene gender (SG) task, participants were instructed to judge whether there was a male or a female figure in the picture. The aesthetic judgment required participants to make a left-finger response to beautiful faces or moral beauty scenes and a right-finger response to common faces or neutral scenes. The gender judgment task, which served as a controlling baseline, required participants to make a left-finger response to male faces or male main characters and a right-finger response to female faces or female main characters.

Procedure

The combination of the two task types (aesthetic *vs* gender judgment) and the two stimulus types (face *vs* scene) yielded four conditions. A blocked design with 12 blocks pertaining to each condition was used. Block orders were fixed and counterbalanced across participants. Each block lasted for 15 s and was followed by 10 s of fixation (see Figure 2). An instruction for task type appeared for 2 s before block onset. Each block included six trials. Within each block, every image was presented for 2 s subsequently after a 500 ms fixation baseline. Participants were instructed to fixate on each image and make judgments, accordingly, using their thumbs on the button box. Each subject had a single functional scan, which lasted ~25 min.

fMRI data acquisition

Whole-brain fMRI data were acquired on a 3T Siemens Trio scanner with 12-channel phase array head coil. Functional images were obtained in one scanning run with a T2*-weighted gradient echo planner imaging sequence, each comprising 32 contiguous axial slices (3 mm thickness, 1 mm gap). The following parameters were used for scanning: Echo Time (TE) = 35 ms; Repetition Time (TR) = 2000 ms; flip angle = 90°; acquisition matrix size = 64×64 ; field of view = 192 mm. In addition, T1-weighted 3D structural image were acquired using a spoiled gradient-recalled sequence in a steady state (voxel size $1 \times 1 \times 1$ mm³; TR = 19 ms, TE = 5 ms, flip angle = 20°).

fMRI data analysis

Data analysis was performed using statistical parametric mapping (SPM8) (<http://www.fil.ion.ucl.ac.uk/spm>). For each participant, the first six volumes, during which a fixation cross was presented, were discarded to allow for T1 equilibration. Images were spatially realigned to the first volume to correct for head movements. No individual runs had >3 mm maximum displacement or >1° rotation. The aligned functional images were first coregistered to the high-resolution T1-weighted structural image, normalized to the standard T1 template

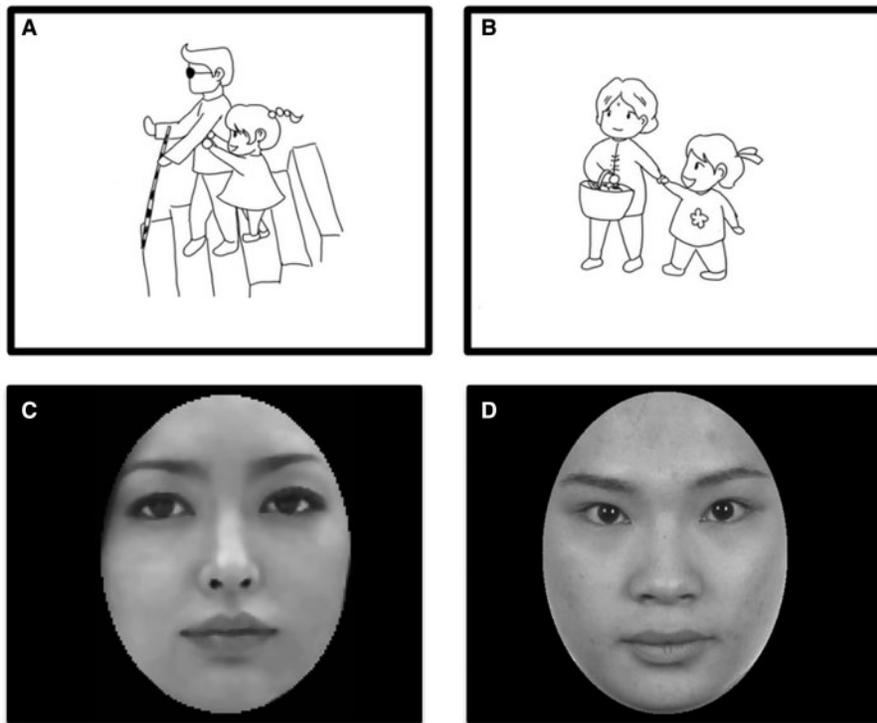


Fig. 1 Examples of stimuli in Experiment 1. Figure (A) and (B) demonstrate two examples of scene drawings. Figure (A) depicts a morally beautiful scene (SB), in which the main character is performing a morally beautiful (i.e. altruistic) behaviour, and Figure (B) demonstrates a morally neutral scene (SN), in which the main character is performing a neutral behavior. Figure (C) is an example of a beautiful face (FB) and Figure (D) is an example of a common face (FC).

volume (MNI) and then resampled with voxel size of $2 \times 2 \times 2 \text{ mm}^3$. The data were then smoothed with an isotropic full-width half-maximum 8 mm Gaussian kernel.

At the single participant level, a general linear model was applied to the fMRI time series where stimulus onset was modelled as single impulse response function and convolved with SPM8's canonical haemodynamic response function (HRF). We modelled four regressors of interest: FA, SA, FG and SG. The four block types were time-locked to the onset of the block with block duration of 15 s. The instructions for task type (see Figure 2) were modelled as a regressor of no interest. Six motion parameters estimated during the realignment procedure were included in the model as covariates of no interest. A high-pass filter with a cut-off period of 128 s was used to remove any low-frequency noise. At the first level, analyses were performed individually for each participant and contrast images were subsequently entered into a second-level analysis treating participants as a random factor.

