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The anterior insular and anterior cingulate cortices in emotional processing for self-face recognition

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Individuals can experience embarrassment when exposed to self-feedback images, depending on the extent of the divergence from the internal representation of the standard self. Our previous work implicated the anterior insular cortex (AI) and the anterior cingulate cortex (ACC) in the processing of embarrassment; however, their exact functional contributions have remained uncertain. Here, we explored the effects of being observed by others while viewing self-face images on the extent of embarrassment, and the activation and connectivity patterns in the AI and ACC. We conducted functional magnetic resonance imaging hyperscanning in pairs of healthy participants using an interaction system that allowed an individual to be observed by a partner in real time. Being observed increased the extent of embarrassment reported when viewing self-face images; a corresponding increase in self-related activity in the right AI suggested that this region played a direct role in the subjective experience. Being observed also increased the functional connectivity between the caudal ACC and prefrontal regions, which are involved in processing the reflective self. The ACC might therefore serve as a hub, integrating information about the reflective self that is used in evaluating perceptual self-face images.

Keywords: anterior cingulate cortex; anterior insular cortex; embarrassment; functional magnetic resonance imaging; self-evaluation of the face

INTRODUCTION

Individuals can experience negative emotions (e.g. embarrassment) when viewing self-feedback images presented via mirrors, photographs or videos, especially if they deviate substantially from the standard self (Duval and Wicklund, 1972; Carver and Scheier, 1981, 1998). These types of negative emotions are distinguished from basic emotions, such as happiness, fear and anger, and are categorized as ‘self-conscious emotions’. One’s own perceptual feedback focuses attention on the self (i.e. self-awareness), which initiates an automatic comparison against the standard self. This comparison process is defined as self-evaluation. The individual can experience a feeling of embarrassment depending on the degree of the discrepancy between the external input of perceptual feedback and the internal representation of the standard self (Buss, 1980; Carver and Scheier, 1998). Negative self-conscious emotions therefore seem to work as an alarm system that detects deviations of our behaviors and attitudes from standards.

Most imaging studies of emotion have reported joint activation of the anterior insular cortex (AI) and the anterior cingulate cortex (ACC) in subjects experiencing a wide range of emotional feelings, including not only basic emotions but also more complex emotions (e.g. romantic love, unfairness and social exclusion) (Blood and Zatorre, 2001; Eisenberger *et al.*, 2003; Wicker *et al.*, 2003; Bartels and Zeki, 2004; Takahashi *et al.*, 2008; Onoda *et al.*, 2010; Moor *et al.*, 2012). The AI and ACC are included in a salience network that facilitates the detection of important and relevant stimuli (Seeley *et al.*, 2007; Menon and Uddin, 2010), rather than being engaged only in the processing of a specific emotional feeling. Indeed, these regions are activated in self-related processing without a specific emotional feeling, although they are not always co-activated. The AI has been implicated in self-agency (Farrer and Frith, 2002), autobiographical memory retrieval (Fink *et al.*, 1996), self-recognition (Kircher *et al.*, 2000, 2001; Devue *et al.*, 2007) and the evaluation of traits concerning the self (Fossati *et al.*, 2003; Modinos *et al.*, 2009). The ACC is recruited when subjects are exposed to self-referential stimuli including auditory verbal feedback (McGuire *et al.*, 1996), short stories (Vogeley *et al.*, 2001) and self-recognition (Kircher *et al.*, 2000, 2001; Sugiura *et al.*, 2000; Devue *et al.*, 2007), as opposed to non-self-referential stimuli. The enhanced activity of these regions during self-related processing can be interpreted as reflecting the detection of self-related salient stimuli or events.

The AI and the ACC could play a key role in the embarrassment associated with self-evaluative processing. We detected robust activation in the bilateral AI and ACC when individuals evaluated facial-feedback photo images of themselves, which in some cases elicited a realistic experience of embarrassment, compared with when evaluating images of others’ faces (Morita *et al.*, 2008, 2012). In individuals with autism spectrum disorders (ASD), we identified the right AI as the basis for producing a feeling of embarrassment during the evaluation of self-face images (Morita *et al.*, 2012). Individuals with ASD demonstrated relatively reduced activity in the right AI during the evaluation of self-face images, which was closely related to their weak coupling between the cognitive evaluation of the self-face images and the related emotional responses (i.e. embarrassment). This finding was consistent with several recent studies reporting ASD-related structural and functional abnormalities of the AI (Di Martino *et al.*, 2009; Uddin and Menon, 2009; Kosaka *et al.*, 2010). However, the exact functional

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contributions of the ACC and the AI to the feeling of embarrassment are still unclear.

The current study investigated the specific roles of the AI and the ACC in the processing of embarrassment associated with self-face recognition using a modified functional magnetic resonance imaging (fMRI) experimental design (Morita *et al.*, 2008, 2012). We introduced the presence of observers to enhance the feeling of embarrassment experienced when participants viewed self-face images. To recreate a realistic social situation in which subjects were observed mutually and equally, we used simultaneous fMRI (hyperscanning) (Montague *et al.*, 2002; King-Casas *et al.*, 2005; Saito *et al.*, 2010), in which paired subjects in different MRI scanners could observe each other's faces via a live video link, and neural activity during the interaction could be measured in real time. In the first condition, the subject viewed self-face images, those of a partner and those of an unfamiliar person while being mutually observed by the partner; this was intended to resemble a social situation in which two people view face images together during daily life. In the second condition, the subject viewed the same face images independently without mutual observation.

We examined whether being observed by a partner elicited an enhanced subjective feeling of embarrassment upon viewing self-face images and how it affected the activation and connectivity patterns in the AI and the ACC. To analyze the fMRI data, we defined two regions of interest (ROIs) for the AI and the ACC based on the locations of peak activations during self-face evaluation compared with the evaluation of others' faces in previous studies (Morita *et al.*, 2008, 2012). In addition to standard subtraction analyses, we used psychophysiological interaction (PPI) analyses to test for other areas that showed a stronger functional coupling with the ROIs when viewing self-face images while being observed by others.

METHODS

Participants

Thirty-two healthy subjects [16 males and 16 females; mean age = 21.3 years, standard deviation (s.d.) = 2.4] participated in the study. None of the participants had seen their partner before the fMRI experiment. All had normal vision or corrected-to-normal vision with contact lenses (not glasses) and were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants had a history of neurological illness. The protocol was approved by the Ethical Committee of the National Institute for Physiological Sciences, Japan. All participants gave their written informed consent to participate in the study.

