Neural Responses to Facial Attractiveness in the Judgments of Moral Goodness and Moral Beauty

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Abstract

The judgments of moral goodness and moral beauty objectively refer to the perception and evaluation of moral traits, which are generally influenced by facial attractiveness. For centuries, people have equated beauty with the possession of positive qualities, but it is not clear whether the association between beauty and positive qualities exerts a similarly implicit influence on people`s responses to moral goodness and moral beauty, how it affects those responses, and what is the neural basis for such an effect. The present study is the first to examine the neural responses to facial attractiveness in the judgments of moral goodness and moral beauty. We found that beautiful faces in both moral judgments activated the left ventral occipitotemporal cortices sensitive to the geometric configuration of the faces, demonstrating that both moral goodness and moral beauty required the automatic visual analysis of geometrical configuration of attractive faces. In addition, compared to beautiful faces during moral goodness judgment, beautiful faces during moral beauty judgment induced unique activity in the ventral medial prefrontal cortex and midline cortical structures involved in the emotional-valenced information about attractive faces. The opposite comparison elicited specific activity in the left superior temporal cortex and premotor area, which play a critical role in the recognition of facial identity. Our results demonstrated that the neural responses to facial attractiveness in the process of higher order moral decision-makings exhibits both task-general and task-specific characteristics. Our findings contribute to the understanding of the essence of the relationship between morality and aesthetics.

Introduction

The face is a highly salient social signal; thus, people pay attention to faces. Facial features that indicate an individual's biological and evolutionary fitness (Darwin, 1871) are commonly considered attractive (Perrett et al., 1999; Rhodes et al., 2001). Attractiveness carries positively valenced stereotypes (i.e., the attractiveness halo effect) (Dion et al., 1972; Nisbett & Wilson, 1977). Facial attractiveness and the positively-valenced stereotypical information with which it is typically associated is believed to come to mind spontaneously upon encountering attractive individuals (Olson & Marshuetz, 2005; van Leeuwen & Macrae, 2004).

The evaluation of facial attractiveness is fast and automatic and serves as the basis for inferences about a person`s socially relevant personal traits (Chatterjee et al., 2009; Locher et al., 1993; Olson & Marshuetz, 2005; Sui & Liu, 2009), initially based on the perception of subtle variations in the facial features that have evolutionary significance (Oosterhof & Todorov, 2008; Zebrowitz et al., 2003). Chatterjee et al (2009) found that the core neural system, which is specialized for early visual processing of face perception and face identity (Fang & He, 2005; Grill-Spector et al., 2017), mainly including the interior occipital gyrus (IOG) and the fusiform face gyrus (FFA), is also involved in the visual processing of attractive faces before object identification, even when subjects were not explicitly attending to the attractive faces (Kranz & Ishai, 2006; Winston et al., 2007; Chatterjee et al., 2009). Iaria et al. (2008) also found that the FFA is activated when making facial attractiveness judgments (Iaria et al., 2008) and that the FFA mainly processes the invariant features (configuration) of the faces. The IOG provide a coarse processing of some aspects of the visual stimulus, then regions more anterior and including visual association cortices (e.g., FFA) construct more extensive, fine-grained perceptual representations that depend more on processing the configuration of the faces (Liu et al., 2010; Pitcher et al., 2011; Steeves et al., 2006). EEG studies have shed light on the temporal dynamics of attractiveness processing, indicating that attractiveness may begin to exert effects as early as the structural encoding stage. Early indices of visual processing, including the early posterior negativity and N170 components, are modulated by facial attractiveness (Marzi & Viggiano, 2010; Zhang & Deng, 2012). The FFA is thought to be the cortical source of the N170 response sensitive to facial attractiveness (Pizzagalli et al., 2002).

The evaluation of facial attractiveness is believed to be an extension of functionally adaptive system for understanding the communicative meaning of emotional expressions, namely, the ability to read affective meanings, whose functional role is to prepare one`s behavior in relation to the other person (e.g., approach or avoidance) (Todorov, 2008). An attractive face is viewed as an approach expression that suggests not only a person *spositiveaffectivestate, butalsoaperson*s capacity to act in a confident, assertive, and friendly way (Montepare & Dobish, 2003). Attractive faces seem to be not simply a consequence of aesthetically pleasing characteristics, but rather an integration of multiple cues including physical appearance, inter-personal engagement, and emotional expression. After the early structural encoding stage of face processing, attractiveness has effects in later stages whereby affective and identity information is extracted from faces (Hahn & Perrett, 2014). Socially relevant positively-valenced information of attractive faces is subsequently labeled by the emotional systems involved in the perception of facial expressions, such as the medial orbotifrontal cortex (mOFC) (Haxby et al., 2000), to which the occipitotemporal cortices (OTC) have direct projections (Rolls, 2007). Previous works (Aharon et al., 2001; Bray & O'Doherty, 2007; Cloutier et al., 2008; Hahn & Perrett, 2014; Liang et al., 2010; O'Doherty et al., 2003; Winston et al., 2007; Zaki et al., 2011) have shown that a number of brain regions activations, including VTA, vmPFC, basal ganglia, and the NAcc, particularly the mOFC, are involved in the emotional evaluation of attractive faces.

Facial attractiveness, considered to be a fundamental aspect of human social interaction, has a profound influence on human social behaviors (Chatterjee, 2015; Kocsor et al., 2013; Maner et al., 2003; Olson & Marshuetz, 2005; Todorov et al., 2008; Zebrowitz & Collins, 1997). The individual facial attractiveness influence the evaluation and judgment on individual`s moral traits, known as the beauty-is-good stereotype (Griffin & Langlois, 2006). This reliance on aesthetic features to infer moral character suggests a close link between aesthetic and moral valuation (Ferrari et al., 2017). In general, the more attractive a person's face is, the more likely he or she is to be perceived as possessing socially desirable personalities, moral traits, such as kindness, honesty, friendliness and trustworthiness and higher moral standards (Dion et al., 1972; Feingold, 1992; Griffin & Langlois, 2006; Langlois et al., 2000; Snyder et al., 1977; Zebrowitz & Montepare, 2008), and to be happier and more successful in later life (French, 2002; Griffin & Langlois, 2006; Langlois et al., 2000; Lewis & Bierly, 1990; Rynes & Gerhart, 1990). Moral traits judgments from faces may reflect the general evaluation of faces or, at least, approximate this evaluation rather well (Todorov et al., 2008).

There is good empirical evidence that the evaluations of facial attractiveness and moral traits may rely on similar neural mechanisms (Luo et al., 2019; Tsukiura & Cabeza, 2011b; Wang et al., 2015). For instance, Tsukiura and Cabeza (2011) found that activity in the mOFC increased as a function of both perceived attractiveness and moral goodness ratings, and the activations elicited by attractive faces and morally positive behaviors were strongly correlated with each other. Wang et al (2015) identified the common involvement of mOFC in the facial attractiveness and moral beauty judgments. Luo et al (2019) further investigated the neural mechanisms underlying the integrated aesthetics of facial attractiveness and moral beauty, and also found that the activity of mOFC was collectively modulated by facial and moral beauty. In these studies, the researchers reasonably interpret the activation of mOFC as related to the positive emotions triggered by rewarding properties of the stimuli that are engaged automatically when viewing attractive faces or viewing positive moral behaviors.

Although neuroimaging research has greatly enhanced our understanding of responses to facial attractiveness and moral judgments, a closer look reveals limitations of previous literature. First, in previous studies, facial attractiveness and moral judgments were mostly investigated separately, and largely at the level of consciousness (Todorov, 2008; Todorov et al., 2008; Tsukiura & Cabeza, 2011b; Wang et al., 2015). In fact, the perceptions of facial attractiveness and moral evaluation are always simultaneously involved in human beings. In reality, the observers are often unaware of the extent to which the individual's facial attractiveness influences their judgments when they make explicit judgments on an individual's moral behaviors or moral traits (Luo et al., 2019). Both types of perceptions are inherently imbued with affect and, most likely, both serve to infer potential intentions of others (Said et al., 2011; Todorov, 2008). As such, it would be of high ecological validity to examine how these forms of information are processed and integrated naturally, which may also provide a window to understand the influence of face appearance on moral judgments. Second, although researchers have shown a profound interaction between facial attractiveness and moral valuation (Dion et al., 1972; Ferrari et al., 2017; Luo et al., 2016; Oosterhof & Todorov, 2008; Stolier et al., 2018; Zhang et al., 2014), they seemed to focus much of their discussion on activations within reward networks, they did not further examine the possibility that perceptual responses to attractive faces might trigger the activation of these reward circuits. Third, the shared neural mechanisms between facial attractiveness and moral judgments are not enough to suggest that facial attractiveness contributes equally to different kinds of moral judgments. Nor it is clear how the positively valenced information of attractive faces generates value signals in different sectors of the reward circuit. Studies have shown that the neural responses to attractive faces depend on the task being performed, specifically, the brain regions of attractive faces activated by explicit aesthetic judgments were different from those activated by age judgments unrelated to facial attractiveness (Chatterjee, 2015; 2009; Chatterjee & Vartanian, 2016; Winston et al., 2007). In other words, the explicit assessment of a face for its attractiveness recruits value signals in the mOFC that are not taken into account when the same face is inspected with respect to other task demands (Chatterjee et al., 2009; Kim et al., 2007).

Moral goodness and moral beauty are two kinds of moral judgments that are often paid attention to in human daily life. They have one thing in common, that is, the object of both judgments is universal human good moral traits (kindness, virtue, etc.) or positive moral behaviors (Cheng et al., 2020). Moral goodness judgment requires the subjects to evaluate how good an individual`s positive moral behavior, whereas moral beauty judgment requires the subjects to assess the inner beauty of the individual who perform the positive moral behavior. Both judgments consist of the appraisal of perceived positive moral traits, such as the virtues of helping others or of sacrificing one's own life for others, and both recruit the inferior temporal cortex (ITC), a ventral visual brain region involved in the perception, recognition and representation of visual objects (Nobre et al., 1994; Vandenberghe et al., 1996), and faces (Haxby et al., 2000), and the lateral orbitofrontal cortex (OFC), a reward circuit that significantly responds positively to rewarding objects in general (Cheng et al., 2020; Troiani et al., 2016).

Although moral beauty and moral goodness objectively refers to the same human moral acts or virtues, they had differences in the strength of emotional reactions and motivations (Cheng et al., 2020; Diessner et al., 2006, 2008; Keltner & Haidt, 2003). When judging a positive moral behavior of an individual as moral goodness, the observer quickly evaluates the level of morality by focusing on the behavior itself, the observation of the behavior and the perception of the visual features of the individual performing the moral behavior (Lieberman, 2007), but the observer might remain emotionally unmoved and un-elevated (Cheng et al., 2020; Diessner et al., 2006; Güsewell & Ruch, 2012; Wang et al., 2015). The object of moral goodness is experienced as part of the material world under the circumstances of no deeply emotional involvement (Diessner et al., 2008). It seems to be concerned with the psychological processes of physical, visible characteristics and behaviors of one person, which are perceived through sensory patterns and experienced as a part of the physical world. In contrast, when evaluating the inner beauty of a person who performs the same positive moral act as moral goodness, the observer focuses on the internal spiritual, emotional and experiential characters of this person (Haidt, 2003) by understanding his or her mental states (i.e., theory of mind, ToM) and vicariously experiencing similar feelings (i.e., empathy) (Cheng et al., 2020). As a kind of aesthetic judgment, moral beauty can generate a aesthetic feeling and triggers emotional elevation (Diessner et al., 2006; Haidt, 2003, 2007; Keltner & Haidt, 2003; Pohling & Diessner, 2016). This moral elevation is an approach-oriented emotion, that is, it can trigger a feeling of warmth and expansion and a common eagerness of self-improvement to prompt the observer to do the similar positive moral behavior in the similar situation (Algoe & Haidt, 2009; Diessner et al., 2013; Haidt, 2003; Haidt & Keltner, 2004; Schnall et al., 2010; Shiota et al., 2014; Van de Vyver & Abrams, 2015, 2017). Whether the brain triggers emotional elevation seems to be the most essential difference between moral goodness and moral beauty judgments.

Therefore, when assessing the level of moral goodness and moral beauty of a particularly good-looking individual's morally positive behavior, will the attractive appearance of the individual have different effects on the observer's judgments of goodness and beauty? For centuries, people have equated beauty with the possession of positive qualities, but it is not clear whether the association between beauty and positive qualities exerts an implicit influence on people`s responses to moral goodness and moral beauty, how it affects, and what is the neural basis for such an effect. Given the introduction above, indicating that moral goodness and moral beauty judgments rely on both common cognitive processes as well as distinct and specific cognitive components, we hypothesize that the visual feature processing of attractive faces is likely to automatically activate the ventral occipitotemporal cortices during the judgments of moral goodness and moral beauty. The lower-level visual analysis of facial attractiveness might play a role in the judgments of moral goodness or moral beauty. In addition, one study showed that brain regions involved in emotional meanings are typically activated by triggering an observer's emotional response (Emery & Amaral, 2000). We speculate that the affective meanings of attractive faces may separate out into different patterns of representation. As a moral judgment and a aesthetic judgment that requires deep emotional involvement, attractive faces in moral beauty judgment task would evoke brain regions related to emotional evaluation. But the moral goodness judgment does not require the observer to be emotionally involved, so an individual's attractive face may not activate the brain regions associated with the representation of emotional meanings. Facial attractiveness may influence both types of judgments in similar and distinct ways.

Methods

Subjects

Twenty-two (mean age = 21.5 years, s.d. = 1.7) healthy, right-handed female undergraduate students with no history of psychiatric and neurological disorders were recruited as subjects in South China Normal University. Only female subjects were invited to participate in the experiment for the purpose of eliminating possible confusion between the gender of the subjects and the gender of the characters pictured in experimental materials (Cheng et al., 2020; Liang et al., 2010; Luo et al., 2019). More importantly, females are reported to generate more consistent aesthetic ratings across subjects for heterosexual faces than males (Luo et al., 2019; Tsukiura & Cabeza, 2011a), and females are more easily moved by scenes of moral judgments than males (Amoyal, 2014; Freeman et al., 2009; Haidt & Keltner, 2004; Janicke & Oliver, 2017; Landis et al., 2009). All subjects were assessed to ensure normal or corrected to normal vision. Informed consent was obtained from all subjects before the experiment according to the requirements of the Research Ethics Review Board of South China Normal University. Subjects received monetary compensation for their participation in the study.