At the group level, analyses were conducted at a voxel threshold of $P < 0.05$ (FWE corrected) and a cluster threshold of $P < 0.05$ (FWE corrected). We first performed the contrasts of 'FA > FG' and 'SA > SG,' respectively, using the flexible factorial analysis in SPM8. Based on our main interest of the common brain regions involved in the above two contrasts, we then computed a conjunction between the 'FA > FG' and 'SA > SG' using the minimum statistic approach (Nichols et al., 2005).

The parameter estimates in the regions of interest (ROI) were obtained by an iterative leave-one-out-cross-validation (LOOCV) analysis, in which all but one participant's data were used to define the ROI for the left-out participant (Kriegeskorte et al., 2009). Each ROI was defined using a sphere with 10 mm radius centred on the peak voxel. This procedure was repeated 28 times by omitting a different participant each time, and the parameter estimates were then averaged across participants and plotted. As a result of the LOOCV analysis, the

data used to define an ROI and the data extracted from this ROI (bar graphs in Figures 3 and 6) are independent.

Results

Behavioral results

We observed no significant differences in the reaction times (RTs) or accuracy between aesthetic judgment and gender judgment for either faces (RTs: $t_{27} = -1.74$, Mean Squared Error (MSE) = 0.03, $P > 0.05$, Cohen's $d = 0.45$; accuracy: $t_{27} = -1.81$, MSE = 49.15, $P > 0.05$, Cohen's $d = 0.34$) or scenes (RTs: $t_{27} = 0.08$, MSE = 0.02, $P > 0.05$, Cohen's $d = 0.08$; accuracy: $t_{27} = -1.61$, MSE = 55.00, $P > 0.05$, Cohen's $d = 0.34$). Thus, the observed brain activation differences could not be attributed to performance variation confounds across the different task types.

Imaging results

For FA judgments, a contrast of 'FA > FG' revealed strong activation in the bilateral medial SFG, left ITG and left inferior OFC (see Table 1 and Supplementary Figure S1). For moral aesthetic judgments, a contrast of 'SA > SG' revealed activation in the bilateral inferior OFC, left SFG, bilateral ITG, left rectus gyri, left middle cingulate, bilateral middle occipital lobe and right precuneus (see Table 1 and Supplementary Figure S1).

Critically, as we predicted, the conjunction analysis of the two previous contrasts of interest showed that the neural networks involved in moral aesthetic judgments overlapped with those involved in facial aesthetic judgments (see Table 1 and Figure 3). To further investigate the neural properties of these key regions, we also conducted an ROI analysis by using a LOOCV procedure. We found that the left inferior OFC, left ITG and bilateral medial SFG were more active during the aesthetic judgment task ($P < 0.05$) (see Figure 3). Together, these

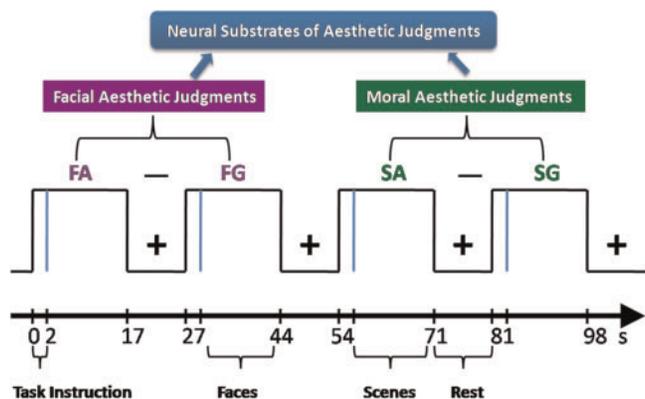


Fig. 2 Experimental design and procedure in Experiment 1. Four types of tasks were performed in separate blocks: FA judgments (beautiful vs common), facial gender (FG) judgments (male vs female), moral aesthetic judgments of scenes (SA; morally beautiful vs neutral) and gender judgments of individuals in scenes (SG; male vs female). The neural substrates underlying the aesthetic judgments for facial beauty were identified by the contrasts of ‘FA-FG’. The neural substrates underlying the aesthetic judgments for moral beauty were identified by the contrasts of ‘SA-SG’. Each block lasted for 15 s and was followed by 10 s of fixation.

findings suggest a common neural mechanism underlying aesthetic judgments irrespective of beauty forms, involving the left inferior OFC, left ITG and bilateral medial SFG, providing direct support for our hypothesis.

EXPERIMENT 2

Experiment 2 investigated the network of facial beauty and moral beauty during implicit perception. That is, while Experiment 1 focused on the difference between tasks (aesthetic vs non-aesthetic), Experiment 2 focused on the difference between stimuli (beautiful vs common or neutral). Besides, as no aesthetic task was involved, we could examine whether people could appreciate beauty (moral or facial) automatically and implicitly.

Materials and methods

Participants

Twenty-two (mean age = 21, range, 18–25 years; 12 females) healthy right-handed college students who did not participate in Experiment 1 with no history of psychiatric and neurological disorders were recruited as participants. All participants were assessed to ensure normal or corrected to normal vision. Informed consent was obtained from all participants before the experiment according to the requirements of the Ethics Committee of Department of Psychology, South China Normal University.

