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ORIGINAL ARTICLE

The neural correlates of internal and external comparisons: an fMRI study

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Abstract Many previous studies have suggested that various comparisons rely on the same cognitive and neural mechanisms. However, little attention has been paid to exploring the commonalities and differences between the internal comparison based on concepts or rules and the external comparison based on perception. In the present experiment, moral beauty comparison and facial beauty comparison were selected as the representatives of internal comparison and external comparison, respectively. Functional magnetic resonance imaging (fMRI) was used to record brain activity while participants compared the level of moral beauty of two scene drawings containing moral acts or the level of facial beauty of two face photos. In addition, a physical size comparison task with the same stimuli as the beauty comparison was included. We observed that both the internal moral beauty comparison and external facial beauty comparison obeyed a typical distance effect and this behavioral effect recruited a common frontoparietal network involved in comparisons of simple physical magnitudes such as size. In addition, compared to external facial beauty comparison, internal moral beauty comparison induced greater activity in more advanced and complex cortical regions, such as the bilateral middle temporal gyrus and middle occipital gyrus, but weaker activity in the putamen, a subcortical region. Our results provide novel neural evidence for the comparative process and suggest that different comparisons may rely on both common cognitive processes as well as distinct and specific cognitive components.

Keywords Internal comparison · External comparison · Moral beauty · Facial beauty · fMRI

Introduction

Comparison is a fundamental aspect of our human psychological functioning. The importance of comparison has long been recognized (Festinger 1954; Kahneman and Miller 1986), and some behavioral characteristics of the comparative process, like influencing factors, stages, outcomes and selective accessibility, have been investigated (Mussweiler 2003; Miyake and Zuckerman 1993; Brewer and Weber 1994; Mussweiler and Bodenhausen 2002). However, with the development of neuroimaging techniques, researchers have only recently begun to focus on the neural mechanisms of comparison.

Previous studies found that number comparison obeys a distance effect, that is, participants are slower at comparing which of two numbers is larger if the numbers are closer together (Gallistel and Gelman 1992; Fulbright et al. 2003), and this distance effect of number comparison recruits a frontoparietal network, especially encompassing the intraparietal sulcus (IPS) (Pinel et al. 2001, 2004; Pesenti et al. 2000; Dehaene 1996; Cohen Kadosh et al. 2005). Based on

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these findings, many studies generally suggested that the IPS serves as a specialized brain module for numerical comparisons (Dehaene et al. 1998, 2003; Zorzi et al. 2002). However, some subsequent studies showed that physical comparisons such as physical size, line length and luminance also obeyed the same distance effect and involved the same brain region, the IPS (Dormal and Pesenti 2009; Pinel et al. 2004; Cohen Kadosh et al. 2005). For example, Dormal and Pesenti (2009) asked healthy volunteers to make numerosity comparisons and length comparisons and found that both comparisons activated the right IPS, which suggested that the two comparisons shared a common processing mechanism. Moreover, the IPS is also recruited by other comparison tasks, such as those regarding beverage taste, time and monetary reward (Rao et al. 2001; Hare et al. 2011; Wunderlich et al. 2009). Thus, most studies suggest the existence of a specific neural comparator mainly located in the IPS that accounts for the comparative process.

Recently, increasing attention has been directed to the neural mechanisms of social comparisons. Researchers have investigated the comparisons of social status (Chiao et al. 2009; Cloutier et al. 2012), intelligence (Kedia et al. 2013; Lindner et al. 2008), body height (Lindner et al. 2008; Kedia et al. 2014), and physical attractiveness (Kedia et al. 2014), and suggested that there was not a consistent brain region activated by these social comparisons. For example, Kedia et al. (2014) found that attractiveness comparisons activated the same frontoparietal network encompassing the IPS as nonsocial comparisons, which supported the hypothesis of a common process underlying different types of comparisons. Moreover, Chiao et al. (2009) demonstrated that social status and number comparisons recruited distinct but overlapping neuronal representations within the inferior parietal cortex. However, a study of intelligence comparison showed that intelligence comparison did not recruit the frontoparietal network, but instead involved the medial frontal, orbitofrontal and limbic areas, and the temporoparietal junction (Lindner et al. 2008). In addition, one study showed that the comparison of animal ferocity did not activate the IPS (Thioux et al. 2005).

In sum, the studies mentioned above led to a consistent conclusion that numerical and physical visual-feature comparisons recruited a common frontoparietal network, especially the IPS; in contrast, comparisons of different domains like social status, intelligence and animal ferocity, separately recruited specific brain regions. However, these studies of comparison have focused only on very specific types of comparisons (i.e., within a specific domain, like numerosity or intelligence). In nature, comparisons can be classified into two types: external comparison, which is based on external perception, or internal comparison, which is based on internalized concepts or rules. External comparisons such as classifying differences in size, length, height, luminance and physical attractiveness are made directly using sensory attributes (Dormal and Pesenti 2009; Pinel et al. 2004; Cohen Kadosh et al. 2005; Kedia et al. 2014). Internal comparisons such as examining differences in intelligence, social status, animal ferocity and trustworthiness are made through the internal transformation of concepts and rules (Chiao et al. 2009; Thioux et al. 2005; Kedia et al. 2013; Lindner et al. 2008; Cloutier et al. 2012). To better understand the neural mechanisms of comparison, it is important to investigate both the similarities and differences between external and internal comparisons. However, to the best of our knowledge, no study has directly compared the neural mechanisms of these different processes. In the present study we hypothesized that there were both commonalities and differences in the spatial layout of the brain activations for the two types of comparisons. Specifically, both the external and internal comparisons might recruit a frontoparietal network, especially encompassing the IPS, because they are both comparative processes in general. Moreover, compared with external comparisons, internal comparisons might recruit more advanced and complex cortical regions due to the indirect and introspective nature of these comparisons.

For this purpose, we adopted a distance effect paradigm (Kedia et al. 2014) to investigate two comparison tasks. One task was a beauty comparison, which required participants to compare the level of moral beauty of two scene drawings containing moral acts or the level of facial beauty of two face photos. The contents of the scene drawings depicted various levels of “moral beauty” (Fig. 1a), a stimulus description which is consistent with many previous studies (Keltner and Haidt 2003; Diessner et al. 2006, 2008, 2013; Takahashi et al. 2008; Wang et al. 2015). The other task was a physical size comparison, which required participants to compare the size of two scene drawings or two face photos. There are two goals for using the size comparison task in this study. One is to explore whether both facial and moral beauty comparisons rely on the same neural correlate as comparisons of simple physical magnitudes such as size. Another is to exclude a possibility that any potential difference in the two beauty comparisons is the result of differences in the stimuli used. We used functional magnetic resonance imaging (fMRI) to record the brain activity while participants took part in the experiment. In the beauty-comparison task, the comparisons of moral beauty and facial beauty belonged to the same domain (i.e., beauty) but were different types of natural comparisons (i.e., the moral-beauty comparison was internal, while the facial-beauty comparison was external). Previous studies found that moral beauty is more complex and abstract (Haidt 2007; Diessner et al. 2006;

