The Role of the Right Prefrontal Cortex in Self-evaluation of the Face: A Functional Magnetic Resonance Imaging Study

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Abstract

■ Individuals can experience negative emotions (e.g., embarrassment) accompanying self-evaluation immediately after recognizing their own facial image, especially if it deviates strongly from their mental representation of ideals or standards. The aim of this study was to identify the cortical regions involved in self-recognition and self-evaluation along with self-conscious emotions. To increase the range of emotions accompanying self-evaluation, we used facial feedback images chosen from a video recording, some of which deviated significantly from normal images. In total, 19 participants were asked to rate images of their own face (SELF) and those of others (OTHERS) according to how photogenic they appeared to be. After scanning the images, the participants rated how embarrassed they felt upon viewing each face. As the photogenic scores decreased, the embarrassment ratings dramatically increased for the participant's own face compared with those of others. The SELF versus OTHERS contrast significantly increased the activation of the right prefrontal cortex, bilateral insular cortex, anterior cingulate cortex, and bilateral occipital cortex. Within the right prefrontal cortex, activity in the right precentral gyrus reflected the trait of awareness of observable aspects of the self; this provided strong evidence that the right precentral gyrus is specifically involved in self-face recognition. By contrast, activity in the anterior region, which is located in the right middle inferior frontal gyrus, was modulated by the extent of embarrassment. This finding suggests that the right middle inferior frontal gyrus is engaged in self-evaluation preceded by self-face recognition based on the relevance to a standard self. ■

INTRODUCTION

The ability to recognize one's own visual image has attracted attention as a potential precursor of the concept of self in primates, including humans. In human infants, self-recognition seems to emerge at about 18 months of age, as measured by the ''rouge test,'' which evaluates an individual's reactions to seeing his or her own reflection in a mirror (Bertenthal & Fischer, 1978; Lewis & Brooks, 1978; Amsterdam, 1972). This type of perceptual feedback from mirrors, photographs, and video/tape recordings focuses attention on the self. Within the theoretical framework of consciousness, the term ''self-awareness'' indicates the state in which an organism directs attention inward toward the self, as distinguished from the state in which an organism directs attention outward toward the environment (Morin, 2006; Carver & Scheier, 1981). As perceptual feedback directs attention toward publicly observable aspects of the self, such as one's own appearance and overt behavior (Buss, 1980), ''public self-awareness'' is induced when we identify the self in perceptual feedback, and thus, is associated with self-recognition. Furthermore, focusing attention on the self initiates an automatic comparison against standards, which comprise mental representations of ideal behaviors or attitudes (Carver & Scheier, 1981, 1998; Duval & Wicklund, 1972). This mental process is defined as self-evaluation. Self-evaluation induces a higher level of self-awareness than public self-awareness because it involves accessing more conceptual and abstract representations of the self, such as autobiographical information and the construction of a self-concept. This greater self-awareness is presumed to be consistent with ''meta self-awareness,'' which is the highest level in the theoretical framework for consciousness (Morin, 2006). If a discrepancy is found between the immediate perception and the standards, the individual can experience a loss of self-esteem, which could lead to a negative affect (Carver & Scheier, 1998; Buss, 1980). Embarrassment and shame are examples of a negative affect that might accompany a negative evaluation, and both are categorized as self-conscious emotions. However, there is an obvious difference in the severity of these emotions: Embarrassment is trivial and momentary, whereas shame is more serious and enduring (Tangney, Miller, Flicker, & Barlow, 1996;

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Buss, 1980). Embarrassed people feel foolish or silly, and experience a temporary loss of self-esteem. By contrast, people who are ashamed feel regretful and depressed, and experience a long-term loss of self-esteem. Exposure to perceptual feedback is unlikely to be serious, even when it deviates from standards; therefore, we suggest that embarrassment, rather than shame, should be closely related to self-evaluation. Thus, embarrassment is a consequence of self-evaluation that involves greater self-awareness than public self-awareness, which is associated with self-recognition.

Neural substrates for self-face recognition have been widely studied. Recent neuroimaging studies suggested that the right parieto-frontal network was mainly involved in self-face recognition (Sugiura et al., 2005, 2006; Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni, 2005; Keenan, Wheeler, Gallup, & Pascual-Leone, 2000). In addition, a few studies have suggested a relationship between self-recognition and self-awareness (Platek, Keenan, Gallup, & Mohamed, 2004; Gallup, 1970). To our knowledge, however, no imaging study has yet provided clear evidence for the relationship between self-recognition and self-awareness. As discussed above, public self-awareness is a transient state that is caused by an inducer (e.g., perceptual feedback). In addition to public self-awareness, an individual might also show a habit, tendency, or disposition to focus on the observable aspect of the self, which is termed as ''public self-consciousness'' (Fenigstein, Scheier, & Buss, 1975). The trait of public self-consciousness and the factor that induces public self-awareness are believed to be closely linked. People who have high public self-consciousness tend to react strongly to factors that induce public self-awareness, whereas people with low public self-consciousness do not (Buss, 1980). This evidence suggests that the neural response to perceptual feedback might also reflect public self-consciousness. We therefore hypothesized that the neural substrates for self-face recognition would be strongly recruited when participants who had a strong disposition to attend to the observable aspects of the self were exposed to feedback face images.

Several imaging studies have examined self-conscious emotions, such as embarrassment or guilt (Takahashi et al., 2004; Berthoz, Armony, Blair, & Dolan, 2002). In these experiments, the subjects were instructed to read various types of sentences depicting embarrassing or guilty situations, and were asked to rate what the participants themselves felt. The medial prefrontal cortex (mPFC), temporal regions, and the orbito-frontal cortex (OFC) were activated. As these tasks required the participants to represent the emotional states of others in these situations, the activated regions should include the neural substrates involved in representing the mental state of others, a process referred to as ''mentalizing'' (Frith & Frith, 1999, 2003; Frith, 2001). Actually, the mPFC and temporal regions are part of the neural substrate of mentalizing. On the other hand, previous clinical and neuroimaging studies have shown that the OFC is involved in the regulation of social behavior (Pietrini, Guazzelli, Basso, Jaffe, & Grafman, 2000; Grafman et al., 1996; Damasio, 1994) and has an essential role in the interplay of self-monitoring and emotional processing to motivate appropriate behaviors (Beer, John, Scabini, & Knight, 2006). Therefore, the OFC is likely to be related to the embarrassment. However, to our knowledge, there have been no studies of the brain activity that occurs when participants make evaluations about themselves and experience self-conscious emotions such as embarrassment.