Materials

The experiment took place over 2 days. On the first day, the participants made short speeches in front of a video camera (Morita *et al.*, 2012). Recordings of each participant's face were made throughout the speeches. Twenty-one black-and-white images of each participant's face, ranging from good (attractive) to bad (unattractive), were selected from the recorded videos by the experimenter, as in our previous study (Morita *et al.*, 2012). Twenty-one images per participant were used as stimuli for the SELF condition of the participant, for the PARTNER condition of the partner and for the OTHERS condition of another participant in the subsequent fMRI experiment.

fMRI experimental procedure and design

A few weeks after the video-recording session, the participants underwent fMRI scanning in pairs. The fMRI experiment was conducted using a dual fMRI system installed in the National Institute for Physiological Sciences. The participants lay in the MRI scanner with their heads immobilized using an elastic band and sponge cushions and their ears plugged. In the scanner, the partner's eyes were presented on the upper half of a screen, and the face stimuli for the task were displayed on the lower half. Participants were asked to rate the extent of the embarrassment they felt upon viewing each face stimulus. In each run, 21 images of the participant's own face (SELF), 21 images of the faces of the partner (PARTNER), 21 images of the faces of an unfamiliar person (OTHERS) and 10 'null events' (in which no stimulus was shown) were presented in a pseudorandom order. Each face stimulus appeared for 3 s. Once the face stimulus had disappeared, a visual analog scale appeared for 3 s, the end points of which were labeled '0 (indicating not at all)' and 'most embarrassed'. During the response period, the participants were required to rate their extent of embarrassment by moving a pointer along a scale, using the index and middle fingers to operate a two-button response box held under the right hand. To discourage response preparation during the stimulus viewing period, the starting position of the pointer was randomly determined for each trial. The visual analog scales were subsequently divided into 100 equal intervals for analyses. The experimental design was based on a rapid event-related paradigm, in which the efficiency was highly dependent upon the temporal pattern of stimulus presentation (Dale, 1999; Friston *et al.*, 1999). The detailed methods required to obtain a highly efficient experimental design are described elsewhere (Morita *et al.*, 2008).

Figure 1 illustrates the two experimental conditions used during the trials. In the non-observation (NOB) condition, participants were instructed to perform different rating tasks, independently without mutual observation, in which a still image of the partner's closed eyes was constantly presented in the upper half of the screen. In the observation (OB) condition, participants were instructed to perform the same rating task with the partner simultaneously in a state of mutual observation. For the paired subjects to share the presented face stimuli, a live video of the partner's eyes was presented to each participant on the upper half of the screen. The task images (generated by Presentation software 14.1, Neurobehavioral Systems, Albany, CA, USA) and the video images of the partner's eyes were combined using a screen splitter, which was part of our dual fMRI system (developed by NAC Image Technology, Tokyo, Japan and Panasonic System Solutions Japan Co. Ltd, Tokyo, Japan). The stimulus size in the OB condition was adjusted to match that in the NOB condition. Throughout the sessions, the visual stimuli were presented on a projection screen by a liquid crystal projector (CP-SX12000J; Hitachi Ltd., Tokyo, Japan), and were viewed by the participants through a mirror. Two consecutive runs, each of which lasted for 7 min 27 s, were performed for each condition. The order of the conditions was randomized across subjects. Before the scanning session, all participants performed a practice task to familiarize themselves with the response device, and observed a 15 s silent video clip selected from the partner's video image that was recorded on the first day, to learn to recognize the partner's face.

Psychological measurements

Immediately following scanning, the participants undertook a self-paced rating task using the stimuli from the fMRI session. Participants were asked to rate the images in terms of 'how photogenic they appeared' on a visual analog scale, the extremes of which were labeled 'Good' and 'Bad'. The visual analog scales were subsequently divided into 100 equal intervals for analyses. Following the rating task, the participants were asked to complete a self-report questionnaire based on the Japanese version of the self-consciousness scale (Fenigstein *et al.*, 1975; Sugawara, 1984), which provides indices for two specific types of self-consciousness: public and private. Public self-consciousness is the tendency to be aware of the publicly displayed

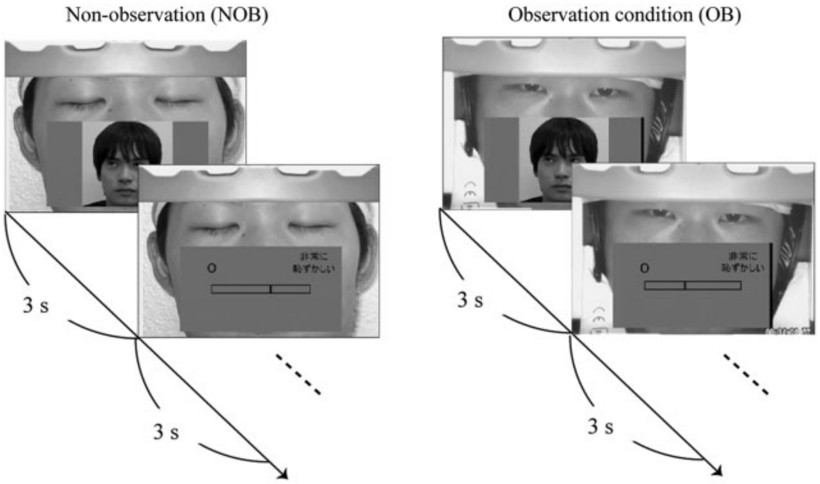

Fig. 1 Sequence of events during trials in the NOB and OB conditions. In each trial, self-faces, partner faces and faces of an unfamiliar person were presented in a random order on the lower half of the screen for 3 s. Participants were required to rate how embarrassed they felt upon viewing each face using a visual analog scale that appeared after each stimulus.

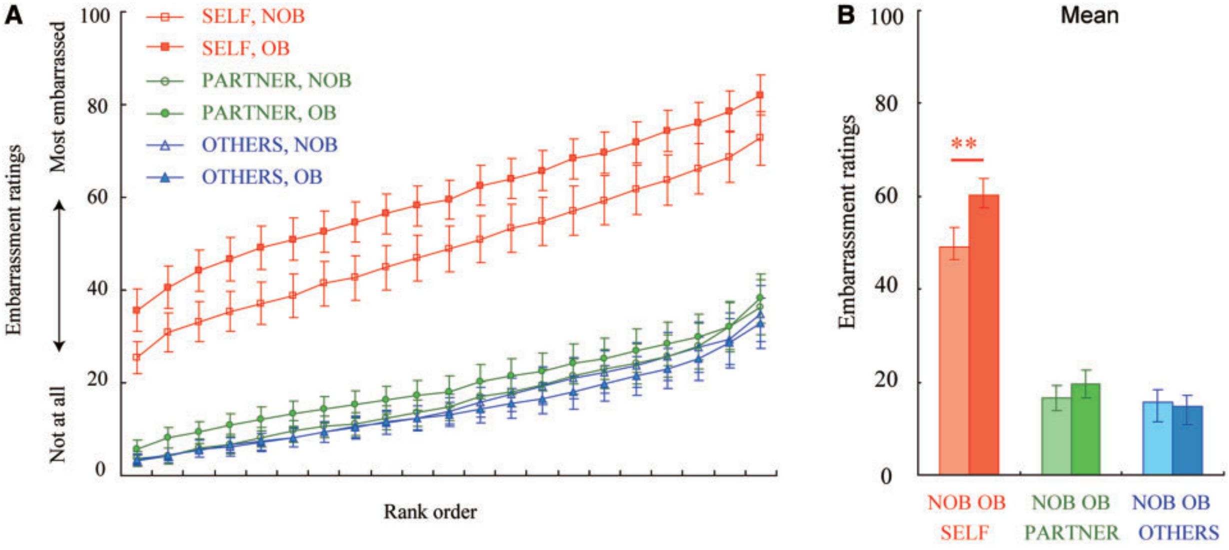

Fig. 2 Results of embarrassment ratings. (**A**) Embarrassment ratings for SELF, PARTNER and OTHERS images rank-ordered according to ratings measured during the fMRI session. (**B**) Mean embarrassment ratings for each condition. Data represent the mean ± standard error (s.e.). Asterisks indicate statistical significance (**$P < 0.01$).

aspects of the self, such as one's physical appearance. In contrast, private self-consciousness is the tendency to be aware of the covert and hidden aspects of the self, such as one's own thoughts and feelings.

