Functional Dissociation of the Left and Right Fusiform Gyrus in Self-Face Recognition

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Abstract: It is well known that the fusiform gyrus is engaged in face perception, such as the processes of face familiarity and identity. However, the functional role of the fusiform gyrus in face processing related to high-level social cognition remains unclear. The current study assessed the functional role of individually defined fusiform face area (FFA) in the processing of self-face physical properties and self-face identity. We used functional magnetic resonance imaging to monitor neural responses to rapidly presented face stimuli drawn from morph continua between self-face (Morph 100%) and a gender-matched friend's face (Morph 0%) in a face recognition task. Contrasting Morph 100% versus Morph 60% that differed in self-face physical properties but were both recognized as the self uncovered neural activity sensitive to self-face physical properties in the left FFA. Contrasting Morphs 50% that were recognized as the self versus a friend on different trials revealed neural modulations associated with self-face identity in the right FFA. Moreover, the right FFA activity correlated with the frequency of recognizing Morphs 50% as the self. Our results provide evidence for functional dissociations of the left and right FFAs in the representations of self-face physical properties and self-face identity. *Hum Brain Mapp 33:2255–2267, 2012.* © 2011 Wiley Periodicals, Inc.

Key words: self-face; fMRI; fusiform face area; cortical midline structure

INTRODUCTION

Orienting consciousness toward the self can be engendered by stimuli that consist of information specific to an

individual such as when viewing one's own face in a mirror [Gallup, 1998]. Behaviorally, self-face recognition in human adults is characterized by faster responses to self-face than to others' faces in a variety of tasks [Keenan et al., 2000; Ma and Han, 2009, 2010; Tong and Nakayama, 1999]. The neural mechanisms underlying self-face recognition have been studied in previous functional magnetic resonance imaging (fMRI) research by monitoring neural responses to one's own face [see Platek et al., 2008 for a review]. Passive viewing or explicit recognition of self-face versus familiar/unfamiliar faces produces increased activity in a neural circuit consisting of the fusiform gyrus, anterior and mid-cingulate, lateral and medial frontal gyri, and prececuneus [Devue et al. 2007; Kircher et al., 2000, 2001; Platek et al., 2004, 2006; Sugiura et al., 2000, 2005, 2006; Sui and Han 2007; Uddin et al., 2005a].

An unresolved issue regarding the neural substrates of self-face recognition is whether the fusiform face area (FFA), a cortical region in the fusiform gyrus that is specialized for the perception of faces [Kanwisher et al., 1997; Kanwisher and Yovel, 2006], is modulated in a specific way by the processing of self-face. Because of the

anatomical location variability of the FFA across subjects, this brain region is usually functionally identified for each individual by contrasting blood oxygenation level-dependent (BOLD) to faces versus objects in a functional localizer scan [Saxe et al., 2006]. Increasing evidence indicates that the FFA plays an important role in the processing of multiple aspects of faces [Haxby et al., 2000; Kanwisher and Yovel, 2006], such as information around the eyes [Gilad et al., 2009], face identity [Rotshtein et al., 2004], face familiarity [Gobbini and Haxby, 2006; Lehmann et al., 2004], and face gender [Freeman et al., 2010]. In addition, the FFAs in the left and right hemispheres seem to play different functional roles in face recognition. The right FFA is more activated by the configural processing of faces compared to the part-based face processing whereas this pattern of activity is reversed in the left FFA [Rossion et al., 2000]. Activity in the left FFA changes in a graded fashion as the image stimuli become increasingly face-like whereas activity in the right FFA shows a step-like response corresponding to a categorical difference between faces and non-faces [Meng et al., 2008]. Face identity specially engages the right FFA as the right, but not the left, FFA increases to a face pair that varies in identity [Rotshtein et al., 2004].

From the evolutionary point of view, the processes of self-face information are important for detection of kin that is critical for survival when living in social groups [Hamilton, 1964] and thus may be solved at the early stage of face processing. Indeed, recent neuroimaging studies suggested that the processing of self-resembling faces recruited the early brain areas in the ventral stream such as the fusiform gyrus [Platek et al., 2005, 2008; Platek and Kemp, 2009]. However, fMRI results regarding the involvement of the FFA in self-face recognition are inconsistent. Some of the previous studies observed increased activity in the fusiform gyrus to self-face than to familiar/unfamiliar faces [Kircher et al., 2000, 2001; Sugiura et al., 2000, 2005; Uddin et al. 2005a] whereas others did not [Devue et al., 2007; Platek et al., 2006; Sui and Han, 2007]. Even the studies that reported modulations of fusiform activity by self-face recognition did not functionally define the brain area in the fusiform gyrus as the FFA. Thus, it remains unclear whether specific processes in the FFA contribute to self-face recognition, and if so, what the functional significance of FFA activity is in self-face recognition. Each individual's own face is different from others' faces in specific physical properties and also induces a unique identity of the self. It is unknown whether the FFA engages in the processing of self-face specific physical properties, or self-face identity, or both, as the contrast of self-face vs. familiar/unfamiliar faces used in the previous work was unable to dissociate the two processes.

The current work aimed to address these issues by combining psychophysical and fMRI methods. We adopted a morphing method that has been used in previous studies of self-face recognition [Keenan et al., 2000, 2001; Platek

et al., 2002, 2003, 2005; Turk et al., 2002; Uddin et al., 2005a,b]. The morphing method generates morph continua from pictures of self-face and a gender matched familiar face. Because the morphed images consist of different amount of information of self-face or familiar faces, systematic variations of neural activity in specific brain regions as a function of amount of information of self-face or familiar faces provide evidence for the involvement of the brain regions in self-face or familiar face recognition. For example, Uddin et al. [2005a] found that activity in the right inferior occipital gyrus, parietal lobule, and inferior frontal gyrus increased as the stimuli contained more "self" whereas the activity in the medial frontal cortex, precuneus, and left superior frontal gyrus increased as the stimuli contained more "other." The morphing method was also used to investigate neural substrates underlying face representations in terms of physical properties and identity categories by contrasting faces that were different in physical properties or face identity [Rotshtein et al., 2004].

To examine whether the FFA is recruited in self-face recognition and to uncover the function of the FFA in the processes of self-face physical properties and self-face identity, the current work first used a localizer scan to functionally identify the FFAs for each subject by contrasting BOLD responses to faces and objects, similar to the previous work [Gilad et al., 2009; Kanwisher et al., 1997; Yovel and Kanwisher, 2005]. We then used fMRI to monitor neural responses to face stimuli drawn from a morph continuum between self-face (Morph 100%) and a gender-matched friend's face (Morph 0%, named Friend A). A personally familiar rather than an unfamiliar face was used in order to exclude confound of face familiarity. In a face recognition task, subjects had to indicate whether they saw a "self" or "Friend A" in the rapidly presented morphs. The FFA activities to the morph continua were then extracted. Differential FFA activity to Morphs 100% and 60% that were different in self-face physical properties but induced the same self-face identity (i.e., both were recognized as the self) revealed neural signals of the representation of self-face physical properties. We also contrasted the ambiguous faces (i.e., Morphs 50%), which differed physically from both self-face and the friend's face by the same distance along the morph continuum, when they were recognized as the self relative to when recognized as Friend A. Face stimuli were rapidly presented and followed by a scrambled face mask so that Morphs 50% was recognized as the self on about half trials and as Friend A on the other trials. Differential neural responses to Morphs 50% recognized as the self vs. friend revealed neural activity involved in the representation of self-face identity independent of the retinal input. If the FFA activity is sensitive to self-face specific physical properties, we would expect different BOLD signals in the FFA to Morphs 100% and 60% when both are recognized as the self. Moreover, if the FFA is involved in the processing of self-face identity, one would predict differential FFA

activity to Morphs 50% that are recognized as the self vs. friend on different trials.