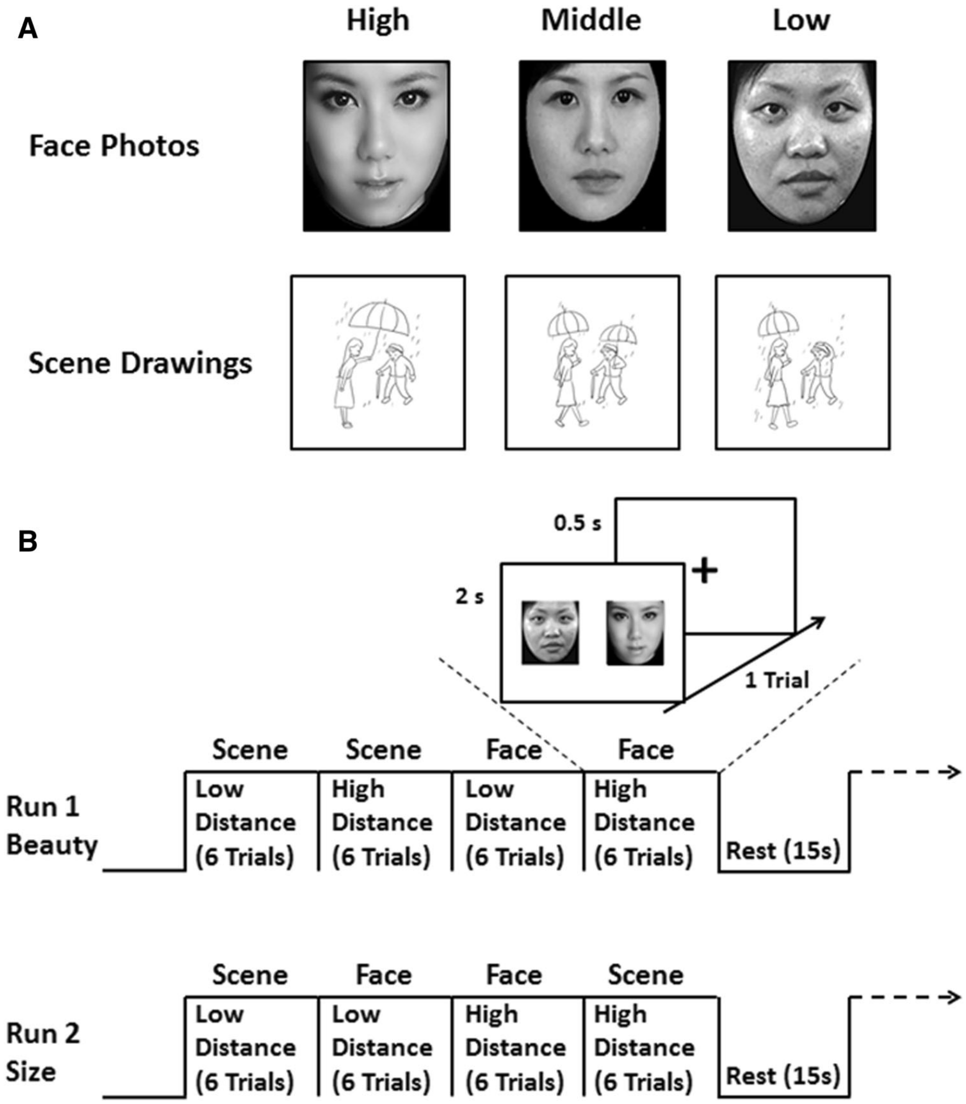

Fig. 1 Experimental materials and design. **a** Exemplars of face photos which were high, middle and low in the level of facial beauty and of scene drawings that were high, middle and low in the level of moral beauty. **b** The experimental flowchart. Stimuli were a pair of scene drawings or face photos. Participants were required to compare the beauty (which drawing is more beautiful in moral beauty or which face is more beautiful in facial beauty?) or size (which drawing or face is larger?) of these targets. The order of the two comparisons was counterbalanced across participants

Keltner and Haidt 2003) and depends on more internal cognitive processes (Wang et al. 2015), such as understanding the minds of others (Avram et al. 2013), while facial beauty mainly depends on external perceptual features (Chatterjee et al. 2009; Iaria et al. 2008; Bzdok et al. 2011). Thus, it is reasonable for us to conclude that classifications of moral beauty are representative of internal comparisons while classifications of facial beauty are representative of external comparison.

Methods

Participants

Twenty-eight (age = 21.0 ± 2.0 years; 14 males) healthy, right-handed volunteers with no history of psychiatric and neurological disorders, and with normal or corrected to normal vision, participated in the present study. All participants were enrolled in South China Normal University, Guangzhou, China. All participants provided written informed consent according to the Declaration of Helsinki, and the protocol was approved by the Research Ethics Review Board of South China Normal University. Participants received monetary compensation for their participation in the study.

Materials

Experimental materials included two types of stimuli, scene drawings and face photos. For facial stimuli, 30 black and white photographs of non-famous Asian human faces (with only neutral facial expressions) were selected from the face databases of South China Normal

University and Beijing Normal University, and were assessed by a separate sample of participants on a 9-point scale, forming 3 face photo sets: 10 high (7.01 ± 0.14), 10 middle (4.52 ± 0.10) and 10 low (2.23 ± 0.14) in the level of perceived facial beauty (Fig. 1a). For scene drawing stimuli, 171 black and white scene drawings depicting the behaviors of cartoon characters in everyday life were created. Similar to the face stimuli, three scene drawing sets were created which showed characters performing acts reflecting high, middle, and low-levels of moral beauty, respectively. To control the visual differences of the paired drawings used in the comparison task, a triplet of scene drawings had identical backgrounds and characters, and only differed in the character's moral actions (i.e., high, middle and low levels of moral beauty). A separate sample of 18 participants assessed the level of moral beauty, visual complexity, and artistry of the candidate drawings on a 7-point scale. Twenty-four triplets with significant differences in moral beauty but not in other indices were selected to achieve a better match of visual processing workload and subjective artistic preference [moral beauty: $F(2, 34) = 178.09$, $p < 0.001$; complexity: $F(2, 34) = 0.60$, $p > 0.05$; artistry: $F(2, 34) = 3.02$, $p > 0.05$], forming 3 sets: 24 high (5.28 ± 0.58), 24 middle (3.81 ± 0.39) and 24 low (2.50 ± 0.46) in the level of moral beauty (Fig. 1a).

Procedure

Our experiment consisted of two comparison tasks, a beauty comparison and a size comparison. In both tasks, two scene drawings or face photos were presented on a computer display at the same time. The center-to-center distance between the two targets subtended a horizontal visual angle of 9.4°. For half of the trials of both tasks, the targets were markedly farther from each other on the compared dimension (high distance conditions); for the other half, the targets were close to each other (low distance conditions).

In the beauty comparison task, the two targets differed in their moral beauty or facial beauty but were of the same size (horizontal visual angle and vertical visual angle were 7.05° for scene drawings; horizontal visual angle was 6.34° and vertical visual angle was 7.05° for face photos). There were four experimental conditions: moral beauty high distance (beauty comparison scene high, or BCSH), consisting of scene drawings high and low in moral beauty; moral beauty low distance (beauty comparison scene low, or BCSL), consisting of scene drawings high and middle (half of the trials) and middle and low (the other half of the trials) in moral beauty; and facial beauty high distance (beauty comparison face high, or BCFH) and low distance (beauty comparison face low, or BCFL), consisting of the same classifications of face photos as described for scene drawings. Each condition included 48 trials.

In the size comparison task, the targets differed in size but were matched for their moral or facial beauty (two targets high, middle, or low in beauty accounted for one-third of trials each). There were also four conditions: size comparison of scenes high distance (SCSH)—the vertical visual angle of the two scene drawings were 6.89° and 7.23°; size comparison of scenes low distance (SCSL)—the vertical visual angle were 7.05° and 7.19°; and size comparison of faces high distance (SCFH) and low distance (SCFL), consisting of face photos in the same vertical visual angles as the scene drawings. We modified the sizes of the original targets used in the beauty comparison task to obtain different degrees of distance to use during the size comparison task, but we kept a consistent ratio of width and height (i.e., 1:1 for scene drawings, and 9:10 for face photos) for all targets. Each condition included 48 trials. The same scene drawings and face photos were used in beauty and size comparison tasks.