MRI scanning procedure

Functional images were acquired using T_2^*-weighted, gradient-echo, echo-planar imaging (EPI) sequences with a 3-T MR imager (MAGNETOM Verio; Siemens, Erlangen, Germany), and a combination of the posterior part of a 32-channel phased-array head coil with a four-channel flex small coil. The latter was placed in front of the participant's forehead using a custom-made holder (Takashima Seisakusho, Tokyo, Japan). During each of the four fMRI runs, 149 volumes were acquired. Each volume consisted of 42 slices that were acquired in ascending order, with a thickness of 3 mm and a 0.5 mm gap, to cover the entire brain. The time interval between each two successive acquisitions of the same slice (TR) was 3000 ms, with an echo time (TE) of 30 ms and a flip angle (FA) of 80°. The field of view (FOV) was 192 × 192 mm, and the matrix size was 64 × 64, giving voxel dimensions of 3 × 3 mm. To acquire a fine structural whole-brain image, magnetization-prepared rapid-acquisition gradient-echo (MP-RAGE) images were obtained [TR = 1800 ms; TE = 2.97 ms; time of inversion (IT) = 800 ms; flip angle = 9°; voxel dimensions = 1 × 1 × 1 mm] with a 32-channel phased-array head coil.

Behavioral data analysis

Behavioral data analysis was carried out using SPSS version 16.0J software (SPSS Japan Inc., Tokyo, Japan). To compare the average embarrassment ratings measured during the MRI scanning depending on face type or observation, we used a two-way repeated measures analysis of variance (ANOVA), with face type (SELF, PARTNER and OTHERS) and observation (NOB and OB) as within-subjects factors. We also performed one-way ANOVA with face type (SELF, PARTNER and OTHERS) for the photogenicity ratings. Results were considered statistically significant at $P < 0.05$.

Imaging data analysis

The first three volumes of each fMRI session were discarded because of unsteady magnetization. Image and statistical analyses were performed using Statistical Parametric Mapping (SPM version 8; The Wellcome

Table 1 Correlation coefficients (*r*) between embarrassment ratings and individual self-consciousness scale scores

Condition	Face type	Public self-consciousness	Private self-consciousness
NOB	SELF	0.265	0.079
	PARTNER	0.098	−0.292
	OTHERS	0.039	−0.199
OB	SELF	0.458^{**}	0.110
	PARTNER	0.148	−0.231
	OTHERS	0.131	−0.088

Asterisks indicate statistical significance ($^{**}P < 0.01$).

Table 2 Significantly activated voxels in mean response for SELF *vs* OTHERS and PARTNER *vs* OTHERS contrasts

Cluster size	Side	Area	MNI coordinates (mm)			*t*-value
			x	*y*	*z*	
SELF vs OTHERS						
6646	Rt	IOC	34	−88	−8	11.50
	Rt	ITG	46	−60	−16	9.36
	Rt	OTPJ	24	−62	54	9.28
5717	Rt	PMv	50	10	34	10.75
	Rt	IC	40	2	6	9.48
	Rt	Mid-IFG	48	42	10	8.79
1311	Rt	Midbrain	8	−32	−4	10.41
	Rt	Thalamus	6	−22	4	7.43
1678	Lt	IC	−36	20	−6	10.04
	Lt	Mid-IFG	−42	32	12	3.30
1326	Lt	IOC	−36	−90	−10	9.24
	Lt	ITG	−44	−62	−14	6.36
	Lt	ITG	−48	−72	−16	5.38
5620	—	MCC	6	−4	30	9.23
	—	SMA	6	14	58	8.18
943	Lt	OTPJ	−22	−68	52	5.72
	Lt	OTPJ	−20	−70	42	5.69
PARTNER vs OTHERS						
6315	Lt	Precuneus	−8	−66	34	8.96
	Lt	TPJ	−48	−58	26	6.69
	Rt	Precuneus	16	−62	32	6.60
3468	–	ACC	−2	40	4	6.62
	Rt	MPFC	8	58	4	5.60
	Lt	MPFC	−6	56	20	5.11
1644	Rt	MFG	44	20	24	5.93
	Rt	MFG	34	4	42	4.80
1971	Lt	MFG	−42	14	36	5.50
	Lt	MFG	−34	8	46	5.08
1010	Rt	IOC	38	−88	−14	4.27
	Rt	ITG	44	−58	−12	4.21
	Rt	IOC	28	−92	0	3.97

Height threshold, $P < 0.005$; extent threshold, $P < 0.05$ corrected. Lt = left; Rt = right; MCC = middle cingulate cortex; SMA = supplementary motor area.

Department of Cognitive Neurology, London, UK) implemented in Matlab 7.7.0 (MathWorks, Sherborn, MA, USA). Initially, EPI images were realigned to the first image and then realigned to the mean image after first realignment. We used slice-timing correction to adjust for differences in slice-acquisition times. We interpolated and re-sampled the data so that, for each time series, the slices were acquired at the same time as the reference slice, which was the middle slice. The high-resolution anatomical images were then co-registered to the mean of the functional images. The co-registered anatomical image was normalized to the Montreal Neurological Institute (MNI) atlas (Evans *et al.*, 1994). The parameters from this normalization process were then applied to each of the functional images. Finally, the spatially normalized functional images were filtered using a Gaussian kernel with a full-width-at-half-maximum of 8 mm in the *x*, *y* and *z* axes. After preprocessing, the task-related activation was evaluated using the general linear model (Friston *et al.*, 1995; Worsley and Friston, 1995). In the single-subject analyses, the design matrix contained three task-related regressors (SELF, PARTNER and OTHERS conditions), three regressors for parametric modulation (the embarrassment scores for each face type), one regressor for motor responses and one constant term (see Morita *et al.*, 2008 for a more detailed explanation of the regressors). We used a high-pass filter, which comprised the discrete cosine basis function with a cutoff period of 128 s, to eliminate the artifactual low-frequency trend. Serial autocorrelation assuming a first-order autoregressive model was estimated from the pooled active voxels using the restricted maximum likelihood procedure and was used to whiten the data (Friston *et al.*, 2002). To calculate the estimated parameters, least-squares estimation was performed on the high-pass filtered and pre-whitened data and design matrix.

The weighted sum of the parameter estimates in the individual analyses constituted contrast images that were used for the second-level analysis. Initially, to identify the brain regions showing significant self- and partner-related activity, we performed one-sample *t*-tests using the contrast images of SELF *vs* OTHERS and PARTNER *vs* OTHERS, respectively. Then, to depict the brain regions in which the self-related activity was modulated by being observed by a partner, we performed paired *t*-tests using the contrast images of SELF *vs* OTHERS in each observation condition. The statistical height threshold in this analysis was $P < 0.005$ ($t > 2.66$), uncorrected. For the *a priori* ROIs (the bilateral AI, rostral ACC and caudal ACC), we applied small-volume corrections (Worsley *et al.*, 1996) with a sphere of 6 mm radius according to the coordinates in our previous studies (Morita *et al.*, 2008, 2012). The MNI coordinates for the small volume correction (SVC) were ($x = 38$, $y = 10$, $z = -8$) for the right AI, ($x = -40$, $y = 22$, $z = -4$) for the left AI, ($x = -4$, $y = 24$, $z = 28$) for the rostral ACC and ($x = 0$, $y = 6$, $z = 30$) for the caudal ACC. To reveal unpredicted effects in areas outside the *a priori* ROIs, we applied a statistical height threshold of $P < 0.005$ ($t > 2.66$) and an extent threshold of $P < 0.05$ corrected for multiple comparisons using the family-wise error correction. In addition, for the brain regions in which the self-related activity was modulated by being observed, we calculated the correlation coefficient (*r*) between the change of the self-related activity and the change of embarrassment ratings for self-face images.