To further examine whether the neural activity is self-face specific rather than reflecting neurocognitive processing of facial physical properties and identity categories in general [Rotshtein et al., 2004], another morph series was created using faces from Friend A and a second friend (named Friend B). Morphed images of the self and Friend A (AS session) and morphed images of Friends A and B (AB session) were presented in different sessions. Similar data analyses were conducted for both AS and AB sessions. Neural activity specifically involved in the processing of self-face physical properties and self-face identify should be observed in the AS session but not in the AB session. The results of the AB session also helped to control for the potential confound of the difference in task uncertainty to the results related to Morphs 100%/60% and Morphs 50%. Our fMRI results suggest dissociable neural substrates in the FFA underlying representations of self-face physical properties and self-face identity.

MATERIALS AND METHODS

Subjects

Twenty right-handed college students (12 females, aged between 19 and 24 years, mean = 22.4 years, SD = 1.3 years) participated in the psychophysical training procedure. All subjects had normal or corrected-to-normal vision and had no history of psychiatric diagnoses. Informed consent approved by a local ethics committee at the Department of Psychology, Peking University, was provided prior to the study. Eighteen of the subjects participated in the fMRI experiment. Two subjects were excluded from data analysis due to excessive head movement, leaving 16 subjects (8 females, age between 19 and 24 years, mean = 22.1 years, SD = 1.4 years) in the reported results of the fMRI experiment.

Stimuli and Task

Digital photographs of neutral faces without glasses, facial hair, or makeup were taken in a full-front view for each subject and two of his/her gender-matched roommates (named Friends A and B). The photographs were processed to remove hair, backgrounds, and everything below the chin, and were then converted into grayscale images. The grayscale images of self-face and Friend A's face, as well as of Friends B and A's faces were paired in order to generate eleven continua using a morphing software (Magic Morph 1.95b, http://www.itinysoft.com/), which produced a linear continuum of images between the two end images. To morph each face pair, we used 120–140 control points on the salient features of each face such as contour ($\sim$ 40 points), eyebrows ($\sim$ 9 points each), eyes ($\sim$ 15 points each), nose ($\sim$ 15 points), and mouth

($\sim$ 20 points). Faces of each pair were calibrated in luminance and contrast before the morphing procedure. For the psychophysical training procedure, we extracted 7 images from each continuum with 100%, 80%, 60%, 50%, 40%, 20%, and 0% of self-information in the face pair of Self/Friend A or of Friend B-information in the face pair of Friends B/A (see Fig. 1). Five images of each continuum (100%, 60%, 50%, 40%, and 0%) were used in the fMRI experiment. Masking stimuli consisted of scrambled faces that were made by segmenting each face image (300 × 336 pixels, 7.96 cm × 8.91 cm width × length) into 50 × 56 square grids that were randomly arranged afterwards. Each face image subtended a visual angle of 5.7 × 6.4° at a viewing distance of 80 cm in the psychophysical training procedure, and of 4.1 × 4.6° at a viewing distance of 110 cm in the fMRI experiment.

Throughout this study, morphed images of the self and Friend A were presented in a random order in one session (AS session) while morphed images of Friends B and A were presented in a random order in another session (AB session). Subjects were asked to perform a face identification task (self vs. Friend A in the AS session or Friend B vs. Friend A in AB the session) by pressing one of the two buttons.

Pilot Study

In order to determine stimulus parameters such as the durations of self/friend faces and masking stimuli, we ran a pilot study on an independent group of 10 subjects (6 females, aged between 19 and 27 years, mean = 24.7 years, SD = 2.5 years). The durations of face stimuli and masks were monitored so that subjects' behavioral performances met the following two criteria: (1) subjects reported about half of Morph 50% as the self in the AS session (and as Friend B in the AB session), indexed by the point of subjective equality (PSE); (2) subjects responded to Morph 100% with a high hit rate (>90%). The pilot procedure initially used a short duration of face stimuli (i.e., 50 ms) and followed by a mask (i.e., a scrambled face) of 150 ms. The duration of face stimuli was increased and the duration of mask stimuli was decreased until performances met the above two criteria; in this case, we found that face stimulus presented for a duration of 80 ms followed by a scrambled face for a duration of 120 ms resulted in desired results.

Psychophysical Training

To make subjects' performance meet the above criteria during the rapid stimuli presentation, we conducted the psychophysical training on each subject in two separate days prior to the scanning procedure. Each training procedure consisted of 6 sessions of 140 trials, resulting in 120 trials for each of the seven images extracted from each continuum. Inter-stimulus intervals (ISI) varied randomly between 1000, 1100, 1200, 1300, and 1400 ms.

The percentages of subjective reports of the self in the AS session or of Friend B in the AB session were plotted as a
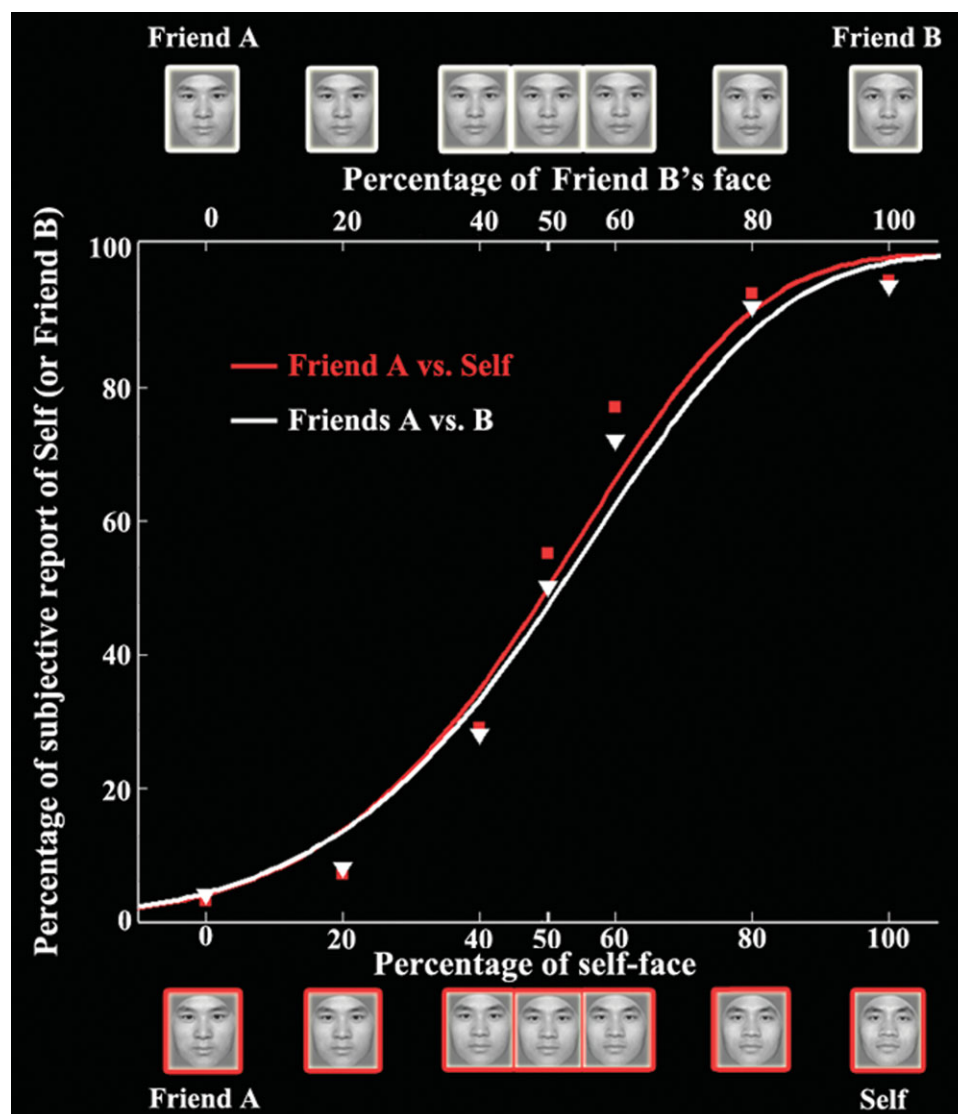
Figure 1.