During the experiment, participants were asked to decide which of the two targets was more beautiful or larger by pressing a button with the corresponding hand (i.e., using their left index finger to indicate the image on the left or right index finger to indicate image on the right). The beauty and size comparison tasks were performed in two separate fMRI scanning runs, respectively. The order of the two tasks was counterbalanced across participants. A blocked design was adopted in each run with eight blocks for each experimental condition (see Fig. 1b). Each block included six trials from the same condition. Each trial consisted of a pair of targets presented for 2 s followed by a 0.5 s fixation cross; therefore, each block lasted 15 s. Block orders were counterbalanced across participants. A block of rest (15 s) consisting of a fixation cross was presented every four active blocks in each run (Kedia et al. 2014). Before the experiment, participants performed a training session outside of the scanner with different stimuli than those used for the fMRI runs.

fMRI data acquisition

All MRI data were obtained on a 3 T Siemens Trio Tim MR scanner with a 12-channel phased array head coil at South China Normal University. The fMRI data were acquired using a gradient-echo-planar imaging (EPI) sequence with the following parameters: TR = 2000 ms, TE = 30 ms, flip angle = 90°, matrix = 64 × 64, FOV = 204 × 204 mm^2, thickness/gap = 3.5/0.8 mm, and 33 axial slices covering the whole brain. In addition, high-resolution brain structural images were obtained using a 3D T1-weighted MP-RAGE sequence with the following parameters: TR = 1900 ms, TE = 2.52 ms, flip angle = 9°, matrix = 256 × 256, FOV = 256 × 256 mm^2, thickness = 1.0 mm, and 176 sagittal slices.

fMRI data analysis

Data analysis was performed using SPM8 (http://www.fil.ion.ucl.ac.uk/spm). For each participant, the two runs were analyzed separately. The first five volumes of each run were removed to allow for scanner equilibration. Slice timing and realignment were performed to correct for the acquisition time delay and head motions. No individual run was excluded according to our criteria (the maximum head motion in any direction was not more than 1.5 mm or 1.5°). The aligned functional images were then coregistered to the high-resolution structural image, normalized to a standard Montreal Neurological Institute (MNI) template, resampled to a voxel size of $3 \times 3 \times 3$ mm^3, and the data were spatially smoothed with an isotropic FWHM 6 mm Gaussian kernel.

At the single participant level, each experimental condition was modeled as a single impulse response convolved with SPM8's canonical hemodynamic response function. A high-pass filter with a cutoff period of 128 s was applied to remove low-frequency noise. The six movement parameters calculated during the realignment were included in the model as parameters of no interest. Contrast images between each experimental condition and the baseline (i.e., the blocks of rest) were created and subsequently entered into a second-level group analysis using a random-effects model.

Whole-brain analyses

The obtained contrast images of all subjects were submitted to two separate 2 (distance) × 2 (target) repeated-measure ANOVAs for the beauty and size tasks, respectively. In line with previous studies (Pinel et al. 2004; Kedia et al. 2014; Dormal and Pesenti 2009), we used the brain activations of the distance effect (i.e., contrast of low distance condition minus high distance) to reflect the neural correlates of comparisons. Thus, at the group level, we mainly focused on the brain activations of the distance effect. To explore the commonalities of external facial beauty and internal moral beauty comparisons, we calculated the main effects of distance in the beauty comparison task [contrast: (BCSL-BCSH) + (BCFL-BCFH)]. The main effects of distance in the size comparison task [contrast: (SCSL-SCSH) + (SCFL-SCFH)] were also calculated. Subsequently, we performed a conjunction analysis of these two contrasts to test whether both facial and moral beauty comparisons rely on a common neural correlate compared with comparisons of simple physical magnitudes such as size.

Next, to explore the different neural correlates between external facial beauty and internal moral beauty comparisons (i.e., the difference between their distance effects), we examined the interactions between the factor distance (i.e., low vs. high) and the factor target (i.e., scenes vs. faces) in the beauty task; that is, contrasts ±[(BCSL-BCSH) − (BCFL-BCFH)]. Meanwhile, to exclude the influence of different stimuli on any potential differences of facial and moral beauty comparisons, the same interactions in the size task, that is, contrasts ±[(SCSL-SCSH) − (SCFL-SCFH)], were also calculated.

To investigate whether the brain activation revealed by distance effects was caused by task difficulty, the same analyses as described above were performed, but in addition, response times were modeled at the group level (for each experimental condition of each participant) as covariates of no interest.

In all whole-brain analyses, including the analysis using response times as covariates of no interest, we report the neural results at a voxel level threshold of $p < 0.001$ (uncorrected) and cluster level threshold of $p < 0.05$ (FWE corrected) to correct for multiple comparisons.

ROI analyses

As described in the Introduction, the IPS is a commonly activated brain region for various comparisons in many previous studies. Importantly, the attractiveness beauty comparisons have been found to recruit the IPS in a recent study (Kedia et al. 2014). Thus, we inferred that the facial beauty and moral beauty comparisons might also recruit the IPS in the present study. We performed a region of interest (ROI) analysis in IPS to investigate this specific hypothesis. In addition, the precuneus has been suggested to be involved in abstract reasoning and moral cognition (Lindner et al. 2008; Ciaramidaro et al. 2007; Bzdok et al. 2012; Avram et al. 2013). During internal comparison, especially the moral beauty comparison used in this study, participants need to reason and understand the behavior of cartoon characters to judge the degree of moral beauty. Thus, we anticipated that the internal comparison may induce more activity in the precuneus than the external comparison, and as such we included the precuneus in our ROI analysis to test this assumption.

For the ROI of the IPS, we used the previous results of a meta-analysis (Kadosh et al. 2008) to define two 10-mm spheres centered on the mean coordinates of bilateral IPS (left IPS: x, y, $z = -31, -50, 45$; right IPS: x, y, $z = 37, -46, 42$). In addition, we applied the WFU PickAtlas Tool version standardized template (Maldjian et al. 2003) to define one ROI covering the bilateral precuneus. In ROI analyses, we report the neural results at the rigorous voxel level threshold of $p < 0.05$ (FWE corrected) and cluster level threshold of $p < 0.05$ (FWE corrected) to correct for multiple comparisons.

Results

Behavioral data

The mean response times (RTs) for each experimental condition in beauty and size comparisons were calculated and each was submitted to a 2 (distance) × 2 (target) repeated-measures ANOVA using SPSS (version 17.0). We calculated mean RTs including the correct trials but removing the incorrect and non-response trials. We mainly focused on the distance effects (Fig. 2). The main effects of distance in both comparisons were significant: participants were faster for high distance than low distance conditions [beauty comparison: $F(1, 27) = 156.3$, $p < 0.001$; size comparison: $F(1, 27) = 173.2$, $p < 0.001$]. Post-hoc two-tailed t tests showed that participants were all faster for high distance than low distance in comparisons of moral beauty [$t(27) = 4.65$, $p < 0.001$], facial beauty [$t(27) = 13.4$, $p < 0.001$], scene drawing size [$t(27) = 11.8$, $p < 0.001$] and face photo size [$t(27) = 11.2$, $p < 0.001$], all corrected using the Bonferroni procedure. In addition, in the beauty comparison, the main effect of target [$F(1, 27) = 577.2$, $p < 0.001$] and the interaction between distance and target [$F(1, 27) = 14.6$, $p = 0.001$] were significant. However, in the size comparison, the main effect of target [$F(1, 27) = 3.98$, $p = 0.056$] and the interaction between distance and target [$F(1, 27) = 0.03$, $p = 0.859$] were non-significant.

fMRI data

Whole-brain analyses

We found that distance effects in beauty [i.e., (BCSL-BCSH) + (BCFL-BCFH)] and size [i.e., (SCSL-SCSH) + (SCFL-SCFH)] comparisons separately involved two almost identical brain networks composed of the bilateral IPS, dorsomedial prefrontal cortex (DMPFC)/supplementary motor area (SMA), and bilateral insula/inferior frontal gyrus (IFG) (Table 1). In addition, compared to the high distance beauty comparison, the low distance beauty comparison elicited stronger activity in the bilateral cerebellum/fusiform and posterior cingulate cortex (PCC), and low distance size comparisons elicited stronger activity than high distance size comparisons in the bilateral cerebellum, bilateral inferior temporal gyrus (ITG), and thalamus (Table 1). A further conjunction analysis of the above two contrasts showed that the bilateral IPS, DMPFC/SMA, bilateral insula/IFG, and left cerebellum were activated by both the distance effects of beauty and size (Table 1; Fig. 3). To gain more specific information of facial beauty and moral beauty comparisons, we also calculated the contrasts of low distance minus high distance in facial beauty and in moral beauty, and performed their conjunction analysis (see Table S1 in Supplementary Materials for these results).