Stimuli

Facial photographs and scene drawings were used as stimuli. For facial stimuli, we used the same stimulus sets used previously as ‘beautiful’ and ‘common’ faces in Experiment 1 (see Figure 4). To reduce the visual differences of moral beauty and non-moral beauty scenes, paired scene drawings were created. In each pair, moral beauty and moral neutral scenes had identical backgrounds and characters, and only differed in the character’s actions. Before the experiment, an independent group of 36 participants rated the visual complexity, familiarity, artistry and degree of moral beauty of the candidate stimuli on a 7-point scale. Thirty-six pairs with significant differences in the moral beauty score but not in other indices were thus selected as stimuli for the purpose of achieving a better match of visual processing workload

and subjective artistic preference (complexity: $t_{35} = -1.33, P > 0.05$; familiarity: $t_{35} = -0.42, P > 0.05$; artistry $t_{35} = 1.79, P > 0.05$; moral beauty: $t_{35} = 22.73, P < 0.05$), forming 36 paired drawings of moral beauty scenes and moral neutral scenes, respectively (see Figure 4).

Task

The same gender judgment task, the details of which were described previously in Experiment 1, was used as the only task of Experiment 2 to keep the participant’s attention fixated on the presented stimuli in the absence of the explicit aesthetic judgment task.

Procedure

We used a blocked design with 12 blocks pertaining to each of the four experimental conditions (FB and FC, SB and SN). Block orders were fixed and counterbalanced across participants. Each block lasted for 15 s and was followed by 10 s of fixation (see Figure 5). Each block included six trials. Within each block, every image was presented for 2 s subsequently after a 500 ms fixation baseline. Participants were instructed to fixate on each image and make judgments, accordingly, using their thumbs on a button box. Each participant had a single functional scan, which lasted ~25 min. After the scan, all participants rated the facial photos based on the degree of facial beauty and the scene drawings based on the degree of moral beauty.

fMRI data acquisition and analysis

The fMRI data acquisition and pre-processing were the same as in Experiment 1. At the single participant level, we modelled four regressors of interest: beautiful face (FB), common face (FC), morally beautiful scene (SB), and neutral scene (SN). The four block types were time-locked to the onset of the block with a block duration of 15 s. Six motion parameters estimated during the realignment procedure were included in the model as covariates of no interest. At the first level, analyses were performed individually for each participant and contrast images were subsequently entered into a second-level analysis treating participants as a random factor.

At the group level, analyses were conducted at a voxel threshold of uncorrected $P < 0.001$ and a cluster threshold of $P < 0.05$ (FWE corrected). We first performed the contrasts of ‘FB > FC’ and ‘SB > SN’, respectively, using the flexible factorial analysis in SPM8. Based on our main interest on the common brain regions involved in the above two contrasts, we then computed a conjunction between the ‘FB > FC’ and ‘SB > SN’ using the minimum statistic approach advocated by Nichols *et al.* (2005). Given the heavy involvement of OFC in mediating beauty in previous studies, we used small volume correction (SVC) on OFC with 10 mm radius centring on the coordinate of the OFC peak voxel ($x = -21, y = 54, z = -9$) from a previous study (Winston *et al.*, 2007). Parameter estimates in each ROI were obtained by a LOOCV analysis (Kriegeskorte *et al.*, 2009). This procedure was repeated 22 times in Experiment 2 by omitting a different participant each time, and the parameter estimates were then averaged across participants and plotted.

Moreover, to further investigate the role of cortical reward region (OFC) and subcortical reward region (putamen) in the cerebral representation of beauty, we used the LOOCV procedure to obtain parameter estimates from OFC and putamen across participants, and then conducted a Pearson correlation analysis to examine the relationship between these parameter estimates and the behavioural ratings of facial and moral beauty obtained at the post-scan session. This procedure ensures that we are not prone to a ‘double dipping’ error in the subsequent correlation analyses (Kriegeskorte *et al.*, 2009). Finally, we examined the difference between correlation coefficients by using the Fisher’s test (Fisher and Bennett, 1973).