Here we aimed to dissociate the brain regions essential for self-face recognition and self-evaluation accompanied by embarrassment. We used event-related functional magnetic resonance imaging (fMRI) to measure regional activation during the evaluation of how well an individual's own face and those of others photographed were (i.e., how photogenic the target person appeared to be). We induced an emotional state of embarrassment while each subject was inside the MRI scanner and was evaluating images of his or her own face. We tried to vary the extent of embarrassment by presenting participants with their own facial images chosen from video recordings, some of which deviated significantly from normal images. We acquired ratings of embarrassment intensity for each face stimulus from each subject after scanning, and used them as parametric covariates in our fMRI analysis (Phan et al., 2003; Büchel et al., 2002). We predicted that the brain regions that responded to embarrassment would reflect the process of embarrassment itself or the self-relevant process, as the feeling of embarrassment is caused by differences between immediate perceptions and standards. Furthermore, on the basis of the difference in the level of self-awareness, we predict that self-evaluation accompanied by an emotional response might not be limited to the cortical elements that are involved in self-face recognition, but might rather recruit additional frontal regions that are specific to self-evaluation and the emotional response.

METHODS

Participants

In total, 9 men and 10 women (mean age = 26.0 ± 4.0 years) participated in the study. All of the subjects were right-handed. The protocol was approved by the Ethical Committee of the National Institute for Physiological Sciences, Japan. All of the volunteers gave written informed consent prior to participation.

Materials

The experiment took place over 2 days. On the first day, the participants made short speeches in front of a video camera. The subjects were informed that the purpose of the recording was to investigate the eye movements that occur when a person speaks, rather than being told the true aim of the study. Initially, the participants were asked to talk for up to 1 min facing the video camera on each of three themes related to their own history and experience (e.g., the hometown where they grew up). Each subject wore a plain black T-shirt and sat in a chair positioned opposite the camera and the experimenter. The subjects gave speeches on each topic in response to the experimenter's instructions.

The recorded video images were imported into a personal computer, and 21 color images, ranging from good to bad as defined below, were selected by the experimenter. We established the following six criteria for the "badness" of each image: first, whether the eyes were totally or partly closed (eyes); second, whether the gaze was averted (gaze); third, whether the mouth was unnaturally open (mouth); fourth, whether the lip stuck out (lip); fifth, whether the chin stuck out (chin); and sixth, whether the expression was strange (expression). "Bad" images that met some of these criteria contained awkward facial expressions, such as those in which the participants showed the whites of their eyes or had their mouths wide open. By contrast, "good" images did not meet any of the criteria, and appeared as if the subjects had posed for a photograph rather than the images having been taken from a video recording. These sets of 21 images were used as the stimuli for the SELF condition in the subsequent fMRI experiment. By contrast, in the OTHERS condition, 21 face images that were selected from three gender-matched unfamiliar individuals (seven images per person) were used.

fMRI Experimental Design

About 2 weeks after the video recording, the participants underwent fMRI scanning. During the fMRI scan, they were asked to evaluate images of either their own face or those of others. The participants lay in the fMRI scanner, with their heads immobilized with an elastic band and sponge cushions, and their ears plugged. Visual stimuli were presented on a projection screen and viewed by the participants through a mirror mounted on the head coil. A handmade MR-compatible five-button key-press device was used with the right hand to record the behavioral responses. Each subject performed four scans. In each scan, 21 images of a subject's own face (SELF condition), 21 images of the faces of others (OTHERS condition), and 7 "null events" in which no stimulus was shown were presented in pseudorandom order. The participants were required to evaluate how photogenic each face was by giving the image a score ranging from 1 (*very bad*) to 7 (*very good*). Each face stimulus (size = 11° × 11°) appeared in the center of the screen for 3 sec. Once the stimulus had disappeared, a small fixation cross appeared in the center of the screen for 500 msec, and was followed by a blank screen for 2.5 sec. The participants were instructed to record their evaluation using the five-button box attached to their right hand when the fixation cross appeared. Each finger was placed on its respective button, and ratings of 1 to 5 were conveyed by a single finger press of the appropriate finger. A rating of 6 was conveyed by a simultaneous thumb and index-finger press, and a rating of 7 was conveyed by a simultaneous thumb and middle-finger press.

Our experimental design was based on a rapid event-related paradigm, in which the efficiency of the design is highly dependent upon the temporal pattern of the stimulus or trial presentations (Dale, 1999; Friston, Zarahn, Josephs, Henson, & Dale, 1999; Dale & Buckner, 1997). We maximized the efficiency of detection of differences between the SELF and OTHER conditions, while maintaining as much as possible the efficiency of estimating the evoked response in the SELF or OTHER condition. To ensure the latter, a null event was included which occurred at a probability of 14% of all events.

The optimization of the design matrix in terms of efficiency was conducted as follows (Dale, 1999; Friston et al., 1999). The order of the 49 events (21 events for each condition and 7 null events) was randomly permutated to generate a set of two vectors (49 × 2 matrix) indicating the presence (1) or absence (0) of a particular event, which embodied information about the order of the conditions. This prototypic design matrix was then transformed into a stimulus function matrix (SF: 3822 × 2 matrix), where SF was at a much finer time resolution (71 msec) than the repetition time (TR = 3000 msec). Finally, a design matrix incorporating two conditions was created by convolving the stimulus function matrix with a hemodynamic response function (HRF) and was down-sampled at the original TR:

$$X = \lfloor \mathrm{SF}_{\mathrm{self}}, \mathrm{SF}_{\mathrm{other}} \rfloor \otimes \mathrm{HRF}.$$

The efficiency of the estimations of SELF–OTHER was evaluated using the inverse of the covariance of the contrast of the parameter estimates (Dale, 1999; Friston et al., 1999):

$$\mathrm{Efficiency} = \left(\mathrm{var}\left(c^T \beta\right)\right)^{-1},$$

$$\mathrm{var}\left(c^T \beta\right) = c^T \left(X^T X\right)^{-1} c.$$

Here, $c = (1, -1)$ for SELF–OTHER. From the 100,000 randomly generated design matrices, we selected the four most efficient ones.