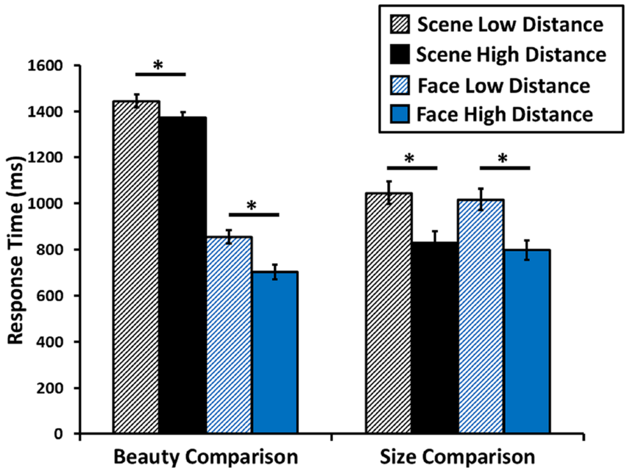

Fig. 2 Response times in all the experimental conditions. *Error bars* represent ±SEM. *$p < 0.001$

Results of interactions between the factor distance and the factor target in beauty comparison indicated that the distance effect of the moral beauty comparison elicited greater activity than that of the facial beauty comparison [i.e., (BCSL-BCSH) > (BCFL-BCFH)] in the bilateral middle temporal gyrus (MTG) and middle occipital gyrus (MOG), precuneus/PCC, and anterior cingulate cortex (ACC) (Table 2; Fig. 4a). Conversely, the distance effect of the moral beauty comparison elicited weaker activity than that of the facial beauty comparison [i.e., (BCSL-BCSH) < (BCFL-BCFH)] in the bilateral putamen (Table 2; Fig. 4b). However, the interaction analyses in the size comparison did not reveal any significant clusters of activated voxels.

All of the above results regarding the distance effects were replicated when response times were treated as covariates of no interest (Tables 1, 2). In these additional analyses, the same threshold (i.e., voxel level $p < 0.001$ uncorrected; cluster level $p < 0.05$, FWE corrected) was adopted. However, it was noted that each corresponding cluster decreased in cluster size (Tables 1, 2), which suggested task difficulty, as measured by response times, may have contributed somewhat to our results. Nevertheless, we believe that our results cannot be explained entirely by differences in task difficulty. To explore this in greater detail, we performed correlation analyses between parameter estimates in the IPS and response times across participants (see Figure S1 in Supplementary Materials). We provide a detailed treatment of this analysis in the Discussion and Supplementary Materials, but in short we found that there was no significant correlation between response times and BOLD signals in both the left and right IPS.

Table 1 Regions showing a distance effect for beauty and size comparisons and their conjunction analyses (voxel level $p < 0.001$, uncorrected; cluster level $p < 0.05$, FWE corrected)

Regions	Side	Whole-brain analysis					Whole-brain analysis with RTs as covariates				
		x	*y*	*z*	*Z* score	CS	*x*	*y*	*z*	*Z* score	CS
Distance effect in the beauty comparison											
IPS	L	−45	−45	48	4.51	244	–	–	–	–	–
IPS	R	33	−66	54	4.96	691	**51**	**−45**	**57**	**3.52**	**20**
DMPFC/SMA	L/R	−3	21	48	7.12	860	−3	21	51	4.84	358
Insula/IFG	L	−30	21	3	7.11	1551	−30	21	3	4.92	90
Insula/IFG	R	30	24	−3	7.25	1845	30	24	−3	4.77	128
PCC	L/R	0	−33	27	5.04	152	**3**	**−36**	**27**	**3.68**	**17**
Cerebelum/fusiform	L/R	−33	−60	−30	5.70	1895	**−42**	**−63**	**−48**	**4.12**	**40**
Distance effect in the size comparison											
IPS	L	−33	−48	51	8.98	1478	−30	−51	48	5.88	505
IPS	R	36	−42	45	8.67	1741	24	−66	45	5.95	639
DMPFC/SMA	L/R	9	27	39	8.16	4484	9	27	39	4.98	165
Insula/IFG	L	−30	21	3	9.11		−30	21	3	5.37	180
Insula/IFG	R	30	21	3	9.71		33	24	3	5.57	121
Cerebelum	L/R	−6	−75	−24	7.21	1325	−6	−72	−21	4.27	113
ITG	L	−45	−63	−6	5.42	137	–	–	–	–	–
ITG	R	48	−57	−6	5.75	126	**48**	**−54**	**−6**	**4.14**	**32**
Thalamus	R	15	−12	3	4.88	160	–	–	–	–	–
Distance effect in conjunction analyses											
IPS	L	−24	−63	42	4.59	246	−36	−48	39	3.83	51
IPS	R	33	−63	54	4.94	512	39	−54	45	3.96	140
DMPFC/SMA	L/R	0	21	51	7.58	496	3	18	51	4.61	198
Insula/IFG	L	−30	21	3	6.99	496	−30	21	3	5.48	150
Insula/IFG	R	30	24	−3	7.29	1108	30	21	3	5.38	118
Cerebelum	L	−33	−60	−30	5.89	439	**−30**	**−54**	**−30**	**3.69**	**41**
IFG	L	−45	9	27	5.54	156	**−51**	**9**	**30**	**3.47**	**13**

Bold fonts represent $p > 0.05$ (FWE corrected) at the cluster level. "–": nonsignificant. Coordinates refer to the stereotactic space of the Montreal Neurological Institute

CS cluster size (voxels), *RTs* response times, *IFG* inferior frontal gyrus, *DMPFC* dorsomedial prefrontal cortex, *SMA* supplementary motor area, *IPS* intraparietal sulcus, *PCC* posterior cingulate cortex, *ITG* inferior temporal gyrus

ROI analyses

ROI analyses indicated that there were significant distance effects over the bilateral IPS for both beauty (left IPS: x, y, $z = -36, -48, 39$, cluster size = 88 voxels, $z = 4.22$; right IPS: x, y, $z = 36, -42, 39$, cluster size = 103 voxels, $z = 4.68$) and size comparisons (left IPS: x, y, $z = -33, -48, 51$, cluster size = 165 voxels, $z = 8.98$; right IPS: x, y, $z = 36, -42, 45$, cluster size = 167 voxels, $z = 8.67$). There was no significant interaction in IPS for both the beauty and size comparisons. Conversely, within the ROI of the precuneus, no distance effect was found for both the beauty and size comparisons; however, a significant effect for beauty—the moral beauty comparison elicited greater activity than the facial beauty comparison—was found (precuneus: $x, y, z = -9, -57, 15$, cluster size = 19 voxels, $z = 5.15$). However, no interaction was found in the precuneus for size comparison. Thus, the results of ROI analyses with a more rigorous correction for multiple comparisons, that is, voxel level threshold of $p < 0.05$ (FWE corrected) and cluster level threshold of $p < 0.05$ (FWE corrected), further support our hypothesis. Moreover, to provide more information, we performed a 2 (task) × 2 (target) × 2 (distance) three-way repeated measures ANOVA in each ROI (the details and results of this analysis are provided in Supplementary Materials). In short we found that the results of three-way repeated measures ANOVAs were quite consistent with the main ROI analyses consisting of two separate 2 (distance) × 2 (target) repeated-measure ANOVAs for the beauty and size comparison tasks.