PPI analyses were used to search for brain regions that showed comparatively greater functional connectivity with seed regions (i.e. the right AI, left AI, rostral ACC and caudal ACC) when viewing self-face images while being observed (Friston *et al.*, 1997; Gitelman *et al.*, 2003) (see details in Supplementary Methods).

RESULTS

Behavioral data

The average public self-consciousness scale scores were 55.63 ± 9.42 in men and 58.31 ± 9.41 in women, whereas the average private self-consciousness scale values were 45.31 ± 7.37 in men and 49.38 ± 7.95 in women. There were no significant differences between genders in

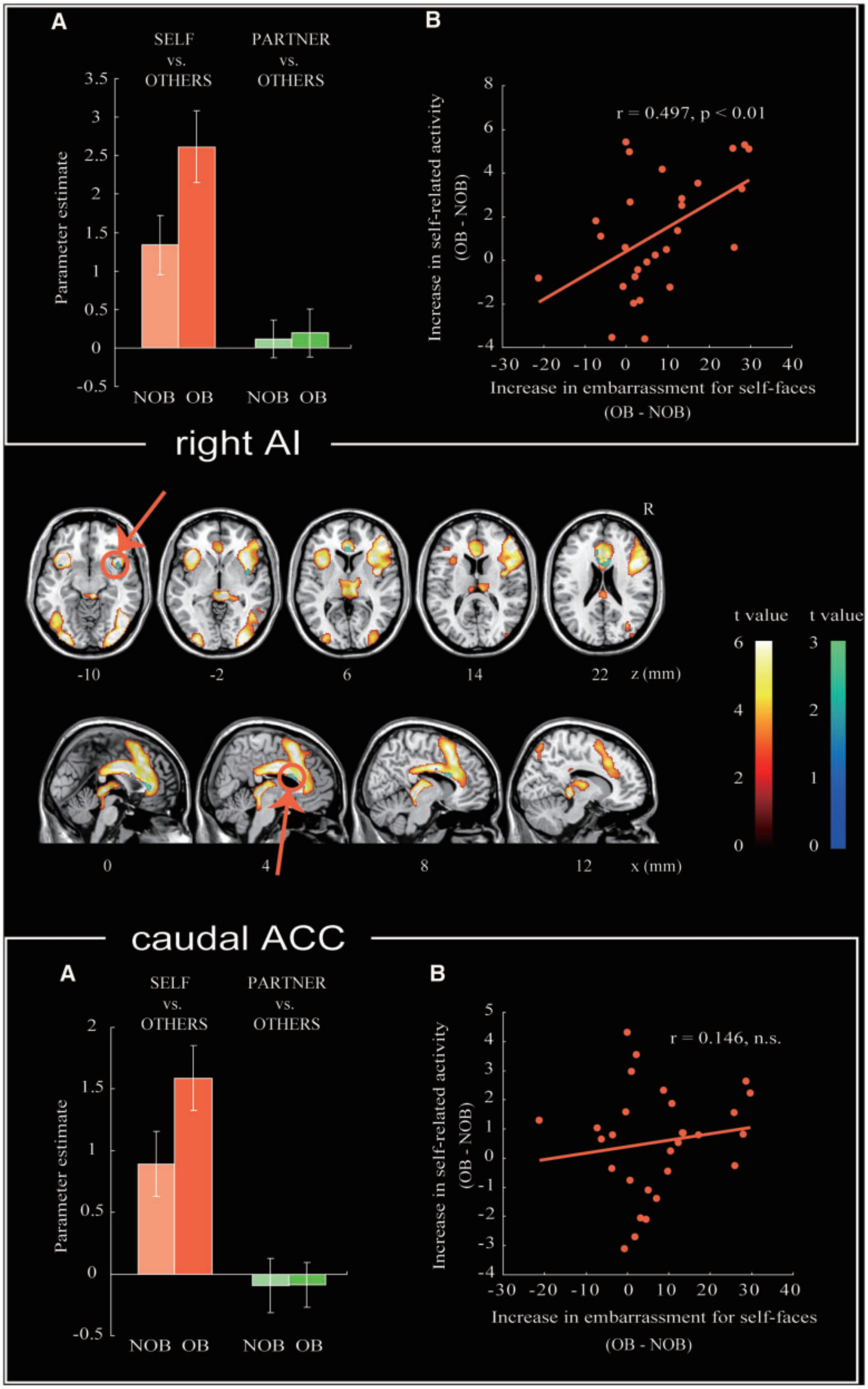

Fig. 3 Results of standard subtraction analyses. Brain regions significantly activated by the SELF *vs* OTHERS contrast are shown in red. The height threshold for this analysis was set at $t > 2.74$ ($P < 0.005$ uncorrected), and $P < 0.05$ corrected for multiple comparisons at the cluster level. Brain regions in which the mean response showed a significant effect of observation (NOB, OB) on self-related activity (SELF *vs* OTHERS) are shown in blue. The height threshold for this analysis was set at $t > 2.74$ ($P < 0.005$ uncorrected). These activities were masked by the areas that were significantly activated by the contrasts of SELF *vs* OTHERS (red regions). The activation of the right AI (40, 14, — 10) and the caudal ACC (—4, 4, 26) persisted after $P < 0.05$ small-volume correction using a 6 mm sphere over coordinates from our previous studies. The activation was superimposed on high-resolution anatomical MR images. (A) Averaged parameter estimates for the mean self- and partner-related activity in each region plotted for each observation condition. (B) Relationship between the increase in the self-related activity and the increase in the individual's self-reported embarrassment for self-face images caused by being observed.

tendency to be aware of the publicly displayed aspects or the covert and hidden aspects of the self [public: $t(30) = 0.81$, $P = 0.43$; private: $t(30) = 1.50$, $P = 0.14$]. The public and private self-consciousness scales were not correlated with one another ($r = 0.06$, $P =$ not significant).

Figure 2 shows the range of embarrassment ratings measured during the fMRI session. A two-way ANOVA with face type (SELF, PARTNER, OTHERS) × observation (NOB, OB) revealed a significant main effect of face type [$F(2,62) = 77.19$, $P < 0.001$]. *Post hoc* multiple comparisons indicated that participants felt more embarrassment in response to self-face images than to those of others partners or unfamiliar people (SELF *vs* OTHERS, $P < 0.001$; SELF *vs* PARTNER, $P < 0.001$). In addition, there was both a significant main effect of observation [$F(1,31) = 8.97$, $P < 0.01$], and a face type × observation interaction [$F(2,62) = 8.70$, $P < 0.001$]. *Post hoc t*-tests indicated that the extent of the embarrassment elicited by self-face images was significantly increased by being observed by a partner [$t(31) = 3.36$, $P < 0.01$]; however, there was no comparable increase of embarrassment when viewing face images of a partner [$t(31) = 1.88$, $P = 0.07$] or an unfamiliar person [$t(31) = 0.87$, $P = 0.39$] (Figure 2B). The relationship between the embarrassment ratings for each type of face and the individual self-consciousness scale scores was explored (Table 1). The ratings for self-face images were significantly positively correlated with the individual public self-consciousness scale scores only in the OB condition. The average photogenicity ratings measured outside the MRI scanner were 33.6 ± 10.1 for SELF images, 48.5 ± 9.3 for PARTNER images and 46.4 ± 8.8 for OTHERS images. The participants reported lower scores for self-face images than those of a partner or unfamiliar person [$F(2,62) = 26.95$, $P < 0.001$; SELF *vs* PARTNER, $P < 0.001$; SELF *vs* OTHERS, $P < 0.001$].

fMRI data

We initially identified the brain regions showing self- and partner-related increases in activity using whole-brain analyses. The SELF *vs* OTHERS contrast revealed activation in the following areas: the bilateral inferior occipital cortex (IOC), inferior temporal gyrus (ITG), occipito-temporo-parietal junction (OTPJ) and insular cortex (IC); the right mid-inferior frontal gyrus (mid-IFG), ventral premotor cortex (PMv), post central gyrus, thalamus and midbrain; and the cingulate cortex extending from the anterior to posterior regions (Table 2 and Figure 3). The PARTNER *vs* OTHERS contrast revealed activation in the following areas: the bilateral medial prefrontal cortex (MPFC), middle frontal gyrus (MFG), ACC, posterior cingulate cortex (PCC) and precuneus; the right IOC and ITG; and the left temporoparietal junction (TPJ) (Table 2).