Psychological Measurements

Immediately following scanning, the participants undertook a self-paced rating task in which they scored all 42 pictures presented on a laptop computer according to the following: how photogenic they appeared on a scale ranging from 1 (*very bad*) to 7 (*very good*); embarrassment intensity (i.e., ''How embarrassed do you feel when viewing each face?'') on a scale ranging from 1 (*not at all*) to 9 (*most embarrassed*); valence (i.e., ''How pleasant or unpleasant do you feel when viewing each face?'') on a scale ranging from 1 (*most unpleasant*) to 9 (*most pleasant*); and arousal (i.e., ''How aroused do you feel when viewing each face?'') on a scale ranging from 1 (*sleepy*) to 9 (*most aroused*). The latter two measurements were based on Russell's affect grid, which was designed to rapidly assess affect (Russell, Weiss, & Mendelsohn, 1989). The photogenic scores were rated outside the MRI scanner, in order to ensure the reliability of the data measured inside the scanner. We used the embarrassment ratings as parametric covariates in our fMRI analysis (Phan et al., 2003; Büchel et al., 2002). After the rating task, the participants completed a questionnaire on the basis of the public and private self-consciousness scales, which are the Japanese versions of Feningstein's original index (Sugawara, 1984; Fenigstein et al., 1975). 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. By contrast, public self-consciousness is the tendency to be aware of the publicly displayed aspects of the self, consisting of one's physical appearance. A representative item used to assess private self-consciousness is ''I'm constantly examining my motives,'' and a representative item used to assess public self-consciousness is ''I'm usually aware of my appearance.''

MRI Scanning Procedure

Functional images were acquired using T2*-weighted gradient echo-planar imaging (EPI) sequences and a 3.0-T MR scanning system (Allegra, Siemens, Erlangen, Germany). There were four fMRI scans, during each of which 96 volumes were acquired. Each volume consisted of 42 slices, with a thickness of 3 mm and a 0.5-mm gap, in order to cover the entire brain. The time interval between each two successive acquisitions of the same slice was 3000 msec, with an echo time (TE) of 30 msec and a flip angle (FA) of 85°. The field of view (FOV) was 192 × 192 mm, and the matrix size was 64 × 64, giving voxel dimensions of 3 × 3 mm. For anatomical reference, T1-weighted magnetization-prepared rapid gradient-echo (MPRAGE) images (TR = 1460 msec; TE = 4.38 msec; FA = 8°; FOV = 192 mm; matrix size = 256 × 256) were collected at the same positions as the EPIs, and three-dimensional (3-D) MPRAGE images (TR = 2500 msec; TE = 4.38 msec; FA = 8°; FOV = 230 mm; matrix size = 256 × 256; slice thickness = 1 mm; a total of 192 trans-axial images) were obtained as a high-resolution anatomical reference for each subject.

Behavioral Data Analysis

Behavioral data analysis was carried out using SPSS version 10.0J software (SPSS Japan, Tokyo, Japan). The photogenic scores rated outside the MRI scanner were used to generate the behavioral statistics. To compare the photogenic scores between the SELF and OTHERS conditions, a paired t test was performed on the average ratings. The relationship between the photogenic score and embarrassment was analyzed using a general linear model (GLM) with face type (SELF vs. OTHERS) as a fixed factor, photogenic score as a covariate, and subject as a random factor. We also performed a GLM with face type (SELF vs. OTHERS) as a fixed factor, valence and arousal as covariates, and subject as a random factor, in order to investigate the relationship between the embarrassment ratings and two dimensions in the affect grid (arousal and valence). The self-consciousness scale data were analyzed with a two-way repeated measures analysis of variance using gender (male or female) as a between-subject factor, and face type (SELF or OTHERS) as a within-subject factor. The results were considered statistically significant at $p < .05$.

Imaging Data Analysis

The first two volumes of each fMRI session were discarded because of unsteady magnetization, and the remaining 94 volumes per session were used for analysis. Image and statistical analyses were performed using the statistical parametric mapping package SPM2 (www.fil.ion.ucl.ac.uk/spm/). Initially, we used slice-timing correction to adjust for differences in slice-acquisition times during echo-planar scanning in ascending order. We interpolated and resampled the data so that for each time series, the slices had been acquired at the same time as the reference slice, which was the middle slice (slice 22 in this case). The images were then realigned using the last image as a reference. The high-resolution 3-D T1-weighted MPRAGE image was coregistered to the last scan in the functional images using T1-weighted MPRAGE MRIs scanned in planes identical to the functional imaging slice. Subsequently, the coregistered high-resolution T1-weighted anatomical image was normalized to a standard T1 template image, as defined by the Montreal Neurological Institute (MNI), involving linear and nonlinear 3-D transformations (Ashburner & Friston, 1999). The parameters from this normalization process were applied to each of the fMRI images. Finally, the anatomically normalized fMRI images were filtered using a Gaussian kernel with a full width at half maximum of 8 mm in the x, y, and z axes.

Statistical analysis was conducted at two levels. First, the individual task-related activation was evaluated (Friston et al., 1995; Worsley & Friston, 1995). Second, to make inferences at a population level, the individual data were summarized and incorporated into a random effect model (Holmes & Friston, 1998). In the single-subject analysis, the design matrix contained two task-related regressors (the SELF and OTHERS conditions), two regressors for parametric modulation (the embarrassment ratings for each condition), and one constant term. The presentation of each face stimulus was embedded in a series of delta functions. The task-related regressor was modeled by convolving it with a canonical HRF. To construct the regressor for parametric modulation, the interaction between the trial and the parameter variable was first calculated for each face condition as follows. The delta function for each stimulus was modulated by the subjective embarrassment ratings made for each face image after fMRI scanning. In other words, the height of the delta function was changed as a function of the embarrassment ratings. Next, the Trial × Parameter interaction term was convolved with the HRF, giving the regressor for the parametric modulation. Finally, the regressor for each face condition was orthogonalized with respect to the corresponding task-related regressor. We used the high-pass filter, which was composed of the discrete cosine basis function with a cutoff period of 128 sec, in order 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 (ReML) procedure, and was used to whiten the data and the design matrix (Friston et al., 2002). To give the estimated parameters, the least-square estimation was performed on the high-pass filtered and prewhitened data and design matrix. The weighted sum of the parameter estimates in the individual analysis constituted contrast images that were used for the second-level analysis. We constructed appropriate contrast images to examine brain areas showing differential effects in the two conditions—that is, areas that showed greater activity during the evaluation of an individual's own face than those of others (SELF vs. OTHERS) and vice versa (OTHERS vs. SELF), as well as the main effects of condition (SELF and OTHERS). We also produced contrast images for parametric modulation, that is, brain areas in which activity covaried with the subjective embarrassment ratings for an individual's own face or the faces of others.