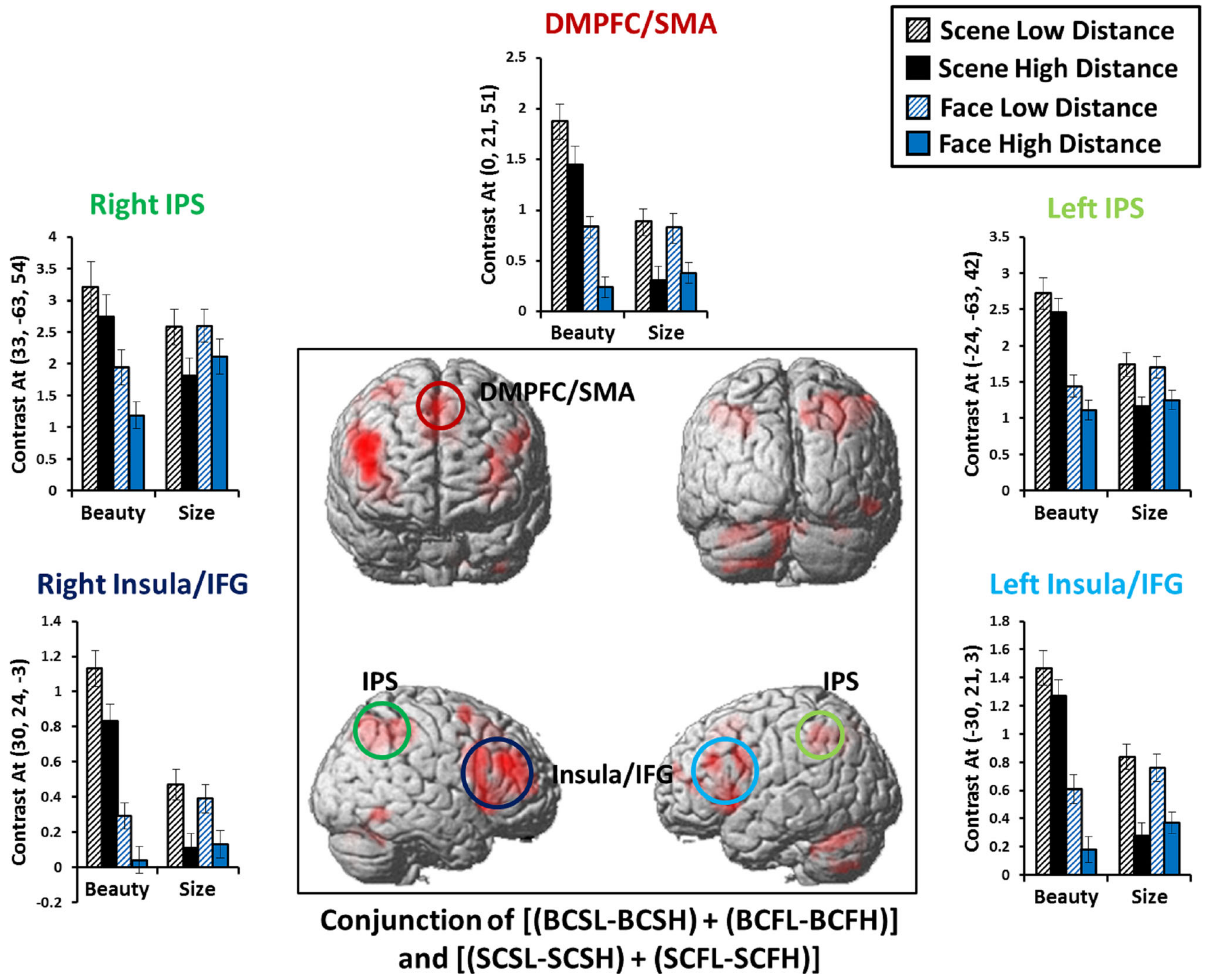

Fig. 3 Distance effect for the conjunction of beauty and size comparisons. Activation maps are shown at a voxel level threshold of $p < 0.001$ (uncorrected), and cluster level threshold of $p < 0.05$ (FWE corrected). Histograms display the parameter estimates at peak voxels in the bilateral IPS, bilateral insula/IFG, and DMPFC/SMA for beauty and size comparisons. The *histograms* are shown for qualitative purposes only and no statistical analyses are conducted on them. Brain regions are *circled* in *corresponding colors*. *Error bars* represent ±SEM

Discussion

To the best of our knowledge, this is the first study to directly explore the neural commonalities and differences of external comparisons and internal comparisons. We have three main findings. First, behavioral results indicated that external facial beauty and internal moral beauty comparisons both obeyed the distance effect with longer response times for near than far distances. Second, neuroimaging results showed that, similar to comparisons of simple physical magnitudes such as size, these distance effects of beauty recruited an overlapping frontoparietal network including the IPS, DMPFC, and insula/IFG. Third, compared to external facial beauty comparisons, internal moral beauty comparisons induced stronger activity in more advanced and complex regions of the cerebral cortex, such as the MTG, MOG, precuneus/PCC, and ACC, but weaker activity in the putamen, a subcortical region.

Common neural correlates of internal and external comparisons

In the field of traditional cognitive psychology, there is a general viewpoint that various complex comparisons involve similar mental processes (Mussweiler 2003; Kahneman and Miller 1986). Corresponding to this viewpoint, recent studies investigating the neural correlates of comparisons such as number (Pinel et al. 2001, 2004; Cohen Kadosh et al. 2005),

Table 2 Regions showing an interaction effect in the beauty comparison (voxel level $p < 0.001$, uncorrected; cluster level $p < 0.05$, FWE corrected)

Regions	Side	Whole-brain analysis					Whole-brain analysis with RTs as covariates				
		x	*y*	*z*	*Z* score	CS	*x*	*y*	*z*	*Z* score	CS
(BCSL-BCSH) > (BCFL-BCFH)											
MTG	L	−33	12	−18	5.23	82	−33	12	−18	4.91	88
MTG	R	54	6	−24	5.36	206	51	3	−24	5.06	203
MOG	L	−39	−81	33	5.61	253	−39	−81	33	5.35	156
MOG	R	48	−75	27	5.11	143	48	−75	27	4.78	106
Precuneus/PCC	L/R	−9	−57	15	5.15	407	−12	−57	18	4.85	308
ACC	L/R	−3	30	−9	5.28	542	12	21	−9	5.08	508
(BCSL-BCSH) < (BCFL-BCFH)											
Putamen	L	−30	0	0	4.42	142	−30	−3	18	4.16	77
Putamen	R	30	−6	15	4.39	111	30	−6	15	4.19	72

Coordinates refer to the stereotactic space of the Montreal Neurological Institute

CS cluster size (voxels), *RTs* response times, *MTG* middle temporal gyrus, *ACC* anterior cingulate cortex, *PCC* posterior cingulate cortex, *MOG* middle occipital gyrus

length (Dormal and Pesenti 2009), luminance (Pinel et al. 2004), social status (Chiao et al. 2009; Cloutier et al. 2012), body height (Lindner et al. 2008) and physical attractiveness (Kedia et al. 2014) all found that these comparisons of different domains involved a common frontoparietal network, mainly encompassing the IPS. Consistent with previous studies, our study also found that the distance effects of internal and external comparisons activated the IPS (Table 1; Fig. 3), suggesting that various comparisons might share a common cognitive component related to the activity of IPS. Interestingly, two fMRI experiments failed to show activity in the IPS for comparison judgments of animal ferocity (Thioux et al. 2005) as well as intelligence (Lindner et al. 2008). However, these two studies did not use a distance effect paradigm but instead used paradigms including noncomparative control conditions. Thus, the inconsistent findings may be attributed to the different experimental paradigms used. In general, however, a large majority of results suggest that the IPS is the main comparator in the brain for many types of comparisons, including internal and external comparisons.

