ORIGINAL ARTICLE

The Neural Correlates of Intelligence Comparison

Xue Wen[1,2], Jonathan S. Cant[3], Yanhui Xiang[4], Ruiwang Huang[1] and Lei Mo[1]

[1]Center for Studies of Psychological Application, Guangdong Key Laboratory of Mental Health and Cognitive Science, School of Psychology, South China Normal University, Guangzhou 510631, China, [2]School of Management, Guangdong University of Technology, Guangzhou, China, [3]Department of Psychology, University of Toronto Scarborough, Toronto ON M1C 1A4, Canada and [4]Cognition an Human Behavior Key Laboratory of Hunan and Department of Psychology, Hunan Normal University, Changsha 410006, China

Address correspondence to Lei Mo, School of Psychology, South China Normal University, Guangzhou 510631, China. Email: molei@m.scnu.edu.cn

Abstract

Social comparison plays an important role in our daily life. Several studies have investigated the neural mechanism of social comparison; however, their conclusions remain controversial. The present study explored the neural correlates of intelligence comparison and nonsocial size comparison using functional magnetic resonance imaging and a distance effect paradigm. We found that both intelligence and size comparisons obeyed the behavioral distance effect—longer response times for near than far distances and this effect involved an overlapping frontal network including the dorsomedial prefrontal cortex and insula. In addition, compared with size comparisons, intelligence comparisons elicited increased activity in the precuneus and angular gyrus, but decreased activity in the inferior parietal lobe. Furthermore, the analysis of seed-based functional connectivity complemented these neural commonalities and differences. Our findings suggest that social and nonsocial comparisons may rely on a common core mechanism, but this mechanism may be supplemented by different domain-specific cognitive components.

Key words: comparison, fMRI, intelligence, physical size, social cognition

Introduction

Various types of judgments and choices that human beings make are accomplished by comparisons in nature. When making an evaluation, from simple physical properties such as size (Pinel et al. 2004; Kadosh et al. 2005) to complex social attributes such as social status (Chiao et al. 2009), people do so in a comparative manner. As a fundamental aspect of human psychological function, the importance of comparison has long been acknowledged (Festinger 1954; Kahneman and Miller 1986). However, the neural correlates of comparisons have only recently been explored by researchers.

Previous studies have found that a frontoparietal network, especially including the intraparietal sulcus (IPS) and dorsomedial prefrontal cortex (DMPFC), was involved in various nonsocial comparisons, such as comparisons of numbers (Dehaene 1996; Pesenti et al. 2000; Pinel et al. 2001; Dehaene et al. 2003), physical size (Fulbright et al. 2003; Pinel et al. 2004), line lengths

(Fias et al. 2003; Dormal and Pesenti 2009), luminance (Pinel et al. 2004; Kadosh et al. 2005), time (Rao et al. 2001), beverage taste (Hare et al. 2011), and monetary rewards (Wunderlich et al. 2009). For example, an fMRI study investigated comparisons of different magnitude in the domains of numerical value, brightness and physical size, and found that a cortical network including the bilateral IPS was activated for all these 3 types of comparisons (Kadosh et al. 2005). Hare et al. (2011) explored the neural mechanisms of decision making processes and found that the values of beverage taste are compared in the regions of DMPFC and IPS. The activation of this frontoparietal network can be attributed to the distance effect, that is, when the 2 compared magnitudes (e.g., 2 numbers) are closer, the comparison is more difficult, and the activity of this network is stronger (Kadosh et al. 2005; Nieder and Dehaene 2009). Based on these findings, researchers suggested that this frontoparietal network may serve as a brain comparator for the general comparative

process (Kadosh et al. 2005; Kedia et al. 2014). However, comparisons in the social realm might be a special case. For example, when comparing the intelligence of 2 persons, people need to make inferences about attitudes, intentions, and intellectual performance of the 2 persons and to take their own subjective bias into account. As such, these complex and subjective social comparisons may involve more brain regions rather than just the so-called nonsocial neural comparator.

Thus far, only a handful of studies have directly investigated the neural mechanisms of social comparisons, including comparisons of intelligence (Lindner et al. 2008; Kedia et al. 2013), social status (Chiao et al. 2009), physical attractiveness (Kedia et al. 2014), and facial and moral beauty (Wen et al. 2017). Chiao et al. (2009) observed that comparisons of both social status and number obeyed a semantic distance effect and recruited the bilateral IPS. Kedia et al. (2014) suggested that the neural correlates of social attractiveness comparisons and nonsocial comparisons overlapped in the same frontoparietal network (IPS and DMPFC). In a previous study, we also observed that both external facial beauty comparisons and internal moral beauty comparisons activated the IPS and DMPFC (Wen et al. 2017). However, Lindner et al. (2008) showed that comparisons of intelligence activated regions involved in processing theory of mind (ToM) (i.e., the medial prefrontal and temporoparietal junction) and emotion-based decision making (i.e., the orbitofrontal and limbic areas), but not the IPS. Moreover, a recent study indicated that intelligence comparisons recruited a network of midline brain areas but not the frontoparietal network (Kedia et al. 2013). A possible reason for these contrary results is that the different experimental paradigms may account for the apparent contradictions. The studies about social status, attractiveness, and facial and moral beauty comparisons had used a distance effect paradigm (Chiao et al. 2009; Kedia et al. 2014; Wen et al. 2017), while the other 2 studies of intelligence comparisons had applied paradigms involving noncomparative control conditions (Lindner et al. 2008; Kedia et al. 2013). We suggest that using a noncomparative control condition may be less suitable to studying comparisons compared with a distance effect paradigm, because these control conditions may not fully conform to the criteria of pure insertion (i.e., a new cognitive component can be purely inserted without affecting the expression of previous ones (Price and Friston 1997)). Thus, the present study adopted a distance effect paradigm to investigate the neural correlates of intelligence comparisons.

The aim of the present study was to test whether intelligence comparisons share overlapping cognitive and neural mechanisms as comparisons of nonsocial magnitudes such as physical size. Particularly, we examined whether intelligence comparisons show a distance effect and whether this distance effect recruited the frontoparietal network mentioned above. We also tested whether any difference exists between intelligence and size comparisons. Moreover, several previous studies argued that different targets (i.e., different stimulus materials) can influence the same kinds of comparison processes (Fulbright et al. 2003; Pinel et al. 2004; Chiao et al. 2009; Kedia et al. 2014), but this conclusion is controversial and requires further investigation. Thus, we examined whether different stimuli (i.e., portraits and names) can influence different types of comparisons (i.e., intelligence and physical size) in a distance effect paradigm (i.e., low and high distance). To this end, we performed a 3-way within-subject experimental design consisting of 2 functional magnetic resonance imaging (fMRI) tasks. One task was an intelligence comparison, which required participants to compare the intelligence of 2 persons displayed as written names or portraits (under conditions of low and high distance). The other task was a size comparison requiring participants to compare the physical size of 2 names or portraits (under conditions of low and high distance). The data for both intelligence and size comparisons were collected from the same participants in the same session, but the intelligence and size tasks were separated into 2 fMRI runs.

Methods

Participants

We recruited 18 (age = 20.6 ± 1.6 years, 9 males) healthy, right-handed participants with normal or corrected-to-normal vision, and with no history of psychiatric and neurological disorders, from the campus of South China Normal University, Guangzhou, China. The study protocol was approved by the Research Ethics Review Board of South China Normal University. Before the fMRI scanning, written informed consent was obtained from all participants according to the Declaration of Helsinki. Participants were paid 150 CNY for their participation in the study.