A random effects model was used to make statistical inferences at the population level (Holmes & Friston, 1998). A one-sample t test was performed using the contrast images specified above. First, we produced a statistical parametric map of the differential effects of the conditions (SELF vs. OTHERS and OTHERS vs. SELF). For this effect, we reported the brain activations with a statistical height threshold of $p < .001$ and a statistical extent threshold of $p < .05$, corrected for multiple comparisons for the entire brain. To confirm the activation patterns of areas showing differential effects, we also conducted a post hoc analysis for the contrast of the main effects (SELF and OTHERS). Second, we searched for brain activities that covaried with the subjective embarrassment rating for individuals' own faces. In this analysis, the search region was restricted to areas showing significant activation during the SELF condition compared with the OTHERS condition. We applied a statistical threshold of $p < .001$ without correction for multiple comparisons to these data. Third, we examined the relationships between brain activation and the public and private self-consciousness scales. For each subject, the fitted response curves for the SELF condition were extracted from each activation focus depicted by the SELF versus OTHERS contrast. The peak values (in units of percentage signal change relative to the mean for the whole brain) of the response curve were then averaged over four sessions to give one representative value for each activation focus in each subject. Linear regression analysis was used to determine the relationship between the percentage signal changes for the peak of the evoked fMRI response and the self-consciousness scales.

RESULTS

Behavioral Data

The photogenic scores for the images of individuals' own faces and those of others were measured during and after the fMRI session, in order to ensure the reliability of the data measured within the scanner. The two measurements were strongly correlated with each other (SELF, $r = .81$; OTHERS, $r = .83$). This result suggested that the other scores for each face obtained outside the MRI scanner must have reflected the mental states when viewing the face inside the scanner. Figure 1 shows the range of photogenic scores measured outside the MRI scanner. A paired t test revealed that the average ratings for individuals' own faces were significantly lower than those for the faces of others [$t(18) = -2.55$, $p < .05$]. The relationship between the photogenic score and embarrassment rating for each face is shown in Figure 2. A GLM analysis revealed significant effects of face type [$F(1, 29) = 61.60$, $p < .001$] and photogenic score [$F(1, 758) = 822.31$, $p < .001$]. As the photogenic scores decreased, the embarrassment ratings dramatically increased for individuals' own faces. In other words, individuals' own faces that were evaluated as "bad" evoked greater embarrassment than those that were evaluated as "good." However, the relationship between the photogenic score and embarrassment rating in the OTHERS condition was distinct from that in the SELF condition [Face type × Rating, $F(1, 758) = 55.2$, $p < .001$]. Interestingly, the embarrassment ratings

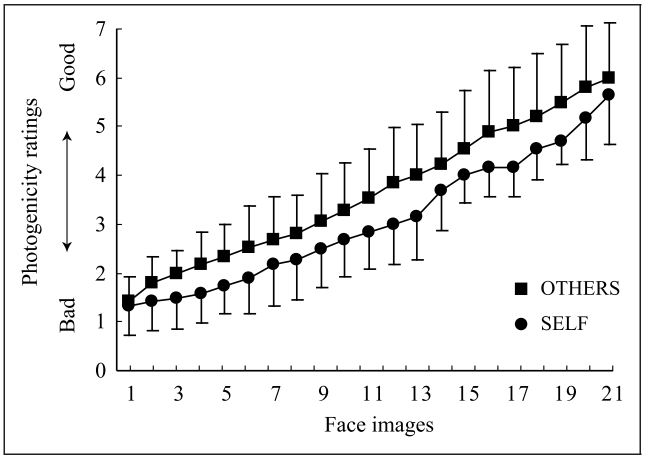


Figure 1. Evaluative photogenic scores for individuals' own face images and those of others rank-ordered according to the ratings (mean ± standard deviation).

for the faces of others varied widely, as the photogenic scores decrease. We next investigated the relationship between the embarrassment rating and the two dimensions constituting the affect grid. A GLM analysis revealed significant main effects of face type [$F(1, 200) = 33.56$, $p < .001$] and valence [$F(1, 754) = 96.32$, $p < .001$]. The Face type × Arousal × Valence interaction was significant [$F(1, 754) = 6.38, p < .05$] as was the Face type × Valence interaction [$F(1, 754) = 20.91$, $p < .001$], whereas the Face type × Arousal interaction was not significant [$F(1, 754) = 3.55$, *ns*]. These results, together with the data presented in Figure 3, suggest that the intensity of embarrassment elicited by individuals' own faces was more strongly correlated with the valence rating than the arousal rating, but that this relationship was not obvious when rating the faces of others.

The average public self-consciousness scale values were 48.2 ± 12.7 in men and 46.4 ± 9.9 in women, whereas the average private self-consciousness scale values were 55.0 ± 7.3 in men and 48.7 ± 6.7 in women. There were no significant differences between genders [men and women, $F(1, 17) = 2.19$, *ns*] or subscales [public and private, $F(1, 17) = 1.81$, *ns*]. Moreover, there was no significant interaction between these two factors [gender and subscale, $F(1, 17) = 0.57$, *ns*]. The public and private self-consciousness scales were not correlated with one another ($r = .06$, *ns*).

fMRI Results

We initially highlighted the contrast of SELF versus OTHERS, in order to specify the brain regions that were more strongly activated during self-evaluation. For this comparison, an inclusive mask was used to rule out the effects that might arise from task-related decreases in activation. Figure 4A and B shows the areas that were more active during the evaluation of individuals' own faces than those of others (SELF vs. OTHERS inclusively masked by SELF). We found significant activation in the right insular cortex/middle inferior frontal gyrus (mIFG), right precentral gyrus, left insular cortex, anterior cingulate cortex (ACC), and bilateral occipito-temporal cortex (Table 1). Clusters located in the right insular cortex/mIFG included the activation foci in the right insular cortex and right mIFG [Brodmann's area (BA) 45/46]. Additionally, there was a broad range of activation within the bilateral occipito-temporal cortex, which had three different foci: the posterior part of the lateral occipital cortex, the anterior part of the ventral occipital cortex, and the occipito-temporo-parietal junction. A post hoc analysis showed that the bilateral ventral occipital cortices and the right precentral gyrus were significantly active even during the evaluation of the faces of others [$t(18) = 2.55$, $p < .01$]. By contrast, the other regions were activated only by the evaluation of individuals' own faces (Figure 4C, Table 1).

The reverse contrast (OTHERS vs. SELF inclusively masked by OTHERS) caused activation of the bilateral amygdala, the medial OFC (mOFC), and the right inferior parietal cortex. Post hoc analysis showed that the bilateral amygdala were significantly active even during the evaluation of individuals' own faces [$t(18) = 2.55$, $p < .01$; Table 2]. By contrast, the mOFC and the right inferior parietal cortex were only activated when evaluating the faces of others.