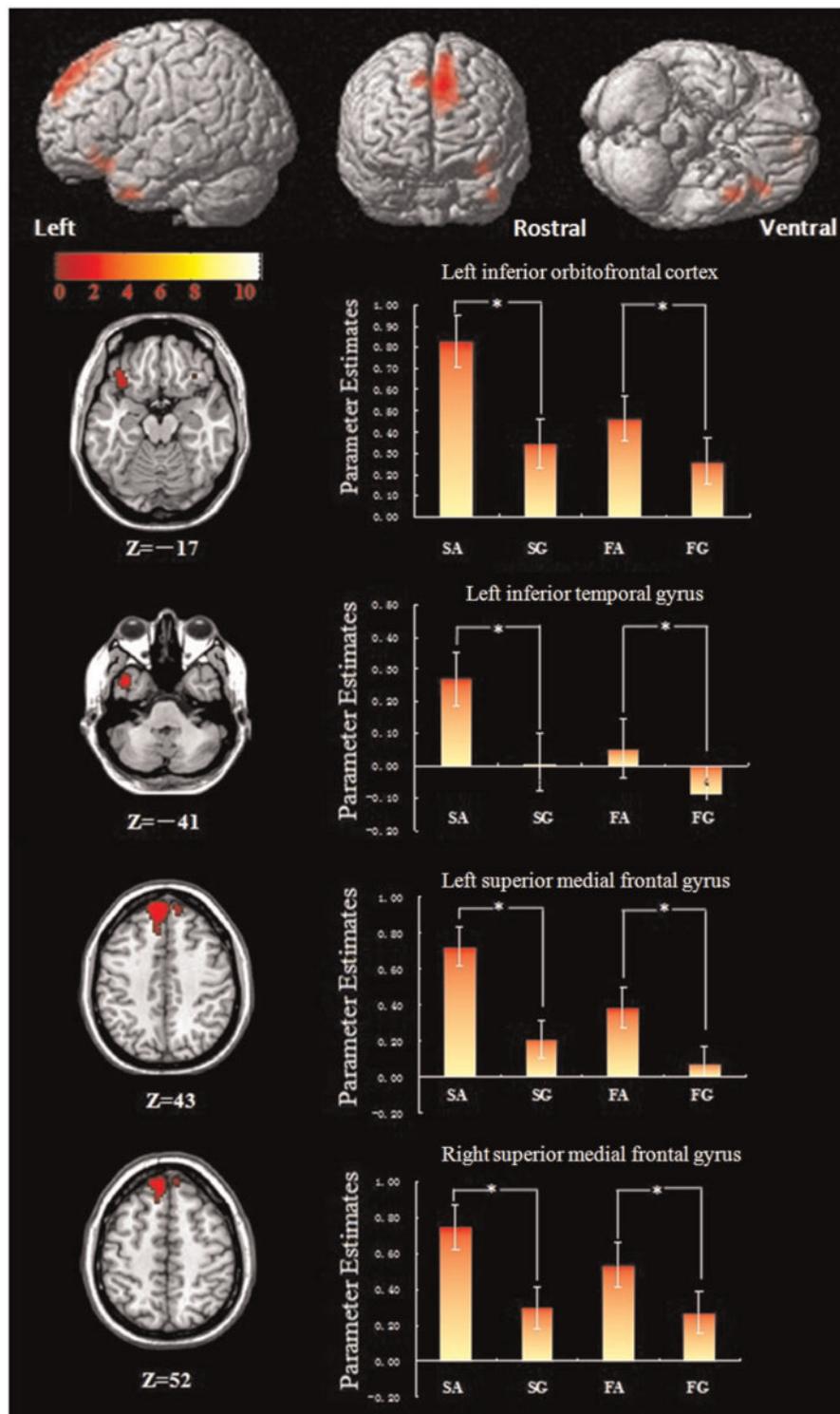


Fig. 3 The conjunction results of FA judgments and moral aesthetic judgments. Left ITG, left inferior OFC and bilateral superior medial frontal gyrus were found to exhibit a conjunction effect in both contrasts of 'aesthetic judgment > gender judgment' for faces and scenes. Mean parameter estimates in left inferior OFC, left ITG and bilateral superior medial frontal gyrus are shown in four conditions: scene aesthetic judgment (SA), scene gender judgment (SG), face aesthetic judgment (FA), and face gender judgment (FG). A LOOCV analysis was performed (see 'fMRI data analysis' for details) to ensure that the data examined within each ROI are independent from the procedure used to define the ROI. * $P < 0.05$.

Results

Behavioral results

Behavioral results in Experiment 2 did not exhibit significant performance differences between beautiful and common faces (RTs: $t_{21} = 0.11$, $MSE = 9.18$, $P > 0.05$, Cohen's $d = 0.01$; accuracy: $t_{21} = -0.48$, $MSE = 0.01$, $P > 0.05$, Cohen's $d = -0.11$), or moral beauty and

moral neutral scenes (RTs: $t_{21} = 0.45$, $MSE = 10.51$, $P > 0.05$, Cohen's $d = 0.04$; accuracy: $t_{21} = -1.79$, $MSE = 0.01$, $P > 0.05$, Cohen's $d = -0.32$). However, for the post-scan rating session, we found significant differences between the ratings of beautiful (5.08 ± 0.46) and common (2.97 ± 0.52) faces ($t_{21} = 11.72$, $MSE = 0.20$, $P < 0.05$, Cohen's $d = 3.87$) as well as significant difference

between ratings of moral beauty (4.84 ± 0.64) and neutral (3.58 ± 0.49) scenes ($t_{21} = 12.85$, $MSE = 0.21$, $P < 0.05$, Cohen's $d = 3.07$), indicating that there was no mismatch between our stimuli

Table 1 Peak voxel size for all regions obtained from the whole-brain random-effects contrasts in Experiment 1 ($P < 0.05$, FWE corrected at the voxel level and $P < 0.05$, FWE corrected at the cluster level)

Anatomical region	Hemisphere	x	y	z	t-score	Voxel size
Facial aesthetic judgment > facial gender judgment						
Superior medial frontal cortex	L	-6	50	43	7.762	341
	R	9	47	52	5.480	20
Inferior tempora lgyrus	L	-42	8	-41	6.159	31
Inferior OFC	L	-39	29	-17	5.819	44
Scene Moral Aesthetic Judgment > scene Gender Judgment						
Inferior OFC	L	-51	29	-2	11.601	9409
	R	45	29	-8	11.410	172
Superior medial frontal cortex	L	-6	50	43	11.270	111
ITG	L	-45	10	-41	7.570	20
Cerebellum	R	24	-82	-32	11.856	899
Rectus gyrus	L	0	47	-20	7.016	23
Middle cingulate	L	-3	-13	37	6.566	33
Middle occipital cortex	R	34	34	34	5.904	45
Precuneus	L	-33	-82	31	5.553	21
Precuneus	R	9	-73	58	5.875	53
Conjunction analysis						
Superior medial frontal cortex	L	-6	50	43	7.762	340
	R	9	47	52	5.480	19
ITG	L	-42	8	-41	6.159	31
Inferior OFC	L	-39	29	-17	5.819	44

Note: The *t*-scores computed by SPM8 quantify the statistical difference between the two conditions. Coordinates refer to the stereotactic space of the Montreal Neurological Institute.

selection criteria and participants' perception of facial and moral beauty.