Stimuli

The stimuli were 15 names (written in Chinese characters) and 15 portraits of celebrities, including scientists, politicians, entertainment, and sport stars. The names and portraits represented different individuals (i.e., 30 total celebrities used). First, the names of the celebrities were assessed for 100% familiarity on a 5-point scale by a separate sample of 21 participants and 30 names were selected from a set of 48 celebrities. Then another separate sample of 20 participants sorted the intelligence of selected celebrities according to their subjective feeling. The selected celebrities were classified into 3 groups, 10 high, 10 middle, and 10 low in the level of perceived intelligence. Finally, the names of half of each group (i.e., 5 celebrities) were replaced by their black and white portrait photographs (participants were trained to learn the relationships of portraits and names to make sure they recognized the portraits before the fMRI experiment). Each name consisted of 3 Chinese characters and was typed in black font (font: Song typeface, size: 36 pt). The dpi of each portrait was width × length = 270 pixel × 300 pixel. The detailed descriptions and results of the pretest of the stimuli are presented in Supplementary Materials.

Experimental Procedure

Two tasks, an intelligence comparison and a size comparison, were adopted in the present experiment. In both tasks, pairs of names or portraits were presented simultaneously on a white background to the left and right of the center of the screen. The distance between centers of the 2 targets was a horizontal visual angle of 9.4°.

In the intelligence comparison task, 2 targets differed in their intelligence levels but had the same physical size. For portraits, the horizontal and vertical visual angles were 6.35° and 7.05°. For names, the vertical visual angle was 1.0° and the horizontal visual angle depended on the number of characters. The task included 4 experimental conditions: intelligence comparison name low distance (ICNL)—consisted of names low and middle in intelligence (half of the trials) and names middle and high in intelligence (the other half of the trials); intelligence comparison name high distance (ICNH)—consisted of names low and high in intelligence; and intelligence comparison portrait low distance (ICPL) and high distance (ICPH)—consisted of

portraits with the same combinations described in the name conditions above. There were 48 trials for each condition. Examples of the portrait conditions are showed in Figure 1A.

In the size comparison task, 2 targets differed in their size but had the same intelligence level. Targets from the same group of high, middle, or low intelligence were assigned to one-third of the trials, respectively. The task also included 4 experimental conditions: size comparison of names low distance (SCNL) and high distance (SCNH), and size comparison of portrait low distance (SCPL) and high distance (SCPH). The vertical visual angles of the 2 portraits were 7.05° and 7.19° in SCPL (a ratio of 1:1.02) and 6.89° and 7.23° in SCPH (a ratio of 1:1.05). The horizontal visual angles of the 2 portraits were 6.35° and 6.47° in SCPL (a ratio of 1:1.02) and 6.20° and 6.51° in SCPH (a ratio of 1:1.05). The ratio of width to length for each portrait used (in both the intelligence and size comparison tasks) was kept constant at 9:10. The vertical visual angles of the 2 names were 1.0° and 1.05° in SCNL (a ratio of 1:1.05) and 0.97° and 1.07° in SCNH (a ratio of 1:1.1). The horizontal visual angle of each name depended on the number of characters. There were 48 trials for each condition.

The same names and portraits were used in both the intelligence and size comparison tasks. Each experimental condition in both the 2 tasks included 48 trials, and there were 384 trials in total. Each trial consisted of a pair of names or portraits which were presented for 2 s followed by a 0.5 s fixation cross. The 2 tasks were carried out in 2 separate fMRI runs (1 run for the intelligence comparison and 1 run for the size comparison) and each run consisted of 192 trials. The order of the 2 runs was counterbalanced across participants. Within each run, a blocked design was adopted with 8 blocks for each condition, and 6 trials per block. The order of blocks was counterbalanced across participants. Every 4 active blocks (i.e., experimental condition blocks) were followed by a rest block (15 s), during which participants fixated a cross at the center of the screen. Thus, each run lasted about 10 min. Figure 1B shows the experimental flowchart.

In the experiment, participants were required to choose which of the 2 persons represented by the portraits or names was more intelligent in intelligence comparisons, and which of the 2 physical sizes (i.e., the number of pixels) of the portraits or names was larger in size comparisons. They made their choices by pressing a button with either their right or left index finger (depending on whether the more intelligent or larger name or portrait was presented on the right, or left, respectively). Before the fMRI experiment, participants learned the
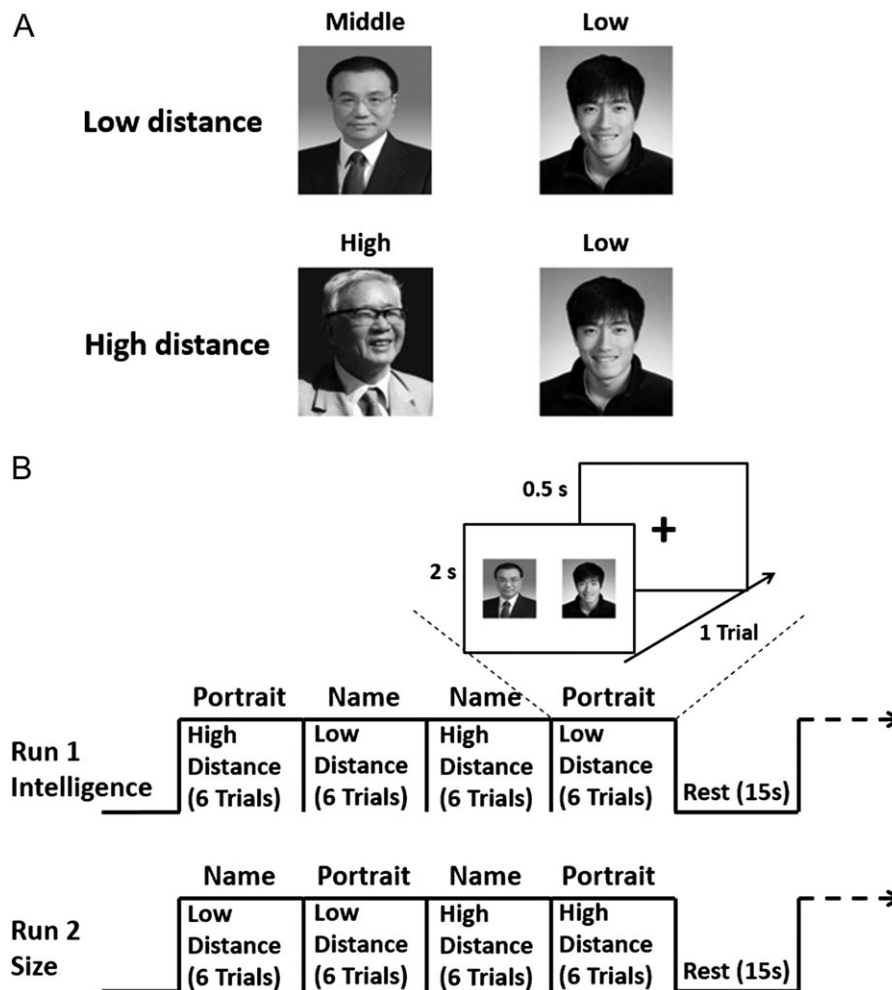