To investigate the brain regions in which activity covaried with the reported embarrassment ratings accompanied by self-evaluation, we performed random effect analyses within areas identified as active by the SELF versus OTHERS contrast. We did not identify any regions in which the activity was positively correlated with the embarrassment ratings. By contrast, the activity in the anterior part of the right mIFG was negatively correlated with the embarrassment ratings for individuals' own faces [$t(18) = 4.53, p < .001$; Figure 5A]—that is, the activity in the right mIFG decreased as the subjective intensity of the embarrassment increased. We compared the slope of the regression lines between

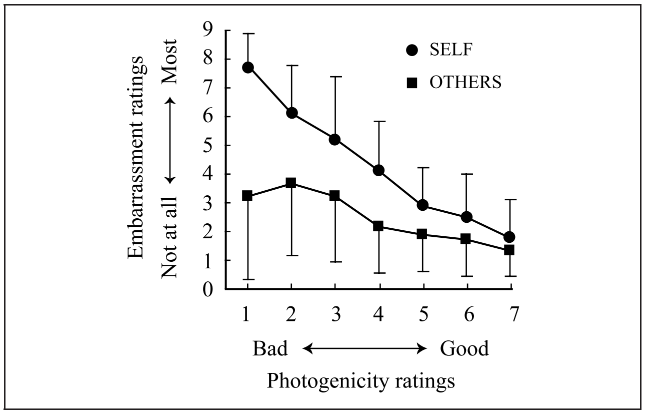
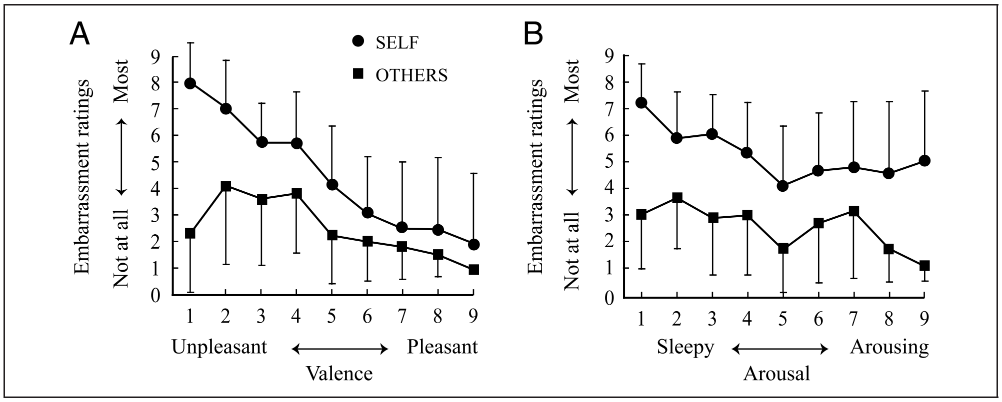


Figure 2. Relationship between the ratings of embarrassment and the photogenic scores for each face.

Figure 3. Relationship between the ratings of embarrassment and the two dimensions of the affect grid (valence and arousal).



the SELF and OTHERS conditions in the right mIFG. A paired t test revealed that the slope in the SELF condition was lesser than that in the OTHERS condition [$t(18) = 1.99$, $p < .05$; Figure 5B].

We performed linear regression analysis to test the hypothesis that the activity of neural substrates for self-face recognition when an individual views their own feedback face image depends upon the consciousness of observable aspects of the self. Within the local maximum depicted by the SELF versus OTHERS contrast, as shown in Figure 4D, the activity in the right precentral gyrus and the right insular cortex was significantly positively correlated with the ratings on the public self-consciousness scale [right precentral gyrus, $t(34) = 2.41$, $p < .05$; right insular cortex, $t(34) = 1.82$, $p < .05$]. By contrast, there was no region in which the activity was correlated with the ratings on the private self-consciousness scale.

DISCUSSION

Embarrassment Ratings

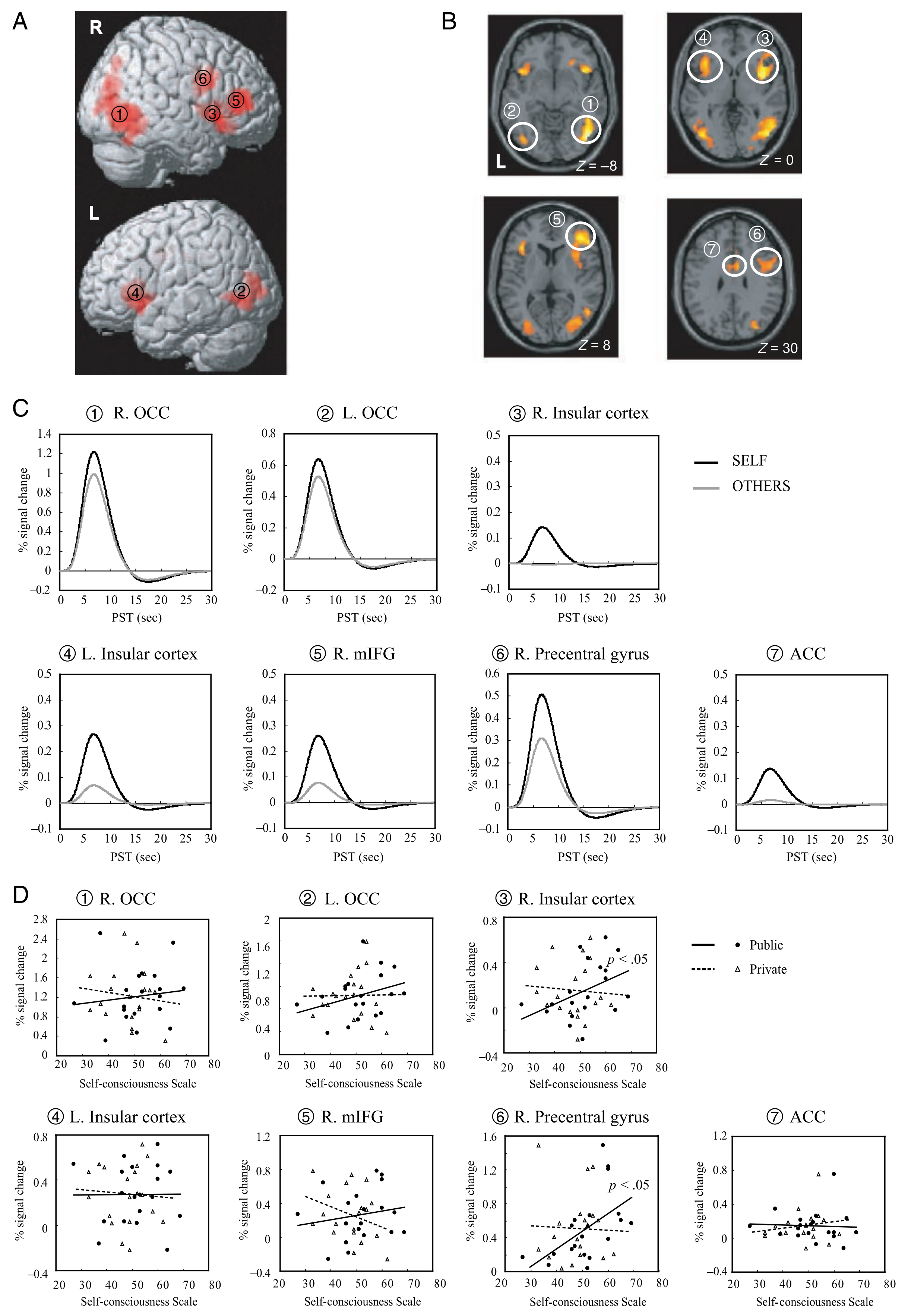
Our results showed that strong feelings of embarrassment arose when individuals viewed an image of their own face which they evaluated as "bad," but not when they viewed images of others. Moreover, the extent of the embarrassment caused by participants' own face images was closely related to the valence or unpleasantness, and not to arousal. These results were consistent with the idea that a discrepancy between an individual's perceptual feedback and standards leads to a reduction in self-esteem and a negative affect (Buss, 1980; Duval & Wicklund, 1972). The embarrassment arising from this situation can be referred to as evaluative embarrassment which is a consequence of the negative evaluation of the self, and which is distinct from exposure embarrassment which occurs when an individual is the object of the attention of others (Lewis, 1992; Edelmann, 1987). We investigated whether the intensity of embarrassment induced by individuals' own faces depended upon their awareness of observable or unobservable aspects of the self. The results showed that the average embarrassment rating was significantly positively correlated with the private self-consciousness scale scores [$t(34) = 2.17$, $p < .05$], but not with the public self-consciousness scale scores [$t(34) = 0.71$, *ns*]. This result was consistent with previous reports showing that high levels of private self-consciousness exaggerate the intensity of pain, moods, emotions, and motives because of increased attention to such inner aspects of the self (Scheier & Carver, 1977). We emphasize that there is no relationship between the extent of public self-consciousness and the embarrassment evoked by the observation of one's own face.