Materials

As described in our previous study (Cheng et al., 2020), experimental materials consisted of a series of black and white scene drawings depicting morally positive behaviors acted by male characters in daily life. In accordance with previous studies (Luo et al., 2019; Wang et al., 2015), short sentences that described morally positive behavior (i.e., He helps the elderly cross the road, he escorts the injured to the hospital, he visits the orphans in the orphanage, etc) were collected. Then, black-and-white scene drawings were created based on the content of these sentences. For each scene, a red capital letter “A” was drawn beside the main character to distinguish the character from other figures shown in the scene drawing. And for each scene, there were two versions of the main character’s facial attractiveness: a beautiful-face version and an ugly-face version, both of which are based on real male photos of beauty and ugliness. The manipulation of facial attractiveness was not limited to the systematic change of a certain facial feature but rather to the random combination of several facial features (Cui et al., 2019). Our research focused on Fechner’s concept of internal psychophysics (the relationship between subjective experience and physical characteristics of neural systems), not on the external psychophysics (the relationship between subjective experience and physical characteristics of stimuli). Although we are interested in the brain areas of neural responses to facial attractiveness on moral goodness and moral beauty, we didn’t know what specific visual features caused such responses.

Twenty-two female subjects (mean age = 21 years, range, 18-24 years; healthy, right-handed college students from South China Normal University with no history of psychiatric and neurological disorders) who had never participated in our similar experiments before, were recruited for the pilot study to validate the scene drawings. The sample size was determined by G*Power (Faul et al., 2007) analysis that would provide sufficient power to detect a medium effect size ($f = 0.25$). Similar to the method of validating materials used in Cui et al (2019), first, subjects were asked to evaluate the moral level of the main character’s behavior described in the scene drawing on a 7-point scale (1= especially good to 7 = especially bad), with the character’s face blurred to prevent the influence of facial attractiveness on the behavior evaluation. According to the results, scene drawings with average scores greater than 4 were excluded to ensure that all the behaviors described in the scene drawings were positive. Second, the same subjects were asked to assess the facial attractiveness of the main character also on a 7-point scale (1= especially beautiful to 7 = especially ugly), with other parts of the drawings blurred to avoid the impact of the scene and the main character’s behavior on the facial attractiveness assessment. Based on the results, drawings with average scores greater than or equal to 4 were excluded for the beautiful-face version scene drawings, and average scores less than or equal to 4 were excluded for the ugly-face version scene drawings. Pilot task orders were counterbalanced across subjects. Finally, a total of 104 scene drawings depicting 4 different moral levels of positive behavior (especially good, rather good, slightly good and neutral), of which each level contained 26 scene drawings. Each scene had one beautiful-face version and one ugly-face version, composing 208 validated scene drawings that were used as the materials for the fMRI experiment (see Fig. 1). Scene drawings were 589×500 pixels.

The scene drawings depicting morally positive behaviors were then randomly assigned to two sets used for different moral judgments, respectively, to avoid the repeated use of the same type of stimuli in different tasks. Each set contained 52 scenes drawings, in which each scene had a beautiful-face version and an ugly-face version. The mean rating scores for each moral level of each version of faces in the two sets of materials were calculated and subjected to a 2 (set: the first vs. the second) × 2 (face: beautiful face vs. ugly face) × 4 (moral level: especially good vs. rather good vs. slightly good vs. neutral) repeated measures ANOVA using JASP to examine whether the materials of the two sets were equivalent. Results showed that the main effect of set was not significant, $p > 0.05$, the main effect of face was not significant, $p > 0.05$, the main effect of moral level was significant, $F(3, 63) = 265.07$, $p < 0.001$, with a reasonable increase observed in the average rating scores as a function of moral levels (*m.d.±s.e.* 1.63±0.07, 2.18±0.07, 2.3±0.07 and 3.5±0.07 for level 1, 2, 3 and 4, respectively). The interactions between set and face, between set and level, between face and level were all not significant, $ps > 0.05$. The three-way interaction among set, face and moral level was also not significant, $p > 0.05$. Results showed no significant difference between the two sets of materials, which ensured that the two sets were equivalent. These results are significantly important because it indicates that the difference in activation of brain regions involved in the judgments of moral goodness and moral beauty was not caused by differences in experimental stimuli.

Thus, for each judgment task, 52 scene drawings depicting 4 different moral levels (i.e., especially good, rather good and slightly good and neutral) were used that contained 52 beautiful-face scene drawings and 52 ugly-face scene drawings. The allocation of these parts of the materials was balanced across different tasks. The selected stimuli generated the following conditions with an equal number in each: the beautiful-face-version stimuli in moral goodness judgment (BFMG), the ugly-face-version stimuli in moral goodness judgment (UFMG), the beautiful-face-version stimuli in moral beauty judgment (BFMB) and the ugly-face-version stimuli in moral beauty judgment (UFMB). Different moral levels contained in each condition were used as parameters to identify brain regions involved in different judgment tasks, which displayed altered activity simply as a function of the moral ratings in the fMRI data analysis.

Experimental Procedure

The fMRI experiment contained two tasks: (i) the moral goodness judgment (MG), (ii) the moral beauty judgment (MB). Another group of twenty-two female subjects, who had not participated in the pilot experiment nor similar experiments before, were recruited and performed the tasks listed above. in moral goodness judgment task, subjects were asked to look at the scene drawings and rate the level of goodness of the main character's moral behavior on a 4-point scale (1 = especially good, 4 = neutral); in moral beauty judgment task, subjects were instructed to look at the scene drawings and rate the inner beauty of the main character on a 4-point scale (1 = especially beautiful, 4 = neutral). Two equivalent sets that were used separately in moral goodness and moral beauty judgments were balanced across subjects. Two tasks constituted two runs of the whole fMRI experiment. Run orders were counterbalanced across subjects. The order of presentation of experimental stimuli was randomized between subjects in these tasks. During scanning, an event-related design was applied with two runs.

As described in Cheng et al (2020), a single trial began with the instrument slide, which enlightened the subjects about the specific tasks to perform next. This slide was presented for 4000 ms. Next, one scene drawing was presented with a 4-point scale under it, in which the number indicated the corresponding level of moral behavior or inner beauty of the main character. Subjects were instructed to assess the moral level of the main character's behavior and the level of inner beauty of the main character depicted in the scene drawing as quickly as possible within 4000 ms. Using a response box with buttons labeled 1 to 4, half of the subjects made a left index finger response (i.e., 1 or 2) for the "especially" and "rather" levels of stimuli and a right index finger response (i.e., 3 or 4) for the "slightly" and "neutral" levels. Reverse responses were used for the other half of subjects to balance any influence of movement on data. Once the response was recorded, the rating bar disappeared and was followed by a blank display for a random period ranging between 500-5000 ms. If the scene drawing slide was not presented for 4000 ms after subjects pressed the key, the scene drawings disappeared, and a blank display will appear for the remaining time. The maximum duration of the presentation of the scene drawing slide was 4000 ms, based on the results of a pre-behavioral test. Each run was scanned for approximately 13 minutes. The detailed experimental procedure (See Fig. 2) is as follows:

After the fMRI scanning, in order to examine the efficiency and the stability of facial features of the main character in the scene drawings, subjects were immediately asked to assess the facial attractiveness on a 7-point scale (1= especially beautiful to 7 = especially ugly). All the stimuli were the same as those applied in fMRI scanning for each subject, except other parts of the drawings blurred to avoid the impact of the scene on the facial attractiveness assessment. Like the pilot experiment, scene drawings with average scores greater than or equal to 4 were excluded for the beautiful-face version scene drawings, and average scores less than or equal to 4 were excluded for the ugly-face version scene drawings.

Fmri Data Acquisition

The fMRI data were acquired using a 3 T Siemens Trio scanner with a 12-channel phase array head coil at South China Normal University. Functional images were obtained with a T2*-weighted gradient echo planner imaging sequence using the following parameters: TR = 2000 ms, TE = 30 ms, flip angle = 900, FOV = 204 × 204 mm^2, acquisition matrix = 64 × 64, and 33 interleaved axial slices (thickness/gap = 3.5/0.8 mm) covering the whole brain. High-resolution anatomical images were also obtained for each participant with a T1-weighted 3D MP-RAGE sequence using the following parameters: TR = 1900 ms, TE = 2.52 ms, flip angle = 9°, FOV = 256 × 256 mm^2, acquisition matrix = 256 × 256, thickness = 1.0 mm, and 176 contiguous sagittal slices.

Fmri Data Analysis

Data preprocessing and statistical analyses of all images were conducted using SPM12 (Welcome Trust Center for Imaging, London, UK; http://www.fil.ion.ucl.ac.uk/spm). For each run of each participant, in preprocessing, images were spatially realigned to the first volume to correct for head movements (no individual run was more than 3.0 mm displacement or 1.0^o rotation). These aligned functional images (coregistered with the anatomical image) were then spatially normalized into the Montreal Neurological Institute (MNI) template and resampled with voxel size of 2×2×2 mm^3. After that, the data were smoothed with an isotropic full-width half-maximum 6 mm Gaussian kernel.

In 208 scene drawings, the facial attractiveness (beautiful face or ugly face) of the main character was assessed by 22 participants on a 7-point scale (1= especially beautiful to 7 = especially ugly, see Fig. 2). Based on the results, drawings with average scores greater than or equal to 4 were excluded for the beautiful-face version scene drawings, and average scores less than or equal to 4 were excluded for the ugly-face version scene drawings.

For the statistical analyses of the functional data, condition-related brain activity changes were estimated using a general linear model (GLM) in four conditions at the single subject level, including the beautiful-face-version stimuli in moral goodness judgment (BFMG), the ugly-face-version stimuli in moral goodness judgment (UFMG), the beautiful-face-version stimuli in moral beauty judgment (BFMB) and the ugly-face-version stimuli in moral beauty judgment (UFMB). We defined each experimental condition as a predictor of interest, that parametrically modeled moral ratings of the presented items, respectively, and convolved these predictors with SPM12's canonical hemodynamic response function. In the given trails, the duration of a predictor of interest was equal to 4000ms. Six head-motion parameters estimated during the realignment were included in the model as predictors of no interest. The missed trials were not modeled and thus were included in the baseline. A high-pass filter (HPF) with a cutoff period of 128 s was applied to remove low-frequency noise. Note that, the task events were designed to minimize corrections, in order to estimate the neural responses to facial attractiveness during moral goodness and moral beauty judgment. For each subject, condition-related brain regions displaying altered activity simply as a function of moral ratings were identified by contrasting the parametrically modulated predictor of interest against baseline. The four first-level individual contrast images were then fed to the second-level analysis employing a whole-brain random-effects model.

First, we calculated the main effect of beautiful faces in moral goodness and moral beauty judgment tasks, respectively (moral goodness, contrast: BFMG–UFMG; moral beauty, contrast: BFMB–UFMB) and the main effect of ugly faces (moral goodness, contrast: UFMG–BFMG; moral beauty, contrast: UFMB–BFMB) to investigate the neural responses to facial attractiveness in these two judgment tasks. We then performed a conjunction analysis between the above two beautiful-face contrasts to identify cortical regions commonly involved in the processing of attractive faces in the judgments of moral goodness and moral beauty. Similarly, we also computed a conjunction analysis between the above two ugly-face contrasts to test whether ugly-face contrast in moral goodness judgment and ugly-face contrast in moral beauty judgment rely on similar neural mechanisms.

Secondly, we computed the direct comparisons between BFMG and BFMB, between UFMG and UFMB, to identify their unique cortical regions activation patterns. In addition, we also performed a conjunction analysis between the parameter-mediated contrasts of moral goodness (BFMG+UFMG) and moral beauty (BFMB+UFMB) to identify cortical regions commonly involved in moral goodness and moral beauty representation irrespective of facial attractiveness, i.e., beautiful-face vs. ugly-face.

Finally, we performed leave-one-subject-out iterative cross-validation (LOOCV) ROI analyses (Kriegeskorte et al., 2009; Pegors et al., 2015; Wang et al., 2015) on the significant clusters resulting from the above whole-brain analysis to test whether activity within any clusters responding to facial attractiveness in the judgments of moral goodness and moral beauty responded differently to beautiful-face versus ugly-face as a function of judgment tasks. In the LOOCV analyses, on each iteration, data from a single subject were held out as the test set. ROIs were then defined based on a group analysis of the n-1 remaining subjects, using a sphere with 6mm radius centered on the peak voxel of each significant cluster. Parameters estimates for each task were extracted from these ROIs in the n^{th} subject, and the procedure repeated 22 times. Parameter estimates were then averaged across subjects and were subjected to repeated-measures 2 (task: MG VS. MB) × 2 (face: beautiful-face VS. ugly-face) ANOVAs. This method gave us an estimate of the response in each ROI to beautiful-face and ugly-face in different judgment tasks, using independent data sets to define the boundary of the cluster and the strength of the effect.

At the group level, the resulting reported voxels are significant at $p < .05$ (FDR corrected), corrected for multiple comparisons across the whole brain. Clusters below the correction level were neither reported nor visualized. Statistical results were visualized with the MRIcron (https://people.cas.sc.edu/rorden/mricron) (McCausland Center for Brain Imaging, University of South Carolina) and BrainNetViewer (http://www.nitrc.org/projects/bnv/) (Xia et al., 2013).

Results

In the present study, we manipulated two kinds of information for the scene drawings used as experimental stimuli: facial attractiveness and moral behaviors. The data of facial attractiveness was obtained by asking the same participants to assess the level of facial attractiveness of the main character in the same material after the fMRI scanning. The first step in the data analysis was to examine whether the classification of facial attractiveness was effective and stable, and then to investigate whether the judgments of moral goodness and moral beauty were affected by facial attractiveness in the same way.

Behavioral Results

In order to examine the efficiency and the stability of facial attractiveness classification in the scene drawings, one independent-sample t-test was conducted on the rating scores of facial attractiveness, which were obtained in the pilot experiment and after the fMRI scanning, separately. The results showed that there was no significant difference in scores between the two experiments ($t = 1.344$, $p > 0.05$, cohen's $d = 0.16$). This result indicated the validity of categorizing experimental stimuli into two versions about the facial attractiveness and the stability of subjects' assessment of facial attractiveness of the main character in scene drawings. In the next behavioral data analysis, task scores for half of the subjects were converted to the same standard as the other half of the subjects (i.e., reverse coded), with largest number representing a neutral level.