Illustration of the stimuli and results during psychophysical training. The bottom pictures show a morphed continuum drawn from self-face and Friend A's face. The bottom *X*-axis denotes the percentage of self-information in the morphed faces. The top pictures show a morphed continuum drawn from faces of Friends A and B. The top *X*-axis denotes the percentage of Friend B's information in the morphed faces. The *Y*-axis denotes the mean percentage of subjective reports of the self in the AS session and of Friend B in the AB session. The performances are fit into the Weibull function. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

function of the morphed face continua for each subject. Responses were fit by a Weibull function, $p_{weil} = 1 - e^{-\left(\frac{x}{\alpha}\right)^{\beta}}$, where p_{weil} = subjective reports of the self in the AS session or of Friend B in the AB session, x = percentage of self-information or Friend B-information in the morphed faces, α = the PSE, and β = the slope of the sigmoidal response function. The points along the continuum were monotonically increasing and the Weibull function fit well with each subject's performances (r^2 ranging from 0.922 to 0.994, mean = 0.971). The average response functions across subjects shown in Figure 1 represented the Weibull functions with mean values of α (PSE) and β (slope) obtained from responses in the AS and AB sessions, respectively.

fMRI Experiment

Design and procedure

Stimuli in the fMRI experiment were presented through an LCD projector onto a rear projection screen, which was

viewed with an angled mirror positioned on the head-coil. A mixed design was used in the fMRI experiment. There were eight functional scans of 397.5 s. Each scan consisted of 5 AS sessions and 5 AB sessions. The order of AS and AB sessions was counterbalanced for each subject. Each session of 39 s began with a 3 s instruction followed by 12 trials (two trials of Morphs 0%, 40%, 60%, 100%, respectively, and four trials of Morph 50%). Four Morph 50% trials were used in each session as subjects identified half of Morphs 50% as the self in the AS session or as Friend B in the AB session. The instructions indicated which face identification task the subjects would complete (self vs. Friend A for AS sessions and Friend A vs. Friend B for AB sessions). On each trial, a face stimulus was presented for 80 ms followed by a 120 ms mask. The ISI consisted of a fixation cross with a duration of 1300, 2800, or 4300 ms. Subjects responded by pressing one of the two buttons using their right middle or index finger. The assignment of fingers to self vs. Friend A or Friends B vs. A was counterbalanced across subjects.

An independent functional localizer scan of 384 s was conducted immediately after the main experiment. A block design was used in which 15 sessions of 18 s were presented. Thirty-six stimuli from one stimulus category (unknown faces, objects or scrambled faces) were displayed in each session with a duration of 300 ms followed by an ISI of 200 ms. Different sessions were separated by a 6 s fixation cross presented on a gray background. Subjects were asked to passively view the presented stimuli. Bilateral regions that responded more to faces than to objects were identified in the FFA and occipital face areas (OFA). After the scanning procedure, subjects were asked to complete the Self-Construal Scale [Singelis, 1994] of 24-items in order to assess their independent/interdependent self-construals on a 7-point Likert scale (1 = strongly disagree, 7 = strongly agree).

Imaging procedure

A 3-T Allegra (Siemens) scanner was used to acquire BOLD gradient echoplanar images (EPIs) (64 × 64 × 30 matrix with 3.13 × 3.13 × 4.8 mm spatial resolution, repetition time (TR) = 1500 ms, echo time (TE) = 26 ms, flip angle = 75°, FOV = 24 × 24 cm) during the functional scans. A high-resolution T1-weighted structural image (256 × 256 × 128 matrix with a spatial resolution of 1 × 1 × 1.33 mm, TR = 2530 ms, TE = 3.39 ms, inversion time (TI) = 1,100 ms, flip angle = 7°) was subsequently acquired.

Imaging analysis

Preprocessing and whole-brain voxel-based analyses were conducted using Statistical Parametric Mapping software (SPM2; the Wellcome Trust Centre for Neuroimaging, London, United Kingdom). The functional images were corrected for slice time acquisition differences and realigned for head movement. Six movement parameters

(translation: x, y, z and rotation: pitch, roll, yaw) were included in the statistical model. The anatomical image was coregistered with the mean realigned image and then normalized to the standard T1 Montreal Neurological Institute (MNI) template. The normalizing parameters were applied to the functional images, which were resampled to 2 mm of isotropic voxel size and spatially smoothed using an isotropic Gaussian kernel of 8 mm full-width half-maximum. The time series in each voxel was high-pass-filtered to 1/256 Hz.

Statistical analyses used a hierarchical random-effect model with two levels. In the first level of each subject, the onsets and durations of each of the stimuli were modeled using a general linear model according to the stimulus types and subjects' responses. Events were modeled using a canonical hemodynamic response function and its time derivatives. The models also included six covariates per run to capture residual movement related artifacts. Random-effect analyses at the group level were then conducted using the individual contrast estimates that were calculated by comparing the same number of trials in two contrasting conditions. Two contrasts were performed for each subject: Morph 100% vs. Morph 60% when both were reported as the self and Morphs 50% identified as self vs. Friend A in the AS session (each contrast was conducted on the same number of trials, for both the contrast of Morph 100% vs. Morph 60%, and for the contrast of Morph 50% recognized as the self vs. Friend A). The contrasts of Morph 100% vs. Morph 60% when both reported as Friend B and Morphs 50% identified as Friend B vs. Friend A were also calculated for the AB session. Areas of significant activation were reported if they exceeded $P < 0.001$ (uncorrected) on the single voxel level and $P < 0.05$ at cluster level (corrected for family-wise error rate using Gaussian random field theory methods).

The regions-of-interest (ROIs) analysis started with the preprocessing of fMRI data in the functional localizer scan that was similar to that used in the main experiment except that the correction for slice time acquisition differences was not recruited during preprocessing because a block design was used in the localizer scan. To define the brain areas sensitive to face stimuli, a fixed effect model was applied to each subject's data by contrasting face stimuli with object stimuli in the localizer scan. This identified significant activation in the left FFA in 12 subjects and the right FFA in 13 subjects at a threshold of $P < 0.0001$ (voxel level, uncorrected). The mean coordinates were −42 (3.1), −55 (8.5), −20 (3.6) for the left FFA and 42 (3.5), −54 (5.2), −20 (3.2) for the right FFA. The contrast of face vs. object stimuli also revealed activation in the left and right OFAs with the mean coordinates being −42 (4.5), −78 (5.2), −14 (4.4) for the left OFA and 40 (4.2), −75 (5.3), −12 (4.1) for the right OFA.

The coordinates from each subject were used to extract signal changes related to morphed faces in AS and AB sessions in the main experiment. BOLD signals were extracted from the ROIs defined as clusters consisting of

voxels above the threshold. The time courses of signal change were extracted from the ROIs. The time course for each condition was then averaged across scans and subjects. The mean BOLD signal was obtained from the mean of three successive points around the peak of the time course. Neural activity in association with the processing of self-face physical properties was defined as BOLD signals that differentiated Morph 100% and Morph 60% when both were reported as the self in the AS session. Neural activity related to self-face identity independent of retinal stimulation was defined as the BOLD signals that differentiated Morphs 50% identified as self vs. Friend A in the AS session. Similar analyses were conducted on the data from the AB session in order to control for confounds such as task difficulty and response selection/execution.