In the current study, some individuals reported mild embarrassment when viewing the faces of others that were rated as "bad," although this effect was not as strong as that reported when viewing their own faces. Embarrassment caused by the feedback images of others is categorized as empathic embarrassment, which occurs when an individual feels embarrassed as a consequence of someone else's predicament (Miller, 1987). Participants must have empathized with the person in the photograph in order to feel mild embarrassment while viewing the faces of others that were rated as "bad."

SELF versus OTHERS

We detected greater activation of the right prefrontal and parietal cortex, bilateral insular cortex, bilateral

Figure 4. (A, B) Brain areas showing significant activation caused by the SELF versus OTHERS contrast are displayed on a surface rendering of the brain and MNI transverse sections (height threshold, $p < .001$; extend threshold corrected, $p < .05$). These activities were masked by the areas activated in the SELF condition. (C) Estimated hemodynamics shown for individuals' own faces (black line) and those of others (gray line) plotted against the first 30-sec poststimulus time (PST) at peak activation within each region. (D) Percentage signal change in each region plotted against the scores from the public and private self-consciousness scales. The right precentral gyrus and the right insular cortex showed significant positive correlations with the ratings of the public self-consciousness scale ($p < .05$).


A
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⑦
C
① R. OCC
② L. OCC
③ R. Insular cortex
④ L. Insular cortex
⑤ R. mIFG
⑥ R. Precentral gyrus
⑦ ACC
% signal change
PST (sec)
SELF
OTHERS
D
① R. OCC
② L. OCC
③ R. Insular cortex
④ L. Insular cortex
⑤ R. mIFG
⑥ R. Precentral gyrus
⑦ ACC
% signal change
Self-consciousness Scale
p < .05
p < .05
● Public
△ Private

Table 1. Significantly Activated Voxels in the Contrast of SELF versus OTHERS Masked with Activation in SELF Condition

	MNI Coordinates					*t*	
Structure	*x*	*y*	*z*	*t*	*Cluster Size (Voxels)*	*SELF*	*OTHERS*
R. Insular cortex/mIFG	36	10	−4	10.15*	1672	2.62	0.07
	48	36	4	7.73*		3.77	1.21
L. Insular cortex	−38	24	0	6.52	661	4.50	1.38
R. Precentral gyrus	52	6	26	5.56	557	5.46	4.04
Anterior cingulate cortex	8	4	30	5.46	445	3.32	0.61
R. Occipital cortex (posterior)/	48	−70	−8	9.26*	2380	9.35	7.93
Occipital cortex (anterior)/	46	−52	−14	8.24*		6.74	5.99
Occipito-temporo-parietal junction	24	−72	42	7.26*		2.62	0.23
L. Occipital cortex	−42	−74	−2	7.97*	800	6.90	6.11

*Indicates FWE corrected $p < .05$ at the voxel level.

occipito-temporal cortex, and ACC when individuals were scoring how photogenic images of their own faces appeared than when evaluating those of others. This result suggests that the self-evaluation of perceptual feedback recruits similar brain regions typically seen in previous researches on self-face recognition, and that right hemisphere dominance can be observed during self-evaluation as well as self-face recognition, as indicated by several previous studies (Sugiura et al., 2005, 2006; Uddin et al., 2005; Keenan, Nelson, O'Connor, & Pascual-Leone, 2001; Keenan et al., 2000). In the right PFC, two conspicuous clusters were observed in the right hemisphere but not in the left; these coincided with the peak locations reported in a previous study on self-face recognition (Sugiura et al., 2006). The two peaks were separated by a distance of approximately 3.5 cm. The posterior peak was located in the precentral gyrus around the borders of BA 6 and BA 44, whereas the anterior peak was located in the mIFG around BA 45 and 46. We focused on the differences between the properties of these two prefrontal regions that implied different roles in self-evaluation.