Figure 1. Illustration of experimental materials and design. (A) Examples of low and high distance conditions consisting of celebrity portraits of high, middle, and low intelligence for intelligence comparisons. (B) The experimental flowchart. Stimuli were either a pair of portraits or a pair of names. Participants were required to compare the intelligence or size of these targets. The order of the 2 comparisons was counterbalanced across participants.

relationships between 15 portraits of celebrities and their names to make sure they recognized the portraits. In addition, to let the participants familiarize with comparison tasks in general, they performed a training session of comparison tasks outside the scanner with another set of stimuli not used in the fMRI session. Following the fMRI session, participants were required to rate the intelligence level of the names and portraits they compared in the scanner on a 7-point scale (ranging from 1—very low intelligence to 7—very high intelligence; results of the post hoc validation of the stimuli are reported in the Supplementary Materials).

fMRI Data Acquisition

MRI data were acquired on a 3 T Siemens Trio Tim MR scanner with a 12-channel head coil in South China Normal University. Functional images were obtained using a T2*-weighted gradient-echo echo-planar imaging (GRE-EPI) sequence with the following parameters: TR = 2000 ms, TE = 30 ms, flip angle = 90°, 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 (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

fMRI data were preprocessed and analyzed using the statistical parametric mapping program (SPM8, http://www.fil.ion.ucl.ac.uk/spm). For the data of each run of each participant, we applied the following steps: (1) discarding the first 5 volumes to allow for scanner equilibration, (2) slice timing correction for acquisition delay, (3) realigning to the first volume to correct for head motions (no individual run was more than 2.0 mm displacement or 2.0° rotation), (4) normalization (coregistered with the anatomical image) to the MNI template and resampling to a voxel size of 3 × 3 × 3 mm^3, and (5) spatially smoothing with an isotropic FWHM 6 mm Gaussian kernel.

At the first level, condition-related brain activity changes were estimated using a general linear model in intelligence and size comparison runs, respectively. We defined each experimental condition (4 per run) as a predictor of interest and convolved these predictors with SPM8's canonical hemodynamic response function. We modeled 6 motion parameters as predictors of no interest. We also applied a high-pass filter (cutoff period of 128 s) to remove low-frequency noise. The contrasts of interest between each experimental condition and the baseline (i.e., the rest period blocks) were then computed and put into a second-level group statistical analysis treating participant as a random factor.

Statistical Analysis

According to previous studies (Chiao et al. 2009; Kedia et al. 2014; Wen et al. 2017), the distance effect (i.e., activations observed for the contrast of low distance minus high distance) was used to examine the neural correlates of comparisons. Thus, at the second level, we computed the main effect of distance in the intelligence conditions (contrast: [ICPL–ICPH] + [ICNL–ICNH]) and size conditions (contrast: [SCPL–SCPH] + [SCNL–SCNH]) to investigate the neural correlates of intelligence and size comparisons, respectively. We then performed a conjunction analysis (i.e., the

intersection) between the above 2 contrasts to test whether intelligence comparisons rely on the same neural mechanisms as size comparisons (irrespective of target, i.e., portrait vs. name). Similarly, we also computed the main effect of distance in the portrait (contrast: [ICPL–ICPH] + [SCPL–SCPH]) and name (contrast: [ICNL–ICNH] + [SCNL–SCNH]) conditions separately, as well as a conjunction analysis between these 2 contrasts to test whether portrait comparisons and name comparisons (irrespective of comparison task, i.e., intelligence vs. size) rely on similar neural mechanisms.

In addition, we computed the difference between distance effects in intelligence and size conditions, that is, the 2-way interaction between the factor distance and the factor task—contrast ± ([ICPL–ICPH + ICNL–ICNH] – [SCPL–SCPH + SCNL–SCNH]), to further examine any difference between the neural correlates of intelligence and size comparisons. Moreover, to test whether the comparative processes of intelligence and size were influenced by different targets, we computed the differences between distance effects in the portraits and in names separately, that is, interactions between the factor distance and the factor target in the intelligence conditions—contrast ± ([ICPL–ICPH] – [ICNL–ICNH]) and size conditions—contrast ± ([SCPL–SCPH] – [SCNL–SCNH]).

It is certainly possible that the brain activations revealed by the distance effect may be affected by task difficulty (here defined as differences in response times [RTs] across conditions). To test this possibility, we performed the same conjunction analyses mentioned earlier, but this time, the RTs were modeled as covariates of no interest at the individual level (for each condition block of each participant).

Furthermore, we ran a full factorial ANOVA for the entire 3-way within-subject design to compute the main effects of task, target and distance, the 3-way interaction, and the remaining 2-way interactions. We have provided a simple summary of the statistical analytical strategy in Table S1 in the Supplementary Materials to help the readers appreciate the full design and analytical procedure of the present study.

When reporting the brain activations for a given contrast, we used a very rigorous correction (family-wise error, FWE) for voxel-wise multiple comparisons at the whole-brain level to reduce false positives (Eklund et al. 2016). That is, we used a voxel level threshold of $P < 0.05$ (FWE corrected) and cluster level threshold of $P < 0.05$ (FWE corrected) and spatial extent of 10 contiguous voxels. It is noted that the FWE procedure was conducted at both the voxel level and the cluster level in the present study. Statistical maps were labeled based on the MRIcro atlas (http://www.mricro.com) and results were visualized with the BrainNet Viewer (http://www.nitrc.org/projects/bnv/) (Xia et al. 2013).

To complement the analyses discussed above, which all focused on neural activation within single cortical regions, we also conducted functional connectivity (FC) analyses to examine relationships across cortical regions (Biswal et al. 1995; Greicius et al. 2003). We first defined 5 regions of interest (ROIs) by using five 5-mm radius spheres centered on the coordinates of the activation peaks of the previous analyses (Tables 2 and 3). We then extracted the time courses of each ROI for each participant using the smoothed fMRI data from intelligence and size runs, separately. For each participant, the FCs among these ROIs were obtained through calculating Pearson's correlation coefficient for the time courses between any pair of ROIs (Biswal et al. 1995; Greicius et al. 2003). Finally, we compared these FCs between intelligence and size comparisons using 2-tailed paired t-tests (Bonferroni corrected to control for inflations to Type-I error rate).

Results

Behavioral Data

The mean RTs for each experimental condition in intelligence and size comparisons were calculated and each was submitted to a 2 (distance) × 2 (target) repeated-measures ANOVA separately using SPSS (version 17.0). Although we created high, middle and low intelligence groups, it is certainly the case that intelligence comparisons are subjective, and thus we did not distinguish "correct" and "incorrect" trials when calculating mean RTs. For the same reason, we did not conduct an accuracy analysis. Instead, we focused on the distance effects for RTs, which were highly reliable (Fig. 2). We found that the main effects of distance in both comparisons were significant: participants were faster for high distance than low distance conditions (intelligence comparison: $F[1, 17] = 46.1$, $P < 0.001$; size comparison: $F[1, 17] = 107.5$, $P < 0.001$). However, no significant main effects of target (intelligence comparison: $F[1, 17] = 0.58$, $P = 0.456$; size comparison: $F[1, 17] = 1.92$, $P = 0.184$) and interactions (intelligence comparison: $F[1, 17] = 2.98$, $P = 0.102$; size comparison: $F[1, 17] = 0.75$, $P = 0.400$) in either the intelligence or size comparison tasks. In addition, post hoc 2-tailed t tests (corrected for multiple comparisons using the Bonferroni procedure) showed that participants were faster for high distance than low distance comparisons of portrait intelligence ($t[17] = 7.22$, $P < 0.001$), name intelligence ($t[17] = 4.25$, $P < 0.001$), portrait size ($t[17] = 7.26$, $P < 0.001$), and name size ($t[17] = 8.09$, $P < 0.001$).