RESULTS

Psychophysical Training

Behavioral performances during the training procedure were shown in Figure 1. The PSE in the AS session (49.3%) and the AB session (50.5%) did not differ significantly from 50% (AS session: $t(1,19) = -0.717$, $P = 0.482$; AB session: $t(1,19) = 0.961$, $P = 0.349$), and the PSE did not differ significantly between AS and AB sessions ($t(1,19) = -1.404$, $P = 0.177$). In addition, the mean response accuracy to Morph 100% was high and did not differ between AS and AB sessions (96.5% vs. 95.8%, $t(1,19) = 0.812$, $P = 0.190$).

fMRI Experiment

Subjects correctly identified Morph 100% on 94.1% and 95.1% of the trials in AS and AB sessions, respectively, during the scanning procedure. The mean PSE did not differ between AS and AB sessions (48.6% vs. 48.8%, $t(1, 15) = -0.198$, $P = 0.838$, see supplementary Fig. S1 for the sigmoidal response function of behavioral performances during scanning). Reaction times (RTs) were subjected to a repeated measures analysis of variance (ANOVA) with session (AS vs. AB) and Morph (Morphs 100% vs. 60% identified as the self in the AS session or as Friend B in the AB session) as independent within-subjects variables. The main effect of Morph ($F(1,15) = 83.71$, $P < 0.001$) was significant, suggesting faster responses to Morph 100% than to Morph 60%. However, this effect did not significantly differ between AS and AB sessions ($F(1,15) = 0.571$, $P = 0.461$, supplementary Fig. S2A). ANOVA of RTs with session (AS vs. AB) and identity (Morphs 50% recognized as the self vs. Friend A in the AS session or as Friend B vs. Friend A in the AB session) as independent within-subjects variables did not show any significant effect ($Ps > 0.1$, supplementary Fig. S2B). These behavioral results suggested comparable task difficulty and attention demand between AS and AB sessions.

Self-face physical properties

Brain imaging data were first analyzed to examine the neural activity sensitive to self-face physical properties by comparing BOLD signals to Morphs 100% and 60%. ROI analyses were first conducted to assess whether the FFA activity was modulated by the variation of self-face physical properties. BOLD signals to morphs in the main experiment were extracted from the FFA of each individual subject defined in the localizer scan (Fig. 2A). We found that Morph 100% elicited significantly greater activity in the left FFA compared to Morph 60% when both were recognized as the self ($t(1,11) = 2.514$, $P = 0.029$, Fig. 2B). BOLD signals extracted from the right FFA, however, did not significantly differ between Morphs 100% and 60% that were both recognized as the self ($t(1,12) = 0.768$, $P = 0.457$, Fig. 2B).

To test whether 40% differences in physical properties of any two familiar faces may cause modulations of the FFA activity, similar ROI analyses were conducted on the FFA activity to Morphs 100% and 60% when both were recognized as Friend B in the AB session. We found that BOLD signals in neither the left nor the right FFA were significantly different between Morphs 100% and 60% when both were recognized as Friend B (left: $t(1,11) = -0.304$, $P = 0.767$; right: $t(1,12) = 1.093$, $P = 0.296$, Fig. 2C), suggesting that 40% differences in physical properties of two familiar faces do not necessarily result in modulations of the FFA activity. The contrasts between BOLD responses to Morphs 100% and 60% in AS and AB sessions indicated that the left FFA was sensitive to self-face physical properties whereas the right FFA was not. To examine whether the modulation of neural activity by the processing of self-face physical properties was specific to the FFA, similar analyses of BOLD signals in the OFA were conducted. The activity in bilateral OFAs did not differ significantly between Morphs 100% and 60% that were identified as the self in the AS session (left: $t(1,12) = 0.515$, $P = 0.616$; right: $t(1,12) = 0.609$, $P = 0.554$, Fig. S3B) or as Friend B in the AB session (left: $t(1,12) = 0.402$, $P = 0.695$; right: $t(1,12) = 0.968$, $P = 0.352$).

To investigate whether other brain areas were also involved in the processing of self-face physical properties, whole-brain statistical parametric mapping analyses of the fMRI data were conducted. The contrast of Morph 100% vs. Morph 60% did not show any significant brain activations in both AS and AB sessions at the threshold of $P < 0.05$ corrected for multiple comparisons at cluster level.

Self-face identity

To uncover the neural activity sensitive to self-face identity, we compared neural activity to Morphs 50% that were recognized as the self or Friend A on different trials in the AS session. The ROI analyses showed that activity in the right FFA reduced significantly to Morph 50% recognized as the self compared to Morph 50% recognized as
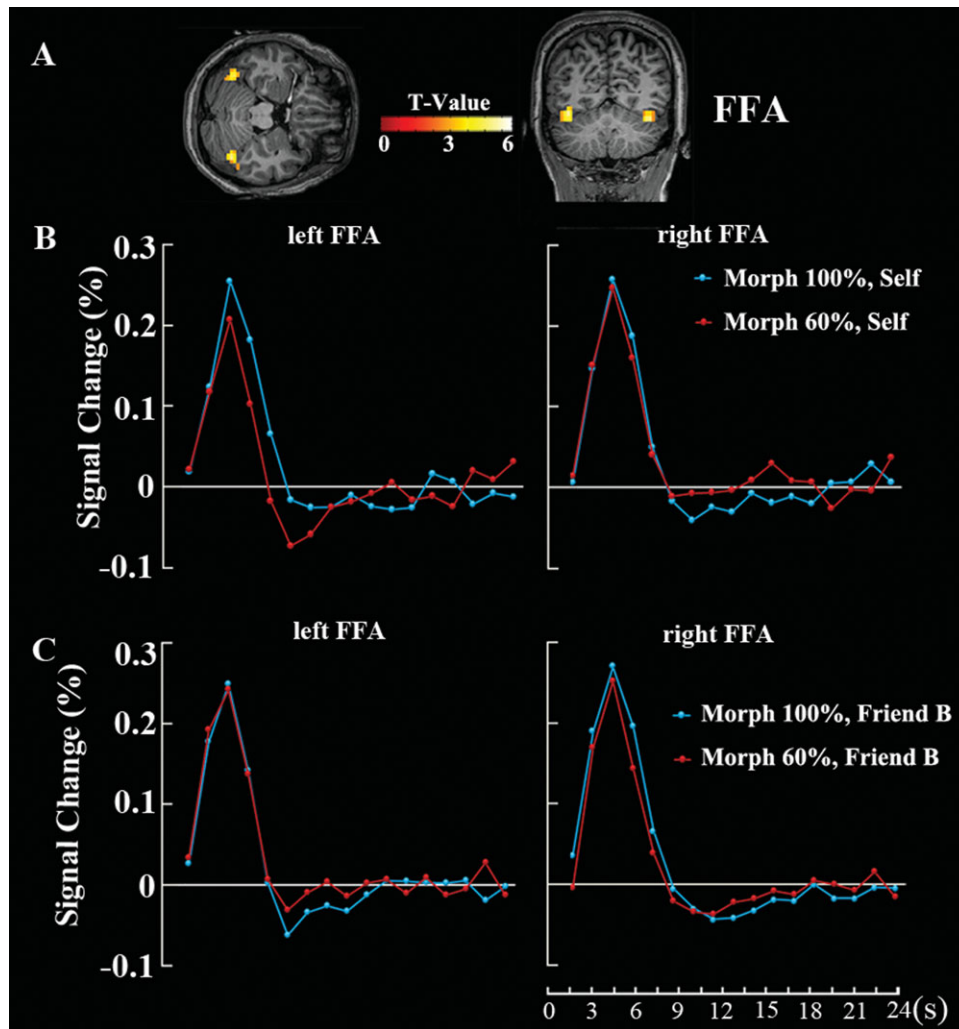
Figure 2.

Neural activity in the FFA associated with the processing of self-face physical properties. **A**: Illustration of the left and right FFA in a representative subject identified in the functional localizer scan. **B**: BOLD responses in the AS session were larger to Morph 100% than to Morph 60% when both were recognized as the self in the left FFA but not in the right FFA. **C**: BOLD responses in the FFA did not differ significantly to Morphs 100% and 60% when both were recognized as Friend B in the AB session. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Friend A ($t(1,12) = -2.302$, $P = 0.04$), whereas BOLD signals in the left FFA did not significantly differ between Morphs 50% recognized as the self or Friend A ($t(1,11) = 0.012$, $P = 0.991$, Fig. 3A), suggesting that the right FFA was modulated by self-face identity associated with the same retinal image whereas the left FFA was not.