Kedia et al. (2014) suggested that the activation of IPS induced by the distance effect can be explained by the mental number line. They stated that “numerically close numbers (e.g., 2 and 3) are spatially closer on the number line than numerically more distant numbers (e.g., 2 and 8), and are therefore more difficult to discriminate and compare” (Kedia et al. 2014). In our study, to compare the moral beauty of two scene drawings or the facial beauty of two faces, participants extract or compute a certain quantity of beauty and may represent it along a mental line to perform the comparison, thus inducing the distance effect and activating the IPS. However, one study implied that the distance effect of the comparison task might reflect a general sensorimotor transformation rather than a mental representation (Cohen Kadosh et al. 2008). Considering that the explanation of the activation in the IPS is still controversial, future research is needed to clarify this issue.

A plausible explanation for the current findings is that the activation in IPS was induced by task difficulty rather than the distance effect (Göbel et al. 2004). However, our analyses suggested that this was unlikely. First, if low distance conditions elicited more IPS activity because they are more difficult, the BOLD signals in IPS would correlate with response times across participants. However, this was not the case (see Figure S1 in Supplementary Materials). Second, to further exclude this possibility, we repeated the same whole-brain analyses but modeled response times as a covariate and found nearly the same brain activations, although each cluster decreased in size (Table 1). This suggested task difficulty may have contributed somewhat to our results. But we believe that differences in task difficulty cannot entirely explain our findings as, in addition to the results described above, the regions activated in both whole-brain analyses were so similar. Moreover, several studies testing the influence of task difficulty on distance effects still found stronger activity in the IPS during numerical comparisons (Ansari et al. 2006; Eger et al. 2003; Kedia et al. 2013). Therefore, our findings of IPS activation seem unlikely to be explained by task difficulty alone, and instead likely reflect the intrinsic neural mechanisms of comparison.

Interestingly, our findings showed that neither external facial beauty nor internal moral beauty comparisons activated the orbitofrontal cortex (OFC), despite the fact that many neuro-aesthetics studies have found a connection

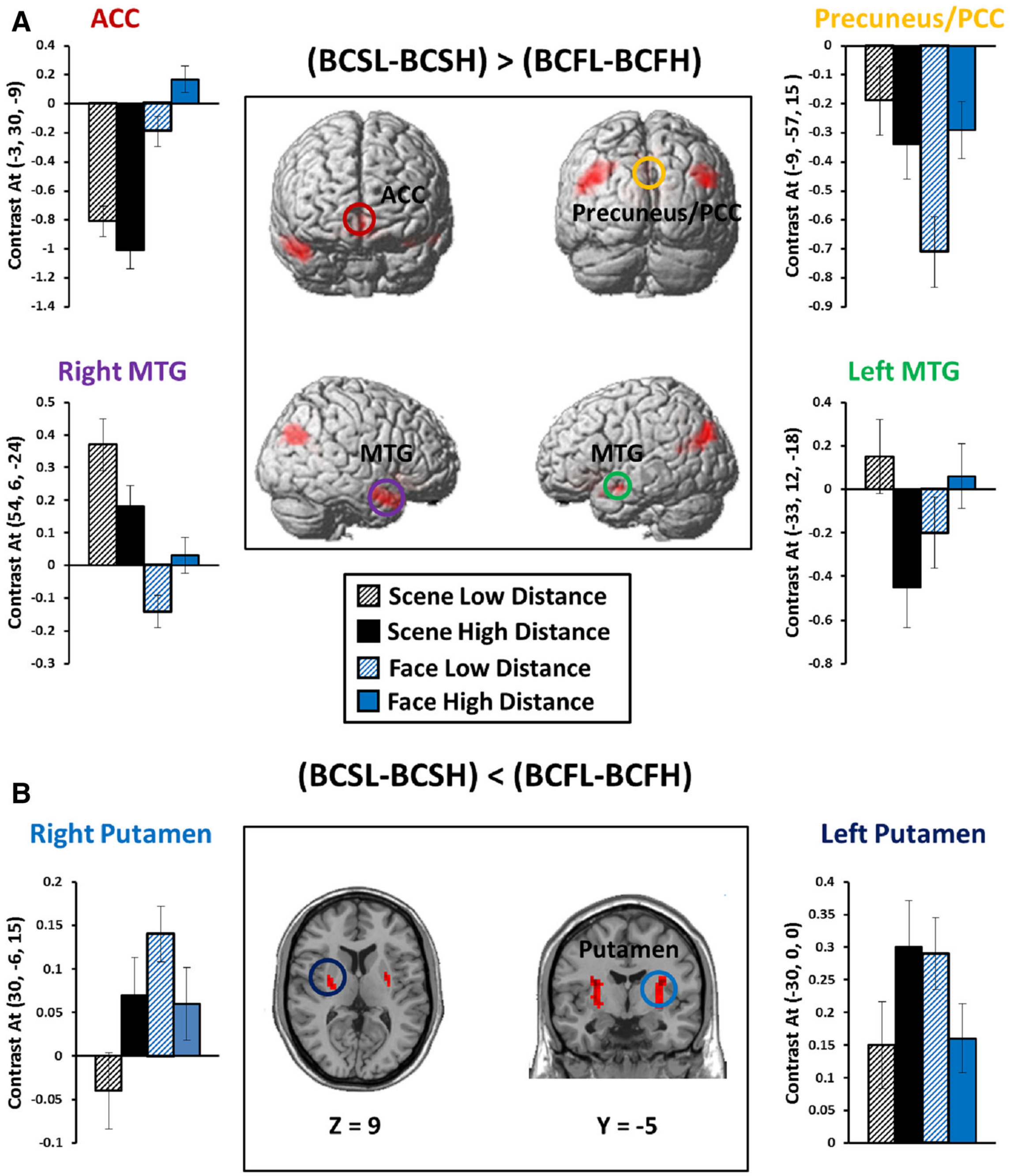

Fig. 4 Differences in the distance effect between moral and facial beauty in beauty comparison. Activation maps are shown at a voxel level threshold of $p < 0.001$ (uncorrected), and cluster level threshold of $p < 0.05$ (FWE corrected). Histograms display the parameter estimates at peak voxels in the precuneus/PCC, ACC, bilateral MTG, and bilateral putamen for beauty comparison. The *histograms* are shown for qualitative purposes only and no statistical analyses are conducted on them. Brain regions are *circled* in *corresponding colors*. **a** Moral beauty elicited greater activity than facial beauty in the precuneus/PCC, ACC, bilateral MTG, and bilateral MOG. **b** Moral beauty elicited weaker activity than facial beauty in the bilateral putamen. *Error bars* represent ±SEM

between this region and many different kinds of beauty, such as facial (Kranz and Ishai 2006; Bray and O'Doherty 2007), musical and visual (Ishizu and Zeki 2011), mathematical (Zeki et al. 2014), artistic (Kawabata and Zeki 2004), and moral beauty (Tsukiura and Cabeza 2011; Wang et al. 2015). Our results are consistent with a previous study (Kedia et al. 2014) which suggested that the comparative process of attractiveness took place outside of the OFC. Thus, we suggest the OFC may account for a representation of beauty values (Kedia et al. 2014), but not a comparison of them. That might explain the lack of a distance effect in the OFC in the present study.

Different neural correlates of internal and external comparisons

In addition to the commonalities described above, our results also revealed differences in the neural correlates of internal moral beauty comparisons and external facial beauty comparisons (Table 2; Fig. 4). However, because we used scene drawings to reflect moral beauty and face photos to reflect facial beauty, it is possible that any difference we observe between the two beauty comparisons is simply the result of differences in the stimuli used. Therefore, we added the physical size comparison tasks of scene drawings and face photos to exclude the influence of stimuli. Our results indicated that the brain activation of distance effects in size comparisons for the two types of stimuli was identical. For both whole-brain analyses and ROI analyses, there were not any significant clusters of activated voxels for the interaction between the factor distance and the factor target in size comparisons. Therefore, the differences of stimuli seem unlikely to account for our main findings using the beauty-comparison task.