fMRI Data

Distance Effect

First, our results showed that distance effects in the intelligence and size conditions separately recruited 2 similar networks, including the bilateral insula, DMPFC/supplementary motor area (SMA), IPS, inferior and middle frontal gyrus (IFG/MFG), and left cerebellum (Table 1 and Fig. 3A,B). In addition, the distance effect in the intelligence conditions activated the bilateral precuneus/posterior cingulate cortex (PCC), superior frontal gyrus (SFG), and right cerebellum (Table 1 and Fig. 3A).
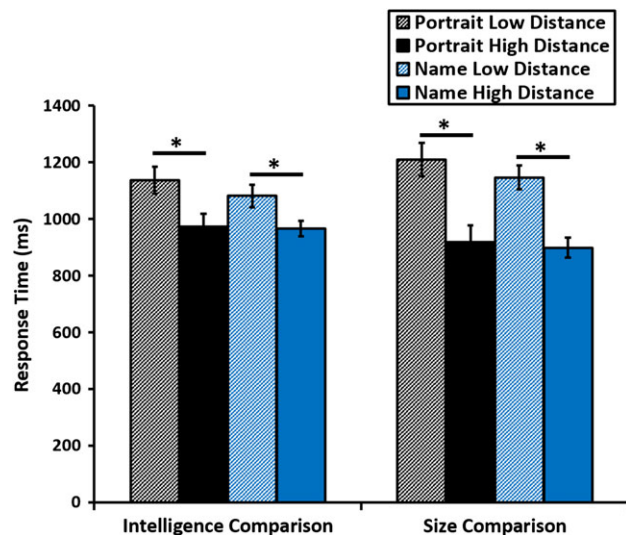

Figure 2. Response times in all the experimental conditions. Error bars represent ± SEM. *P < 0.001.

Second, the distance effects in the portrait and name conditions also separately involved 2 similar networks, including the bilateral insula and DMPFC/SMA (Table 1). It is noted that the activations of DMPFC/SMA and insula for the distance effect in the portrait conditions are partially uncorrected results (Table 1), which should be interpreted conservatively. In addition, the distance effect in the portrait conditions activated a cluster located in widely distributed occipital and temporal areas, including the bilateral superior occipital gyrus (SOG), middle occipital gyrus (MOG), lingual gyrus and fusiform gyrus. In contrast, the distance effect in the name conditions activated the bilateral IPS and right IFG/MFG (Table 1).

Third, the conjunction analysis of the distance effects of intelligence and size comparisons revealed significant overlap in the bilateral insula, the DMPFC, the right MFG, and the left cerebellum (Table 2 and Fig. 3C), which is consistent with our hypothesis. In addition, the conjunction analysis of the distance effects of portrait and name comparisons significantly overlapped in the bilateral insula and DMPFC (Table 2). We noticed that the 2 conjunction analyses did not activate the IPS, although Table 1 showed that both the distance effects of intelligence and size recruited the bilateral IPS. Thus, we applied a small volume correction to further investigate this issue. When performing the small volume correction, we defined two 5-mm radius spheres centered on the mean coordinates of bilateral IPS (left IPS: x, y, $z = -31, -50, 45$; right IPS: x, y, $z = 37, -46, 42$) according to a previous study (Kadosh et al. 2008). Again, we found no activation for the 2 conjunction analyses in the bilateral IPS.

Moreover, all of the distance effect results for the conjunction analyses were replicated when RTs were treated as covariates of no interest (Table 2). These control analyses suggested that task difficulty, as measured by differences in RTs across conditions, did not account for the results we observed. To further justify the relationship between activations of distance effects and task difficulty, we performed correlation analyses between parameter estimates in the DMPFC/SMA (one of the most consistently activated regions across analyses) and RTs across participants (see Fig. S1 in Supplementary Materials). In short, we found no significant correlation between RTs and neural activation in the DMPFC/SMA. This again indicated that our neural results cannot be explained solely in terms of differences in task difficulty across conditions.

Interactions

Table 3 and Figure 4A show that distance effect for intelligence comparisons elicited stronger activity than that of size comparisons in widely distributed frontal and parietal regions, including the bilateral precuneus/PCC, medial orbitofrontal cortex (mOFC), SFG/MFG and angular gyrus, left OFC, left IFG, and right cerebellum. The distance effect for size comparisons elicited stronger activity than that of intelligence comparisons in the right IPL/supramarginal gyrus(the coordinates are close to the IPS), and a peak located in the right IFG. These results showed that, despite the similarities discussed above, intelligence and size comparisons also recruit distinct cortical regions.

When examining the interactions between distance and target in the intelligence task (Table 3), we observed that the distance effect for portraits triggered stronger activity than for names in the bilateral occipital cortex including the lingual gyrus and MOG. No differential activation was found for the opposite contrast. Similarly, in the size comparison task, the distance effect for portraits induced increased activity compared with the names in the bilateral occipital cortex, including the lingual

Table 1 Regions showing activation for distance effects (voxel level $P < 0.05$, FWE corrected; cluster level, $P < 0.05$, FWE corrected and spatial extent of 10 contiguous voxels)

Regions	Hemisphere	x	y	z	t Score	Cluster size (# voxels)
Distance effect in the intelligence conditions: (ICPL–ICPH) + (ICNL–ICNH)						
DMPFC/SMA	L/R	−6	18	48	7.85	139
Insula	L	−30	21	3	7.19	44
	R	30	24	0	7.11	28
Precuneus/PCC	L/R	0	−63	33	10.63	265
IPS	L	−30	−60	45	6.10	36
	R	39	−63	42	5.88	18
IFG/MFG	L	−51	24	30	8.29	222
	R	42	30	24	6.86	142
MFG	L	−48	48	−3	6.62	57
SFG	L	−18	39	51	7.62	80
	R	36	18	57	6.79	17
Cerebellum	L	−6	−78	−27	7.84	64
	L	−33	−66	−45	6.31	36
	R	9	−84	−33	6.82	43
	R	33	−66	−45	6.82	64
	R	3	−54	−45	6.60	25
Distance effect in the size conditions: (SCPL–SCPH) + (SCNL–SCNH)						
DMPFC/SMA	L/R	−3	15	51	7.53	101
Insula	L	−33	15	6	6.90	56
	R	33	21	3	8.03	79
IPS	L	−21	−63	48	6.90	122
	R	42	−39	45	7.73	340
IFG	L	−48	6	21	6.26	57
	R	51	9	27	7.83	127
MFG	R	27	−3	48	6.29	37
	R	48	39	30	6.21	29
Cerebellum	L	−21	−69	−48	7.18	20
Distance effect in the portrait conditions: (ICPL–ICPH) + (SCPL–SCPH)						
DMPFC/SMA	L/R	−3	18	48	5.70	272
Insula	L	−33	18	3	5.09	90
	R	33	21	3	5.47	85
SOG	L	−15	−93	9	9.49	1029
	R	12	−93	9	9.69	
MOG	L	−30	−87	12	7.22	
	R	33	−81	18	8.59	
Lingual gyrus	L	−9	−81	−6	7.05	
	R	12	−75	−6	7.25	
Fusiform gyrus	L	−30	−78	−15	5.73	
	R	30	−66	−9	6.28	
Distance effect in the name conditions: (ICNL–ICNH) + (SCNL–SCNH)						
DMPFC/SMA	L/R	−3	21	45	6.29	52
Insula	L	−30	21	3	6.68	35
	R	30	24	0	6.43	32
IPS	R	36	−54	39	5.62	13
IFG/MFG	R	42	30	24	6.73	61
IOG/MOG	L	−27	−99	−6	7.14	47
ITG	L	−45	−54	−12	6.05	18