Next, we identified the brain regions in which the self-related activity (SELF *vs* OTHERS) was significantly modulated by being observed by a partner. Among the *a priori* ROIs, the right AI and the caudal ACC showed significantly increased self-related activities associated with being observed (Table 3 and Figure 3), while the left AI and the rostral ACC did not. In contrast to the self-related activity, the partner-related activity in either the right AI or the caudal ACC was not modulated by being observed (Figure 3A). In addition, we conducted a correlation analysis between the increase in the self-related activity of the right AI or the caudal ACC and the increase in participants' embarrassment ratings for self-face images, including all data within ± 2 s.d. of the mean. The results showed a significant positive correlation only in the right AI ($r = 0.497$, $P < 0.01$) (Figure 3B).

We also found self-related activity that was modulated by being observed in the left middle temporal gyrus (MTG) (Table 3). This cluster of activation survived a threshold of $P < 0.05$, corrected for multiple comparisons at the cluster level. However, as the left MTG showed self-related deactivation, it is not discussed further here.

Table 3 Brain regions exhibiting increased self-related activity when being observed by a partner

Cluster size	Side	Area	MNI coordinates (mm)			*t*-value
			x	*y*	*z*	
A priori areas (SVC)						
15	Rt	AI	40	14	−10	2.98
4	Lt	Caudal ACC	−4	4	28	2.84
Non-predicted areas						
630	Lt	MTG	−62	−6	−8	3.83
	Lt	MTG	−50	−12	−12	3.53

The first section shows *a priori* areas that survived $P < 0.05$ small-volume correction using a 6 mm sphere over coordinates from previous studies. The second section shows areas for which no prediction was made. Our analysis applied a statistical threshold of $P < 0.005$ for height, corrected to $P < 0.05$ for multiple comparisons using cluster size. Lt = left; Rt = right.

We assessed how being observed modulated functional connectivity between the seed regions and other brain regions when viewing self-face images. Within four seed regions, the left IC showed enhanced connectivity for the OB condition compared with the NOB condition with the left MFG and subcortical regions (Figure 4A and Table 4), and the caudal ACC showed enhanced connectivity with left lateral prefrontal regions (LPFCs) including the MFG, IFG, AI, and dorsal and ventral parts of the MPFC (Figure 4B and Table 4). These enhanced connectivities in response to being observed were specific to the self-face images. In addition, no regions showed decreased connectivity with any seed region in the OB condition compared with the NOB condition.

DISCUSSION

Enhancement of embarrassment ratings by being observed

We confirmed that participants felt more embarrassed when viewing self-face images than the face images of a partner or unfamiliar person, which was in line with previous studies (Morita *et al.*, 2008, 2012). In addition, being observed led to an increase in the subjective feeling of embarrassment in response to self-face images, but not in response to face images of others. Recent social psychological experiments have shown that when individuals are observed by others, they are concerned about how they are viewed and want to earn a good reputation, which can work as an incentive for prosocial behaviors (Haley and Fessler, 2005; Bateson *et al.*, 2006; Bénabou and Tirole, 2006). Similarly, in the present study, when participants' own face images were observed by a partner, they were expected to want to acquire a good reputation based on the physical aspects of self. This could raise the level of the internal standard self, leading to an increase in the discrepancy between the actual self and the internal standard self, and eventually increasing the subjective feeling of embarrassment.

Furthermore, in the presence of an observer, individuals with high public self-consciousness reported stronger embarrassment when viewing self-face images than individuals with low public self-consciousness (Table 1). Both receiving perceptual feedback and being observed by others are inducers of public self-awareness, in which an individual's attention is focused on the publicly observable aspects of the self (Buss, 1980). When viewing self-face images while being observed, individuals with higher public self-consciousness would be expected to react strongly to the inducers, causing a stronger feeling of embarrassment.

Enhancement of self-related activity by being observed

We confirmed stronger self-related activity (SELF *vs* OTEHRS) in the prefrontal, parietal and occipital cortices, and several limbic systems including the AI and ACC. Several previous studies focusing on

