Differential responses in the fusiform region to same-race and other-race faces

Alexandra J. Golby, John D. E. Gabrieli, Joan Y. Chiao and Jennifer L. Eberhardt

Departments of Radiology and Psychology, Jordan Hall-Building 420, Stanford University, Stanford, California 94305, USA
Correspondence should be addressed to J.L.E. (jle@psych.stanford.edu)

Many studies have shown that people remember faces of their own race better than faces of other races. We investigated the neural substrates of same-race memory superiority using functional MRI (fMRI). European-American (EA) and African-American (AA) males underwent fMRI while they viewed photographs of AA males, EA males and objects under intentional encoding conditions. Recognition memory was superior for same-race versus other-race faces. Individually defined areas in the fusiform region that responded preferentially to faces had greater response to same-race versus other-race faces. Across both groups, memory differences between same-race and other-race faces correlated with activation in left fusiform cortex and right parahippocampal and hippocampal areas. These results suggest that differential activation in fusiform regions contributes to same-race memory superiority.

People are better at recognizing faces of their own race than faces of other races[1–3]. The same-race advantage has been demonstrated with behavioral studies involving a wide variety of protocols, face stimuli, participants and cultural settings. Despite its robustness, this finding has defied a simple explanation. One theory, the contact hypothesis, proposes that the same-race advantage results from greater experience with faces from one's own race[1,2,4,5]. This is consistent with the finding that in the United States the race effect is stronger for European Americans, who may have limited experience with African-American faces, than for African Americans, who, by virtue of being a minority, generally have greater experience with European-American faces.

There are several lines of evidence that expertise in face processing is a skill that develops over many years of practice[6]. This specialization is thought to be a neurobiological solution to the perceptual challenge of identifying individual faces from among many similar faces that share common features (eyes, nose, mouth) and that differ on the basis of relatively subtle configural relationships among those features. Because such expertise is built upon practice in particular experiences, it is closely tied to those experiences. Support for this type of experiential specificity comes from studies demonstrating that inversion of faces disrupts recognition disproportionately compared to other stimuli[7,8]. Presumably, this reflects the lack of experience in identifying inverted faces. By extension, most people's limited experience with faces from other races may influence how they process such faces. For example, recognition of other-race faces is less affected by inversion than same-race faces[5,9]. An alternate explanation posits that superior memory for same-race faces emerges because of differential saliency of same-race and other-race faces[10]. Sorting out the relative contributions of experience and saliency has proven difficult because differences in exposure to other-race faces may be confounded by differences in perceived saliency, attitude or attention. Understanding the basis of memory differences for same-race and other-race faces has important practical implica-

tions, including assessment of the reliability of eyewitness identification[11]. In addition, how people classify and identify individuals from other races likely influences their relationships, and such classification can contribute to stereotyping.

We investigated the neural substrates underlying the differences in memory for same-race and other-race faces. Lesion and functional imaging studies have implicated an area in or near the fusiform gyrus as essential for face processing. Prosopagnosia, a specific deficit in face recognition, arises from lesions to the ventral occipital cortex that involve the fusiform gyrus[12–14]. Despite intact perception in non-visual modalities and relatively preserved visual capacities for recognition of non-face objects, prosopagnosic patients are unable to identify people, including family members. Functional neuroimaging studies using positron emission tomography (PET)[15,16] and functional magnetic resonance imaging[17,18] have further investigated the neural basis of face perception. A face-selective region in the ventral occipitotemporal cortex has been identified that responds preferentially to faces compared to objects (such as houses)[17]. This functionally defined region varies across individuals in precise location and extent, but is typically in the fusiform gyrus or adjacent sulci and has been called the fusiform face area (FFA). Moreover, studies have indicated that the FFA responds more strongly to faces than to other human anatomical parts, such as hands[17].

Other functional imaging evidence suggests that increased activation in the fusiform region is due in part to practiced visual expertise. All humans may be expert at recognizing faces due to daily social interactions with other people. With expertise developed through practice, non-face objects may selectively recruit areas in or near the fusiform gyrus. For example, bird and car experts show increased FFA activation when perceiving birds and cars, respectively[19]. FFA activation increases in response to artificial objects (greebles) after participants are trained extensively to identify and categorize these objects[20]. Together with the neuropsychological studies, these studies suggest that fusiform regions form

Fig. 1. Race effect on memory and fusiform face area (FFA) activation. (**a**) Discriminability (*d′*) scores for post-scan memory test demonstrate better memory for same-race faces by members of both groups with a larger effect in the European American (EA) participants than in the African American (AA) participants. (**b**) Average signal change within the functionally defined FFA for the nine participants who had a FFA by $p < 0.0001$ criterion demonstrates greater signal change when viewing same-race faces ($p < 0.025$). (**c**) Average signal change within the FFA for 19 participants as defined by $t = 2$ criterion shows the same effect ($p < 0.01$).


the substrates for visual processes tuned by long-term experience to identify specific members of a visually similar category.