Similarly, to examine whether an identity change of an ambiguous face morphed from any two familiar faces might lead to modulations of FFA activity, we compared the FFA activity to Morphs 50% that were recognized as Friend B vs. Friend A on different trials in the AB session. This, however, did not show any significant difference in

the left or right FFA activity between Morphs 50% that were recognized as Friend B or Friend A (left: $t(1,11) = 1.479$, $P = 0.165$; right: $t(1,12) = 0.399$, $P = 0.697$, Fig. 3B). Thus, the modulations of FFA activity in association with morphs produced by self-face and a friend's face did not reflect neurocognitive processes of familiar faces in general, but revealed neural signatures of the processes specifically related to self-face identity during face recognition. To assess whether the modulation of the processing of self-face identity was specific to the FFA, BOLD signals in the OFA were compared between Morphs 50% identified as self or friend. This, however, did not show any
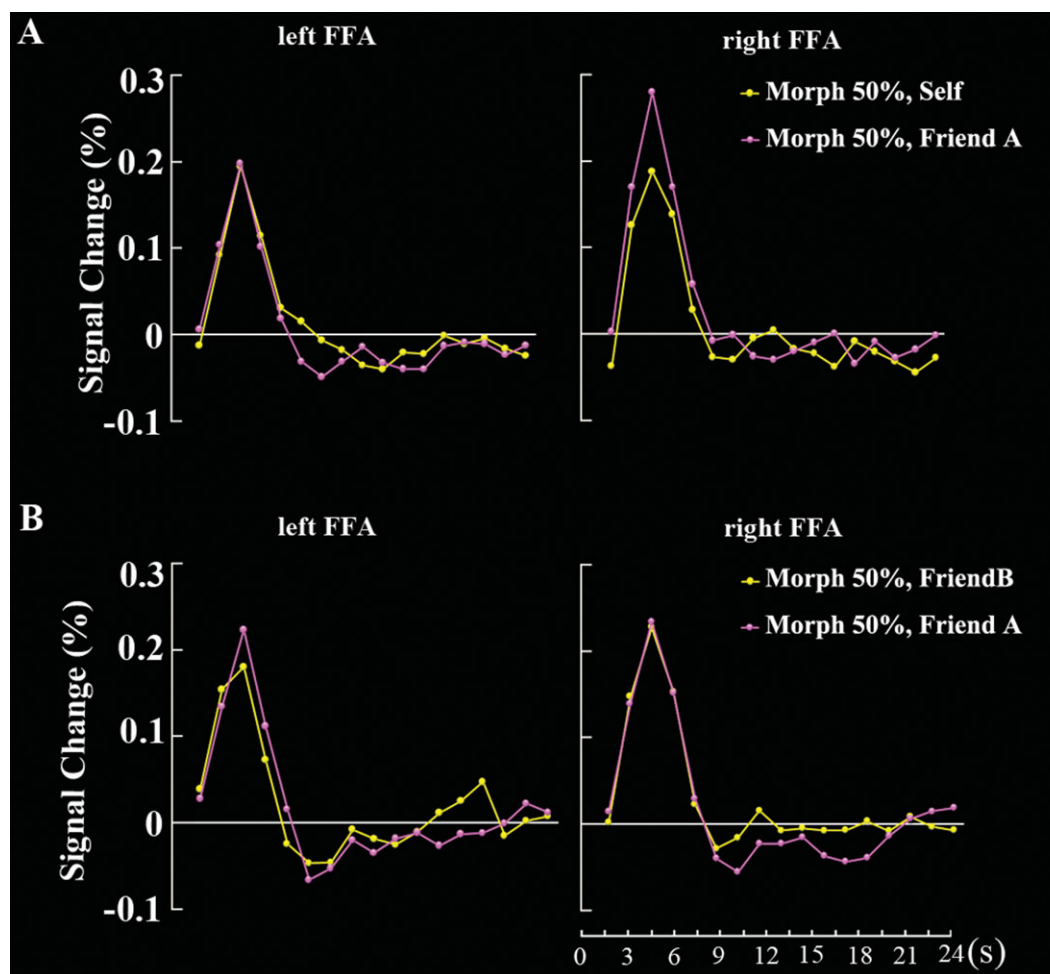
Figure 3.
Neural activity in the FFA associated with the processing of self-face identity. **A**: BOLD responses in the AS session were smaller to Morph 50% when it was recognized as the self than as Friend B in the right FFA but not in the left FFA. **B**: BOLD responses in the FFA did not differ significantly to Morph 50% when it was recognized as Friend A or Friend B in the AB session. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

significant difference between the two conditions (left OFA: $t(1,12) = -0.916$, $P = 0.378$; right OFA: $t(1,12) = 0.462$, $P = 0.652$; Fig. S3B). Similarly, neither the left ($t(1,12) = -0.551$, $P = 0.592$) nor the right OFA ($t(1,12) = -1.196$, $P = 0.255$) differentiated Morphs 50% that were identified as Friend A or B in the AB session.

Whole-brain statistical parametric mapping analyses were conducted to explore other brain activations associated with self-face identity. The contrast of Morphs 50% recognized as the self vs. Friend A in the AS session revealed activations in the medial prefrontal cortex (MPFC: $x, y, z = -2, 44, 4$, BA 32/10, $Z = 3.66$, number of voxels = 147), the posterior cingulate (PCC: $x, y, z = 2, -28, 44$, BA 31, $Z = 4.52$, number of voxels = 208), and the right precuneus ($x, y, z = 10, -68, 28$, BA 31, $Z = 3.74$, number of voxels = 157, Fig. 4). The reverse contrast did

not show any significant activation. To assess whether these brain activations were specific to self-face identity, similar contrast was conducted for fMRI data of the AB session. However, the contrast of Morphs 50% recognized as Friend B vs. Friend A failed to show any significant activation under the same threshold value. Thus the activations in the cortical midline structures shown in the contrast of Morphs 50% recognized as self vs. Friend A did not reflect the process of face identity in general but were specific to self-face identity.

To assess the link between behavioral and neural markers of self-face identity during face recognition, we conducted a correlation analysis of BOLD responses and the frequency that Morphs 50% were recognized as the self in the AS session. We found a significant negative correlation between the right FFA activity and the percentage
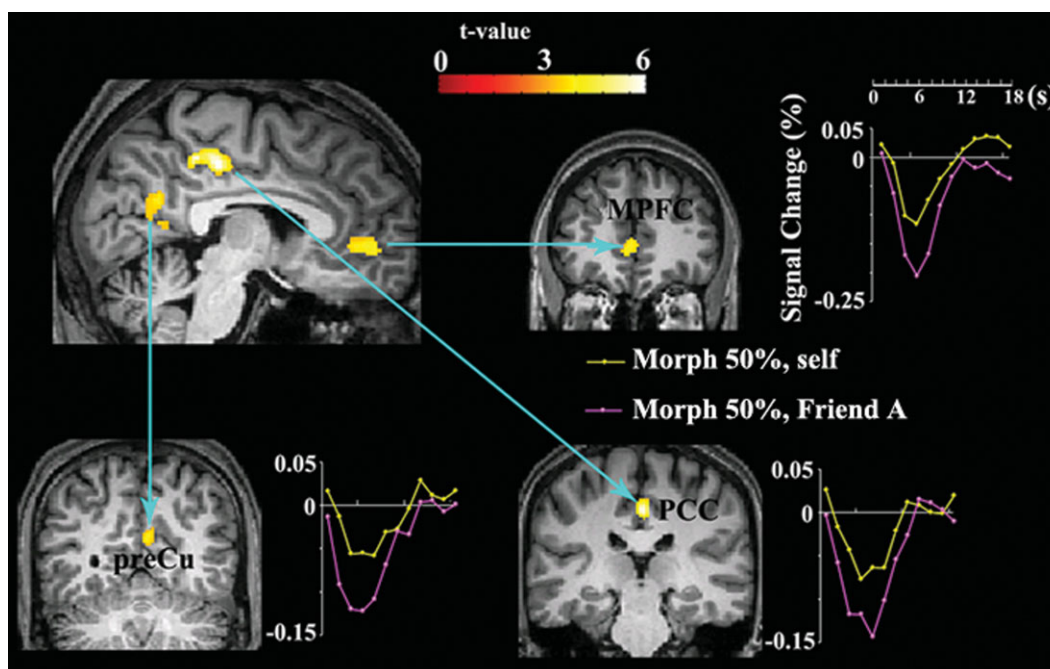
Figure 4.