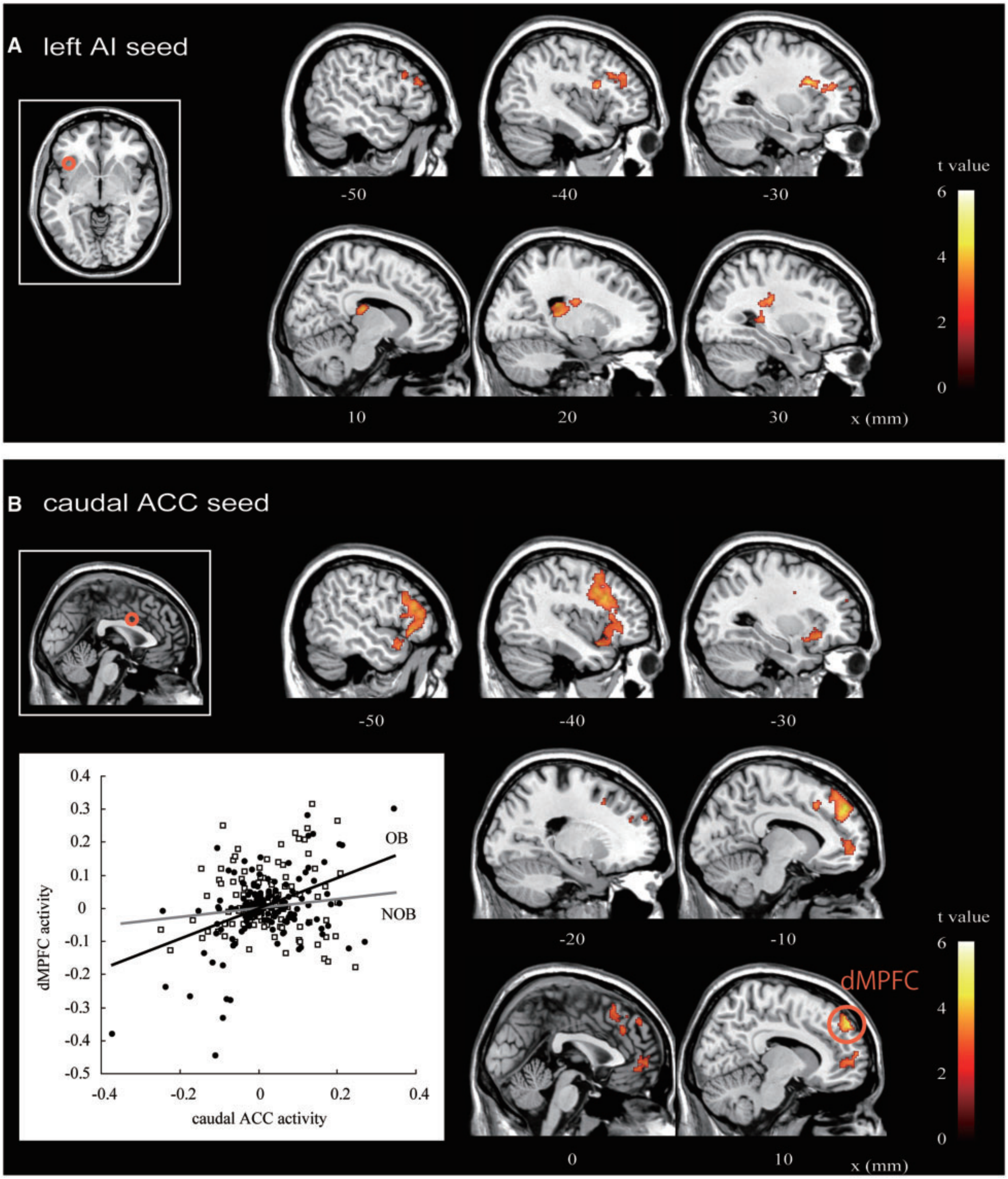

Fig. 4 Results of PPI analysis. Brain areas showing enhanced connectivity with seed regions (**A**, left AI; **B**, caudal ACC) when viewing self-face images as a result of being observed by a partner. The random-effects statistical parametric activation map [SPM(t)] was superimposed on a high-resolution anatomical MR image. The height threshold was set at $t > 2.74$ ($P < 0.005$ uncorrected), and at $P < 0.05$ corrected for multiple comparisons at the cluster level. The scatter plot on the left shows the relationship between the activity in the caudal ACC and the dorsal MPFC ($x = 10$, $y = 54$, $z = 42$) in a representative participant when viewing self-face images in each of the NOB and OB conditions. The regression slopes were 0.14 and 0.46 for the NOB and OB conditions, respectively. The activities are mean adjusted (arbitrary units).

cognitive aspects of self-face recognition have reported activity in similar regions of the prefrontal and parietal cortices in the right hemisphere (Platek *et al.*, 2004, 2006, 2008; Sugiura *et al.*, 2005, 2006, 2012; Uddin *et al.*, 2005; Devue *et al.*, 2007). In addition, a few studies reported self-related activation in the AI and ACC (Kircher *et al.*, 2000, 2001; Devue *et al.*, 2007; Morita *et al.*, 2008, 2012). As discussed in our previous studies, the potential causes of the self-related activation of the limbic regions may be emotional processing associated with self-face recognition.

Within *a priori* ROIs placed on the AI and the ACC, we found that being observed by a partner led to an increase in the self-related activity of the right AI and the caudal ACC. Of these, the increase in

Table 4 PPIs in each seed

Seed	Cluster size	Side	Area	MNI coordinates (mm)			*t*-value
				x	*y*	*z*	
Right AI	No significant activation						
Left AI	605	Rt	CN	26	−28	22	7.07
		Rt	Thalamus	8	−22	16	4.14
	719	Lt	MFG	−44	36	22	3.93
Rostral ACC	No significant activation						
Caudal ACC	1219	Rt	dMPFC	10	54	42	4.75
		Lt	dMPFC	−8	48	40	4.69
	1999	Lt	MFG	−36	8	38	4.23
		Lt	IFG	−44	32	0	4.10
	575	Lt	vMPFC	−6	52	−6	4.05
		Rt	vMPFC	20	56	−4	3.61

This analysis applied a statistical threshold of $P < 0.005$ for height, corrected to $P < 0.05$ for multiple comparisons using cluster size. Lt = left; Rt = right; CN = caudate nucleus; dMPFC = dorsal medial prefrontal cortex; vMPFC = ventral medial prefrontal cortex.

self-related activity was positively correlated with the increase in the subjective feeling of embarrassment for self-face images only in the right AI. The AI is recruited in the processing of various emotional feelings (Blood and Zatorre, 2001; Eisenberger *et al.*, 2003; Wicker *et al.*, 2003; Bartels and Zeki, 2004; Takahashi *et al.*, 2008; Onoda *et al.*, 2010; Moor *et al.*, 2012). It is also active during self-related processing without a specific emotional feeling (Fink *et al.*, 1996; Kircher *et al.*, 2000, 2001; Farrer and Frith, 2002; Fossati *et al.*, 2003; Coull, 2004; Deary *et al.*, 2004; Devue *et al.*, 2007; Livesey *et al.*, 2007; Modinos *et al.*, 2009). To explain this wide range of insular functions within a unitary account, Craig (2009) proposed a meta-representational model of integration across the IC, in which diverse information including homeostatic, environmental, hedonic, motivational, social and cognitive activity are integrated to produce subjective awareness, which represents the sentient self at a particular moment in time. Craig *et al.* (2000) reported that the activity of the AI, especially in the right hemisphere, was correlated with the strength of subjective ratings of sensations or feelings in some cases (Craig, 2009). Previously, we showed that the right AI was strongly recruited when participants evaluated self-face images compared with images of others; however, we did not detect changes in right AI activity dependent on intra-subjective variation in ratings of embarrassment for self-face images. One reason for the lack of a positive correlation could be relatively small variability in the extent of embarrassment. Another could be differences in physical properties according to the stimulus. In the present study, we introduced the presence of observers to enhance the extent of embarrassment while using the same set of external inputs; we could therefore detect increased activity in the right AI depending on the increase in the extent of embarrassment. This approach revealed that the right AI is specialized in creating the subjective feeling of embarrassment resulting from self-evaluative processing, as well as other emotional feelings.

Modulation of functional connectivity by being observed

Functional connectivity analyses revealed that the caudal subdivision of the ACC showed stronger connectivity with dorsal and ventral parts of the MPFC, and the left LPFC including the MFG, IFG and AI, when viewing self-face images while being observed than when doing so without observation. In addition, the left AI showed stronger connectivity with the left MFG, which is included in the abovementioned network centered on the caudal ACC.

It is well known that the MPFC has an important role in representing others' minds (i.e. mentalizing) (Gallagher and Frith, 2003; Frith and Frith, 2006). In the current study, the MPFC was significantly activated when viewing face images of a partner compared with those of an unfamiliar person, which would reflect a mentalizing process automatically induced by the face (Gobbini *et al.*, 2004). In addition, the MPFC has recently been implicated in the processing of the self, which is reflected in the eyes or minds of others (Ochsner *et al.*, 2005; Amodio and Frith, 2006; D'Argembeau *et al.*, 2007; Frith and Frith, 2008; Izuma *et al.*, 2008, 2010; Sugiura *et al.*, 2012). In contrast, in the left PFC, the left IFG corresponding to Brodmann's area (BA) 44/47 is frequently recruited during processing of the psychological aspects of the self, such as self-appraisal (Gusnard *et al.*, 2001; Ochsner *et al.*, 2004), autobiographical memory retrieval (Maguire and Frith, 2003; Piolino *et al.*, 2004) and judgments of personality traits (Kircher *et al.*, 2000; Kelley *et al.*, 2002; Lou, *et al.*, 2004; Morin and Michaud, 2007). Taken together, the MPFC and the left PFC seem to be involved in processing of the reflective self, which Gallagher (2000) denotes as 'narrative self' that is extended in time to include memories of the past and intentions toward the future. Therefore, the increased connectivity between these frontal regions and the caudal ACC in the presence of an observer may suggest that the social situation increased access to information about the reflective self that is used in self-evaluative processing. Thus, we used functional connectivity analysis to observe the effect of being observed in the prefrontal regions, which was not considered in a standard subtraction analysis. In some cases, employing both connectivity and standard subtraction analyses may provide greater insight into the neural mechanisms underlying social cognitive processes (Zaki *et al.*, 2007).