Imaging results

We found that compared with FCs, FBs elicited stronger activation in the left inferior OFC, left putamen, left SFG and right middle occipital cortex (see Table 2 and Supplementary Figure S2). Stronger brain activation related to scenes conveying moral beauty (contrasted with those related to SNs) was observed in a large-scale brain network, including the left inferior OFC, right medial OFC, left middle temporal gyrus, left middle frontal gyrus, angular gyrus, right paracentral lobule,

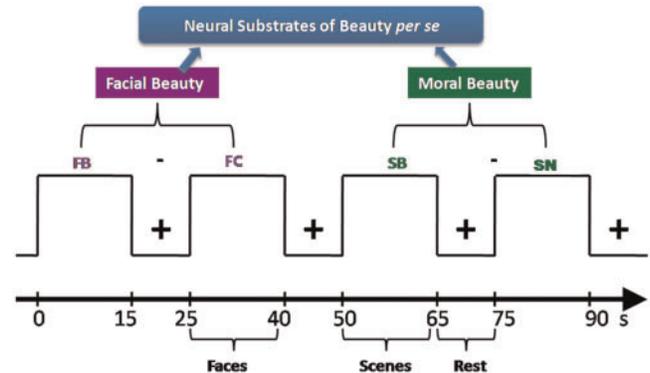


Fig. 5 Experimental design and procedure in Experiment 2. Participants viewed stimuli in four different types of blocks: FB, FC, SB and SN. The neural substrates of facial beauty were identified by the contrast of 'FB-FA'. The neural substrates of moral beauty were identified by the contrast of 'SB-SN'. Each block lasted for 15 s and was followed by 10 s of fixation.

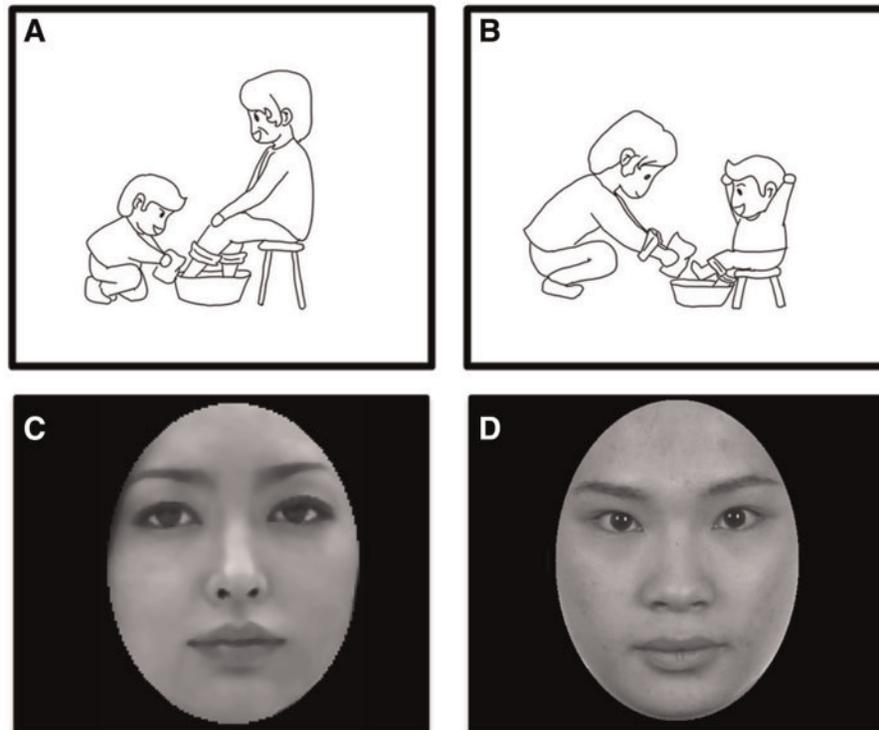


Fig. 4 Examples of stimuli in Experiment 2. Figure (A) and (B) demonstrate two examples of scene drawings, which are matched for visual complexity, familiarity and artistry with identical main character and background. Figure (A) depicts moral beauty scenes, in which the main character is performing a morally beautiful behaviour, and Figure (B) demonstrates morally neutral scene, in which the main character is performing a neutral behaviour. Figure (C) is an example of beautiful face, and Figure (D) is an example of common face.

bilateral middle cingulate, left post cingulate, and left precuneus (see Table 2 and Supplementary Figure S2).

A conjunction analysis of the above two contrasts showed that the left inferior OFC was activated by both facial beauty and moral beauty

Table 2 Peak voxel size for all regions obtained from the whole-brain random-effects contrasts in Experiment 2 ($P < 0.001$, uncorrected at the voxel level and $P < 0.05$, FWE corrected at the cluster level)

Anatomical region	Hemisphere	x	y	z	t-Score	Voxel size
Beautiful Face > common Face						
Putamen	L	-28	-8	10	5.18	1743
Inferior OFC	L	-38	42	-10	4.80	837
SFG	L	-16	30	44	4.44	408
Middle occipital cortex	R	38	-72	18	4.38	458
Moral beauty scenes > ordinary scenes						
Middle temporal gyrus	L	-64	-16	-18	6.94	589
Middle frontal gyrus	L	-40	18	48	5.03	379
Paracentral lobule	R	4	-36	70	5.01	2444
Middle cingulate	L	-4	-16	40	4.69	292
	R	4	-22	40	4.37	81
Post cingulate	L	0	-36	28	4.15	200
Precuneus	L	-14	-60	36	4.03	81
Medial OFC	R	12	52	-10	4.81	875
Angular	L	-42	-58	38	4.76	748
	R	48	-60	52	3.89	502
Inferior OFC	L	-36	40	-14	4.72	651
Conjunction						
Inferior OFC ^a	L	-38	44	-14	4.55	101

Note: The t -scores computed by SPM8 quantify the statistical difference between the two conditions. Coordinates refer to the stereotactic space of the Montreal Neurological Institute.
^aRefers to the fact that the activation was further corrected by a SVC analysis.