The average rating scores and the average response times (RTs) of ratings for each level of moral behaviors of the main character with different facial attractiveness were calculated in moral goodness (MG) and moral beauty (MB) judgments of the fMRI experiment and subjected to a 2 (task: MG vs. MB) × 2 (face: beautiful-face vs. ugly-face) × 4 (moral level: especially good/beautiful vs. rather good/beautiful vs. slightly good/beautiful vs. neutral) repeated measures ANOVA using JASP. The Greenhouse-Geisser correction for non-sphericity of data was applied as necessary. The uncorrected degree of freedom, corrected p-values and effect sizes (partialη^2) are reported. The p-values of the pairwise comparisons were adjusted using a Bonferroni correction. For all analyses, the significance level was set to .05. The results of average rating scores revealed that the main effect of task was marginally significant, $F(1, 21) = 3.72$, $p = 0.07$, partial$\eta^2 = 0.15$, showing that compared with moral goodness, positive moral behaviors were more likely to be rated beautiful (*m.d.±s.e.* MB:2.31±0.1; MG:2.39±0.11); the main effect of face was marginally significant, $F(1, 21) = 3.85$, $p = 0.06$, partial$\eta^2 = 0.16$, showing that the main character with beautiful-face was rated as behaving more beautiful or better (*m.d.±s.e.* BF:2.33±0.11; UF:2.36±0.11) than ugly-face; the main effect of moral level was significant, $F(3, 63) = 150.85$, $p < 0.001$, partial$\eta^2 = 0.88$, with a reasonable increase observed in the average rating scores as a function of moral levels (*m.d. ±s.e.* 1.54±0.09, 2.12±0.12, 2.24±0.12 and 3.5±0.09 for levels 1, 2, 3 and 4, respectively). The interactions between task and face, between task and level were all not significant, $ps > 0.05$. The interaction between face and moral level was significant, $F(3, 63) = 4.9$, $p < 0.01$, post hoc comparisons showed that the behavior of the main character with beautiful-face was significantly rated either the most beautiful or the best on the moral level 1, $t(21) = 3.35$, $p = 0.03$. In addition, the behavior of the main character with beautiful-face also showed a tendency to be more beautiful or better than that with ugly-face on the moral level 2 and 3. The three-way interaction among task, face and moral level was not significant, $p > 0.05$ (see Fig. 3).

The analysis of the response times (RTs) of ratings revealed that the main effects of task and face were all not significant, $ps > 0.05$. The main effect of moral level was significant, $F(3, 63) = 9.21$, $p < 0.001$, with the fastest responses observed for the "especially" level of moral behaviors (*m.d.±s.e.* 1845.81±72.51 for level 1) and the slowest responses observed for the "neutral" level (*m.d.±s.e.* 2132.15±80 for level 4). Importantly, the interaction between both variables was not significant, $ps > 0.05$. This result is very important because it indicates that fMRI analyses focused on the activity of brain regions involved in the processing of facial attractiveness occurred in the judgment tasks of moral goodness and moral beauty, and were not confounded by differences in task difficulty.

Fmri Results

Whole-brain analyses

To investigate the neural responses to facial attractiveness (beautiful faces, BFs and ugly faces, UFs), that occurred in the judgment tasks of moral goodness and moral beauty, our main analysis in GLM included 4 critical morally positive events (i.e., BFMG, UFMG, BFMB and UFMB) which parametrically modeled the moral ratings of the presented items, respectively.

First, compared to UFs, the condition of BFs in moral goodness judgment task significantly activated the left ventral occipitotemporal cortex (OTC), left superior temporal cortex (STC), left anterior temporal lobe (ATL) and left precentral gyrus/inferior frontal gyrus (IFG) (see Fig. 4A and Table 1), the opposite contrast showed no significant region; whereas compared to UFs, the condition of BFs in moral beauty judgment task significantly activated the left ventral occipitotemporal visual cortex (the left IOG and left FFA/lingual gyrus), left PCC/precuneus and vmPFC (refers to the ACC extended to mOFC) (see Fig. 4B and Table 1), the opposite contrast showed that the condition of UFs significantly activated the medial PFC (i.e., ACC), left middle frontal gyrus (MFG) and left temporo-parietal junction (TPJ) (see Fig. 4C and Table 1). Our results showed that the BFs in the judgment tasks of moral goodness and moral beauty commonly recruited 2 similar neural activations: left FFA (Temporal Fusiform Cortex, posterior division) and left IOG (Occipital Face Area, OFA). The conjunction analysis revealed significant overlap in the left IOG/OFA. We noticed that the conjunction analysis also activated the FFA, but did not reach a statistical significance, thus, we applied a small volume correction (SVC) to further check this issue. When performing the SVC, we defined a 10-mm radius sphere centered on the peak voxel of the left FFA. We found significant activation for the conjunction analysis in this area (see Fig. 5A and Table 1). To confirm a similar role of the left OTC on attractive faces in the judgments of moral goodness and moral beauty, we also calculated the correlation between the left IOG activations and between the left FFA activations under the conditions of attractive face for both tasks across subjects (see Fig. 5B). In the cluster of left IOG, we found a highly significant positive correlation ($r = 0.69$, $p < 0.001$), indicating that subjects with stronger IOG activation for moral goodness ratings also showed stronger IOG activation for moral beauty ratings. But left FFA correlations did not reach to be statistically significant and only just showed a positive trend ($r = 0.31$, $p = 0.16$).

Second, compared to BFs in moral goodness judgment, the BFs in moral beauty judgment uniquely activated the cingulate cortex, including the left PCC/precuneus and ACC extending to mOFC. The opposite contrast showed that the BFs in moral goodness judgment uniquely activated the left promotor area extending to the opercular part of the frontal area (precentral gyrus/IFG). In addition, compared to UFs in moral goodness judgment, the UFs in moral beauty judgment uniquely activated the left TPJ. And no differential activation was found for the opposite contrast (see Fig. 5C and Table 1).

Third, the conjunction analysis between the parameter-mediated contrasts of moral goodness and moral beauty irrespective of facial attractiveness revealed significant overlap in the right lateral OFC (see Fig. 6A). Further, we performed a LOOCV ROI analysis on this cluster to test whether activity responding to both moral goodness and moral beauty appreciations responded differently to beautiful-face versus ugly-face in those two different judgment tasks. It was found that there was not any significant effect, demonstrating that the activity in cortical region commonly involved in the judgments of moral goodness and moral beauty was not affected by facial attractiveness (see Fig. 6B).

Loocv Rois Analyses

To assess whether any of the above significant clusters responded selectively to beautiful or ugly faces in different judgment tasks, we performed a cross-validation analysis in which we iteratively defined the ROIs on n-1 subjects and then extracted parameters estimates for the “left-out” subject. Repeated measures ANOVAs indicated that there were significant effects of BFs over the left FFA and IOG/OFA, with no significant interactions for either moral goodness or moral beauty judgments. These results suggest that the left FFA (Fig. 7A) and IOG/OFA (Fig. 7B) respond similarly to variation in BFs for these two judgment tasks (FFA, $F(1, 21) = 5.37$, $p = 0.03$, partial$\eta^2 = 0.22$; IOG/OFA, $F(1, 21) = 4.45$, $p = 0.05$, partial$\eta^2 = 0.18$), demonstrating the general role of the ventral occipitotemporal cortex in the automatic processing of BFs in both the judgments of moral goodness and moral beauty. In contrast, within the ROIs of the left PCC/precuneus (Fig. 7C) and vmPFC (i.e., ACC extending to mOFC) (Fig. 7D), the main effects of task and face were all significant (PCC/precuneus, task: $F(1, 21) = 7.58$, $p = 0.01$, partial$\eta^2 = 0.27$; face: $F(1, 21) = 21.29$, $p < 0.001$, partial$\eta^2 = 0.5$; ACC/mOFC, task: $F(1, 21) = 14.98$, $p < 0.001$, partial$\eta^2 = 0.42$; face: $F(1, 21) = 3.82$, $p = 0.06$, partial$\eta^2 = 0.15$), and more importantly, the interactions between face and task were significant (PCC/precuneus, $F(1, 21) = 4.04$, $p = 0.05$, partial$\eta^2 = 0.2$; ACC/mOFC, $F(1, 21) = 4.75$, $p = 0.04$, partial$\eta^2 = 0.2$), which were mainly driven by higher activity in BFs in moral beauty judgment than UFs in moral beauty judgment (PCC/precuneus, $t(21) = 4.53$, $p < 0.001$; ACC/mOFC, $t(21) = 3.12$, $p < 0.001$), and higher than BFs in moral goodness judgment (PCC/precuneus, $t(21) = 3.41$, $p < 0.01$; ACC/mOFC, $t(21) = 4.16$, $p < 0.001$). These results demonstrated the unique roles of the left PCC/precuneus and ACC/mOFC in the processing of BFs in moral beauty judgment. Although the ACC was also significantly activated by ugly faces in moral beauty judgment, the ROI results showed that the activity of beautiful faces was significantly higher than that of ugly faces. Within the left TPJ (Fig. 7E), a significant effect for task - the moral beauty judgment elicited greater activity than the moral goodness judgment ($F(1, 21) = 7.55$, $p = 0.01$, partial$\eta^2 = 0.26$) - was found. No interaction between task and face was found in this area, but there was obviously a trend for higher activity in UFs than BFs in moral beauty judgment. Within the left MFG (Fig. 7F), there was significant effect of task - the moral beauty judgment elicited greater activity than the moral goodness judgment ($F(1, 21) = 10.89$, $p < 0.01$, partial$\eta^2 = 0.33$), and significant interaction ($F(1, 21) = 7.48$, $p = 0.01$, partial$\eta^2 = 0.25$), which was mainly driven by higher activity in UFs in moral beauty judgment than BFs in moral beauty judgment ($t(21) = 2.74$, $p = 0.01$), and higher than UFs in moral goodness judgment ($t(21) = 3.97$, $p < 0.001$). These results demonstrated that the left TPJ and MFG might play a critical role in the processing of UFs in moral beauty judgment. Within the ROI of the left precentral gyrus/IFG (Fig. 7G), significant effects for task and face were found, with higher activity in BFs in moral goodness judgment, but no significant interaction. This result indicated the unique role of left premotor area/IFG in the processing of BFs in moral goodness judgment.

Table 1
Coordinates, Voxel Count, and Peak t Values for Significant Clusters showing activation for effects of facial attractiveness comparing moral goodness (MG) to moral beauty (MB) judgments (whole-brain maps for each contrast were thresholded at *p* < .05, FDR-corrected)

Regions	R/L	BA	x	y	z	*t* score	size
Neural activity of beautiful faces in the MG judgment_(BFMG-UFMG)							
IOG	R	18	27	-87	-9	4.35	119
STC	L		-39	-75	24	4.18	95
FFA	L	37	-33	-30	-15	4.52	86
Precentral gyrus/IFG	L	9	-48	6	33	4.52	82
ATL	L	38	-48	12	-21	4.45	75
IOG	L	18	-33	-84	-9	3.76	40
Neural activity of ugly faces in the MG judgment_(UFMG-BFMG)							
No activation							
Neural activity of beautiful faces in the MB judgment_(BFMB-UFMB)							
PCC/Precuneus/FFA/Lingual Gyrus	L	31	-12	-48	33	5.73	642
vmPFC (ACC/mOFC)	L	32	-18	27	39	4.61	563
IOG	L	18	-27	-90	-9	4.72	82
Neural activity of ugly faces in the MB judgment_(UFMB-BFMB)							
TPJ (IPL/SMG)	L	40	-57	-45	48	5.15	379
ACC/mPFC	L/R	32	-6	42	9	4.26	135
MFG	L	8	-33	27	42	4.73	70
Conjunction of BFMG-BFMB_[(BFMG-UFMG) ∩ (BFMB-UFMB)]							
IOG	L	18	-33	-84	-9	3.76	29
FFA	L	36/37	-27	-36	-12	3.6	20(SVC)
Conjunction of UFMG-UFMB_[(UFMG-BFMG) ∩ (UFMB-BFMB)]							
No activation							
Conjunction of MG-MB_[(BFMG+UFMG) ∩ (BFMB+UFMB)]							
Inferior OFC/IFG/insular	R	45	30	27	3	4.89	61
Differences between facial attractiveness in the MG and MB judgments							
Unique regions of BFMG_(BFMG-BFMB)							
Precentral Gyrus/IFG	L	9/6	-51	21	30	4.1	159
Unique regions of UFMG_(UFMG-UFMB)							
No activation							
Unique regions of BFMB_(BFMB-BFMG)							
vmPFC (ACC/mOFC)	L	32/10	-9	45	-3	4	34
Unique regions of UFMB_(UFMB-UFMG)							
TPJ (IPL/SMG/Angular)	L	40	-51	-42	30	4.26	190
Note: The t-scores computed using SPM12 quantify the statistically significant differences between the two conditions. Coordinates refer to the stereotactic space of the Montreal Neurological Institute. *mOFC* medial orbitofrontal cortex, *IFG* inferior frontal gyrus, *FFA* fusiform face area, *IOG* inferior occipital gyrus, *STC* superior temporal cortex, *ATL* anterior temporal lobule, vmPFC ventral medial prefrontal cortex, *ACC* anterior cingulate cortex, *PCC* posterior cingulate cortex, *SMG* supramarginal gyrus, *IPL* inferior parietal lobule, *TPJ* temporo-parietal junction							

Discussion

The judgments of moral goodness and moral beauty objectively refer to the evaluation of moral behaviors or moral traits (i.e., kindness, virtue, etc.), which is generally influenced by facial attractiveness. But it is not clear whether facial attractiveness has similar or different influence on the judgments of moral goodness and moral beauty. In the current study, we investigated the neural responses to facial attractiveness under two conditions of higher order moral decision-makings: moral goodness judgment and moral beauty judgment. The same subjects were required to evaluate the level of goodness about the positive moral behavior and the level of inner beauty of the person doing that same behavior with different levels of facial attractiveness (beautiful or ugly face). During the whole experiment, subjects were not instructed to pay attention to an individual $sface, butwereasked \rightarrow makem$ or $aljudgmentsbasedonthis \in \div al$s moral behavior. So, what we're talking about is whether the subjects' judgments on the moral behavior of an individual is affected by the individual`s facial attractiveness, with the focus on the influence of implicit perception of facial attractiveness on higher social decisions, which is more in line with natural situations and reality in terms of decision making and has certain ecological validity.

We have four main findings. First, behavioral results indicated that the morally positive behaviors performed by individuals with beautiful faces were more likely to be evaluated as morally good and morally beautiful than behaviors performed by individuals with ugly faces, as indexed by the rating scores but not response time. Second, neuroimaging results showed that, similar to beautiful faces in moral goodness judgment trials, beautiful faces in moral beauty judgment trials recruited an overlapping of the left ventral occipitotemporal extrastriate cortices (OTC) sensitive to the early perceptual processing of faces, including inferior occipital gyrus (IOG) and fusiform face area (FFA). Third, compared to beautiful faces during moral goodness judgment, beautiful faces during moral beauty judgment induced specific activity in the ventral medial prefrontal cortex (vmPFC) (i.e., ACC extending to mOFC) and left PCC/precuneus. The opposite comparison elicited specific activity in the left premotor area extending to the opercular part of the inferior frontal gyrus (IFG). Moreover, compared to ugly faces during moral goodness judgment, ugly faces during moral beauty judgment induced specific activity in the left temporo-parietal junction (TPJ). The opposite comparison elicited no significant cluster. Fourth, the right lateral orbitofrontal cortex (OFC) was commonly involved in the representations of moral goodness and moral beauty, but was not regulated by facial attractiveness. Our results demonstrated that the neural responses to facial attractiveness in the process of higher moral decision-makings exhibits both task-general and task-specific characteristics. Facial attractiveness contributes similarly and differently to the judgments of moral goodness and moral beauty.