Right mIFG

Consistent with our prediction, we identified no activity in the mPFC and temporal regions engaged in the evaluative process of embarrassment (Takahashi et al., 2004; Berthoz et al., 2002) when the subjects experienced embarrassment associated with self-evaluation. The reduced activity in these areas suggested that the actual experience of embarrassment did not require mentalizing activity. Within the brain regions highlighted by the SELF versus OTHERS contrast, only the activity in the anteroventral part of the right PFC located in the mIFG was modulated by the extent of embarrassment caused to individuals viewing their own faces. We observed a negative correlation between the right mIFG activity and embarrassment ratings, whereby the activity decreased as the intensity of embarrassment increased. The correlation analysis of the embarrassment intensity was performed at the within-subject level, and thus, was more sensitive than the between-subject correlation analysis involving the private self-consciousness scale, which was correlated with the averaged intensity of embarrassment for all of the subjects' own faces. The photogenic rating was inversely correlated with the intensity of the induced embarrassment on the SELF trial, but not on the OTHERS trial. This finding indicated that the embarrassment was caused by the self-evaluation because the photogenic rating was a type of evaluation and because the evaluation of others did not elicit embarrassment. This negative correlation made it unlikely that the right mIFG represented the induced embarrassment itself. As the right mIFG was selectively activated during the evaluation of one's own face, but not the faces of others, it might be related to the self-evaluation that induces embarrassment. Several functional imaging studies have reported activation of the right lateral PFC during self-referential processing, including autobiographical memory retrieval (Vogeley, Kurthen, Falkai, & Maier, 1999; Fink et al., 1996), or evaluation of traits concerning the self (Ochsner et al., 2005; Schmitz, Kawahara-Baccus, & Johnson, 2004). Schmitz et al. (2004) suggested that the increased activity in the right PFC during self-evaluation is associated with increased self-relevance. This explanation fits well with previous reports showing activation of the right prefrontal region close to the mIFG that is specific to observations of individuals' own faces or bodies (Sugiura et al., 2006), as well as increases in signal intensity above the baseline associated with stimuli that contain more ''self'' elements when using morphed faces (Uddin et al., 2005). As the standard for an individual's face appears to be recognized as one's own representative

Table 2. Significantly Activated Voxels in the Contrast of OTHERS versus SELF Masked with Activation in OTHERS Condition

	MNI Coordinates					*t*	
Structure	*x*	*y*	*z*	*t*	*Cluster Size (Voxels)*	*SELF*	*OTHERS*
L. Amygdala	−18	−8	−14	6.20	69	3.00	5.44
R. Amygdala	20	−8	−12	5.83	36	3.68	4.88
Medial orbito-frontal cortex	6	46	−16	5.33	125	0.51	3.20
Inferior parietal cortex	48	−54	36	4.18	33	1.59	3.21

face, it could be the most self-relevant stimulus. Individuals whose own faces are rated as "good" tend to be close to the standard and these individuals experience relatively little embarrassment. Therefore, in the current study, an increase in the right mIFG activity associated with reduced embarrassment would reflect increased relevance to the standard self, which could be regarded as self-relevance. In addition, the activity of the right mIFG did not depend on public self-consciousness; this was in agreement with our finding that the extent of embarrassment was not associated with public self-consciousness. Taken together, our results suggest that the right mIFG is selectively engaged in the self-evaluation, reflecting self-relevance.

Right Precentral Gyrus

Unlike the right mIFG, activity in the posterior peak located within the right precentral gyrus was not correlated with the embarrassment ratings for individuals' own faces. However, the right precentral gyrus was strongly activated when individuals with high public self-consciousness viewed their own faces and evaluated their photogenic scores, compared with individuals with low public self-consciousness. People with high public self-consciousness tend to react strongly and become publicly self-aware when they are exposed to inducers of public self-awareness, such as perceptual feedback (Buss, 1980). This implies that individuals with high and low public self-consciousness differ in the sensitivity of their neural responses to inducers of public self-awareness. In the current study, activity in the right precentral gyrus related to public self-consciousness reflected individual differences in the sensitivity of the neural responses to individuals' own facial images. That is, the brain regions involved in self-face recognition were expected to be strongly activated when individuals with high public self-consciousness viewed images of their own face, regardless of whether they deviated from standards. We therefore proposed that the right precentral gyrus was one of the neural substrates involved in self-face recognition. Indeed, the observed peak in the precentral gyrus was close to the peak of activation associated with self-face recognition in some previous studies (Sugiura et al., 2005, 2006; Platek et al., 2004; Keenan et al., 2000) (Table 3). Moreover, the observed peak overlapped with premotor areas that are associated with the observation and imitation of mouth movements (Buccino et al., 2001), dynamic emotional facial expressions in movies (Leslie, Johnson-Frey, & Grafton, 2004), or static facial emotional expressions (Dapretto et al., 2006; Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Table 3). The premotor areas are thought to be a key component of the mirror-neuron system, which is a shared representation of the actual execution and observation of actions. Observing a face might automatically recruit similar brain areas to those involved in the motor actions of facial expression; this is supported by our finding that the right precentral gyrus is active even while evaluating the faces of others. Moreover, in the present study, the enhanced activity in the right precentral gyrus during self-evaluation can be interpreted as showing that the perception of one's own face can more easily access the internal representation of one's own actions than the perception of others' faces. This idea

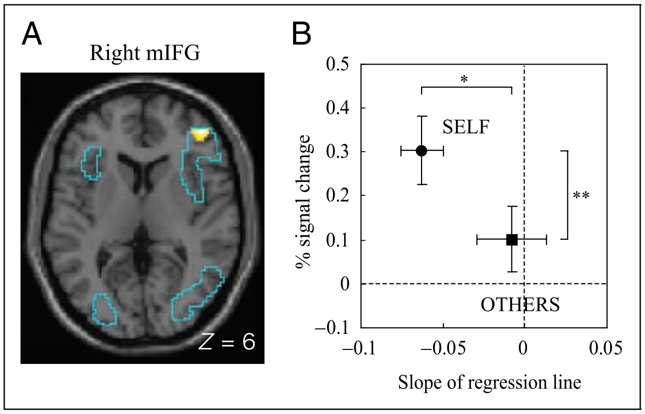

Figure 5. (A) Brain activity in the right mIFG negatively correlated with the embarrassment ratings for individuals' own faces. A random effects statistical parametric activation map (SPM$\{t\}$) was overlaid on a canonical transverse section. The height threshold was set at $p < .01$ at each voxel level for display purposes. The light blue outlines indicate areas that were significantly activated by the SELF versus OTHERS contrast. (B) The x-axis indicates the slope of the regression lines between the embarrassment ratings for each face and the right mIFG activities. The y-axis indicates the average percentage signal change of the right mIFG in each condition. The asterisks indicate statistically significant differences ($^{*}p < .05$, $^{**}p < .001$, paired t test).