(see Table 2 and Figure 6). Given the heavy involvement of the OFC in mediating beauty in previous studies, we corrected for the multiple comparison error rate by applying an SVC on the statistical results (see 'Materials and Methods' section). The ROI was defined as a 20 mm sphere centred on the peak voxel in the OFC ($x = -21$, $y = 54$, $z = -9$), identified from a previous study (Winston et al., 2007). As a result, we discovered significant activation of the OFC ($x = -36$, $y = 38$, $z = -14$, peak $t = 4.58$) in the conjunction analysis (SVC, $P < 0.05$, FWE corrected). So, while the conjunction analysis revealed that there is a common cortical reward region (OFC) involved in the implicit perception of both facial and moral beauty, interestingly, the facial and moral beauty analyses revealed that the implicit perception of facial beauty involves both cortical (OFC) and subcortical (putamen) reward regions, whereas the implicit perception of moral beauty involves only a cortical reward region (OFC).

To further understand the neural properties of the OFC and the putamen in relation to facial and moral beauty, we conducted an ROI-based correlation analysis (see 'Materials and Methods' section for details). Both OFC and putamen activity positively correlated with facial beauty ratings (OFC: $r_{21} = 0.49$, $P < 0.05$; putamen: $r_{21} = 0.44$, $P < 0.05$) (see Figure 7A and B). Fisher's test (Fisher and Bennett, 1973) showed that there were no significant difference between the above correlation coefficients, $z = 0.15$, $P > 0.05$, indicating similar involvement of both cortical and subcortical reward systems in the perception of facial beauty. Additionally, we found a significant positive correlation between OFC activity and moral beauty ratings ($r_{21} = 0.67$, $P < 0.05$) (see Figure 7C) but no relationship between putamen activity and moral beauty ratings ($r_{21} = 0.21$, $P > 0.05$) (see Figure 7D). Fisher's test revealed a significant difference between the above correlation coefficients,

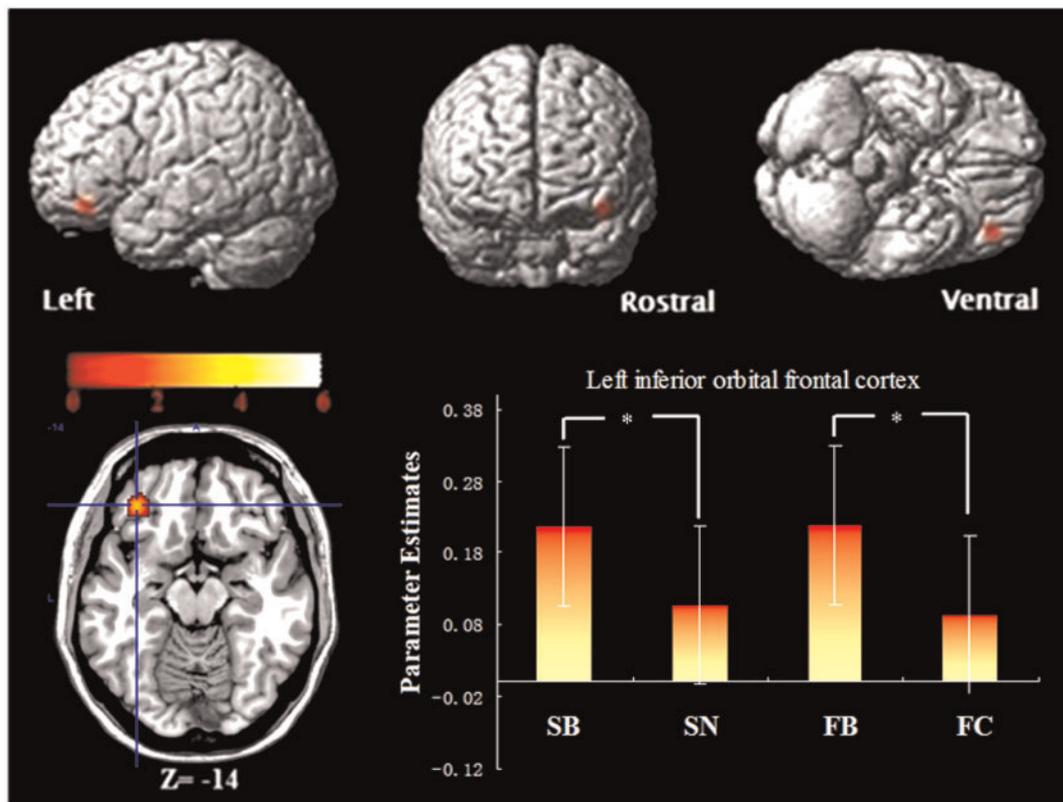


Fig. 6 The conjunction results of perception of physical and moral beauty. Left inferior OFC was found to exhibit a conjunction effect in both contrasts of 'beautiful faces > common faces' and 'moral beauty scenes > neutral scenes'. Mean parameter estimates in left inferior OFC are shown in four conditions: SB, SN, FB, and FC.