Coordinates refer to the MNI stereotactic space. Bold fonts indicate the threshold of voxel level $P < 0.001$ (uncorrected) and cluster level $P < 0.05$ (FWE corrected). IFG/MFG/SFG, inferior/middle/superior frontal gyrus; IOG/MOG/SOG, inferior/middle/superior occipital gyrus; ITG, inferior temporal gyrus.

gyrus, calcarine gyrus and SOG. Again, no differential activation was found for the opposite contrast (Table 3). These results suggested that intelligence and size comparisons were influenced by different stimulus materials in a similar way.

The results of the full factorial ANOVA, including the main effects of task, target and distance, the 3-way interaction of task by target by distance and the 2-way interactions of task by target and target by distance, are shown in Table S2 in the Supplementary Materials.

Functional Connectivity

So far, we have shown the neural commonalities and differences between intelligence and size comparisons at the level of functional activation within single cortical regions. To provide complementary evidence for these results, we also calculated FCs among the ROIs of the left and right insula, bilateral DMPFC/SMA, bilateral precuneus/PCC, and right IPL/supramarginal gyrus. We found that the FCs among the regions common to both tasks (i.e., bilateral insula and DMPFC/SMA) were not significantly different
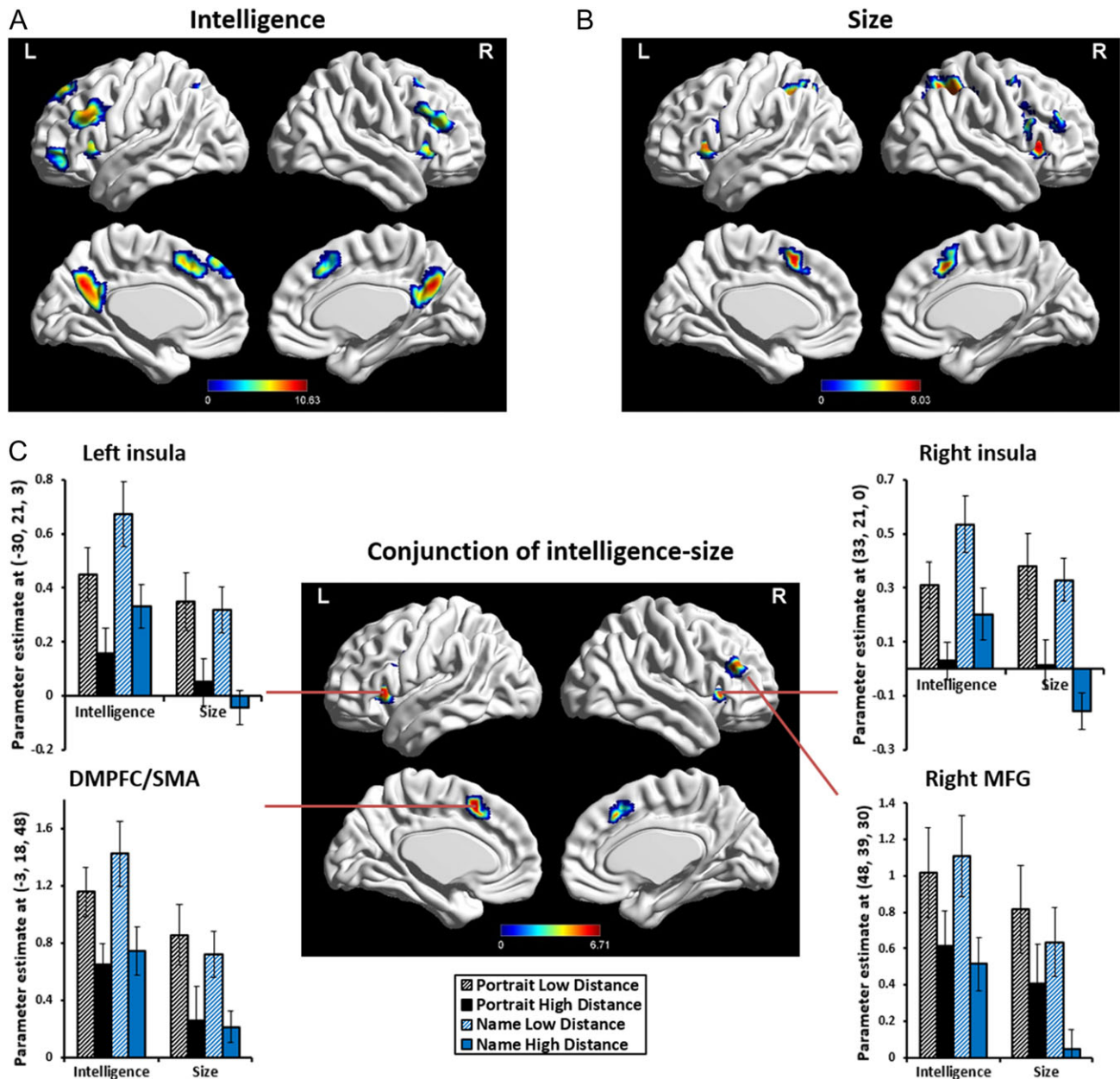
Figure 3. Distance effects. Activation maps are shown at a voxel level threshold of $P < 0.05$ (FWE corrected) and cluster level threshold of $P < 0.05$ (FWE corrected). Images were plotted with the BrainNet Viewer (http://www.nitrc.org/projects/bnv/). (A) and (B) Distance effects in the intelligence and size conditions separately. (C) Conjunction of the intelligence and size distance effects. Histograms display the parameter estimates at peak voxels in the bilateral DMPFC/SMA, bilateral insula, and right MFG. The histograms are shown for qualitative purposes only and no statistical analyses are conducted on them. Error bars represent ± SEM.

between the intelligence and size comparisons (Fig. 4B). However, the FCs between the precuneus/PCC and the bilateral insula and DMPFC/SMA were significantly stronger in intelligence comparisons compared with size comparisons (Fig. 4B). Conversely, the FCs between the IPL/supramarginal gyrus and the bilateral insula and DMPFC/SMA were significantly stronger in size comparisons compared with intelligence comparisons (Fig. 4B). The detailed FC values and P-values comparing FCs in the intelligence and size tasks are listed in Table S3 (Supplementary Materials).

Discussion

This study used the distance effect paradigm to explore the neural and cognitive mechanisms of social intelligence comparison and nonsocial physical size comparison. We report the following findings: (1) both intelligence and size comparisons obeyed the behavioral distance effect—longer RTs for near than far distances; (2) these distance effects involved an overlapping frontal network including the DMPFC and insula; (3) contrast to size comparisons, intelligence comparisons elicited increased neural activity in the precuneus/PCC, SFG/MFG, and angular gyrus, but decreased activity in the IPL/supramarginal gyrus; and (4) FC analysis further complemented the relationship between intelligence and size comparisons. These results provided evidence for the neural commonalities and differences in the comparison of subjective intelligence and objective nonsocial values.