Illustration of neural activity in the cortical midline structures associated with self-face identity. Identification of Morph 50% as the self resulted in increased activity in the medial prefrontal cortex (MPFC), the posterior cingulate cortex (PCC), and the right precuneus (preCu). BOLD signals illustrated in each brain area were extracted from spheres of 5-mm radii centered at the peak voxel in the activated clusters identified in the random effect analysis. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

of subjective report of Morph 50% as self ($r = -0.665$, $P = 0.013$, Fig. 5A), the weaker the right FFA response to Morphs 50%, the more frequently subjects reported Morph 50% as the self. Similarly, we also found a significant positive correlation between differential PCC activity to Morph 50% identified as self vs. Friend A and the percentage of subjective reports of Morphs 50% as self ($r = 0.586$, $P = 0.017$, Fig. 5B), suggesting that the stronger the PCC activity differentiated Morphs 50% recognized as the self vs. Friend A, the more frequently subjects reported Morphs 50% as the self. We also found a significant negative correlation between activities in the PCC and right FFA in association with Morph 50% identified as the self ($r = -0.669$, $P = 0.012$, Fig. S4). This provided further evidence for the involvement of the cortical midline structures in the processing of self-face identity. We also calculated correlations between subjective reports and the mPFC/precuneus activity, but failed to find significant results (P's > 0.5).

DISCUSSION

By functionally defining the FFAs, our results provide direct evidence for the involvement of the FFA in self-face specific processing. Moreover, the FFA activity in the left and right hemispheres was modulated by self-face physical properties and self-face identity in different fashions.

Such modulations were specific to self-face because personally familiar faces with different physical properties or different face-identity in the AB session did not induce any changes in FFA activity. In addition, our results indicate that modulations of the occipito-temporal activity by self-face recognition were specific to the FFA because neural activity in the OFA, which may engage in the processing of face-part information at an early stage in the face-processing stream [Pitcher et al., 2007] did not vary as a function of self-face physical properties or self-face identity[1].

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[1]Unlike Rotshtein et al. [2004], our work did not observe modulations of OFA activity by physical properties of faces stimuli. There were several differences between Rotshtein et al. [2004] and our work. Rotshtein et al. presented a pair of famous faces with a short interstimulus interval (75 or 500 ms) but a long duration (500 ms) on each trial. Subjects had to judge whether the two faces showed the same or different persons. BOLD repetition-related decrease was used to index OFA sensitivity to the difference in physical properties. Our work used self-face and personally familiar faces. The interstimulus interval was much longer (1300, 2800, or 4300 ms) and the stimulus duration was short (a face stimulus was presented for 80 ms followed by a 120 ms masking). It is likely that the paradigm used in our work were not sensitive enough to uncover the repetition effect that may reveal the involvement of the OFA in the processing of physical properties of personally familiar faces.
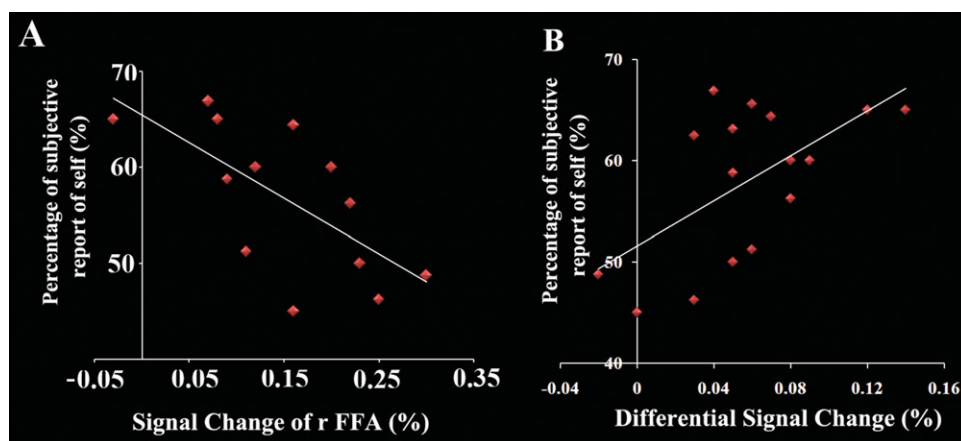
Figure 5.

Correlation between neural activity and behavioral performances. **A**: The BOLD signals in the right FFA to Morph 50% identified as the self negatively correlated with the percentage of subjective reports of Morphs 50% as the self. **B**: The differential BOLD signals in the PCC to Morph 50% identified as the self vs. Friend A negatively correlated with the percentage of subjective reports of Morphs 50% as the self. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Our findings suggest dissociation of representations of self-face physical properties and self-face identity in the left and right FFAs. Specifically, we showed that activity in the left FFA was modulated by changes in the physical properties of faces that were identified as the self (i.e., Morphs 100% and 60% in the AS session). In contrast, activity in the right FFA was modulated by faces that did not differ in physical properties but induced different facial identities of the self vs. nonself (i.e., Morphs 50% in the AS session were recognized as the self or Friend A). Furthermore, our results indicate that the modulations of FFA activity do not reflect neurocognitive processes of facial structures or face identity in general as the modulations of FFA activity were not observed with personally familiar faces in the AB session. The AB session also required similar processes of facial physical properties and face identity, involved the same task uncertainty, and differed from the AS session only in that a friend's image replaced the self image. However, fMRI data from the AB session did not show modulations of FFA activity by variation of a friend's specific retinal image or the consciously perceived identity of friends. Therefore, the modulations of FFA activity in the AS session could not simply arise from the difference in task uncertainty in responding to clear or ambiguous face-identification properties.

More interestingly, we found a different pattern of modulations of the left and right FFAs by self-face recognition. Self-face specific physical properties were associated with increased activity in the left FFA (i.e., Morph 100% vs. Morph 60%, both identified as self in the AS session), whereas self-face identity was associated with decreased activity in the right FFA (i.e., Morph 50% identified as self

vs. friend in the AS session). The increased activity in the left fusiform gyrus has been previously observed for self-face relative to familiar/unfamiliar faces [Kircher et al., 2000, 2001; Sugiura et al., 2000, 2005]. However, the functional role of the fusiform gyrus in self-processing was not yet understood [Platek et al., 2008]. Our fMRI results suggest that at least two types of self-face specific neural computations are conducted in the FFA and are dissociated in the left and right hemispheres. The increased left FFA activity in association with self-face physical properties may not simply reflect coding of physical features of familiar faces because we showed that 40% differences in physical properties between two familiar (nonself) faces did not cause the modulations of left FFA activity. Rather, the left FFA plays a pivotal role in the low level processing of self-face by encoding self-face specific physical properties. Our results provide further understanding of the functional role that the left FFA played in processing human faces. Previous studies showed that the FFA activity increases with the amount of general face-like information [Meng et al., 2008]. The FFA activity also increases to same-race than other-race faces [Golby et al., 2001] and to ingroup than outgroup members' faces [Van Bavel et al., 2008]. The modulation of the FFA activity by social categorization of individuals may arise from enhanced covert attention to physically familiar faces. Our results suggest that the FFA is also engaged in categorization of people in terms of self versus others. Heightened familiarity with the physical features of one's own face may also induce enhanced attention to self-face and result in the increased left FFA activity.