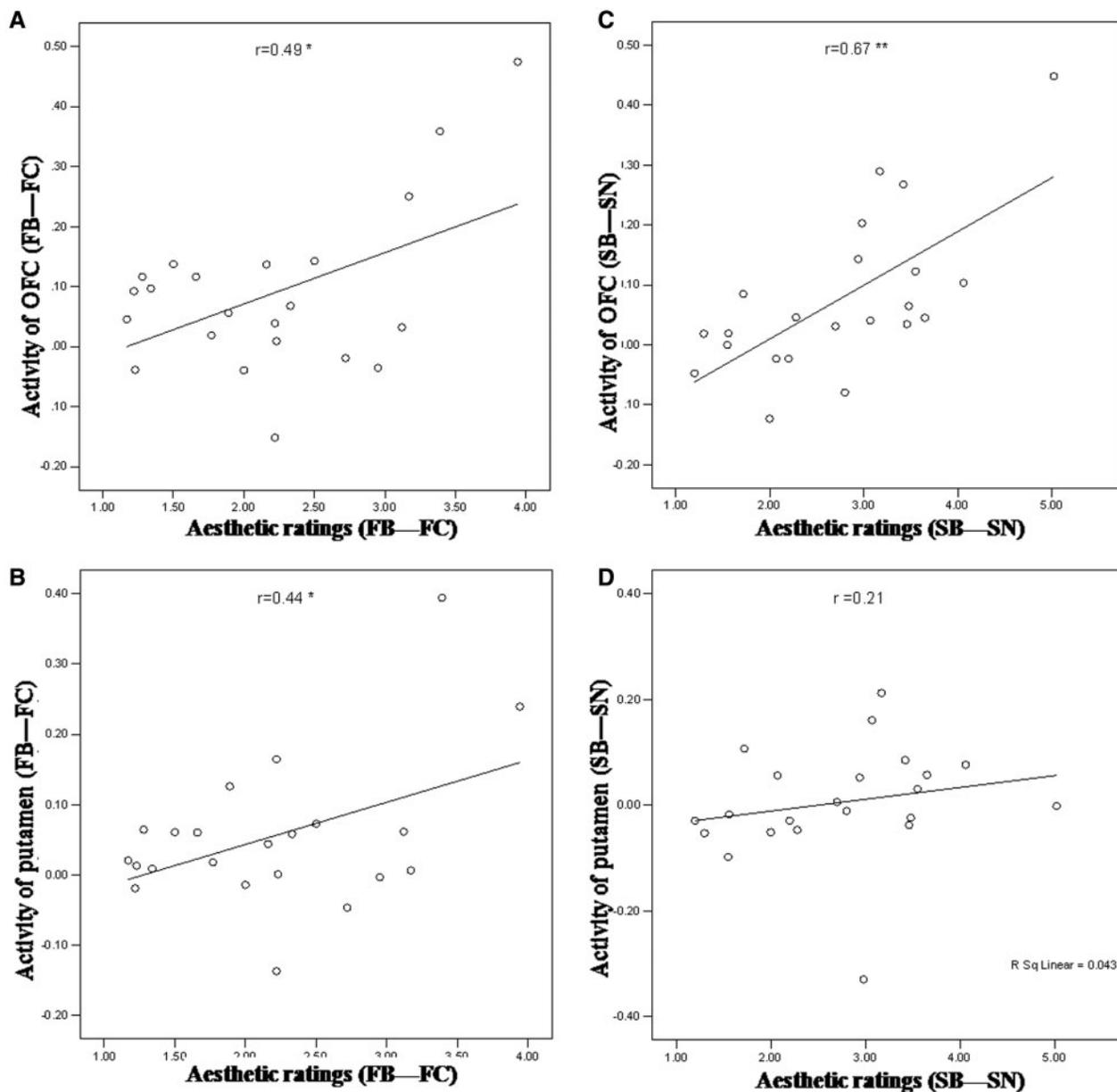


Fig. 7 The correlation analysis between brain activity and aesthetic ratings. (A) Correlation results of the activation of OFC with the rating difference of 'beautiful face > common face' (FB-FC). (B) Correlation results of the activation of putamen with the rating difference of 'beautiful face > common face' (FB-FC). (C) Correlation results of the activation of OFC with the rating difference of 'moral beauty scene > neutral scene' (SB-SN). (D) Correlation results of the activation of putamen with the rating difference of 'moral beauty scene > neutral scene' (SB-SN). $^*P < 0.05$; $^{**}P < 0.01$.

$z = 1.79$, $P < 0.05$, suggesting a stronger cortical (i.e. OFC) than subcortical involvement in the perception of moral beauty.

DISCUSSION

This study aimed to explore whether the cerebral representation of moral beauty is different from the cerebral representation of facial beauty. Experiment 1 investigated the network of moral aesthetic judgments and FA judgments (compared with non-aesthetic gender judgments). That is, Experiment 1 focused on the difference between tasks (aesthetic vs non-aesthetic). We identified the common involvement of the bilateral medial SFG, left ITG and left inferior OFC in moral aesthetic judgments and facial aesthetic judgments. Experiment 2 examined the network of facial beauty and moral beauty during implicit perception. That is, Experiment 2 focused on the difference between

stimuli (beautiful vs common or neutral). Besides, as no aesthetic task was involved, we could examine whether people could appreciate beauty (moral or facial) automatically and implicitly. We found that implicit perception of beauty also involved the activity of reward system. Facial beauty involved both the cortical reward region OFC and the subcortical reward region putamen, whereas moral beauty involved only the OFC. Moreover, compared with facial beauty, moral beauty spanned a larger-scale cortical network, indicating more advanced and complex cerebral representations characterizing moral beauty.