Shared response to attractive faces in the judgments of moral goodness and moral beauty

In the current study, we hypothesized that the judgments of moral goodness and moral beauty would be associated with enhanced activations in regions involved in the early perceptual processing of attractive faces, given that visual features pertaining to facial attractiveness would be apprehended automatically (Hung et al., 2016; Palermo & Rhodes, 2007) at a glance (Olson & Marshuetz, 2005) and influence people’s social judgments made about others (Chatterjee, 2003, 2015; Chatterjee et al., 2009; Chatterjee & Vartanian, 2016; Moonja Park Kim & Rosenberg, 1980; Todorov et al., 2008; Winston et al., 2007). Consistent with our expectation, we found that the left ventral occipitotemporal visual cortices, including IOG and FFA, responded to the beautiful faces independent of judgment task, showing a similar magnitude of activation during both judgments of moral goodness and moral beauty.

Previous studies confirmed that the apprehension of attractive faces is associated with an identifiable neural response, specifically, attractive faces automatically activate the ventral occipitotemporal cortices, particularly sensitive to face perception, including IOG and FFA (Chatterjee et al., 2009; Kranz & Ishai, 2006; Winston et al., 2007). An attractive face is a salient social signal that reflect the overall effect of all physical attributes of a face (Rhodes, 2006). Regions of the occipital and posterior temporal visual cortices involved in the lower-level visual processing of perceptual features of faces plays a critical role in the perceptual processing of attractive faces (Chatterjee et al., 2009). Recent fMRI studies also showed that the cognitive and neural mechanisms involved in the perceptual analyses of faces and attractive faces were considerably overlapping (Calder & Young, 2005; Fisher et al., 2016; Li et al., 2019; Redfern & Benton, 2017; Sun et al., 2015). The face-selective neurons in the occipitotemporal cortical visual areas is tuned to the identity of faces (Eick et al., 2020), and has representations that are invariant with respect to, for example, retinal position, size and even view. These invariant representations are ideally suited to provide the inputs to brain regions such as mOFC that is involved in social communication and emotional behaviors.

Combining our behavioral findings, that individuals with a beautiful face who perform moral behaviors are more likely to be judged as morally good and internally beautiful, compared with individuals with an ugly face who perform the same behaviors, our imaging result, that the neural activity involved in the perceptual apprehension of attractive faces was activated in both judgment tasks of moral goodness and moral beauty, demonstrates that both the judgments of moral goodness and moral beauty require the automatic visual analysis of the geometrical configuration of attractive faces of individuals performing moral behaviors, before attractive information can be transmitted to the extended emotional system involving in emotional representations. Our result is consistent with the previous findings that the occipital and posterior temporal visual cortices are responsive to the perceptual processing of attractive faces and remain present even when subjects are not attending explicitly to facial attractiveness (Chatterjee et al., 2009; Winston et al., 2007). We suggest that the perceptual processing of visual features of attractive faces is equally crucial for both forms of moral decision-making. It is in line with the view that the perceptual response to attractive faces involves a pattern of domain nonspecific regional activations (Chatterjee et al., 2009).

Different response to attractive faces in the judgments of moral goodness and moral beauty

In addition to the overlapping brain regions (IOG and FFA) activated by the beautiful faces, we also found that beautiful faces activated unique brain regions for each task, specifically, in moral goodness judgment, the left superior temporal cortex (STC), anterior temporal lobule (ATL) and premotor area extending to the opercular part of the inferior frontal gyrus (IFG) showed a significant increase in activation for beautiful faces compared to ugly faces; the left premotor area extending to the opercular part of the IFG was more activated by beautiful faces compared with the activity of beautiful faces in moral beauty judgment; whereas in moral beauty judgment, the midline cortical structures (MCS), including vmPFC/ACC/mOFC, PCC and precuneus, showed a significant increase in activation for beautiful faces. That beautiful faces in different judgment tasks activated different brain regions might imply that the representation of emotional aspects of attractive faces is task-specific, that is, different moral judgments might interpret emotional signals expressed by attractive faces in different ways.

Early perceptual processing of the attractive faces needs to be linked to many other brain structures which are mainly involved in emotional representations, to accomplish the evaluation of attractive faces. Because attractiveness has effects in later stages whereby identity and affective qualities are extracted from faces after the early structural encoding stage of face perception (Hahn & Perrett, 2014). Calder and Young (2005) proposed that the invariant and variable features (geometrical configuration) of faces may be encoded by the same perceptual characterization system, followed by separation (Li et al., 2019). Separate representations are constructed that make explicit information useful for recognizing facial identity or recognizing the affective qualities of faces at a step that is subsequent to perceptual processing. Recognizing actions (variant changes in facial expressions) and emotions from perceptual information in faces form the basis for understanding the intentions and feelings of others and allow us to successfully navigate our social world (McArthur & Baron, 1983; Thornhill & Gangestad, 1999).

Neural responses to attractive faces in moral goodness judgment task

The recognition of identity is based on the perception of aspects of facial structure that are invariant across changes in expression and other movements of the eyes and mouth, generally recruits the FFA, which is especially involved in representing the static features of faces, and the superior temporal sulcus (STS) especially involved in representing the dynamic, changeable features of faces (Bruce & Young, 1986; Hasselmo et al., 1989; Haxby et al., 2000, 2002; Hoffman & Haxby, 2000; Winston et al., 2004). STS and FFA neurons could be form detectors sensitive to particular configurations of the face surface, together, encoding a sequence of face configurations corresponding to a particular facial expression, act as a motion pattern detector (Giese & Poggio, 2003; Said et al., 2011). An additional face-selective region has been identified in the anterior temporal lobule (ATL) (Jonas et al., 2016), associated with dynamic aspects of face perception (Calder et al., 2007; Pitcher et al., 2011). In addition to the STC, an extended network for facial expression perception reaches the frontal operculum and premotor cortex. IFG and nearby motor areas show activity during the perception of facial expression and may have a causal role in their recognition (Pitcher et al., 2008; Pitcher, Dilks, et al., 2011). The STC serves as the visual input of the dynamics of the facial expression, and posterior IFG and adjacent ventral premotor cortex, which generates higher-level motor plans of expression action (Dijksterhuis & Bargh, 2001; Iacoboni & Dapretto, 2006; Monfardini et al., 2013; Yang et al., 2015). The recognition of facial identity is particularly well suited for the mirror neurons hypothesis, as it is known that humans mimic the facial expression of people they are interaction with and produce micro-expressions when simply looking at expressive face images (Dijksterhuis & Bargh, 2001; Dimberg, 1982; Dimberg et al., 2000; Monfardini et al., 2013). When perceiving and decoding other individuals $\exp ressionsignals \text{ and } \in ferr \in gtheirunderly \in g\int entions, theobservermaytry \rightarrow unders\text{tand}w\hat{t}heactionswodmean \text{ if } theythemselveswe$

s self is much more prominent and the understanding of others` actions is relatively self-based (Iacoboni & Dapretto, 2006; Yang et al., 2015).

Our results showed that the brain networks of beautiful faces in moral goodness judgment task appeared to be consistent with the neural activity in the recognition of facial identity. The attractive face of the main character who performs a moral behavior captures the observer's attention (Chen et al., 2012; Leder et al., 2010), and the perceptual processing of attractive face might rely heavily on the observer`s self. The observation and understanding of the action here should refer to the visual features of attractive faces, rather than the moral action itself, because individuals with an ugly face also performs the same moral behavior, but there are no significant brain regions activated. We noticed that in moral goodness judgment task, information about the perceptual processing of beautiful faces was not transmitted to the brain regions responsible for processing the emotional aspects of attractive faces, for example, the vmPFC, and particularly the mOFC. This result is consistent with the affective-meaning-centered view of vmPFC, that is, vmPFC and its subcortical connections are not essential for simple forms of affects, valuation and affective learning, but are essential when conceptual information drives affective physiological and behavioral responses (Benoit et al., 2014; Roy et al., 2012). Indeed, the appreciation of attractive faces unfolds as a neurobiological process in which sensory information is projected to the reward circuit, which generates levels of pleasure (Skov & Nadal, 2020). Although the perceptual representation of a face is obviously important to how it is appreciated, its positive emotional impact is not inherent to this perceptual representation. Rather, emotional values must be understood as a gloss that applied onto sensation by the mesocorticolimbic system (Ellingsen et al., 2015). We speculate that in moral goodness judgment, the observers were likely to observe and imitate the specific facial features and expressions to mediate the influence of attractive faces on the moral goodness judgment, and did not concern themselves with the emotional meanings of attractive faces.

Neural responses to attractive faces in moral beauty judgment task

The recognition of emotional meanings is derived from facial features that resemble facial expressions signaling approach/avoidance behaviors (Todorov et al., 2008), and is generally modulated by a network of structures, including mOFC, cingulate cortex and ventral striatum (Maddock et al., 2003; Rolls, 2019; Vuilleumier et al., 2001). Most brain structures that participate in the recognition of emotions or the social significance of faces involve both perceptual processing - identifying the geometric configuration of facial features in order to discriminate among different stimuli on the basis of their appearance - and recognition of the emotional meaning of a stimulus - knowing that a certain expression signals an emotion (Adolphs, 2002). in moral beauty judgment, beautiful faces of the main characters who perform morally positive behaviors did not activate the superior temporal cortex (STC) and mirror nervous system, but significantly evoked the vmPFC (i.e., ACC extending to the mOFC) and left PCC/precuneus, which seemed to be consistent with the neural activity in the recognition of emotional aspects of attractive faces.

Work from fMRI studies have consistently shown that the vmPFC, particularly the mOFC, is relevant to the evaluation of attractive faces (Aharon et al., 2001; Bray & O'Doherty, 2007; Cloutier et al., 2008; Hampshire et al., 2012; Ishizu & Zeki, 2011; Kawabata & Zeki, 2004; Kawasaki et al., 2001; Liang et al., 2010; Marinkovic et al., 2000; O'Doherty et al., 2003; Smith et al., 2016; Tsukiura & Cabeza, 2011a, 2011b; Winston et al., 2007; Zaki et al., 2011). The vmPFC has been shown not only to underlie subjective experiences of emotional value, but also, more specifically, to underlie valuation that incorporates conceptual information to produce "affective meaning" (Aydogan et al., 2018; Roy et al., 2012; Winecoff et al., 2013). Neurons located in vmPFC, especially the mOFC, appear to integrate information from different sources (Knutson & Genevsky, 2018) and drive affective physiological and behavioral responses (Roy et al., 2012). The vmPFC also plays an important role in emotional regulation of behavior, particularly at the intersection of emotion and decision-making. Damaged to the vmPFC, results in both blunted emotional responses, demonstrated by reduced psychophysiological responses to emotional stimuli, and abnormal decision making (Rolls & Grabenhorst, 2008). The extensive connections between occipitotemporal visual regions and the prefrontal cortex (Seltzer & Pandya, 1989) provide for an effective source of perceptual input to the vmPFC and also make it plausible that the vmPFC could play a role in recognizing facial emotion via direct modulation of activity in occipitotemporal cortex via feedback (Adolphs, 2002). In addition, there is evidence that the recognition and experience of emotion are closely related, and in principle, consistent with the idea that the mOFC participates in emotion recognition via triggering an emotional response in the observer, and more importantly, this process depends on the context and the task (Emery & Amaral, 1999). That brain regions associated with reward information respond to attractive faces suggests physical attractiveness may hold incentive salience (Berridge & Robinson, 2003) and influence the observer`s perception of moral beauty.

Moreover, a number of fMRI studies have found that the midline cortical structures (MCS), including ACC, PCC and precuneus, are related to the self-referential processing, and self-referential thought, related to hopes and aspirations, tends to be associated with the anterior midline regions whereas self-referential thought related to duties and obligations is associated with the posterior midline regions (Johnson et al., 2006; Nejad et al., 2013). The result that the ACC, PCC and precuneus tended to respond more strongly to attractive faces than unattractive faces in moral beauty judgment suggests that MCS activations might be involved in the higher order processing of self and positive emotional-related information (Quevedo et al., 2018; Sugiura, 2015) and this processing is more likely to occur in moral beauty judgments than moral goodness judgment. Once again, this pattern of activations bears a strong resemblance to that associated with positive emotional expressions (Dolan et al., 1996; Kesler-West et al., 2001; Phillips et al., 1998). The highly consistent presence of these areas suggests that under certain tasks, attractive faces modulate activity in emotional meanings regions of the brain. This result is very important. For a long time, the academic has proposed that the generation of aesthetic feelings is influenced by the external image of the object, while the generation of moral sense is not affected (Zaidel & Nadal, 2011), but this is only from a speculative perspective. The results of the present study not only provide empirical evidence for this important principle, but uncover this critical difference only exist in the late encoding stage of object perception.

In addition, it is important to note that we found that the common neural representations of moral goodness and moral beauty was localized in the right lateral OFC, but its activity was not affected by facial attractiveness in either of judgment tasks. This result is consistent with some findings of the OFC`s role in social reward value, that lateral portions of the OFC are significantly more responsive to rewarding objects in general, while medial portions are involved in processing the emotional aspects of faces, including emotional valence and facial attractiveness (Aharon et al., 2001; Chatterjee et al., 2009; Cloutier et al., 2008; Ishai, 2007; Kawabata & Zeki, 2004; Liang et al., 2010; Pegors et al., 2015; Troiani et al., 2016). This result is also in line with the view that the brain requires a domain-general common currency signal, localize in the ventrolateral PFC, when comparing and deciding between different rewards (Delgado, 2007; Levy & Glimcher, 2012; Peters & Buchel, 2009; Sescousse et al., 2015), whereas adaptive behavior may require a domain-specific value signal generally located in the central OFC (Heinzelmann et al., 2020; Howard et al., 2015; Howard & Kahnt, 2017). In the present study, subjects were asked to compare and decide between different morally positive behaviors, and they were not directed to attend to the faces, which are value signals of adaptive behaviors, of individuals who perform moral behaviors. Although some studies have found that the lateral OFC also responds to beautiful faces (left latOFC: Winston et al., 2007; right latOFC: Tsukiura & Cabeza, 2011), this activity for face attractiveness may only arise when participants are explicitly evaluating face attractiveness (Pegors et al., 2015). Other studies have found that the role of the lateral OFC in aesthetic preference is not limited to the representation of the reward value of stimuli regarded as beautiful, it also seems to play a role in the processing of stimuli rated as not beautiful (Munar et al., 2012).

In brief, the present study directly compared the facial attractiveness under two conditions of higher order moral decision-makings: moral judgment and moral beauty judgment and examined the commonalities and differences in the neural responses to facial attractiveness during these two processes through an experimental approach. However, there are also several limitations in this study. First, we must admit that scene drawings used as experimental materials could lower the ecological validity of the study. Although the drawings give us a high level of control, in "real life," we look at human faces in action; even looking at a still photo drops ecological validity, but has more than a cartoon drawing. Second, we only recruited female subjects to participate in the experiment. Although we were doing it to eliminate the possible confusion between the gender of the subjects and the gender of the protagonist in the experimental stimulus, we must admit that this is also a limitation of the current study. Therefore, in future studies, we should recruit male subjects to complete different types of moral judgments and further explore whether there are gender differences in the neural mechanisms of facial attraction's influence on higher order moral decision-making. This will help us determine the extent to which we hold people responsible for those positive moral actions and reactions.