There are 2 viewpoints regarding the mental processes of comparisons. One is that comparisons within different realms

Table 2 Regions showing activation for conjunction analyses without and with response times (RTs) as covariates (voxel level $P < 0.05$, FWE corrected; cluster level, $P < 0.05$, FWE corrected and spatial extent of 10 contiguous voxels)

Regions	Hemisphere	Without RTs as covariates					With RTs as covariates				
		x	y	z	t Score	CS	x	y	z	t Score	CS
Conjunction analyses of the intelligence and size distance effects											
DMPFC/SMA	L/R	−3	18	48	6.71	78	−3	18	48	6.74	76
Insula	L	−30	21	3	6.47	42	−30	21	3	6.48	40
	R	33	21	0	5.63	15	33	21	0	6.64	14
MFG	R	48	39	30	6.18	37	48	39	30	6.13	35
Cerebellum	L	−6	−75	−24	5.97	11	–	–	–	–	–
Conjunction analyses of the portrait and name distance effects											
DMPFC/SMA	L/R	−3	18	48	5.76	38	−3	18	48	5.79	33
Insula	L	−33	18	3	5.51	11	−33	18	3	5.52	11
	R	30	21	3	5.61	11	33	21	3	5.63	11

Coordinates refer to the MNI stereotactic space. "–": nonsignificant. CS, cluster size (# voxels); DMPFC, dorsomedial prefrontal cortex; SMA, supplementary motor area; MFG, middle frontal gyrus.

Table 3 Regions showing activation for interactions between the factor distance and the other 2 factors (voxel level, $P < 0.05$, FWE corrected; cluster level, $P < 0.05$, FWE corrected and spatial extent of 10 contiguous voxels)

Regions	Hemisphere	x	y	z	t Score	Cluster size (# voxels)
Two-way interaction of distance by task						
Intelligence distance effect (ICPL–ICPH + ICNL–ICNH) > size distance effect (SCPL–SCPH + SCNL–SCNH)						
Precuneus/PCC	L/R	0	−60	30	10.05	714
SFG/MFG	L/R	24	30	54	8.18	670
Angular gyrus	L	−48	−69	33	7.16	241
	R	51	−66	36	8.86	262
mOFC	L/R	3	45	−15	6.53	112
OFC	L	−39	36	−12	8.39	51
IFG	L	−51	24	30	6.63	66
MTG	R	63	−6	−21	6.05	34
Cerebellum	R	42	−72	−36	5.94	52
	R	9	−51	−42	6.33	21
	R	18	−81	−27	6.17	56
Size distance effect (SCPL–SCPH + SCNL–SCNH) > intelligence distance effect (ICPL–ICPH + ICNL–ICNH)						
IPL/supramarginal gyrus	R	60	−27	45	−6.65	136
IFG	R	54	9	24	−6.55	40
Interaction between distance and target in intelligence task						
Portrait distance effect (ICPL–ICPH) > name distance effect (ICNL–ICNH)						
Lingual gyrus	L	−21	−75	−9	6.34	31
	R	6	−81	−6	6.87	28
MOG	L	−15	−99	9	6.26	16
	R	12	−96	6	6.73	13
Name distance effect (ICNL–ICNH) > portrait distance effect (ICPL–ICPH)						
No activation						
Interaction between distance and target in size task						
Portrait distance effect (SCPL–SCPH) > name distance effect (SCNL–SCNH)						
Calcarine gyrus	L	−9	−93	6	6.34	178
	R	9	−90	6	9.72	
SOG	L	−15	−96	12	6.53	
Lingual gyrus	L	−12	−78	−6	6.26	
Name distance effect (SCNL–SCNH) > portrait distance effect (SCPL–SCPH)						
No activation						

Coordinates refer to the MNI stereotactic space. MTG, middle temporal gyrus; IPL, inferior parietal lobule. The regions of calcarine gyrus, SOG, and lingual gyrus belong to one and the same cluster (178 voxels) but have different local peaks.

involve similar psychological mechanisms (Kahneman and Miller 1986; Mussweiler 2003). The other viewpoint posits that the neural representation of comparative judgments may be organized along basic content domains into different realms, such as social and nonsocial realms (Lindner et al. 2008). Our results showed that intelligence comparisons and size comparisons obeyed the same distance effect and the neural mechanisms of these distance effects overlapped in the DMPFC and insula (Table 2). These findings partly supported the former viewpoint. Furthermore, comparisons of portraits and names
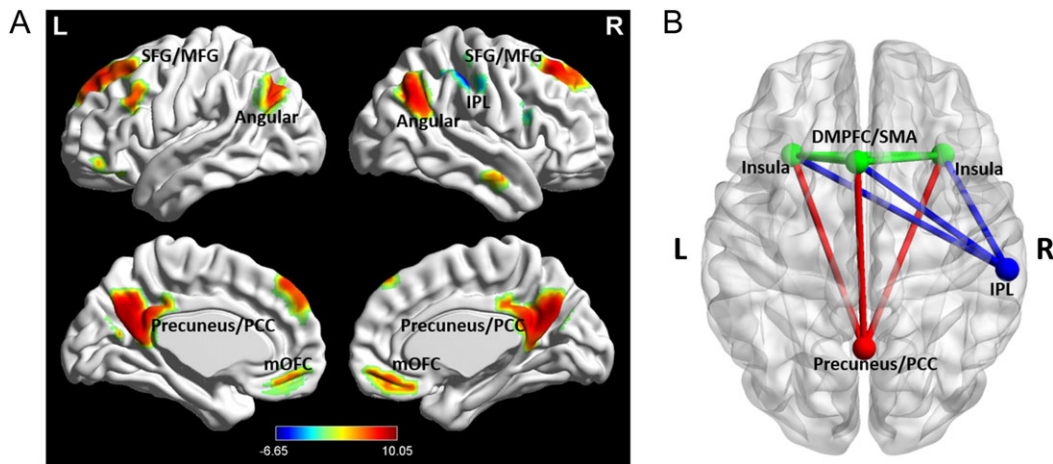
Figure 4. Differences between intelligence and size comparisons. Images were plotted with the BrainNet Viewer (http://www.nitrc.org/projects/bnv/). (A) Differences in distance effects. Activation maps are shown at a voxel level threshold of $P < 0.05$ (FWE corrected) and cluster level threshold of $P < 0.05$ (FWE corrected). Warm (cold) color indicates that intelligence comparisons elicited greater (weaker) activity than size comparisons. (B) Differences in functional connectivity (FC). Red (blue) color indicates increased (decreased) FCs for the intelligence comparisons compared with the size comparisons; green color indicates no significant difference in FC between the intelligence and size comparisons.

also overlapped in these regions (Table 2), which indicated that these distance effects were consistent across different targets. Our results are consistent with previous studies, which suggested that comparisons on various domains like number (Ansari et al. 2006; Chiao et al. 2009), beverage taste (Hare et al. 2011), monetary rewards (Wunderlich et al. 2009), social status (Chiao et al. 2009), physical attractiveness (Kedia et al. 2014), and facial and moral beauty (Wen et al. 2017) all recruited a frontoparietal network, mainly including the DMPFC and IPS. Taken together, our results suggest that different types of comparison may involve a common core neural mechanism.