Table 3. List of Functional MRI Studies That Have Reported Activation in the Right Prefrontal Cortex during Face Presentation

				MNI Coordinates		
Author	*Task*	*Name*	*BA*	*x*	*y*	*z*
Precentral gyrus						
Keenan et al., 2001	self-face recognition	inferior frontal gyrus	–	–	–	–
Platek et al., 2004	self-face recognition	inferior frontal gyrus	–	42	8	27
Sugiura et al., 2005	self-face recognition	frontal operculum	–	44	8	12
Sugiura et al., 2006	self-face recognition	precentral gyrus	–	53	7	35
Leslie et al., 2004	imitating/observing face	mid premotor	6/44	48	10	24
Buccino et al., 2001	observing mouth actions	premotor	6/44	53	−2	35
Carr et al., 2003	imitating/observing emotions	premotor face area	6	48	7	31
Dapretto et al., 2006	imitating facial expressions	precentral gyrus	6	48	−1	22
mIFG						
Uddin et al., 2005	self-face recognition	inferior frontal gyrus	–	48	42	−2
Sugiura et al., 2006	self-face recognition	mid-inferior frontal gyrus	–	46	39	13

Coordinates reported in previous studies on Talairach's coordinate systems were transformed to MNI coordinates.

is compatible with previous studies suggesting that a fronto-parietal ''mirror'' network, including the premotor area, is involved in self-face recognition relative to the recognition of others' faces as well as the discrimination of self from others (Uddin et al., 2005; Platek et al., 2004). Thus, the right precentral gyrus appears to play a crucial role in self-face recognition, which is a prerequisite for self-evaluation. We found a functional dissociation between the mIFG and the precentral gyrus in the right PFC; this is consistent with evidence from developmental studies, showing that the emergence of self-recognition precedes the emergence of self-evaluation and the self-conscious emotion associated with self-evaluation (Stipek, Gralinski, & Kopp, 1990; Lewis, 1989; Dunn, 1987; Emde, Johnson, & Easterbrooks, 1987; Kagan, 1984).

Insular Cortex

The activity observed in the right anterior insula also correlated with the scores on the public self-consciousness scale. This indicated that the right anterior insula was strongly activated when individuals who are strongly inclined to be concerned about observable aspects of the self viewed their own face images. Furthermore, the activity in the bilateral anterior insula increased only during the evaluation of one's own face, and not those of others. These findings suggest that the anterior insula is one of the specific neural substrates for self-face recognition. This is consistent with recent studies showing engagement of the anterior insula in the processing of one's own face or personally familiar face (e.g., partner's face) (Platek et al., 2006; Kircher et al., 2000, 2001). Other self-related processing, such as that for self-related episodic memories, activates the anterior insula (Fink et al., 1996). These activities during self-related processing have been attributed to high autonomic arousal in response to self-related salient stimuli. In agreement with this interpretation, the specific anterior insula activation observed during self-evaluation might result from autonomic arousal related to self-face recognition. However, our results demonstrated that the level of arousal did not covary with the extent of embarrassment. Furthermore, the anterior insula activity was not modulated by the embarrassment ratings for individuals' own faces. This evidence suggests that the anterior insula reflects enhanced autonomic arousal caused by self-face recognition, but does not reflect emotional responses associated with self-evaluation.

Occipital Cortex

The bilateral occipital areas extending over the fusiform and inferior temporal gyri were more strongly activated during the evaluation of individuals' own faces than those of others. This activated area overlapped with the right fusiform face area that is selectively involved in face processing (Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Asgari, Gore, & McCarthy, 1996), and the bilateral extrastriate body area that is selectively involved in the visual processing of human bodies and faces (Downing, Jiang, Shuman, & Kanwisher, 2001). Activation of the fusiform and inferior temporal gyrus has been reported in many previous studies on self-face recognition (Sugiura et al., 2005, 2006; Kircher et al., 2000, 2001). Sugiura et al. (2005, 2006) reported self-specific activation of the ventral occipito-temporal cortex, suggesting that the self-face is processed as a word-like visual stimulus or a symbol. However, in the present study, most of the activation within the occipital cortices caused by the SELF versus OTHERS contrast occurred not only during the evaluation of individuals' own faces but also during the evaluation of the faces of others. The enhanced activity within the occipital cortices reflected increased attention to the emotional salience of individuals' own faces compared with those of others, as reported in previous studies (Takahashi et al., 2004, 2006; Uddin et al., 2005; Phan, Wager, Taylor, & Liberzon, 2002).

OTHERS versus SELF

The OTHERS versus SELF contrast revealed activation of the bilateral amygdala, the mOFC, and the right inferior parietal cortex. Within these areas, only the activation of the mOFC has been reported previously, in a study contrasting familiar faces of others with one's own face (Uddin et al., 2005). Neurophysiological studies in monkeys and neuroimaging studies in humans have demonstrated that the amygdala and the OFC respond to novel faces or novel stimuli (Rolls, Browning, Inoue, & Hernadi, 2005; Frey & Petrides, 2003; Schwartz et al., 2003; Wilson & Rolls, 1993). In agreement with these findings, the enhanced activity of the amygdala and the mOFC in the OTHERS condition in the current study was probably due to the novelty of the unfamiliar faces compared with the participants' own face. If these areas respond to the novelty of stimuli, habituation might have been expected during the second half of the experiment due to repeated presentation. In the first-level analysis, we constructed contrast images in order to examine the brain areas that were more strongly activated in the first half of the four sessions ($1\text{st} + 2\text{nd} - 3\text{rd} - 4\text{th}$) for each condition. A one-sample t test was performed using the abovementioned contrast images in the second-level analysis. A decrease in activity was observed in the amygdala during the third and fourth sessions of the OTHERS condition; no such trend was observed in the mOFC, even at lower thresholds ($p < .05$). In addition, the mOFC was activated only during the evaluation of the faces of others, which differed from the amygdala activity. These findings suggest that the mOFC plays a different role in the evaluation of the faces of others. In recent studies, the regions of the mOFC that respond to reward stimuli were also shown to be involved in the judgment of facial attractiveness (Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007; O'Doherty et al., 2003). In the current study, a difference was expected between the evaluation of one's own face and those of others. The evaluation of one's own face involves comparing the presented face with the standard for one's own face image (Carver & Scheier, 1981). By contrast, the evaluation of the faces of others might be based on their attractiveness. Thus, the enhanced activity in the mOFC might reflect judgments of the facial attractiveness of others.

Limitations of the Study

We did not find any positive correlations between the neural activities and the induced embarrassment. This might have been due to the rarity of the event, and the small size of the effect. Another possibility is that the neural substrates might have been located in the posterior portion of the OFC, which fMRI cannot depict because of susceptibility artifacts. These occur at tissue–air and tissue–bone interfaces, and thus, are most prominent at the skull base (Fischer & Ladebeck, 1998).

Conclusion

The process of evaluating individuals' own faces appears to be implemented by a neural network containing the right mIFG, right precentral gyrus, insular cortex, occipital cortex, and ACC. Our findings highlight a functional dissociation between the right mIFG and the right precentral gyrus: The latter is mainly involved in self-face recognition, which is tightly coupled with public self-awareness; the former is selectively engaged in the self-evaluation of perceptual feedback, which is based on estimating the relevance to a standard self. This functional segregation reflects the developmental course of self-recognition followed by self-evaluation and the self-conscious emotion associated with self-evaluation, which is closely related to the development of self-awareness.

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