Conclusions

The present study aimed to directly compare the neural responses to facial attractiveness in the judgments of moral goodness and moral beauty. With this goal, scene drawings were chosen as suitable experimental materials for they have a significant advantage of simultaneously providing information on both characters

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emotional response or engagement driven by relevant conceptual information when subjects were asked to assess their inner beauty, so, emotional representations of attractive faces recruited different brain regions between the two types of judgments. We suggest that the neural responses to attractive faces involves patterns of task-general and task-specific regional activations. Our findings contribute to the understanding of the relationship between the relationship between the sense of morality and aesthetic and the perception of face.

Declarations

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Qiuping Cheng, Xuchu Weng and Lei Mo constructed the research idea. All authors of this paper contributed to the experimental design of the work. Qiuping Cheng and Zhili Han collected and analyzed the data. Qiuping Cheng wrote the main manuscript text. Qiuping Cheng, Zhili Han, Shun Liu, Yilong Kong, Xuchu Weng and Lei Mo provided critical revisions. Qiuping Cheng and Zhili Han contributed equally to this study. All authors approved the final version of the manuscript for submission.

Ethics declarations

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Informed consent

Informed consent in research involving Human Participants: Informed consent was obtained from all subjects before the experiment according to the requirements of the Research Ethics Review Board of South China Normal University. Subjects received monetary compensation for their participation in the study. (please see paragraph 'Participants' in section 'Methods').

Availability of data and material

All data analyzed in this study are available from the corresponding author upon reasonable request.

References

1. Adolphs R (2002) Neural systems for recognizing emotion. Curr Opin Neurobiol 12(2):169–177. https://doi.org/10.1016/S0959-4388(02)00301-X
2. Aharon I, Etcoff N, Ariely D, Chabris CF, O'Connor E, Breiter HC (2001) Beautiful Faces Have Variable Reward Value. Neuron 32(3):537–551. https://doi.org/10.1016/S0896-6273(01)00491-3
3. Algoe SB, Haidt J (2009) Witnessing excellence in action: The 'other-praising' emotions of elevation, gratitude, and admiration. The Journal of Positive Psychology 4(2):105–127. https://doi.org/10.1080/17439760802650519
4. Amoyal N (2014) *Moral Elevation and its Relation to the Altruistic Health Behavior of Becoming an Organ and Tissue Donor* [University of Rhode Island]. https://doi.org/10.23860/diss-amoyal-nicole-2014
5. Aydogan G, Flaig N, Ravi SN, Large EW, McClure SM, Margulis EH (2018) Overcoming Bias: Cognitive Control Reduces Susceptibility to Framing Effects in Evaluating Musical Performance. Sci Rep 8(1):6229. https://doi.org/10.1038/s41598-018-24528-3
6. Benoit RG, Szpunar KK, Schacter DL (2014) Ventromedial prefrontal cortex supports affective future simulation by integrating distributed knowledge. *Proceedings of the National Academy of Sciences*, *111*(46), 16550–16555. https://doi.org/10.1073/pnas.1419274111
7. Berridge KC, Robinson TE (2003) Parsing reward. Trends Neurosci 26(9):507–513. https://doi.org/10.1016/S0166-2236(03)00233-9
8. Bray S, O'Doherty J (2007) Neural coding of reward-prediction error signals during classical conditioning with attractive faces. J Neurophysiol 97(4):3036–3045. https://doi.org/10.1152/jn.01211.2006
9. Bruce V, Young A (1986) Understanding face recognition. Br J Psychol 77(3):305–327. https://doi.org/10.1111/j.2044-8295.1986.tb02199.x
10. Calder AJ, Young AW (2005) Understanding the recognition of facial identity and facial expression. Nat Rev Neurosci 6(8):641–651. https://doi.org/10.1038/nrn1724
11. Chatterjee A (2003) *Prospects for a cognitive neuroscience of visual aesthetics* [Data set]. American Psychological Association. https://doi.org/10.1037/e514602010-003
12. Chatterjee A (2015) The Neuropsychology of Visual Art. In: Huston JP, Nadal M, Mora F, Agnati LF, Conde CJC (eds) Art, Aesthetics, and the Brain. Oxford University Press, pp 341–356. https://doi.org/10.1093/acprof:oso/9780199670000.003.0017
13. Chatterjee A, Thomas A, Smith SE, Aguirre GK (2009) The neural response to facial attractiveness. Neuropsychology 23(2):135–143. https://doi.org/10.1037/a0014430

14. Chatterjee A, Vartanian O (2016) Neuroscience of aesthetics: Neuroscience of aesthetics. Ann N Y Acad Sci 1369(1):172–194. https://doi.org/10.1111/nyas.13035
15. Chen W, Liu CH, Nakabayashi K (2012) Beauty Hinders Attention Switch in Change Detection: The Role of Facial Attractiveness and Distinctiveness. PLoS ONE 7(2):e32897. https://doi.org/10.1371/journal.pone.0032897
16. Cheng Q, Cui X, Lin J, Weng X, Mo L (2020) Neural correlates of moral goodness and moral beauty judgments. Brain Res 1726:146534. https://doi.org/10.1016/j.brainres.2019.146534
17. Cloutier J, Heatherton TF, Whalen PJ, Kelley WM (2008) Are Attractive People Rewarding? Sex Differences in the Neural Substrates of Facial Attractiveness. J Cogn Neurosci 20(6):941–951. https://doi.org/10.1162/jocn.2008.20062
18. Cui X, Cheng Q, Lin W, Lin J, Mo L (2019) Different influences of facial attractiveness on judgments of moral beauty and moral goodness. Sci Rep 9(1):12152. https://doi.org/10.1038/s41598-019-48649-5
19. Darwin C (1871) The Descent of Man and Selection in Relation to Sex, Volume 1. *London: John Murray, Albemarle Street*, 436
20. Delgado MR (2007) Reward-Related Responses in the Human Striatum. Ann N Y Acad Sci 1104(1):70–88. https://doi.org/10.1196/annals.1390.002
21. Diessner R, Iyer R, Smith MM, Haidt J (2013) Who engages with moral beauty? Journal of Moral Education 42(2):139–163. https://doi.org/10.1080/03057240.2013.785941
22. Diessner R, Rust T, Solom RC, Frost N, Parsons L (2006) Beauty and hope: A moral beauty intervention. Journal of Moral Education 35(3):301–317. https://doi.org/10.1080/03057240600874430
23. Diessner R, Solom RC, Frost NK, Parsons L, Davidson J (2008) Engagement with beauty: Appreciating natural, artistic, and moral beauty. The Journal of Psychology 142(3):303–329. https://doi.org/10.3200/JRLP.142.3.303-332
24. Dijksterhuis A, Bargh JA (2001) The perception–behavior expressway: Automatic effects of social perception on social behavior. In *Advances in experimental social psychology, Vol. 33* (pp. 1–40). Academic Press
25. Dimberg U (1982) Facial Reactions to Facial Expressions. Psychophysiology 19(6):643–647. https://doi.org/10.1111/j.1469-8986.1982.tb02516.x
26. Dimberg U, Thunberg M, Elmehed K (2000) Unconscious Facial Reactions to Emotional Facial Expressions. Psychol Sci 11(1):86–89. https://doi.org/10.1111/1467-9280.00221
27. Dion K, Berscheid E, Walster E (1972) What is beautiful is good. J Pers Soc Psychol 24(3):285–290. https://doi.org/10.1037/h0033731
28. Dolan RJ, Fletcher P, Morris J, Kapur N, Deakin JFW, Frith CD (1996) Neural Activation during Covert Processing of Positive Emotional Facial Expressions. NeuroImage 4(3):194–200. https://doi.org/10.1006/nimg.1996.0070
29. Eick CM, Kovács G, Rostalski S-M, Röhrig L, Ambrus GG (2020) The occipital face area is causally involved in identity-related visual-semantic associations. Brain Structure Function 225(5):1483–1493. https://doi.org/10.1007/s00429-020-02068-9
30. Ellingsen D-M, Leknes S, Kringelbach M (2015) Hedonic value. In: Handbook of Value: Perspectives from Economics, Neuroscience, Philosophy, Psychology and Sociology, 265-286. Eds: David Sander and Tobias Brosch. *Oxford University Press*
31. Emery NJ, Amaral DG (2000) The role of the amygdala in primate social cognition. In: Cognitive neuroscience of emotion. Oxford University Press, pp 156–191
32. Fang F, He S (2005) Cortical responses to invisible objects in the human dorsal and ventral pathways. Nat Neurosci 8(10):1380–1385. https://doi.org/10.1038/nn1537
33. Faul F, Erdfelder E, Lang A-G, Buchner A (2007) G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. Behav Res Methods 39(2):175–191. https://doi.org/10.3758/BF03193146
34. Feingold A (1992) Gender differences in mate selection preferences: A test of the parental investment model. Psychol Bull 112(1):125–139. https://doi.org/10.1037/0033-2909.112.1.125
35. Ferrari C, Nadal M, Schiavi S, Vecchi T, Cela-Conde CJ, Cattaneo Z (2017) The dorsomedial prefrontal cortex mediates the interaction between moral and aesthetic valuation: A TMS study on the *beauty-is-good* stereotype. Social Cognitive Affective Neuroscience 12(5):707–717. https://doi.org/10.1093/scan/nsx002
36. Fisher K, Towler J, Eimer M (2016) Facial identity and facial expression are initially integrated at visual perceptual stages of face processing. Neuropsychologia 80:115–125. https://doi.org/10.1016/j.neuropsychologia.2015.11.011
37. Freeman D, Aquino K, McFerran B (2009) Overcoming Beneficiary Race as an Impediment to Charitable Donations: Social Dominance Orientation, the Experience of Moral Elevation, and Donation Behavior. Pers Soc Psychol Bull 35(1):72–84. https://doi.org/10.1177/0146167208325415
38. French MT (2002) Physical appearance and earnings: Further evidence. Appl Econ 34(5):569–572. https://doi.org/10.1080/00036840010027568
39. Giese MA, Poggio T (2003) Neural mechanisms for the recognition of biological movements. Nature Reviews Neuroscience 4(3):179–192. https://doi.org/10.1038/nrn1057
40. Griffin AM, Langlois JH (2006) Stereotype Directionality and Attractiveness Stereotyping: Is Beauty Good or is Ugly Bad? Social Cognition 24(2):187–206. https://doi.org/10.1521/soco.2006.24.2.187
41. Grill-Spector K, Weiner KS, Kay K, Gomez J (2017) The Functional Neuroanatomy of Human Face Perception. Annual Review of Vision Science 3(1):167–196. https://doi.org/10.1146/annurev-vision-102016-061214
42. Güsewell A, Ruch W (2012) Are only Emotional Strengths Emotional? Character Strengths and Disposition to Positive Emotions. Applied Psychology: Health Well-Being 4(2):218–239. https://doi.org/10.1111/j.1758-0854.2012.01070.x

43. Hahn AC, Perrett DI (2014) Neural and behavioral responses to attractiveness in adult and infant faces. Neuroscience Biobehavioral Reviews 46:591–603. https://doi.org/10.1016/j.neubiorev.2014.08.015
44. Haidt J (2003) Elevation and the positive psychology of morality. In *Flourishing: Positive psychology and the life well-lived* (pp. 275–289). American Psychological Association. https://doi.org/10.1037/10594-012
45. Haidt J (2007) The New Synthesis in Moral Psychology. Science 316(5827):998–1002. https://doi.org/10.1126/science.1137651
46. Haidt J, Keltner D (2004) Appreciation of beauty and excellence [awe, wonder, elevation]. In: Character strengths and virtues, Edited by: Peterson, C and Seligman, MEP. 537–551. New York. *Oxford University Press*, *NY*
47. Hampshire A, Chaudhry AM, Owen AM, Roberts AC (2012) Dissociable roles for lateral orbitofrontal cortex and lateral prefrontal cortex during preference driven reversal learning. NeuroImage 59(4):4102–4112. https://doi.org/10.1016/j.neuroimage.2011.10.072
48. Hasselmo ME, Rolls ET, Baylis GC, Nalwa V (1989) Object-centered encoding by face-selective neurons in the cortex in the superior temporal sulcus of the monkey. Exp Brain Res 75(2):417–429. https://doi.org/10.1007/BF00247948
49. Haxby JV, Hoffman EA, Gobbini MI (2000) The distributed human neural system for face perception. Trends in Cognitive Sciences 4(6):223–233. https://doi.org/10.1016/S1364-6613(00)01482-0
50. Haxby JV, Hoffman EA, Gobbini MI (2002) Human neural systems for face recognition and social communication. Biol Psychiat 51(1):59–67. https://doi.org/10.1016/S0006-3223(01)01330-0
51. Heinzelmann NC, Weber SC, Tobler PN (2020) Aesthetics and morality judgments share cortical neuroarchitecture. Cortex 129:484–495. https://doi.org/10.1016/j.cortex.2020.04.018
52. Hoffman EA, Haxby JV (2000) Distinct representations of eye gaze and identity in the distributed human neural system for face perception. Nat Neurosci 3(1):80–84. https://doi.org/10.1038/71152
53. Howard JD, Gottfried JA, Tobler PN, Kahnt T (2015) Identity-specific coding of future rewards in the human orbitofrontal cortex. *Proceedings of the National Academy of Sciences*, *112*(16), 5195–5200. https://doi.org/10.1073/pnas.1503550112
54. Howard JD, Kahnt T (2017) Identity-Specific Reward Representations in Orbitofrontal Cortex Are Modulated by Selective Devaluation. The Journal of Neuroscience 37(10):2627–2638. https://doi.org/10.1523/JNEUROSCI.3473-16.2017
55. Hung S-M, Nieh C-H, Hsieh P-J (2016) Unconscious processing of facial attractiveness: Invisible attractive faces orient visual attention. Sci Rep 6(1):37117. https://doi.org/10.1038/srep37117
56. Iacoboni M, Dapretto M (2006) The mirror neuron system and the consequences of its dysfunction. Nat Rev Neurosci 7(12):942–951. https://doi.org/10.1038/nrn2024
57. Iaria G, Fox CJ, Waite CT, Aharon I, Barton JJS (2008) The contribution of the fusiform gyrus and superior temporal sulcus in processing facial attractiveness: Neuropsychological and neuroimaging evidence. Neuroscience 155(2):409–422. https://doi.org/10.1016/j.neuroscience.2008.05.046
58. Ishai A (2007) Sex, beauty and the orbitofrontal cortex. Int J Psychophysiol 63(2):181–185. https://doi.org/10.1016/j.ijpsycho.2006.03.010
59. Ishizu T, Zeki S (2011) Toward A Brain-Based Theory of Beauty. PLoS ONE 6(7):e21852. https://doi.org/10.1371/journal.pone.0021852
60. Janicke SH, Oliver MB (2017) The relationship between elevation, connectedness, and compassionate love in meaningful films. Psychology of Popular Media Culture 6(3):274–289. https://doi.org/10.1037/ppm0000105
61. Johnson MK, Raye CL, Mitchell KJ, Touryan SR, Greene EJ, Nolen-Hoeksema S (2006) Dissociating medial frontal and posterior cingulate activity during self-reflection. Social Cognitive Affective Neuroscience 1(1):56–64. https://doi.org/10.1093/scan/nsl004
62. Kawabata H, Zeki S (2004) Neural Correlates of Beauty. J Neurophysiol 91(4):1699–1705. https://doi.org/10.1152/jn.00696.2003
63. Kawasaki H, Adolphs R, Kaufman O, Damasio H, Damasio AR, Granner M, Bakken H, Hori T, Howard MA (2001) Single-neuron responses to emotional visual stimuli recorded in human ventral prefrontal cortex. Nat Neurosci 4(1):15–16. https://doi.org/10.1038/82850
64. Keltner D, Haidt J (2003) Approaching awe, a moral, spiritual, and aesthetic emotion. Cogn Emot 17(2):297–314. https://doi.org/10.1080/02699930302297
65. Kesler-West ML, Andersen AH, Smith CD, Avison MJ, Davis CE, Kryscio RJ, Blonder LX (2001) Neural substrates of facial emotion processing using fMRI. Cogn Brain Res 11(2):213–226. https://doi.org/10.1016/S0926-6410(00)00073-2
66. Kim H, Adolphs R, O'Doherty JP, Shimojo S (2007) Temporal isolation of neural processes underlying face preference decisions. *Proceedings of the National Academy of Sciences*, *104*(46), 18253–18258. https://doi.org/10.1073/pnas.0703101104
67. Knutson B, Genevsky A (2018) Neuroforecasting Aggregate Choice. Curr Dir Psychol Sci 27(2):110–115. https://doi.org/10.1177/0963721417737877
68. Kocsor F, Feldmann A, Bereczkei T, Kállai J (2013) Assessing facial attractiveness: Individual decisions and evolutionary constraints. Socioaffective Neuroscience Psychology 3(1):21432. https://doi.org/10.3402/snp.v3i0.21432
69. Kranz F, Ishai A (2006) Face Perception Is Modulated by Sexual Preference. Curr Biol 16(1):63–68. https://doi.org/10.1016/j.cub.2005.10.070
70. Kriegeskorte N, Simmons WK, Bellgowan PSF, Baker CI (2009) Circular analysis in systems neuroscience: The dangers of double dipping. Nat Neurosci 12(5):535–540. https://doi.org/10.1038/nn.2303
71. Landis SK, Sherman MF, Piedmont RL, Kirkhart MW, Rapp EM, Bike DH (2009) The relation between elevation and self-reported prosocial behavior: Incremental validity over the Five-Factor Model of Personality. The Journal of Positive Psychology 4(1):71–84. https://doi.org/10.1080/17439760802399208
72. Langlois JH, Kalakanis L, Rubenstein AJ, Larson A, Hallam M, Smoot M (2000) Maxims or myths of beauty? A meta-analytic and theoretical review. Psychol Bull 126(3):390–423. https://doi.org/10.1037/0033-2909.126.3.390