The DMPFC is an important common region for intelligence and size comparisons in our study. A previous study has argued that the DMPFC is a natural region to implement a comparison process (Hare et al. 2011), as it is functionally interconnected with response-related areas like SMA and valuation-related areas like ventromedial prefrontal cortex (Picard and Strick 2001; Beckmann et al. 2009). Another study showed that neurons in DMPFC encoded several different decision variables (Kennerley et al. 2009), which makes this region an ideal candidate to compare different options. In addition, the DMPFC has been confirmed to be engaged in decision making and action selection (Amodio and Frith 2006). Thus, it is not surprising that both intelligence and size comparisons involved the DMPFC in the present study, as the 2 comparison tasks both contained the processes of decision making and response selection.

The insula is another region responding to both intelligence and size comparisons. While few studies have focused on the role of the insula in comparative processes, several studies have nevertheless demonstrated that the insula was indeed recruited in comparisons of number (Kadosh et al. 2005; Ansari et al. 2006; Dormal and Pesenti 2009), physical size (Fulbright et al. 2003; Kadosh et al. 2005; Wen et al. 2017), body height and physical attractiveness (Kedia et al. 2014), and facial and moral beauty (Wen et al. 2017). Since the insula has been associated with various motor processes (Augustine 1996; Kurth et al. 2010; Menon and Uddin 2010), we could not exclude the possibility that the activation in the insula may be explained by motor processing associated with manual button responses. However, given the fact that all our experimental conditions included a motor response and our results showed no

activation in the primary motor cortex (Tables 1 and 2), we suggest that the activation in the insula cannot be explained solely by motor processing. Given the issue of reverse inference (Poldrack 2006), more studies, particularly experiments that do not contain a motor response, are needed to clarify the role of the insula in comparative processing in detail.

An alternative explanation for the overlapping neural correlates of intelligence and size comparisons is that the activations of DMPFC and insula reflect differences in task difficulty rather than evidence of common internal representations for different types of comparisons. However, several previous studies have indicated that task difficulty cannot account for this neural distance effect activations of comparisons (Chiao et al. 2009; Kedia et al. 2014; Wen et al. 2017). In addition, if the fact that low distance conditions minus high distance conditions activated DMPFC and insula was due to the low distance conditions being more difficult, then activity in these regions should correlate with RTs. However, we showed that this was not the case (Fig. S1 in Supplementary Materials). Moreover, when we treated RTs as covariates of no interest and reanalyzed our data (i.e., performed the same conjunction analyses), we observed strikingly similar neural activations compared with our original analyses (Table 2). These robust results help to further exclude the possibility that task difficulty can account for our findings. Hence, taken together, we suggest that the common activation of DMPFC and the insula induced by intelligence and size comparisons is not likely explained by task demands alone.

In this study, our conjunction analysis showed that the overlapping neural correlates of intelligence and size comparisons did not include the IPS (Table 2), although the distance effects resulting from intelligence and size comparisons separately activated the IPS (Table 1). As mentioned above, the IPS is consistently recruited by various types of comparisons, and as such we must address this issue here. At first, we hypothesized that the IPS was missed in the conjunction analysis because of the very rigorous standard for multiple correction that we employed (i.e., FWE correction at the whole brain level). We thus performed a small volume correction to investigate this possibility, but no cluster in the bilateral IPS survived this analysis. Next, we carefully examined our results and found that the activation of the bilateral IPS in intelligence

comparisons was restricted to small clusters, while the clusters of the bilateral IPS in size comparisons were much larger (Table 1). The IPS is thought to be associated with processing magnitude, hierarchy and ordinality (Fias et al. 2007; Kadosh et al. 2008; Chiao et al. 2009). A possible explanation was that the IPS was indeed involved in intelligence comparisons, however, its involvement was attenuated because intelligence comparisons were more subjective and had no clear ordinality. Conversely, there was more activation in IPS in size comparisons due to the fact that size comparisons contained an objectively clearer ordinal component.

Besides the commonly activated regions, our results also demonstrated differences in activation between the neural mechanisms of intelligence and size comparisons (Table 3 and Fig. 4A). This partly support the viewpoint that the neural processing of comparative judgments may be mediated by domain specific mechanisms (Lindner et al. 2008). Specifically, the distance effect of intelligence comparisons triggered stronger activity than that of size comparisons in the precuneus/PCC, SFG/MFG, and angular gyrus. The precuneus/PCC has been suggested to be implicated in ToM tasks (Gallagher et al. 2000; Reuveni et al. 2003; Spreng et al. 2009). Several functional neuroimaging studies suggested that bilateral angular gyrus involved in ToM or mentalizing tasks (Spreng et al. 2009; Mar 2011; Seghier 2013). The SFG is thought to be involved in self-related tasks like introspection and self-judgments (Goldberg and Harel 2006). In the present study, in contrast to standard physical size and numerical comparisons, intelligence comparisons required participants to extract their knowledge about the 2 celebrities in question since they were unlikely explicitly aware of their intelligence before conducting the task. This characteristic may account for the engagement of these ToM-related and self-related regions in intelligence comparisons.

Conversely, the distance effect of size comparisons elicited greater activity than that of intelligence comparisons in the right IPL/supramarginal gyrus (Table 3 and Fig. 4A). This result is consistent with previous studies. For example, Kedia et al. (2013) found that body height comparisons showed greater activity than intelligence comparisons in this brain region. Moreover, another study from the same laboratory showed that comparisons of body height minus comparisons of physical attractiveness activated the supramarginal gyrus in the left hemisphere (Kedia et al. 2014). Chiao et al. also found greater activation in the right supramarginal gyrus for numerical comparisons but not for social status comparisons (Chiao et al. 2009). Considering these results, we suggest that more activity in the IPL/supramarginal gyrus for size comparisons can be explained using the same reasoning we offered for IPS above. That is, compared with intelligence comparisons, size and numerical comparisons show a clearer objective hierarchy and ordinality.

In addition to the functional activation observed within single cortical regions, the results of FC analyses provided further evidence about the relationship between intelligence and size comparisons. In the present study, similar FC values within bilateral insula and DMPFC (Fig. 4B) may reflect the similar pattern of interactions between these regions for both intelligence and size comparisons. The greater values of precuneus/PCC-based FCs for intelligence comparisons and IPL-based FCs for size comparisons (Fig. 4B) further support the existence of different comparison-specific neural mechanisms. Specifically, FC is suggested to reflect the level of functional communication between spatially remote regions (Van Den Heuvel and Pol 2010), and thus, the similar and different FC patterns may indicate that the human brain keeps a core functional communication channel for the general comparative process but changes minor channels for different comparisons, such as intelligence and size comparisons. However, it is important to remember that the results of our FC analyses cannot support causal inferences, but this can be examined using methods of effective connectivity in future experiments.

As for the interactions between factor distance (low vs. high) and factor target (portrait vs. name), both intelligence and size comparison tasks separately recruited partially distinct occipital regions (Table 3). This indicates that the detected neural mechanisms mediating the 2 types of comparisons might be influenced by different stimulus materials. Considering the different visual information inherent between portraits and names, we suggest that this influence may occur at the stage of visual perception. Specifically, our results of stronger activation in occipital regions for perceiving portraits compared with names, and no differential activation for the opposite contrast (i.e., names > portraits), might be explained by the fact that portraits have more complex visual content than names. In fact, it is still a controversial issue whether or not different stimulus materials can influence the same comparison processes (Fulbright et al. 2003; Pinel et al. 2004; Chiao et al. 2009; Kedia et al. 2014). For instance, Chiao et al. (2009) found significant interactions between distance and stimulus domain when participants performed social status comparisons of cars, uniforms and faces. However, Kedia et al. (2014) showed no such interaction when participants made physical attractiveness or height comparisons of women and dogs. Thus, further research is needed to clarify this issue.