In conclusion, we suggest a functional dissociation between the ACC and the AI in the emotional processing associated with self-face recognition. The caudal ACC could serve as a hub, integrating information about the reflective self required for self-evaluative processing, depending on the situation. In contrast, the right AI appears to be involved in creating the subjective experience of embarrassment.

SUPPLEMENTARY DATA

Supplementary data are available at *SCAN* online.

Conflict of Interest

None declared.

REFERENCES

Amodio, D.M., Frith, C.D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, *7*, 268–77.

Bartels, A., Zeki, S. (2004). The neural correlates of maternal and romantic love. *NeuroImage*, *21*, 1155–66.

Bateson, M., Nettle, D., Roberts, G. (2006). Cues of being watched enhance cooperation in a real-world setting. *Biology Letters*, *2*, 412–4.

Bénabouu, R., Tirole, J. (2006). Incentives and prosocial behavior. *American Economic Review*, *96*, 1652–78.

Blood, A.J., Zatorre, R.J. (2001). Intensely pleasurable responses to music correlate with activity in brain regions implicated in reward and emotion. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 11818–23.

Buss, A.H. (1980). *Self-Consciousness and Social Anxiety*. San Francisco: W.H. Freeman and Company.

Carver, C.S., Scheier, M.F. (1981). *Attention and Self-Regulation: A Control Theory Approach to Human Behavior*. New York: Springer.

Carver, C.S., Scheier, M.F. (1998). *On the Self-Regulation of Behavior*. New York: Cambridge University Press.

Coull, J.T. (2004). fMRI studies of temporal attention: allocating attention within, or towards, time. *Cognitive Brain Research*, *21*, 216–26.

Craig, A.D. (2009). How do you feel now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, *10*, 59–70.

Craig, A.D., Chen, K., Bandy, D., Reiman, E.M. (2000). Thermosensory activation of insular cortex. *Nature Neuroscience*, *3*, 184–90.

D'Argembeau, A., Ruby, P., Collette, F., et al. (2007). Distinct regions of the medial prefrontal cortex are associated with self-referential processing and perspective taking. *Journal of Cognitive Neuroscience*, *19*, 935–44.

Dale, A.M. (1999). Optimal experimental design for event-related fMRI. *Human Brain Mapping*, *8*, 109–14.

Deary, I.J., Simonotto, E., Meyer, M., et al. (2004). The functional anatomy of inspection time: an event-related fMRI study. *NeuroImage*, *22*, 1466–79.

Devue, C., Collette, F., Balteau, E., et al. (2007). Here I am: the cortical correlates of visual self-recognition. *Brain Research*, *1143*, 169–82.

Di Martino, A., Ross, K., Uddin, L.Q., Sklar, A.B., Castellanos, F.X., Milham, M.P. (2009). Functional brain correlates of social and nonsocial processes in autism spectrum disorders: an activation likelihood estimation meta-analysis. *Biological Psychiatry*, *65*, 63–74.

Duval, T.S., Wicklund, R.A. (1972). *A Theory of Objective Self-Awareness*. New York: Academic Press.

Eisenberger, N.I., Lieberman, M.D., Williams, K.D. (2003). Does rejection hurt? An FMRI study of social exclusion. *Science*, *302*, 290–2.

Evans, A.C., Kamber, M., Collins, D.L., MacDonald, D. (1994). An MRI-based probalistic atlas of neuroanatomy. In: Shorvon, S.D., editor. *Magnetic Resonance Scanning and Epilepsy*. New York: Plenum Press.

Farrer, C., Frith, C.D. (2002). Experiencing oneself vs another person as being the cause of an action: the neural correlates of the experience of agency. *NeuroImage*, *15*, 596–603.

Fenigstein, A., Scheier, M.F., Buss, A.H. (1975). Public and private selfconsciousness. *Journal of Consulting and Clinical Psychology*, *43*, 522–7.

Fink, G.R., Markowitsch, H.J., Reinkemeier, M., Bruckbauer, T., Kessler, J., Heiss, W.D. (1996). Cerebral representation of one's own past: neural networks involved in autobiographical memory. *Journal of Neuroscience*, *16*, 4275–82.

Fossati, P., Hevenor, S.J., Graham, S.J., et al. (2003). search of the emotional self: an FMRI study using positive and negative emotional words. *American Journal of Psychiatry*, *160*, 1938–45.

Friston, K.J., Buechel, C., Fink, G.R., Morris, J., Rolls, E., Dolan, R.J. (1997). Psychophysiological and modulatory interactions in neuroimaging. *NeuroImage*, *6*, 218–29.

Friston, K.J., Holmes, A.P., Poline, J.B., et al. (1995). Analysis of fMRI time-series revisited. *NeuroImage*, *2*, 45–53.

Friston, K.J., Penny, W., Phillips, C., Kiebel, S., Hinton, G., Ashburner, J. (2002). Classical and Bayesian inference in neuroimaging: theory. *NeuroImage*, *16*, 465–83.

Friston, K.J., Zarahn, E., Josephs, O., Henson, R.N., Dale, A.M. (1999). Stochastic designs in event-related fMRI. *NeuroImage*, *10*, 607–19.

Frith, C.D., Frith, U. (2006). The neural basis of mentalizing. *Neuron*, *50*, 531–4.

Frith, C.D., Frith, U. (2008). Implicit and explicit processes in social cognition. *Neuron*, *60*(3), 503–10.

Gallagher, S. (2000). Philosophical conceptions of the self: implications for cognitive science. *Trends in Cognitive Sciences*, *4*, 14–21.

Gallagher, H.L., Frith, C.D. (2003). Functional imaging of 'theory of mind'. *Trends in Cognitive Sciences*, *7*, 77–83.

Gitelman, D.R., Penny, W.D., Ashburner, J., Friston, K.J. (2003). Modeling regional and psychophysiologic interactions in fMRI: the importance of hemodynamic deconvolution. *NeuroImage*, *19*, 200–7.

Gobbini, M.I., Leibenluft, E., Santiago, N., Haxby, J.V. (2004). Social and emotional attachment in the neural representation of faces. *NeuroImage*, *22*, 1628–35.

Gusnard, D.A., Akbudak, E., Shulman, G.L., Raichle, M.E. (2001). Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 4259–64.

Haley, K.J., Fessler, D.M.T. (2005). Nobody's watching? Subtle cues affect generosity in an anonymous economic game. *Evolution and Human Behavior*, *26*, 245–56.

Izuma, K., Saito, D.N., Sadato, N. (2008). Processing of social and monetary rewards in the human striatum. *Neuron*, *58*, 284–94.

Izuma, K., Saito, D.N., Sadato, N. (2010). The roles of the medial prefrontal cortex and striatum in reputation processing. *Social Neuroscience*, *5*, 133–47.

Kelley, W.M., Macrae, C.N., Wyland, C.L., Caglar, S., Inati, S., Heatherton, T.F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience*, *14*, 785–94.

King-Casas, B., Tomlin, D., Anen, C., Camerer, C.F., Quartz, S.R., Montague, P.R. (2005). Getting to know you: reputation and trust in a two-person economic exchange. *Science*, *308*, 78–83.