73. Leder H, Tinio PPL, Fuchs IM, Bohrn I (2010) When attractiveness demands longer looks: The effects of situation and gender. Quarterly Journal of Experimental Psychology 63(9):1858–1871. https://doi.org/10.1080/17470211003605142
74. Levy DJ, Glimcher PW (2012) The root of all value: A neural common currency for choice. Curr Opin Neurobiol 22(6):1027–1038. https://doi.org/10.1016/j.conb.2012.06.001
75. Lewis KE, Bierly M (1990) Toward a profile of the female voter: Sex differences in perceived physical attractiveness and competence of political candidates. Sex Roles: A Journal of Research 22(1–2):1–12. https://doi.org/10.1007/BF00288150
76. Li J, He D, Zhou L, Zhao X, Zhao T, Zhang W, He X (2019) The Effects of Facial Attractiveness and Familiarity on Facial Expression Recognition. Front Psychol 10:2496. https://doi.org/10.3389/fpsyg.2019.02496
77. Liang X, Zebrowitz LA, Zhang Y (2010) Neural activation in the "reward circuit" shows a nonlinear response to facial attractiveness. Soc Neurosci 5(3):320–334. https://doi.org/10.1080/17470911003619916
78. Lieberman MD (2007) Social Cognitive Neuroscience: A Review of Core Processes. Annu Rev Psychol 58(1):259–289. https://doi.org/10.1146/annurev.psych.58.110405.085654
79. Liu J, Harris A, Kanwisher N (2010) Perception of Face Parts and Face Configurations: An fMRI Study. J Cogn Neurosci 22(1):203–211. https://doi.org/10.1162/jocn.2009.21203
80. Locher P, Unger R, Sociedade P, Wahl J (1993) At first glance: Accessibility of the physical attractiveness stereotype. Sex Roles 28(11):729–743. https://doi.org/10.1007/BF00289990
81. Luo Q, Hanlin W, Dzhelyova M, Huang P, Mo L (2016) Effect of Affective Personality Information on Face Processing: Evidence from ERPs. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.00810
82. Luo Q, Yu M, Li Y, Mo L (2019) The neural correlates of integrated aesthetics between moral and facial beauty. *Scientific Reports*, *9*(1), 1980. https://doi.org/10.1038/s41598-019-38553-3
83. Maddock RJ, Garrett AS, Buonocore MH (2003) Posterior cingulate cortex activation by emotional words: FMRI evidence from a valence decision task. Hum Brain Mapp 18(1):30–41. https://doi.org/10.1002/hbm.10075
84. Maner JK, Kenrick DT, Becker DV, Delton AW, Hofer B, Wilbur CJ, Neuberg SL (2003) Sexually Selective Cognition: Beauty Captures the Mind of the Beholder. J Pers Soc Psychol 85(6):1107–1120. https://doi.org/10.1037/0022-3514.85.6.1107
85. Marinkovic K, Trebon P, Chauvel P, Halgren E (2000) LOCALISED FACE PROCESSING BY THE HUMAN PREFRONTAL CORTEX: FACE-SELECTIVE INTRACEREBRAL POTENTIALS AND POST-LESION DEFICITS. Cognitive Neuropsychology, 17(1–3), 187–199. https://doi.org/10.1080/026432900380562
86. Marzi T, Viggiano MP (2010) Deep and shallow encoding effects on face recognition: An ERP study. Int J Psychophysiol 78(3):239–250. https://doi.org/10.1016/j.ijpsycho.2010.08.005
87. McArthur L, Baron R (1983) Toward an ecological theory of social perception. Psychol Rev 90:215–238. https://doi.org/10.1037/0033-295X.90.3.215
88. Monfardini E, Gazzola V, Boussaoud D, Brovelli A, Keysers C, Wicker B (2013) Vicarious Neural Processing of Outcomes during Observational Learning. PLoS ONE 8(9):e73879. https://doi.org/10.1371/journal.pone.0073879
89. Montepare JM, Dobish H (2003) THE CONTRIBUTION OF EMOTION PERCEPTIONS AND THEIR OVERGENERALIZATIONS TO TRAIT IMPRESSIONS. J Nonverbal Behav 27(4):237–254. https://doi.org/10.1023/A:1027332800296
90. Moonja Park, Kim, Rosenberg S (1980) Comparison of two structural models of implicit personality theory. J Pers Soc Psychol 38(3):375–389. https://doi.org/10.1037/0022-3514.38.3.375
91. Munar E, Nadal M, Rosselló J, Flexas A, Moratti S, Maestú F, Marty G, Cela-Conde CJ (2012) Lateral Orbitofrontal Cortex Involvement in Initial Negative Aesthetic Impression Formation. PLoS ONE 7(6):e38152. https://doi.org/10.1371/journal.pone.0038152
92. Nejad AB, Fossati P, Lemogne C (2013) Self-Referential Processing, Rumination, and Cortical Midline Structures in Major Depression. *Frontiers in Human Neuroscience*, *7*. https://doi.org/10.3389/fnhum.2013.00666
93. Nisbett RE, Wilson TD (1977) Telling more than we can know: Verbal reports on mental processes. Psychol Rev 84(3):231–259. https://doi.org/10.1037/0033-295X.84.3.231
94. Nobre AC, Allison T, McCarthy G (1994) Word recognition in the human inferior temporal lobe. Nature 372(6503):260–263. https://doi.org/10.1038/372260a0
95. O'Doherty J, Winston J, Critchley H, Perrett D, Burt DM, Dolan RJ (2003) Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. Neuropsychologia 41(2):147–155. https://doi.org/10.1016/S0028-3932(02)00145-8
96. Olson IR, Marshuetz C (2005) Facial Attractiveness Is Appraised in a Glance. Emotion 5(4):498–502. https://doi.org/10.1037/1528-3542.5.4.498
97. Oosterhof NN, Todorov A (2008) The functional basis of face evaluation. *Proceedings of the National Academy of Sciences*, *105*(32), 11087–11092. https://doi.org/10.1073/pnas.0805664105
98. Palermo R, Rhodes G (2007) Are you always on my mind? A review of how face perception and attention interact. Neuropsychologia 45(1):75–92. https://doi.org/10.1016/j.neuropsychologia.2006.04.025
99. Pegors TK, Kable JW, Chatterjee A, Epstein RA (2015) Common and Unique Representations in pFC for Face and Place Attractiveness. J Cogn Neurosci 27(5):959–973. https://doi.org/10.1162/jocn_a_00777
100. Perrett DI, Burt DM, Penton-Voak IS, Lee KJ, Rowland DA, Edwards R (1999) Symmetry and Human Facial Attractiveness. Evolution Human Behavior 20(5):295–307. https://doi.org/10.1016/S1090-5138(99)00014-8

101. Peters J, Buchel C (2009) Overlapping and Distinct Neural Systems Code for Subjective Value during Intertemporal and Risky Decision Making. J Neurosci 29(50):15727–15734. https://doi.org/10.1523/JNEUROSCI.3489-09.2009
102. Phillips ML, Young AW, Scott SK, Calder AJ, Andrew C, Giampietro V, Williams SC, Bullmore ET, Brammer M, Gray JA (1998) Neural responses to facial and vocal expressions of fear and disgust. *Proceedings of the Royal Society B: Biological Sciences*, *265*(1408), 1809–1817. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1689379/
103. Pitcher D, Dilks DD, Saxe RR, Triantafyllou C, Kanwisher N (2011) Differential selectivity for dynamic versus static information in face-selective cortical regions. NeuroImage 56(4):2356–2363. https://doi.org/10.1016/j.neuroimage.2011.03.067
104. Pitcher D, Garrido L, Walsh V, Duchaine BC (2008) Transcranial Magnetic Stimulation Disrupts the Perception and Embodiment of Facial Expressions. J Neurosci 28(36):8929–8933. https://doi.org/10.1523/JNEUROSCI.1450-08.2008
105. Pitcher D, Walsh V, Duchaine B (2011) The role of the occipital face area in the cortical face perception network. Exp Brain Res 209(4):481–493. https://doi.org/10.1007/s00221-011-2579-1
106. Pohling R, Diessner R (2016) Moral Elevation and Moral Beauty: A Review of the Empirical Literature. Review of General Psychology 20(4):412–425. https://doi.org/10.1037/gpr0000089
107. Quevedo K, Harms M, Sauder M, Scott H, Mohamed S, Thomas KM, Schallmo M-P, Smyda G (2018) The neurobiology of self face recognition among depressed adolescents. J Affect Disord 229:22–31. https://doi.org/10.1016/j.jad.2017.12.023
108. Redfern AS, Benton CP (2017) Expression Dependence in the Perception of Facial Identity. I-Perception 8(3):204166951771066. https://doi.org/10.1177/2041669517710663
109. Rhodes G (2006) The Evolutionary Psychology of Facial Beauty. Annu Rev Psychol 57(1):199–226. https://doi.org/10.1146/annurev.psych.57.102904.190208
110. Rhodes G, Yoshikawa S, Clark A, Lee K, McKay R, Akamatsu S (2001) Attractiveness of Facial Averageness and Symmetry in Non-Western Cultures. Search of Biologically Based Standards of Beauty *Perception* 30(5):611–625. https://doi.org/10.1068/p3123
111. Rolls ET (2007) The representation of information about faces in the temporal and frontal lobes. Neuropsychologia 45(1):124–143. https://doi.org/10.1016/j.neuropsychologia.2006.04.019
112. Rolls ET (2019) The cingulate cortex and limbic systems for emotion, action, and memory. Brain Structure Function 224(9):3001–3018. https://doi.org/10.1007/s00429-019-01945-2
113. Rolls ET, Grabenhorst F (2008) The orbitofrontal cortex and beyond: From affect to decision-making. Prog Neurobiol 86(3):216–244. https://doi.org/10.1016/j.pneurobio.2008.09.001
114. Roy M, Shohamy D, Wager TD (2012) Ventromedial prefrontal-subcortical systems and the generation of affective meaning. Trends in Cognitive Sciences 16(3):147–156. https://doi.org/10.1016/j.tics.2012.01.005
115. Rynes SL, Gerhart B (1990) Interviewer assessments of applicant “fit”: An exploratory investigation. Pers Psychol 43(1):13–35. https://doi.org/10.1111/j.1744-6570.1990.tb02004.x
116. Said CP, Haxby JV, Todorov A (2011) Brain systems for assessing the affective value of faces. Philosophical Transactions of the Royal Society B: Biological Sciences 366(1571):1660–1670. https://doi.org/10.1098/rstb.2010.0351
117. Schnall S, Roper J, Fessler DMT (2010) Elevation Leads to Altruistic Behavior. Psychol Sci 21(3):315–320. https://doi.org/10.1177/0956797609359882
118. Seltzer B, Pandya DN (1989) Frontal lobe connections of the superior temporal sulcus in the rhesus monkey. J Comp Neurol 281(1):97–113. https://doi.org/10.1002/cne.902810108
119. Sescousse G, Li Y, Dreher J-C (2015) A common currency for the computation of motivational values in the human striatum. Social Cognitive Affective Neuroscience 10(4):467–473. https://doi.org/10.1093/scan/nsu074
120. Shiota MN, Thrash TM, Danvers AF, Dombrowski JT (2014) Transcending the self: Awe, elevation, and inspiration. In: Handbook of positive emotions. The Guilford Press, pp 362–377
121. Skov M, Nadal M (2020) A Farewell to Art: Aesthetics as a Topic in Psychology and Neuroscience. Perspectives on Psychological Science 15(3):630–642. https://doi.org/10.1177/1745691619897963
122. Smith ML, Cottrell GW, Gosselin F, Schyns PG (2016) Transmitting and Decoding Facial Expressions: *Psychological Science*. https://journals.sagepub.com/doi/10.1111/j.0956-7976.2005.00801.x
123. Snyder M, Tanke ED, Berscheid E (1977) Social perception and interpersonal behavior: On the self-fulfilling nature of social stereotypes. J Pers Soc Psychol 35(9):656–666. https://doi.org/10.1037/0022-3514.35.9.656
124. Steeves JKE, Culham JC, Duchaine BC, Pratesi CC, Valyear KF, Schindler I, Humphrey GK, Milner AD, Goodale MA (2006) The fusiform face area is not sufficient for face recognition: Evidence from a patient with dense prosopagnosia and no occipital face area. Neuropsychologia 44(4):594–609. https://doi.org/10.1016/j.neuropsychologia.2005.06.013
125. Stolier RM, Hehman E, Keller MD, Walker M, Freeman JB (2018) The conceptual structure of face impressions. *Proceedings of the National Academy of Sciences*, *115*(37), 9210–9215. https://doi.org/10.1073/pnas.1807222115
126. Sugiura M (2015) Three faces of self-face recognition: Potential for a multi-dimensional diagnostic tool. Neurosci Res 90:56–64. https://doi.org/10.1016/j.neures.2014.10.002
127. Sui J, Liu CH (2009) Can Beauty Be Ignored? Effects of Facial Attractiveness on Covert Attention. Psychon Bull Rev 16(2):276–281. https://doi.org/10.3758/PBR.16.2.276