In contrast, our results indicate that the right FFA was involved in registration of self-face identity independently

of self-face specific physical features. This finding has not been reported in the previous research using the contrast of self-face vs. familiar/unfamiliar faces. In such designs, self-face identity depends largely on self-face specific physical properties, making it difficult to dissociate the two processes. Our results suggest the existence of a separate mechanism in the right FFA that contributes to conscious perception of self-face identity independently of retinal inputs during face recognition.

A related question is why activity in the right FFA decreased to Morph 50% identified as the self compared to as a friend. As it has been shown that the FFA responds to low-level features of face stimuli such as the frontal face configuration and presence of specific face parts [Kanwisher and Yovel, 2006], a possible account is that weaker encoding of low-level features is needed for Morphs 50% when recognized as a self than a friend, or in other words, stronger encoding of low-level features of Morphs 50% is required when a face is recognized as a nonself, possibly due to increased attentional load for encoding a nonself face [Reddy et al., 2007]. As the midline cortical structure showed enhanced activity to Morph 50% recognized as the self compared to as a friend, it may be further assumed that the modulation of the right FFA activity might reflect the interaction between the processes of self-face identity in the right FFA and those in the cortical midline structures. To assess this, we calculated correlations between activity in the right FFA and activity in the midline cortical structures associated with self-face identity and found a significant negative correlation between activities in the PCC and right FFA in association with Morph 50% identified as the self. The fact that the increased PCC activity to Morph 50% recognized as the self could predict the decreased right FFA activity across subjects implicates interactions between the two brain areas during the processing of self-face identity.

Increased activities in the MPFC and PCC/precuneus were correlated with Morphs 50% in the AS session that were recognized as the self compared to as a friend. These activities were obtained by contrasting the same retinal image (i.e., Morph 50%) that was recognized as the self or a friend and thus could not result from task uncertainty or conflict generated by the morphs as these were matched well in the two conditions. No differential activity in these brain areas was observed for stimuli that were different in physical properties but induced the same self-face identity (i.e., Morphs 100% and 60% in the AS session). The MPFC and PCC/precuneus activations have been also observed in the contrast of familiar vs. unfamiliar faces [Gobbini and Haxby, 2006], faces similar vs. dissimilar to the self [Platek et al., 2005], and sibling faces vs. friend faces [Platek and Kemp, 2009]. Our results complement the previous work by showing that the cortical midline structures are also recruited in categorization of faces in terms of self vs. nonself in the condition that face physical properties do not provide any information for such categorization processes. Together, these results are consistent with the hy-

pothesis that brain regions such as the posterior medial substrates are involved in face categorization when faces are familiar or express some level of visual familiarity [Platek et al., 2008]. Such mechanism can explain why the MPFC and PCC/precuneus activity was observed in the AS session but not in the AB session. Subjects categorized faces in terms of self vs. nonself in the AS session. However, as both Friends A and B belong to the category of "familiar faces," subjects might respond to Morph 50% in the AB session as two individual faces in the same category and thus the categorization process was not necessarily engaged.

Previous neuroimaging studies have found that self-face recognition recruits the lateral frontal cortex [Platek et al., 2006; Sui and Han, 2007; Uddin et al. 2005a], whereas self-reflective thought of personal traits engages the cortical midline structures [Han et al., 2008; Kelley et al., 2002; Ma and Han, 2011; Northoff and Bermpohl, 2004; Northoff et al., 2006; Zhu et al., 2007]. These are in agreement with the proposal that the lateral and medial frontoparietal networks functionally dissociate from each other, with the former underlying the processes of visible features and actions and the latter underpinning human mental states in a more abstract and evaluative fashion [Lieberman, 2007; Uddin et al., 2007]. We showed here that the cortical midline structures also engage in the processing of self-face identity during a face recognition task. However, self-face identity associated with Morph 50% in the AS session occurred independent of self-specific retinal images and thus was essentially initiated by internal mental processes mediated by the cortical midline structures. This provides further evidence for the functional role of the cortical midline structures in internal voluntary mental activity underlying self-related processing.

It should be noted that the current work only recruited Chinese subjects. Recent cultural neuroscience studies have shown increasing evidence for cultural difference in neural substrates of human cognition [Chiao, 2009; Han and Northoff, 2008; Kitayama and Uskul, 2011]. The neural activity in the brain regions involved in face processing is also influenced by cultures. Goh et al. [2010] found more right lateralization of the FFA activity in Chinese but more selectivity for faces in Westerners in the left FFA. Although the cultural difference in the hemispheric lateralizations of the FFA activity was observed with the processing of others' faces, it raises the possibility that self-face processing may also exhibit cultural difference. Specifically, it is possible that the right FFA modulation by self-face identity reflects the interdependent self-construal style in East Asian culture [Markus and Kitayama, 1991]. To assess the relation between the interdependent self-construals and the FFA activity, we calculated the correlation between the rating scores of Self-Construal Scale [Singelis, 1994] and the magnitude of the FFA activity to self-face. Neither the interdependent self-construal score (Mean $\pm$ SE $= 65.88 \pm 1.49$) nor the independent self-construal score (Mean $\pm$ SE $= 56.88 \pm 1.99$) was significantly correlated with the FFA activity ($r = 0.024$ and -0.062, $P =$

0.934 and 0.825). In any case, future research needs to clarify whether the specific pattern of FFA activity to self-face physical properties and self-face identity is common for different cultures.

In summary, our fMRI results uncovered dissociable neural signatures of representations of self-face physical properties and self-face identity during face recognition. While previous neuroimaging findings indicate that the FFA engages in conscious perception of faces in general, our fMRI findings demonstrate that the FFA contributes to the processing of one's own face. Specifically, the left FFA is sensitive to self-face physical properties and the right FFA is sensitive to self-face identity or categorization of faces in terms of self vs. nonself. This supplements our understanding of the functional role of the FFA in that the right FFA not only underpins the categorization of faces vs. non-faces [Kanwisher et al., 1997; Meng et al., 2008] but also contributes to categorization of faces in terms of self vs. nonself. Such function of the FFA may evolve to mediate the computation of self-facial resemblance that plays a key role in differentiation between kin and non-kin members of one's social group [Platek et al., 2005, 2008; Platek and Kemp, 2009]. Our fMRI results also suggested that the midline cortical structures such as the PCC/precuneus interact with the FFA to generate self-face identity in the absence of self-specific physical properties in faces. The fMRI findings shed new light on the neurocognitive processes involved in self-face recognition.

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REFERENCES

Chiao JY (2009): Cultural neuroscience: A once and future discipline. Prog Brain Res 178:287–304.

Devue C, Collette F, Balteau E, Degueldre C, Luxen A, Maquet P, Brédart S (2007): Here I am: The cortical correlates of visual self-recognition. Brain Res 1143:169–182.

Freeman JB, Rule NO, Adams RB, Ambady N (2010): The neural basis of categorical face perception: Graded representations of face gender in fusiform and orbitofrontal cortices. Cereb Cortex 20:1314–1322.

Gallup GG (1998): Self-awareness and the evolution of social intelligence. Behav Process 42:239–247.

Gilad S, Meng M, Sinha P (2009): Role of ordinal contrast relationships in face encoding. Proc Natl Acad Sci USA 106:5353–5358.

Gobbini MI, Haxby JV (2006): Neural response to the visual familiarity of faces. Brain Res Bull 71:76–82.

Goh JO, Leshikar ED, Sutton BP, Tan JC, Sim SK, Hebrank AC, Park DC (2010): Culture differences in neural processing of faces and houses in the ventral visual cortex. Soc Cogn Affect Neurosci 5:227–235.

Golby AJ, Gabrieli JDE, Chiao JY, Eberhardt JL (2001): Differential responses in the fusiform region to same-race and other-race faces. Nat Neurosci 4:845–850.

Han S, Northoff G (2008): Culture-sensitive neural substrates of human cognition: A transcultural neuroimaging approach. Nat Rev Neurosci 9:646–654.