Kircher, T.T., Senior, C., Phillips, M.L., et al. (2000). Towards a functional neuroanatomy of self processing: effects of faces and words. *Cognitive Brain Research*, *10*, 133–44.

Kircher, T.T., Senior, C., Phillips, M.L., et al. (2001). Recognizing one's own face. *Cognition*, *78*, B1–15.

Kosaka, H., Omori, M., Munesue, T., et al. (2010). Smaller insula and inferior frontal volumes in young adults with pervasive developmental disorders. *NeuroImage*, *50*, 1357–63.

Livesey, A.C., Wall, M.B., Smith, A.T. (2007). Time perception: manipulation of task difficulty dissociates clock functions from other cognitive demands. *Neuropsychologia*, *45*, 321–31.

Lou, H.C., Luber, B., Crupain, M., et al. (2004). Parietal cortex and representation of the mental self. *Proceedings of the National Academy of Sciences of the United States of America*, *101*, 6827–32.

Maguire, E.A., Frith, C.D. (2003). Aging affects the engagement of the hippocampus during autobiographical memory retrieval. *Brain*, *126*, 1511–23.

McGuire, P.K., Silbersweig, D.A., Frith, C.D. (1996). Functional neuroanatomy of verbal self-monitoring. *Brain*, *119*, 907–17.

Menon, V., Uddin, L.Q. (2010). Saliency, switching, attention and control: a network model of insula function. *Brain Structure and Function*, *214*, 655–67.

Modinos, G., Ormel, J., Aleman, A. (2009). Activation of anterior insula during self-reflection. *PLoS One*, *4*, e4618.

Montague, P.R., Berns, G.S., Cohen, J.D., et al. (2002). Hyperscanning: simultaneous fMRI during linked social interactions. *NeuroImage*, *16*, 1159–64.

Moor, B.G., Guroglu, B., Op de Macks, Z.A., Rombouts, S.A., Van der Molen, M.W., Crone, E.A. (2012). Social exclusion and punishment of excluders: neural correlates and developmental trajectories. *NeuroImage*, *59*, 708–17.

Morin, A., Michaud, J. (2007). Self-awareness and the left inferior frontal gyrus: inner speech use during self-related processing. *Brain Research Bulletin*, *74*, 387–96.

Morita, T., Itakura, S., Saito, D.N., et al. (2008). The role of the right prefrontal cortex in self-evaluation of the face: a functional magnetic resonance imaging study. *Journal of Cognitive Neuroscience*, *20*, 342–55.

Morita, T., Kosaka, H., Saito, D.N., et al. (2012). Emotional responses associated with self-face processing in individuals with autism spectrum disorders: an fMRI study. *Social Neuroscience*, *7*, 223–39.

Ochsner, K.N., Beer, J.S., Robertson, E.R., et al. (2005). The neural correlates of direct and reflected self-knowledge. *NeuroImage*, *28*, 797–814.

Ochsner, K.N., Knierim, K., Ludlow, D.H., et al. (2004). Reflecting upon feelings: an fMRI study of neural systems supporting the attribution of emotion to self and other. *Journal of Cognitive Neuroscience*, *16*, 1746–72.

Oldfield, R.C. (1971). The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, *9*, 97–113.

Onoda, K., Okamoto, Y., Nakashima, K., et al. (2010). Does low self-esteem enhance social pain? The relationship between trait self-esteem and anterior cingulate cortex activation induced by ostracism. *Social Cognitive and Affective Neuroscience*, *5*, 385–91.

Piolino, P., Giffard-Quillon, G., Desgranges, B., Chetelat, G., Baron, J.C., Eustache, F. (2004). Re-experiencing old memories via hippocampus: a PET study of autobiographical memory. *NeuroImage*, *22*, 1371–83.

Platek, S.M., Keenan, J.P., Gallup, G.G. Jr, Mohamed, F.B. (2004). Where am I? The neurological correlates of self and other. *Cognitive Brain Research*, *19*, 114–22.

Platek, S.M., Loughead, J.W., Gur, R.C., et al. (2006). Neural substrates for functionally discriminating self-face from personally familiar faces. *Human Brain Mapping*, *27*, 91–8.

Platek, S.M., Wathne, K., Tierney, N.G., Thomson, J.W. (2008). Neural correlates of self-face recognition: an effect-location meta-analysis. *Brain Research*, *1232*, 173–84.

Saito, D.N., Tanabe, H.C., Izuma, K., et al. (2010). 'Stay tuned': inter-individual neural synchronization during mutual gaze and joint attention. *Frontiers in Integrative Neuroscience*, *4*, 127.

Seeley, W.W., Menon, V., Schatzberg, A.F., et al. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. *Journal of Neuroscience*, *27*, 2349–56.

Sugawara, K. (1984). Ji-ishiki-shakudo nihon-go-ban sakusei no kokoromi [An attempt to construct the self-consciousness scale for Japanese.]. *Shinrigaku Kenkyu: The Japanese Journal of Psychology*, *55*, 184–8.

Sugiura, M., Kawashima, R., Nakamura, K., et al. (2000). Passive and active recognition of one's own face. *NeuroImage*, *11*, 36–48.

Sugiura, M., Sassa, Y., Jeong, H., et al. (2006). Multiple brain networks for visual self-recognition with different sensitivity for motion and body part. *NeuroImage*, *32*, 1905–17.

Sugiura, M., Sassa, Y., Jeong, H., et al. (2012). Self-face recognition in social context. *Human Brain Mapping*, *33*, 1364–74.

Sugiura, M., Watanabe, J., Maeda, Y., Matsue, Y., Fukuda, H., Kawashima, R. (2005). Cortical mechanisms of visual self-recognition. *NeuroImage*, *24*, 143–9.

Takahashi, H., Matsuura, M., Koeda, M., et al. (2008). Brain activations during judgments of positive self-conscious emotion and positive basic emotion: pride and joy. *Cerebral Cortex*, *18*, 898–903.

Uddin, L.Q., Kaplan, J.T., Molnar-Szakacs, I., Zaidel, E., Iacoboni, M. (2005). Self-face recognition activates a frontoparietal 'mirror' network in the right hemisphere: an event-related fMRI study. *NeuroImage*, *25*, 926–35.

Uddin, L.Q., Menon, V. (2009). The anterior insula in autism: under-connected and under-examined. *Neuroscience & Biobehavioral Reviews*, *33*(8), 1198–203.

Vogeley, K., Bussfeld, P., Newen, A., et al. (2001). Mind reading: neural mechanisms of theory of mind and self-perspective. *NeuroImage*, *14*, 170–81.

Wicker, B., Keysers, C., Plailly, J., Royet, J.P., Gallese, V., Rizzolatti, G. (2003). Both of us disgusted in My insula: the common neural basis of seeing and feeling disgust. *Neuron*, *40*, 655–64.

Worsley, K.J., Friston, K.J. (1995). Analysis of fMRI time-series revisited. *NeuroImage*, *2*(3), 173–81.

Worsley, K.J., Marrett, S., Neelin, P., Vandal, A.C., Friston, K.J., Evans, A.C. (1996). A unified statistical approach for determining significant signals in images of cerebral activation. *Human Brain Mapping*, *4*, 58–73.

Zaki, J., Ochsner, K.N., Hanelin, J., Wager, T.D., Mackey, S.C. (2007). Different circuits for different pain: patterns of functional connectivity reveal distinct networks for processing pain in self and others. *Social Neuroscience*, *2*, 276–91.