128. Sun D, Chan CCH, Fan J, Wu Y, Lee TMC (2015) Are Happy Faces Attractive? The Roles of Early vs. Late Processing. *Frontiers in Psychology*, *6*. https://doi.org/10.3389/fpsyg.2015.01812
129. Thornhill R, Gangestad SW (1999) The scent of symmetry: A human sex pheromone that signals fitness? Evolution Human Behavior 20(3):175–201. https://doi.org/10.1016/S1090-5138(99)00005-7
130. Todorov A (2008) Evaluating Faces on Trustworthiness: An Extension of Systems for Recognition of Emotions Signaling Approach/Avoidance Behaviors. Ann N Y Acad Sci 1124(1):208–224. https://doi.org/10.1196/annals.1440.012
131. Todorov A, Baron SG, Oosterhof NN (2008) Evaluating face trustworthiness: A model based approach. Social Cognitive Affective Neuroscience 3(2):119–127. https://doi.org/10.1093/scan/nsn009
132. Troiani V, Dougherty CC, Michael AM, Olson IR (2016) Characterization of Face-Selective Patches in Orbitofrontal Cortex. *Frontiers in Human Neuroscience*, *10*. https://doi.org/10.3389/fnhum.2016.00279
133. Tsukiura T, Cabeza R (2011a) Remembering beauty: Roles of orbitofrontal and hippocampal regions in successful memory encoding of attractive faces. NeuroImage 54(1):653–660. https://doi.org/10.1016/j.neuroimage.2010.07.046
134. Tsukiura T, Cabeza R (2011b) Shared brain activity for aesthetic and moral judgments: Implications for the Beauty-is-Good stereotype. Social Cognitive Affective Neuroscience 6(1):138–148. https://doi.org/10.1093/scan/nsq025
135. Van de Vyver J, Abrams D (2015) Testing the prosocial effectiveness of the prototypical moral emotions: Elevation increases benevolent behaviors and outrage increases justice behaviors. J Exp Soc Psychol 58:23–33. https://doi.org/10.1016/j.jesp.2014.12.005
136. Van de Vyver J, Abrams D (2017) Is moral elevation an approach-oriented emotion? The Journal of Positive Psychology 12(2):178–185. https://doi.org/10.1080/17439760.2016.1163410
137. van Leeuwen ML, Macrae CN (2004) Is Beautiful Always Good? Implicit Benefits of Facial Attractiveness. Social Cognition 22(6):637–649. https://doi.org/10.1521/soco.22.6.637.54819
138. Vandenberghe R, Price C, Wise R, Josephs O, Frackowiak RSJ (1996) Functional anatomy of a common semantic system for words and pictures. Nature 383(6597):254–256. https://doi.org/10.1038/383254a0
139. Vuilleumier P, Armony JL, Driver J, Dolan RJ (2001) Effects of Attention and Emotion on Face Processing in the Human Brain. Neuron 30(3):829–841. https://doi.org/10.1016/S0896-6273(01)00328-2
140. Wang T, Mo L, Mo C, Tan LH, Cant JS, Zhong L, Cupchik G (2015) Is moral beauty different from facial beauty? Evidence from an fMRI study. Social Cognitive Affective Neuroscience 10(6):814–823. https://doi.org/10.1093/scan/nsu123
141. Winecoff A, Clithero JA, Carter RM, Bergman SR, Wang L, Huettel SA (2013) Ventromedial Prefrontal Cortex Encodes Emotional Value. J Neurosci 33(27):11032–11039. https://doi.org/10.1523/JNEUROSCI.4317-12.2013
142. Winston JS, Henson RNA, Fine-Goulden MR, Dolan RJ (2004) FMRI-Adaptation Reveals Dissociable Neural Representations of Identity and Expression in Face Perception. J Neurophysiol 92(3):1830–1839. https://doi.org/10.1152/jn.00155.2004
143. Winston JS, O'Doherty J, Kilner JM, Perrett DI, Dolan RJ (2007) Brain systems for assessing facial attractiveness. Neuropsychologia 45(1):195–206. https://doi.org/10.1016/j.neuropsychologia.2006.05.009
144. Xia M, Wang J, He Y (2013) BrainNet Viewer: A network visualization tool for human brain connectomics. PloS One 8(7):e68910. https://doi.org/10.1371/journal.pone.0068910
145. Yang DY-J, Rosenblau G, Keifer C, Pelphrey KA (2015) An integrative neural model of social perception, action observation, and theory of mind. Neuroscience Biobehavioral Reviews 51:263–275. https://doi.org/10.1016/j.neubiorev.2015.01.020
146. Zaidel DW, Nadal M (2011) Brain Intersections of Aesthetics and Morals: Perspectives from Biology, Neuroscience, and Evolution. Perspect Biol Med 54(3):367–380. https://doi.org/10.1353/pbm.2011.0032
147. Zaki J, Schirmer J, Mitchell JP (2011) Social Influence Modulates the Neural Computation of Value. Psychol Sci 22(7):894–900. https://doi.org/10.1177/0956797611411057
148. Zebrowitz LA, Collins MA (1997) Accurate Social Perception at Zero Acquaintance: The Affordances of a Gibsonian Approach. Personality Social Psychology Review 1(3):204–223. https://doi.org/10.1207/s15327957pspr0103_2
149. Zebrowitz LA, Fellous J-M, Mignault A, Andreoletti C (2003) Trait Impressions as Overgeneralized Responses to Adaptively Significant Facial Qualities: Evidence from Connectionist Modeling. Personality Social Psychology Review 7(3):194–215. https://doi.org/10.1207/S15327957PSPR0703_01
150. Zebrowitz LA, Montepare JM (2008) Social Psychological Face Perception: Why Appearance Matters. Soc Pers Psychol Compass 2(3):1497–1517. https://doi.org/10.1111/j.1751-9004.2008.00109.x
151. Zhang Y, Kong F, Zhong Y, Kou H (2014) Personality manipulations: Do they modulate facial attractiveness ratings? Personality Individ Differ 70:80–84. https://doi.org/10.1016/j.paid.2014.06.033
152. Zhang Z, Deng Z (2012) Gender, facial attractiveness, and early and late event-related potential components. Journal of Integrative Neuroscience 11(04):477–487. https://doi.org/10.1142/S0219635212500306

Figures

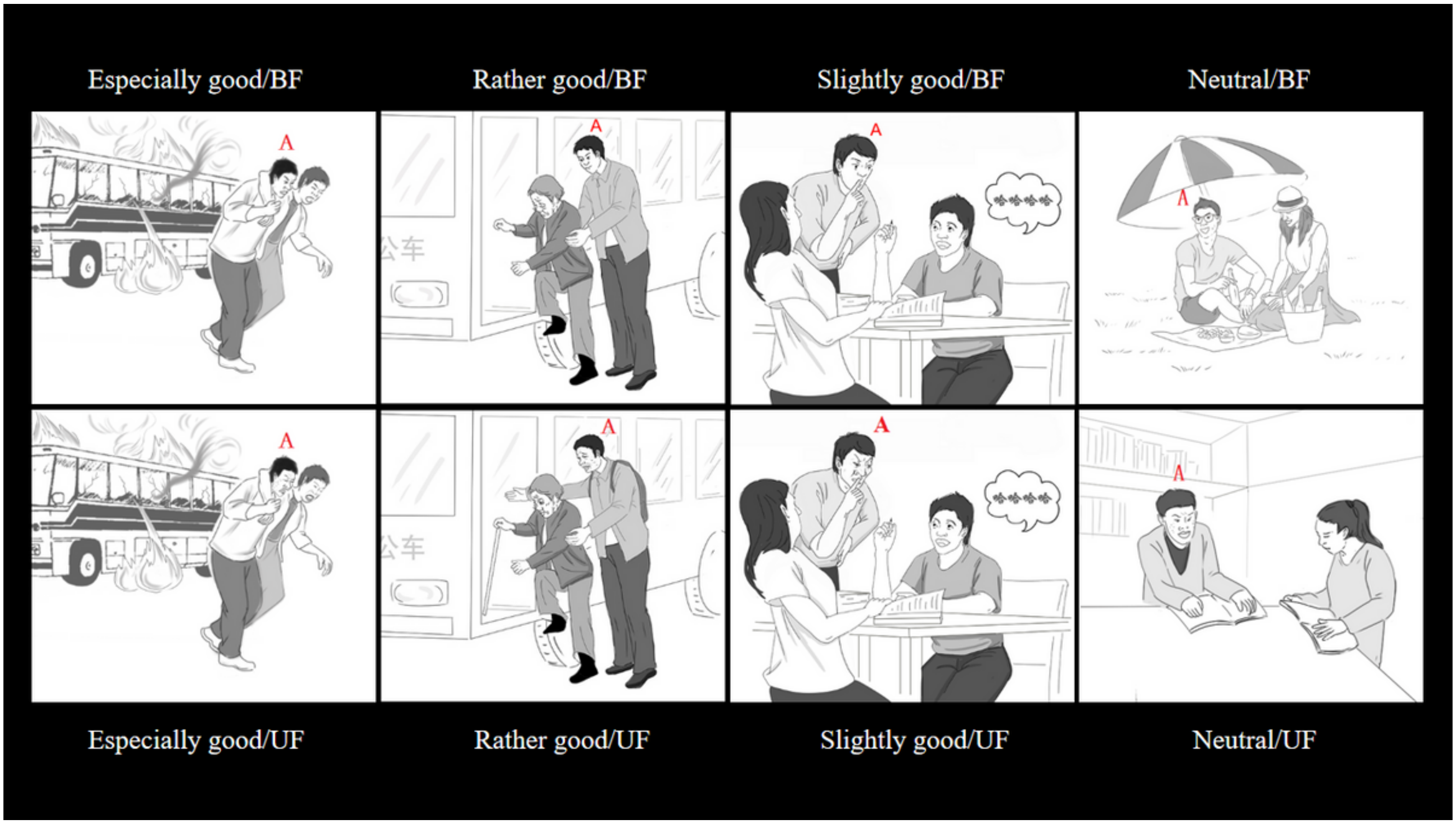

Figure 1

Examples of stimuli used in the fMRI experiment. Stimuli were hand drawn by the first author Qiuping Cheng. There are two versions of the main character`s facial attractiveness for each scene: the above shows behavior with different moral levels acted by the main character with a beautiful face (BF); the below shows the same behavior but acted by the main character with an ugly face (UF).

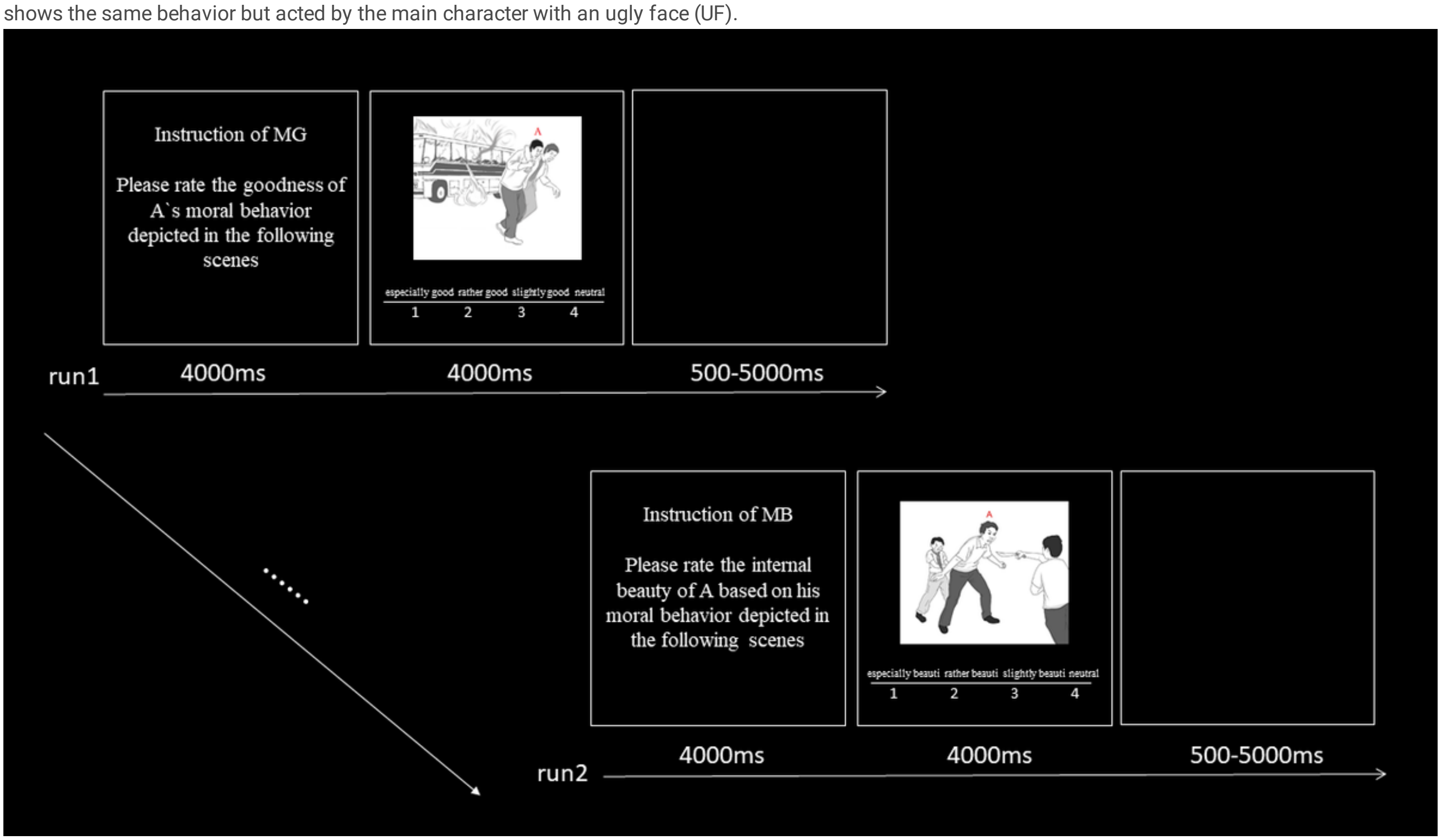

Figure 2

The experimental flowchart. Each subject completed 2 judgment tasks which constituted 2 runs of the whole fMRI experiment. Stimuli were a set of scene drawings depicting morally positive behaviors. Subjects were required to rate the level of moral goodness and inner beauty of A`s behavior in the scene drawings. Run orders were counterbalanced across subjects. The order of presentation of experimental stimuli was randomized between subjects in two tasks.