Next, we further discuss the specific brain regions that are separately activated by internal comparison and external comparison in detail. First, the distance effect of internal comparison (moral beauty) elicited greater activity than that of external comparison (facial beauty) in the MTG, MOG, precuneus/PCC, and ACC. It has been suggested that the MTG plays a critical role in processing complex motion knowledge (Wallentin et al. 2011; Lingnau and Downing 2015; Watson et al. 2013) and the MOG is more activated during spatial relative to non-spatial visual tasks (Renier et al. 2010; Collignon et al. 2011). The precuneus/PCC are regions related to theory of mind and moral cognition (Young and Dungan 2012; Bzdok et al. 2012; Avram et al. 2013; Nakao et al. 2012). The ACC is known for its central role in cognitive control and conflict monitoring (van Veen et al. 2001; Carter and Van Veen 2007; MacDonald et al. 2000), as well as in moral decision-making (Nakao et al. 2012). In the present study, the internal comparison task was a moral beauty comparison during which participants were required to judge the level of moral beauty using the behavior of a cartoon character in a scene drawing. This complex process includes apparent motion and visual spatial information as well as moral cognition, and as a result, might require more conflict monitoring compared to the process of judging facial beauty. Therefore, the involvement of these regions in moral beauty comparisons is in agreement with previous studies. However, since the precuneus/PCC and ACC showed decreased activations (see the histograms in Fig. 4), our interpretation about the involvement of these regions in moral beauty comparisons should be treated conservatively and should thus be investigated in greater detail in subsequent studies. Second, facial beauty comparisons elicited greater activity than moral beauty comparisons in the bilateral putamen (Table 2; Fig. 4). In line with our results, Wang et al. (2015) found that the implicit perception of facial beauty and moral beauty both recruited neural reward systems; however, the reward system of facial beauty included the orbitofrontal cortex, a cortical region, and the putamen, a subcortical region, whereas moral beauty did not involve the putamen. A possible explanation is that the putamen is related to the physiological component of processing beautiful faces (Wang et al. 2015). Additionally, moral beauty mainly refers to high-level social need but not physiological need (Haidt 2003; Haidt et al. 2004; Keltner and Haidt 2003). Thus, compared with moral beauty comparisons, greater activity in the putamen was found for facial beauty comparisons in the present study. It is noteworthy that the explanation of the above activated brain regions are based on findings from previous studies. Further research is needed to explore this possibility in greater detail.

In brief, previous studies mainly focused on a classification of comparison from the aspect of domain or content; the present study distinguished comparison into internal and external comparisons and examined the commonalities and differences in the neural correlates of the two comparisons through an experimental approach. However, the present study is limited in that it only used moral beauty and facial beauty as representatives of internal comparison and external comparison; future studies using other types of internal and external comparisons should be performed to verify our findings. In addition, to exclude the influence of different types of stimuli, we used visual images (i.e., scene drawings and face photos) as experimental materials. It would be interesting to determine whether the same results could be found if semantic stimuli, such as poems and moral statements (Avram et al. 2013), were used to induce the external and internal comparisons.

Conclusion

In conclusion, we explored the neural correlates of internal moral beauty comparison and external facial beauty comparison using fMRI and a distance effect paradigm. We found that internal and external comparisons (along with comparisons of simple physical magnitude such as size) both obey a typical distance effect and this behavioral effect recruits a common frontoparietal network encompassing the IPS. In addition, compared with external comparisons, internal comparisons elicit greater activity in the more advanced and complex cerebral cortex but weaker activity in the putamen, a subcortical region. These findings suggest that the two comparisons rely on both common cognitive processes as well as distinct and specific cognitive components. Our study thus provides novel neural evidence of the comparative process and advances the current knowledge of the neural mechanisms underlying comparison.

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References

Ansari D, Fugelsang JA, Dhital B, Venkatraman V (2006) Dissociating response conflict from numerical magnitude processing in the brain: an event-related fMRI study. Neuroimage 32(2):799–805

Avram M, Gutyrchik E, Bao Y, Pöppel E, Reiser M, Blautzik J (2013) Neurofunctional correlates of esthetic and moral judgments. Neurosci Lett 534:128–132

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. doi:10.1152/jn.01211.2006

Brewer MB, Weber JG (1994) Self-evaluation effects of interpersonal versus intergroup social comparison. J Pers Soc Psychol 66(2):268–275

Bzdok D, Langner R, Caspers S, Kurth F, Habel U, Zilles K, Laird A, Eickhoff SB (2011) ALE meta-analysis on facial judgments of trustworthiness and attractiveness. Brain Struct Funct 215(3–4):209–223. doi:10.1007/s00429-010-0287-4

Bzdok D, Schilbach L, Vogeley K, Schneider K, Laird AR, Langner R, Eickhoff SB (2012) Parsing the neural correlates of moral cognition: ALE meta-analysis on morality, theory of mind, and empathy. Brain Struct Funct 217(4):783–796. doi:10.1007/s00429-012-0380-y

Carter CS, Van Veen V (2007) Anterior cingulate cortex and conflict detection: an update of theory and data. Cogn Affect Behav Neurosci 7(4):367–379

Chatterjee A, Thomas A, Smith SE, Aguirre GK (2009) The neural response to facial attractiveness. Neuropsychology 23(2):135–143. doi:10.1037/a0014430

Chiao JY, Harada T, Oby ER, Li Z, Parrish T, Bridge DJ (2009) Neural representations of social status hierarchy in human inferior parietal cortex. Neuropsychologia 47(2):354–363. doi:10.1016/j.neuropsychologia.2008.09.023

Ciaramidaro A, Adenzato M, Enrici I, Erk S, Pia L, Bara BG, Walter H (2007) The intentional network: how the brain reads varieties of intentions. Neuropsychologia 45(13):3105–3113

Cloutier J, Ambady N, Meagher T, Gabrieli JD (2012) The neural substrates of person perception: spontaneous use of financial and moral status knowledge. Neuropsychologia 50(9):2371–2376. doi:10.1016/j.neuropsychologia.2012.06.010

Cohen Kadosh R, Henik A, Rubinsten O, Mohr H, Dori H, van de Ven V, Zorzi M, Hendler T, Goebel R, Linden DE (2005) Are numbers special? The comparison systems of the human brain investigated by fMRI. Neuropsychologia 43(9):1238–1248. doi:10.1016/j.neuropsychologia.2004.12.017

Cohen Kadosh R, Brodsky W, Levin M, Henik A (2008) Mental representation: what can pitch tell us about the distance effect? Cortex 44(4):470–477. doi:10.1016/j.cortex.2007.08.002

Collignon O, Vandewalle G, Voss P, Albouy G, Charbonneau G, Lassonde M, Lepore F (2011) Functional specialization for auditory–spatial processing in the occipital cortex of congenitally blind humans. Proc Natl Acad Sci 108(11):4435–4440

Dehaene S (1996) The organization of brain activations in number comparison: event-related potentials and the additive-factors method. J Cogn Neurosci 8(1):47–68

Dehaene S, Dehaene-Lambertz G, Cohen L (1998) Abstract representations of numbers in the animal and human brain. Trends Neurosci 21(8):355–361

Dehaene S, Piazza M, Pinel P, Cohen L (2003) Three parietal circuits for number processing. Cogn Neuropsychol 20(3):487–506. doi:10.1080/02643290244000239

Diessner R, Rust T, Solom RC, Frost N, Parsons L (2006) Beauty and hope: a moral beauty intervention. J Moral Educ 35(3):301–317

Diessner R, Solom RD, Frost NK, Parsons L, Davidson J (2008) Engagement with beauty: appreciating natural, artistic, and moral beauty. J Psychol 142(3):303–332