Finally, we noticed that 2 previous fMRI studies have failed to report the involvement of the frontoparietal network mentioned above for comparisons of intelligence (Lindner et al. 2008; Kedia et al. 2013). We suggest that these contradictions with the present study can be explained by the different experimental paradigms used. Specifically, the 2 studies both used paradigms involving noncomparative control conditions rather than a distance effect, which was an important aspect of our experimental paradigm. Control conditions may be less suitable to explore comparisons compared with the distance effect due to the problem of pure insertion (Price and Friston 1997). For instance, a control condition may activate the frontoparietal network as well, and thus when subtracting activation in the noncomparative control condition from the comparative condition, no differential activation is observed in this network. Similarly, a study of number comparison also used noncomparative control tasks and failed to show activity in IPS (Göbel et al. 2004), which contradicts the results seen in other studies (Pesenti et al. 2000; Pinel et al. 2001; Dehaene et al. 2003). However, since the present study did not directly examine how different paradigms can lead to differences in neural comparison results, further research is needed to better clarify this issue.

In summary, the present study explored the neural correlates of social intelligence comparisons and nonsocial size comparisons using functional MRI and a distance-effect paradigm. Our findings of commonalities and differences between intelligence and size comparisons suggest that various types of comparison may rely on a core mechanism, involving regions in frontal cortex (i.e., DMPFC and the insula), but this core neural mechanism may be supplemented by different cortical mechanisms depending on the nature of the specific domains in question (i.e., social vs. nonsocial comparisons). In other words, the neural substrates mediating comparative processing may rely on an interaction between domain general and domain specific cortical mechanisms.

Supplementary Material

Supplementary data is available at *Cerebral Cortex* online.

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Notes

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References

Amodio DM, Frith CD. 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat Rev Neurosci. 7:268–277.

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. 32:799–805.

Augustine JR. 1996. Circuitry and functional aspects of the insular lobe in primates including humans. Brain Res Rev. 22:229–244.

Beckmann M, Johansenberg H, Rushworth MFS. 2009. Connectivity-based parcellation of human cingulate cortex and its relation to functional specialization. J Neurosci. 29:1175–1190.

Biswal B, Zerrin Yetkin F, Haughton VM, Hyde JS. 1995. Functional connectivity in the motor cortex of resting human brain using echo-planar MRI. Magn Reson Med. 34: 537–541.

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. 47:354–363.

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

Dehaene S, Piazza M, Pinel P, Cohen L. 2003. Three parietal circuits for number processing. Cogn Neuropsychol. 20:487–506.

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

Eklund A, Nichols TE, Knutsson H. 2016. Cluster failure: why fMRI inferences for spatial extent have inflated false-positive rates. Proc Natl Acad Sci USA. 113:7900.

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

Fias W, Lammertyn J, Caessens B, Orban GA. 2007. Processing of abstract ordinal knowledge in the horizontal segment of the intraparietal sulcus. J Neurosci. 27:8952.

Fias W, Lammertyn J, Reynvoet B, Dupont P, Orban GA. 2003. Parietal representation of symbolic and nonsymbolic magnitude. J Cogn Neurosci. 15:47–56.

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. 24:193–200.

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

Gallagher HL, Happé F, Brunswick N, Fletcher PC, Frith U, Frith CD. 2000. Reading the mind in cartoons and stories: an fMRI study of 'theory of mind' in verbal and nonverbal tasks. Neuropsychologia. 38:11–21.

Goldberg II, Harel MR. 2006. When the brain loses its self: prefrontal inactivation during sensorimotor processing. Neuron. 50:329–339.

Greicius MD, Krasnow B, Reiss AL, Menon V. 2003. Functional connectivity in the resting brain: a network analysis of the default mode hypothesis. Proc Nat Acad Sci USA. 100: 253–258.

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

Kadosh RC, Henik A, Rubinsten O, Mohr H, Dori H, Ven VVD, Zorzi M, Hendler T, Goebel R, Linden DEJ. 2005. Are numbers special?: The comparison systems of the human brain investigated by fMRI. Neuropsychologia. 43:1238–1248.

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

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

Kedia G, Lindner M, Mussweiler T, Ihssen N, Linden DE. 2013. Brain networks of social comparison. Neuroreport. 24: 259–264.

Kedia G, Mussweiler T, Mullins P, Linden DE. 2014. The neural correlates of beauty comparison. Soc Cogn Affect Neurosci. 9:681–688.

Kennerley SW, Dahmubed AF, Lara AH, Wallis JD. 2009. Neurons in the frontal lobe encode the value of multiple decision variables. J Cogn Neurosci. 21:1162–1178.

Kurth F, Zilles K, Fox PT, Laird AR, Eickhoff SB. 2010. A link between the systems: functional differentiation and integration within the human insula revealed by meta-analysis. Brain Struct Funct. 214:519–534.

Lindner M, Hundhammer T, Ciaramidaro A, Linden DE, Mussweiler T. 2008. The neural substrates of person comparison—an fMRI study. Neuroimage. 40:963–971.

Mar RA. 2011. The neural bases of social cognition and story comprehension. Annu Rev Psychol. 62:103.

Menon V, Uddin LQ. 2010. Saliency, switching, attention and control: a network model of insula function. Brain Struct Funct. 214:655–667.

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

Nieder A, Dehaene S. 2009. Representation of number in the brain. Annu Rev Neurosci. 32:185.

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: 461–479.

Picard N, Strick PL. 2001. Imaging the premotor areas. Curr Opin Neurobiol. 11:663.

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

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: 983–993.

Poldrack RA. 2006. Can cognitive processes be inferred from neuroimaging data? Trends Cogn Sci. 10:59–63.

Price CJ, Friston KJ. 1997. Cognitive conjunction: a new approach to brain activation experiments. Neuroimage. 5:261–270.

Rao SM, Mayer AR, Harrington DL. 2001. The evolution of brain activation during temporal processing. Nat Neurosci. 4:317–323.

Reuveni S, Meilijson I, Kupiec M, Ruppin E, Tuller T. 2003. People thinking about thinking people. The role of the temporo-parietal junction in "theory of mind". Neuroimage. 19:1835.

Seghier ML. 2013. The angular gyrus: multiple functions and multiple subdivisions. Neuroscist. 19:43–61.

Spreng RN, Mar RA, Kim AS. 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. J Cogn Neurosci. 21:489–510.

Van Den Heuvel MP, Pol HEH. 2010. Exploring the brain network: a review on resting-state fMRI functional connectivity. Eur Neuropsychopharmacol. 20:519–534.

Wen X, Xiang Y, Cant JS, Wang T, Cupchik G, Huang R, Mo L. 2017. The neural correlates of internal and external comparisons: an fMRI study. Brain Struct Funct. 222:563–575.

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

Xia M, Wang J, Yong H. 2013. BrainNet viewer: a network visualization tool for human brain connectomics. PLoS One. 8:e68910.