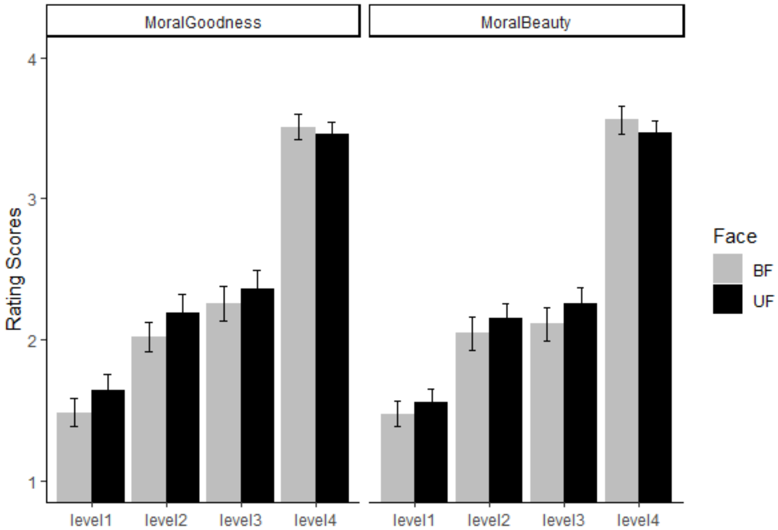

Figure 3

Results obtained from the behavioral data. Mean rating scores are presented as a function of moral level and facial attractiveness in the judgments of moral goodness and moral beauty.

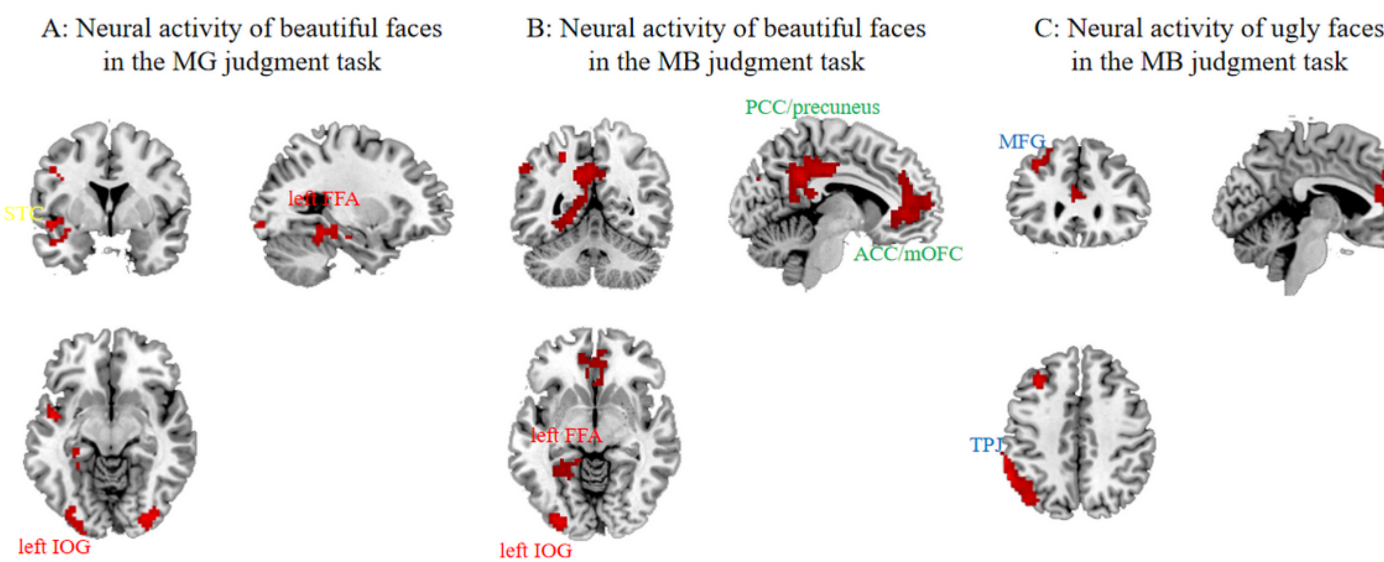

Figure 4

Neural responses to beautiful and ugly faces in the judgments of moral goodness and moral beauty. The image on the left (A) shows the neural responses to beautiful faces in moral goodness judgment. The central figure (B) shows changes in left IOG and FFA activity as a function of moral goodness and moral beauty ratings were correlated. The right figure (C) shows the neural responses to beautiful faces in moral beauty judgment. The right figure (C) shows the neural responses to ugly faces in moral beauty judgment. Activation maps are shown at a whole-brain level of $p < 0.05$, FDR corrected for multiple comparisons.

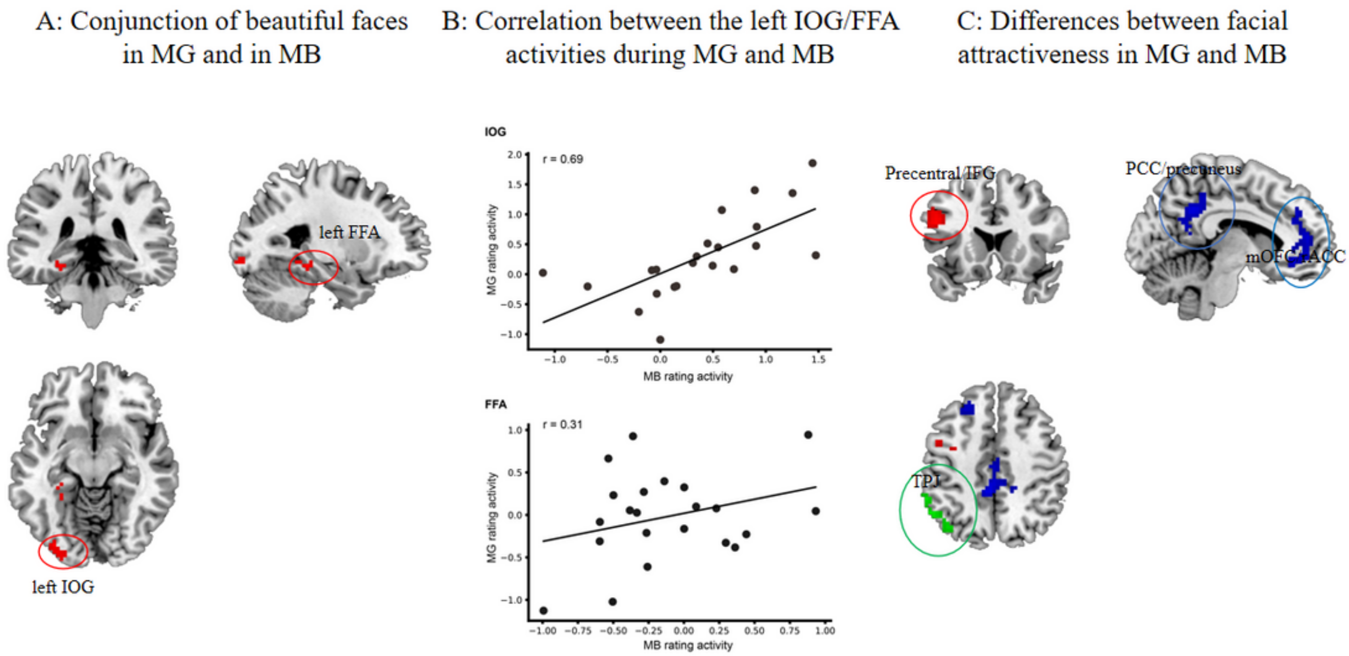

Figure 5

Neural activations revealed by comparing facial attractiveness in the judgments of moral goodness and moral beauty. The image on the left (A) shows a conjunction effect of the beautiful faces in moral goodness and moral beauty judgments. The central figure (B) shows differences between facial attractiveness in moral goodness and moral beauty judgments. Red region indicates that beautiful faces in moral goodness judgment elicited greater activity than beautiful faces in moral beauty judgment; Blue regions indicate that beautiful faces in moral beauty judgment elicited greater activity than beautiful faces in moral goodness judgment; Green region indicates that ugly faces in moral beauty judgment elicited greater activity than ugly faces in moral goodness judgment. Activation maps are shown at a whole-brain level of $p < 0.05$, FDR corrected for multiple comparisons.

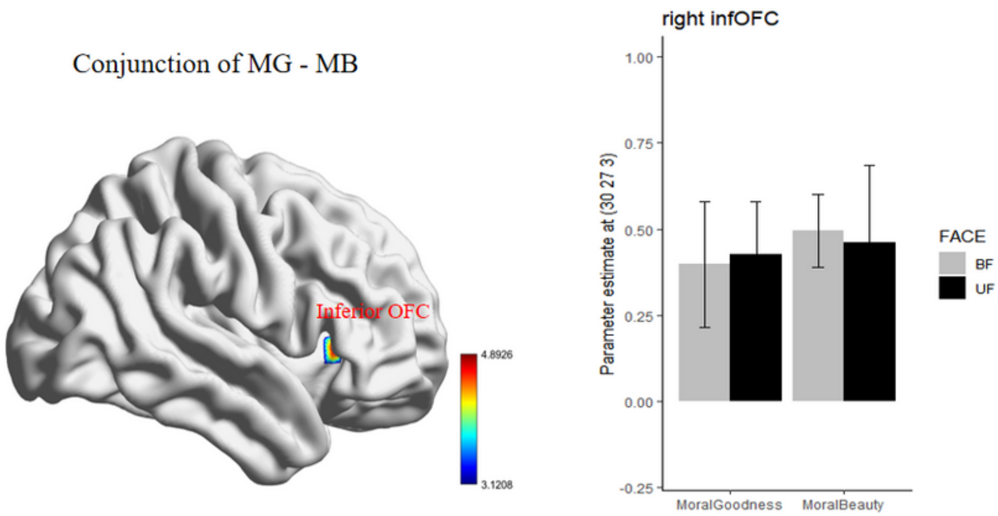

Figure 6

The image on the left (A) shows a conjunction effect of moral goodness and moral beauty. The right image (B) shows mean parameter estimates for beautiful faces and ugly faces in moral goodness and moral beauty judgments within the right inferior OFC. Error bars represent standard error of means. Activation maps are shown at a whole-brain level of $p < 0.05$, FDR corrected for multiple comparisons.

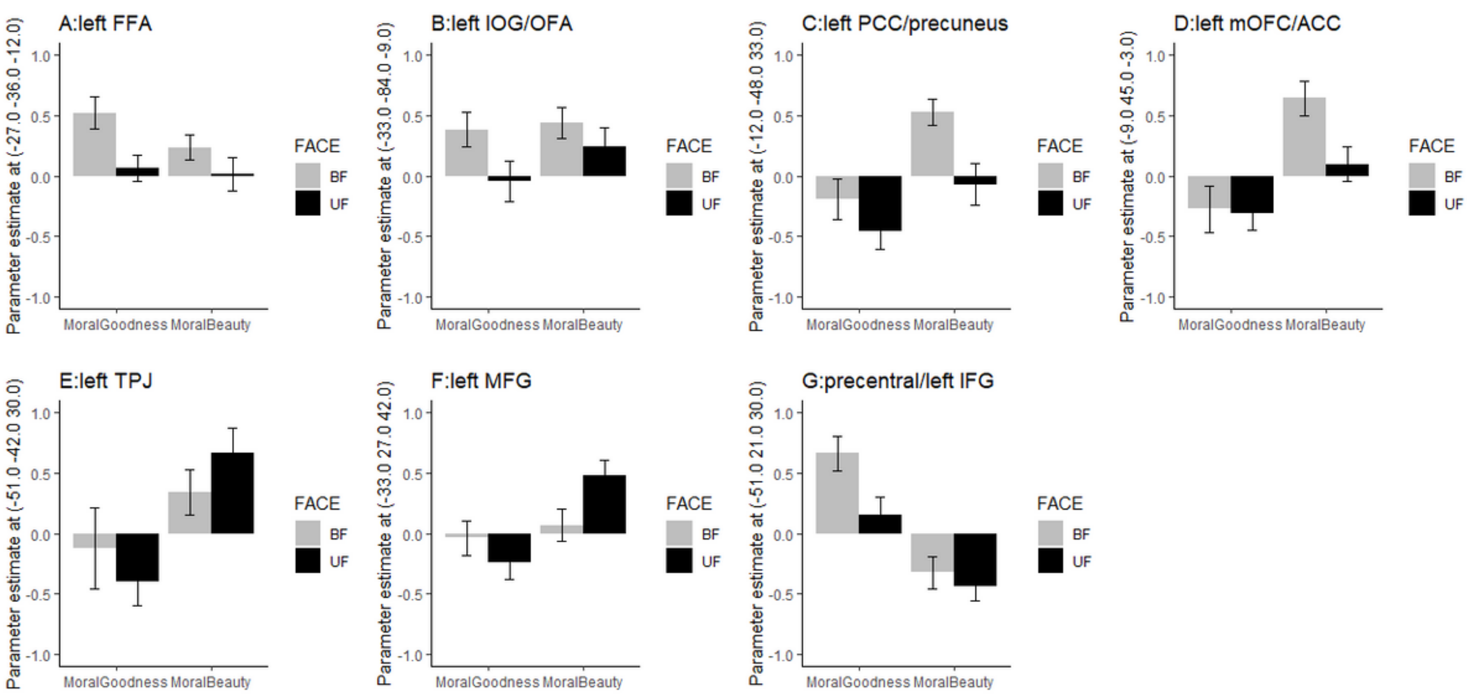

Figure 7

The results of LOOCV ROIs analysis of the effects of beautiful faces versus ugly faces and task. Results are shown for the left FFA (A), left IOG (B), left PPC/precuneus (C), left vmPFC (D), left TPJ (E), left MFG (F), and left premotor/IFG (G). Parameter estimates (beta values) of the 4 conditions (BFMG, UFMG, BFMB and UFMB) were extracted from the above defined ROIs and fed into repeated-measures 2 (task: moral goodness vs. moral beauty) × 2 (face: beautiful-face vs. ugly-face) ANOVAs. Error bars indicate standard error of means.