Han S, Mao L, Gu X, Zhu Y, Ge J, Ma Y (2008): Neural consequences of religious belief on self-referential processing. Soc Neurosci 3:1–15.

Hamilton WD (1964): The genetical evolution of social behavior I, II. J Theoret Biol 7:17–52.

Haxby JV, Hoffman EA, Gobbini MI (2000): The distributed human neural system for face perception. Trends Cogn Sci 4:223–233.

Kanwisher NG, Yovel G (2006): The fusiform face area: A cortical region specialized for the perception of faces. Phil Trans R Soc B 361:2109–2128.

Kanwisher NG, McDermott J, Chun MM (1997): The fusiform face area: A module in human extrastriate cortex specialized for face perception. J Neurosci 17:4302–4311.

Keenan JP, Freund S, Hamilton RH, Ganis G, Pascual-Leone A (2000): Hand response differences in a self-face identification task. Neuropsychologia 38:1047–1053.

Keenan JP, Nelson A, O'Connor M, Pascual-Leone A (2001): Self recognition and the right hemisphere. Nature 409:305.

Kelley WM, Macrae CN, Wyland CL, Caglar S, Inati S, Heatherton TF (2002): Finding the self? An event-related fMRI study. J Cogn Nenrosci 14:785–794.

Kircher T, Senior C, Phillips ML, Benson PJ, Bullmore ET, Brummer M, Simmons A, Williams SC, Bartels M, David AJ (2000): Towards a functional neuroanatomy of self-processing: Effects of faces and words. Cogn Brain Res 10:133–144.

Kircher TTJ, Senior C, Phillips ML, Rabe-Hesketh S, Benson PJ, Bullmore ET, Brammer M, Simmons A, Bartels M, David A (2001): Recognizing one's own face. Cognition 78:B1–B15.

Kitayama S, Uskul AK (2011): Culture, mind, and the brain: Current evidence and future directions. Annu Rev Psychol 62:419–449.

Lehmann C, Mueller T, Federspiel A, Hubl D, Schroth G, Huber O, Strik W, Dierks T (2004): Dissociation between overt and unconscious face processing in fusiform face area. Neuroimage 21:75–83.

Lieberman MD (2007): Social cognitive neuroscience: A review of core processes. Ann Rev Psychol 58:259–280.

Ma Y, Han S (2009): Self-face advantage is modulated by social threat—Boss effect on self-face recognition. J Exp Soc Psychol 45:1048–1051.

Ma Y, Han S (2010): Why respond faster to the self than others? An implicit positive association theory of self advantage during implicit face recognition. J Exp Psychol: Hum Percept Perform 36:619–633.

Ma Y, Han S (2011): Neural representation of self-concept in sighted and congenitally blind adults. Brain 134:235–246.

Markus HR, Kitayama S (1991): Culture and the self: Implication for cognition, emotion and motivation. Psychol Rev 98:224–253.

Meng M, Singal G, Cherian T, Sinha P (2008): Neural correlates of categorical face perception. J Vision 8:407.

Northoff G, Bermpohl F (2004): Cortical midline structures and the self. Trends Cogn Sci 8:102–107.

Northoff G, Heinzel A, de Greck M, Bermpohl F, Dobrowolny H, Panksepp J (2006): Self-referential processing in our brain—A meta-analysis of imaging studies on the self. Neuroimage 31:440–457.

Pitcher D, Walsh V, Yovel G, Duchaine B (2007): TMS evidence for the involvement of the right occipital face area in early face processing. Curr Biol 18:1568–1573.

Platek SM, Kemp SM (2009): Is family special to the brain? An event-related fMRI study of familiar, familial, and self-face recognition. Neuropsychologia 47:849–858.

Platek SM, Burch RL, Panyavin IS, Wasserman BH, Gallup GG Jr (2002): Reactions towards children's faces: Resemblance matters more for males than females. Evol Hum Behav 23:159–166.

Platek SM, Critton SR, Burch RL, Frederick DA, Myers TE, Gallup GG Jr (2003): How much paternal resemblance is enough? Sex differences in the reaction to resemblance but not in ability to detect resemblance. Evol Hum Behav 24:81–87.

Platek SM, Keenan JP, Gallup GG Jr, Mohamed FB (2004): Where am I? The neurological correlates of self and other. Brain Res Cogn Brain Res 19:114–222.

Platek SM, Keenan JP, Mohame FB (2005): Sex differences in the neural correlates of child facial resemblance: An event-related fMRI study. NeuroImage 25:1336–1344.

Platek SM, Loughead JW, Gur RC, Busch S, Ruparel K, Phend N, Panyavin IS, Langleben DD (2006): Neural substrates for functionally discriminating self-face from personally familiar faces. Hum Brain Mapp 27:91–98.

Platek SM, Wathne K, Tierney NG, Thomson JW (2008): Neural correlates of self-face recognition: An effect-location meta-analysis. Brain Res 1232:173–184.

Reddy L, Moradi F, Koch C (2007): Top-down biases win against focal attention in the fusiform face area. Neuroimage 38:730–379.

Rossion B, Dricot L, Devolder A, Bodart J, Crommelinck M, de Gelder B, Zoontjes R (2000): Hemispheric asymmetries for whole-based and part-based face processing in the human fusiform gyrus. J Cogn Neurosci 15:793–802.

Rotshtein P, Henson RN, Treves A, Driver J, Dolan RJ (2004): Morphing Marilyn into Maggie dissociates physical and identity face representations in the brain. Nat Neurosci 8:107–113.

Saxe R, Brett M, Kanwisher N (2006): Divide and conquer: A defense of functional localizaers. NeuroImage 30:1088–1096.

Singelis TM (1994): The measurement of independent and interdependent self-construals. Pers Soc Psychol Bull 20:580–591.

Sugiura M, Kawashima R, Nakamura K, Okada K, Kato T, Nakamura A, Hatano K, Itoh K, Kojima S, Fukuda H (2000): Passive and active recognition of one's own face. NeuroImage 11:36–48.

Sugiura M, Watanabe J, Maeda Y, Matsue Y, Fukuda H, Kawashima R (2005): Cortical mechanisms of visual self-recognition. NeuroImage 24:143–149.

Sugiura M, Sassa Y, Jeong H, Miurab N, Akitsukib Y, Horied K, Satod S, Kawashima R (2006): Multiple brain networks for visual self-recognition with different sensitivity for motion and body part. NeuroImage 32:1905–1917.

Sui J, Han S (2007): Self-construal priming modulates neural substrates of self-awareness. Psychol Sci 18:861–866.

Tong F, Nakayama K (1999): Robust representations for faces: Evidence from visual search. J Exp Psychol: Hum Percep Perform 25:1016–1035.

Turk DJ, Heatherton TF, Kelley WM, Funnell MG, Gazzaniga MS, Macrae CN (2002): Mike or me? Self-recognition in a split-brain patient. Nat Neurosci 5:841–842.

Uddin LQ, Kaplan JT, Molnar-Szakacs I, Zaidel E, Iacoboni M (2005a): Self-face recognition activates a frontoparietal "mirror" network in the right hemisphere: An event-related fMRI study. NeuroImage 25:926–935.

Uddin LQ, Rayman J, Zaidel E (2005b): Split-brain reveals separate but equal self-recognition in the two cerebral hemispheres. Consci Cogn 14:633–640.

Uddin LQ, Iacoboni M, Lange C, Keenan JP (2007): The self and social cognition: The role of cortical midline structures and mirror neurons. Trends Cogn Sci 11:153–157.

Van Bavel JJ, Packer DJ, Cunningham WA (2008): The neural substrates of in-group bias: A functional magnetic resonance imaging investigation. Psychol Sci 19:1131–1139.

Yovel G, Kanwisher N (2005): The neural basis of the behavioral face-inversion effect. Curr Biol 15:2256–2262.

Zhu Y, Zhang L, Fan J, Han S (2007): Neural basis of cultural influence on self representation. Neuroimage 34:1310–1317.