The network of moral aesthetic judgments and facial aesthetic judgments

Our finding of the bilateral medial SFG, left ITG and left inferior OFC activation in aesthetic judgment tasks was consistent with previous

studies (Moll et al., 2002, 2007; Greene et al., 2004; Heekeren et al., 2005; Jacobsen et al., 2006; Cupchik et al., 2009; Di Dio et al., 2011; Avram et al., 2012). It has been established that the ITG plays a critical part in recognition and representation of visual objects (Ungerleider, 1982; Nobre et al., 1994; Vandenberghe et al., 1996). The SFG is relevant for social cognition (Moll et al., 2002, 2007; Greene et al., 2004; Heekeren et al., 2005; Jacobsen et al., 2006), and the OFC is known for its central role in emotional processing (Camille et al., 2004; Kringelbach, 2005). Hence, the involvement of these regions in the aesthetic judgments is also in agreement with aesthetic theories, which pose that aesthetic judgment consists of perceptual, cognitive and emotional processing (Berlyne, 1971; Cupchik, 2002; Di Dio et al., 2011). As we hypothesized, our results clearly indicated that the aesthetic judgments, moral and facial alike, commonly relied on the orchestration of perceptual, cognitive and emotional components.

Notably, in addition to the overlapping regions activated during both tasks, moral aesthetic judgments also recruited several cortical regions, including the precuneus, rectus gyri, middle cingulate and middle occipital lobe (see Table 1, Supplementary Table S1 and Supplementary Material). Previous studies have demonstrated that precuneus and middle cingulate are related to theory of mind and empathy (Moll et al., 2002, 2005; Avram et al., 2012), whereas the rectus gyri is crucial for self-reference (Bai et al., 2012). Therefore, it is likely that activation in these additional regions served as the extra neural resources recruited for more advanced and comprehensive mental processing of moral aesthetic judgments. It is noteworthy that the explanations of the above activated brain areas are based on findings from previous studies. Further research is needed to explore these possibilities in greater detail.

The network of facial beauty and moral beauty

Our results showed that, similar to earlier findings, highly selective activity in response to beautiful faces was observed in the bilateral inferior OFC and putamen, even during implicit perception (Kranz and Ishai, 2006; Bray and O'Doherty, 2007), indicating that facial beauty is simultaneously mediated by both cortical (OFC) and subcortical (putamen) mechanisms. Furthermore, OFC activity was tuned by moral beauty, as evidently manifested in our ROI-based correlation analysis results. Furthermore, enhanced activity was discovered in a large-scale neural circuit including the left inferior OFC, right medial OFC, left middle temporal gyrus, left middle frontal gyrus, left post cingulate, bilateral middle cingulate and bilateral angular gyrus when contrasting the activation induced by moral beauty scenes to that induced by neutral scenes (see Table 2, Supplementary Table S2 and Supplementary Material). Previous studies have identified that the middle frontal gyrus is responsible for the memory storage (Leung et al., 2002). Angular gyrus, post and middle cingulate are evidenced to be involved in theory of mind and moral cognition (Zaidel and Nadal, 2011; Young and Dungan, 2012). The middle temporal gyrus is an important part in the neural representation of motor knowledge (Kourtzi and Kanwisher, 2000; Ruby and Decety, 2001; Phillips et al., 2002; Hauk et al., 2004; Wallentin et al., 2011). To summarize, the recruitment of regions lends direct support to our hypothesis of a more advanced and complex neural representation of moral beauty that spanned from regions responsible for basic perceptual processing to regions executing higher-order functionalities, even during implicit perception. However, further research is needed to directly explore these ideas in greater detail.

Critically, regions exhibiting preference for moral beauty did not involve any part of striatum (Figure 7). Both OFC and striatum are important constituents of the reward circuit (Wise, 2002). The striatum is known for its vital contribution to the cerebral representation

of the primary reinforcement that directly satisfies basic physiological needs (Wise, 2002; Pelchat et al., 2004; Grabenhorst et al., 2010; Haber and Knutson, 2010), while a number of studies have identified the significant role of OFC in mediating the mental pleasure related not only to the primary reinforcement, but also to the secondary reinforcement with social implications (Kriegeskorte et al., 2009; Brown et al., 2011; Tsukiura and Cabeza, 2011). Whereas previous studies have interpreted the preference of the OFC and putamen to processing beautiful faces as being related to both the social and physiological needs of humans, the subcortical insensitivity coupled with the OFC sensitivity to moral beauty scenes might entail intrinsic, exclusive association between moral beauty and high-level, non-physiological needs of humans, as implicated in the perspective of aesthetic theorists that moral beauty emerges on condition that individuals have internalized social norms and social expectations (Haidt, 2003a; Keltner and Haidt, 2003; Haidt et al., 2004).

In conclusion, this study suggests that moral aesthetic judgments and facial aesthetic judgments both involved the joint participation of perceptual, emotional and cognitive components. However, for the neural substrates of beauty, we found that implicit perception of beauty also involved the reward systems. The overlapping but different reliance on the reward systems implies that facial beauty is associated with both physiological and social needs, whereas moral beauty is associated with merely social needs. Moreover, moral beauty spanned a much larger-scale cortical network, indicating more advanced and complex cerebral representations characterizing moral beauty. Our work thus provides novel and compelling neural evidence in relation to the essence of moral beauty and advances the current knowledge of the neural mechanisms underlying aesthetic processing.

SUPPLEMENTARY DATA

Supplementary data are available at SCAN online.

Conflict of Interest

None declared.

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