Diessner R, Iyer R, Smith MM, Haidt J (2013) Who engages with moral beauty? J Moral Educ 42(2):139–163

Dormal V, Pesenti M (2009) Common and specific contributions of the intraparietal sulci to numerosity and length processing. Hum Brain Mapp 30(8):2466–2476

Eger E, Sterzer P, Russ MO, Giraud A-L, Kleinschmidt A (2003) A supramodal number representation in human intraparietal cortex. Neuron 37(4):719–726

Festinger L (1954) A theory of social comparison processes. Hum Relat 7(2):117–140

Fulbright RK, Manson SC, Skudlarski P, Lacadie CM, Gore JC (2003) Quantity determination and the distance effect with letters, numbers, and shapes: a functional MR imaging study of number processing. AJNR Am J Neuroradiol 24(2):193–200

Gallistel CR, Gelman R (1992) Preverbal and verbal counting and computation. Cognition 44(1):43–74

Göbel SM, Johansen-Berg H, Behrens T, Rushworth MF (2004) Response-selection-related parietal activation during number comparison. J Cogn Neurosci 16(9):1536–1551

Haidt J (2003) Elevation and the positive psychology of morality. In: Keyes CLM, Haidt J (eds) Flourishing: Positive Psychology and the Life Well-Lived. American Psychological Associaton, Washington, DC, p 276–289

Haidt J (2007) The new synthesis in moral psychology. Science 316(5827):998–1002. doi:10.1126/science.1137651

Haidt J, Keltner D, Peterson C, Seligman ME (2004) Appreciation of beauty and excellence. In: Peterson C, Seligman MEP (eds) Character Strengths Virtues. American Psychological Associaton, Washington, DC, p 537–551

Hare TA, Schultz W, Camerer CF, O'Doherty JP, Rangel A (2011) Transformation of stimulus value signals into motor commands during simple choice. Proc Natl Acad Sci 108(44):18120–18125

Iaria G, Fox CJ, Waite CT, Aharon I, Barton JJ (2008) The contribution of the fusiform gyrus and superior temporal sulcus in processing facial attractiveness: neuropsychological and neuroimaging evidence. Neuroscience 155(2):409–422. doi:10.1016/j.neuroscience.2008.05.046

Ishizu T, Zeki S (2011) Toward a brain-based theory of beauty. PLoS One 6(7):e21852. doi:10.1371/journal.pone.0021852

Kadosh RC, Lammertyn J, Izard V (2008) Are numbers special? An overview of chronometric, neuroimaging, developmental and comparative studies of magnitude representation. Prog Neurobiol 84(2):132–147

Kahneman D, Miller DT (1986) Norm theory: comparing reality to its alternatives. Psychol Rev 93(2):136

Kawabata H, Zeki S (2004) Neural correlates of beauty. J Neurophysiol 91(4):1699–1705. doi:10.1152/jn.00696.2003

Kedia G, Lindner M, Mussweiler T, Ihssen N, Linden DE (2013) Brain networks of social comparison. Neuroreport 24(5):259–264. doi:10.1097/WNR.0b013e32835f2069

Kedia G, Mussweiler T, Mullins P, Linden DE (2014) The neural correlates of beauty comparison. Soc Cogn Affect Neurosci 9(5):681–688. doi:10.1093/scan/nst026

Keltner D, Haidt J (2003) Approaching awe, a moral, spiritual, and aesthetic emotion. Cogn Emot 17(2):297–314

Kranz F, Ishai A (2006) Face perception is modulated by sexual preference. Curr Biol 16(1):63–68

Lindner M, Hundhammer T, Ciaramidaro A, Linden DE, Mussweiler T (2008) The neural substrates of person comparison–an fMRI study. Neuroimage 40(2):963–971. doi:10.1016/j.neuroimage.2007.12.022

Lingnau A, Downing PE (2015) The lateral occipitotemporal cortex in action. Trends Cogn Sci 19(5):268–277. doi:10.1016/j.tics.2015.03.006

MacDonald AW, Cohen JD, Stenger VA, Carter CS (2000) Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. Science 288(5472):1835–1838

Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2003) An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. Neuroimage 19(3):1233–1239

Miyake K, Zuckerman M (1993) Beyond personality impressions: effects of physical and vocal attractiveness on false consensus, social comparison, affiliation, and assumed and perceived similarity. J Pers 61(3):411–437

Mussweiler T (2003) Comparison processes in social judgment: mechanisms and consequences. Psychol Rev 110(3):472–489

Mussweiler T, Bodenhausen GV (2002) I know you are, but what am I? Self-evaluative consequences of judging in-group and out-group members. J Pers Soc Psychol 82(1):19–32

Nakao T, Ohira H, Northoff G (2012) Distinction between externally vs. internally guided decision-making: operational differences, meta-analytical comparisons and their theoretical implications. Front Neurosci 6:31. doi:10.3389/fnins.2012.00031

Pesenti M, Thioux M, Seron X, Volder Ad (2000) Neuroanatomical substrates of Arabic number processing, numerical comparison, and simple addition: a PET study. J Cogn Neurosci 12(3):461–479

Pinel P, Dehaene S, Riviere D, LeBihan D (2001) Modulation of parietal activation by semantic distance in a number comparison task. Neuroimage 14(5):1013–1026

Pinel P, Piazza M, Le Bihan D, Dehaene S (2004) Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. Neuron 41(6):983–993

Rao SM, Mayer AR, Harrington DL (2001) The evolution of brain activation during temporal processing. Nat Neurosci 4(3):317–323. doi:10.1038/85191

Renier LA, Anurova I, De Volder AG, Carlson S, VanMeter J, Rauschecker JP (2010) Preserved functional specialization for spatial processing in the middle occipital gyrus of the early blind. Neuron 68(1):138–148. doi:10.1016/j.neuron.2010.09.021

Takahashi H, Kato M, Matsuura M, Koeda M, Yahata N, Suhara T, Okubo Y (2008) Neural correlates of human virtue judgment. Cereb Cortex 18(8):1886–1891

Thioux M, Pesenti M, Costes N, De Volder A, Seron X (2005) Task-independent semantic activation for numbers and animals. Brain Res Cogn Brain Res 24(2):284–290. doi:10.1016/j.cogbrainres.2005.02.009

Tsukiura T, Cabeza R (2011) Shared brain activity for aesthetic and moral judgments: implications for the Beauty-is-Good stereotype. Soc Cogn Affect Neurosci 6(1):138–148. doi:10.1093/scan/nsq025

van Veen V, Cohen JD, Botvinick MM, Stenger VA, Carter CS (2001) Anterior cingulate cortex, conflict monitoring, and levels of processing. Neuroimage 14(6):1302–1308. doi:10.1006/nimg.2001.0923

Wallentin M, Nielsen AH, Vuust P, Dohn A, Roepstorff A, Lund TE (2011) BOLD response to motion verbs in left posterior middle temporal gyrus during story comprehension. Brain Lang 119(3):221–225. doi:10.1016/j.bandl.2011.04.006

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. Soc Cogn Affect Neurosci 10(6):814–823

Watson CE, Cardillo ER, Ianni GR, Chatterjee A (2013) Action concepts in the brain: an activation likelihood estimation meta-analysis. J Cogn Neurosci 25(8):1191–1205

Wunderlich K, Rangel A, O'Doherty JP (2009) Neural computations underlying action-based decision making in the human brain. Proc Natl Acad Sci 106(40):17199–17204

Young L, Dungan J (2012) Where in the brain is morality? Everywhere and maybe nowhere. Soc Neurosci 7(1):1–10

Zeki S, Romaya JP, Benincasa DMT, Atiyah MF (2014) The experience of mathematical beauty and its neural correlates. Front Hum Neurosci 8:68. doi:10.3389/fnhum.2014.00068

Zorzi M, Priftis K, Umilta C (2002) Brain damage: neglect disrupts the mental number line. Nature 417(6885):138–139. doi:10.1038/417138a