These studies have examined the neural substrates of visual expertise in participants with unusual expertise in a given class, or with training in the recognition of artificial non-human objects. This research is theoretically important, but describes types of expertise that are rare. In the present study, we sought to identify the neural substrates of visual expertise gained from everyday exposure to faces of people from different racial groups. We used fMRI to explore whether same-race faces activate visual–perceptual areas associated with faces and expertise to a greater extent than do other-race faces. During the experiment, AA and EA participants viewed EA faces, AA faces, objects (antique radios) and fixation crosses under intentional encoding conditions. Antique radios were chosen as a category of objects that share with faces a limited set of similar features (knobs, speakers) arranged similarly across exemplars. The contrast of faces to objects was used to define a face-selective region, which was interrogated for differential response to same-race and other-race faces. Based on same-race memory superiority, we predicted that encoding other-race faces would not recruit these brain regions to the same degree as same-race faces. We then investigated whether there is a correlation between superior memory for same-race versus other-race faces and activation in response to viewing the faces.

RESULTS
Behavioral results

Behavioral results were available for 19 of the 20 participants. There was no significant difference ($t_8 = 0.23$, $p = 0.41$) between AA participants (discriminability, *d′* = 0.78) and EA participants (0.94) in memory for antique radios, a class of objects with which they have had equal and minimal experience. Average *d′* for all faces across both participant groups was 0.97 ± 0.19 (s.e.m.). Participants were better at recognizing same-race faces in comparison to other-race faces ($t_{18} = 1.84$, $p < 0.05$, one-tailed; **Fig. 1a**). The same race advantage was significant for the EA group alone (*d′* difference = 0.97, $t_8 = 2.10$, $p = 0.03$) but not for the AA group (*d′* difference = 0.31, $t_9 = 0.63$, $p > 0.05$). AA (*d′* = 1.16) and EA (1.07) participants did not differ in their memory for EA faces ($t_{17} = 0.15$, $p > 0.05$), but did differ significantly in their memory for AA faces ($t_{17} = 3.41$, $p = 0.002$). AA participants had enhanced memory for AA faces (*d′* = 1.46) relative to EA faces, whereas EA participants had decreased memory for AA faces (*d′* = 0.10) relative to EA faces. Participants varied substantially in their relative memory performance for same-race and other-race faces. The average discriminability score advantage for same-race versus other-race faces was 0.62, but varied from −3.43 to 3.29. Seven AA participants had better memory for faces of their own race, two for faces of the other race and one had equivalent memory. Seven EA participants had superior memory for faces of their own race and two for faces of the other race.
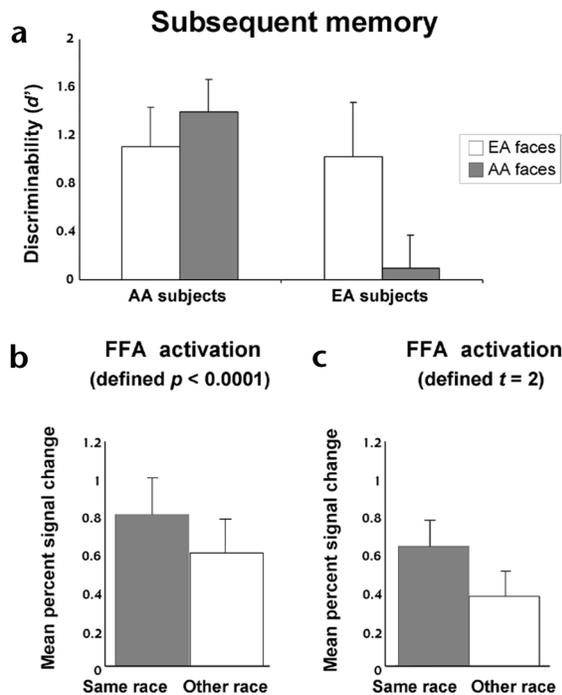
FFA response to same-race and other-race faces

The FFA was defined for individual participants as those voxels within the fusiform gyrus and/or adjacent sulci that were significantly more active when viewing faces of both races compared to objects. In order not to bias the results toward same-race faces, we used the contrast between both same-race and other-race faces versus objects to define the FFA. We used two previously established criteria for defining the FFA, one with a more stringent threshold of $p < 0.0001$ (ref. 17) and another with a less stringent threshold of $t = 2$ (ref. 19).

Five AA participants and four EA participants demonstrated an FFA by the more stringent criterion (**Fig. 2**). Using a threshold of $p < 0.0001$, the face-selective region was on the right in eight participants and on the left in one. The FFA was in the mid-fusiform in five participants, in the posterior fusiform in three, and along the lateral bank of the collateral sulcus in one. All five AA participants and three of four EA participants had greater response within the FFA when viewing same-race compared to other-race faces. There was significantly greater average signal change within the functionally defined FFA for same-race versus other-race faces ($t_8 = 2.34$, $p = 0.02$, one-tailed; **Fig. 1b**). This subset of participants had memory scores similar to the whole group (*d′* same race, 1.26; other race, 0.81).

Nine AA and all 10 EA participants demonstrated a FFA by the second criterion (**Fig. 2**). Using the $t = 2$ criterion, six participants exhibited an FFA on the right only, four on the left only and nine on both the left and right. For participants exhibiting bilateral FFAs, we analyzed the FFA that was most statistically reliable, which was on the right for all nine participants. These face-selective regions were located in the anterior fusiform in one participant, the mid-fusiform in eight participants, and the posterior fusiform in eight. In two participants, the face-responsive region was at the medial edge of the fusiform gyrus along the lateral bank of the collateral sulcus. All nine AA participants and seven of ten EA participants had greater response within the FFA when viewing same-race compared to other race faces ($t_{18} = 2.58$, $p < 0.01$, one-tailed; **Fig. 1c**).
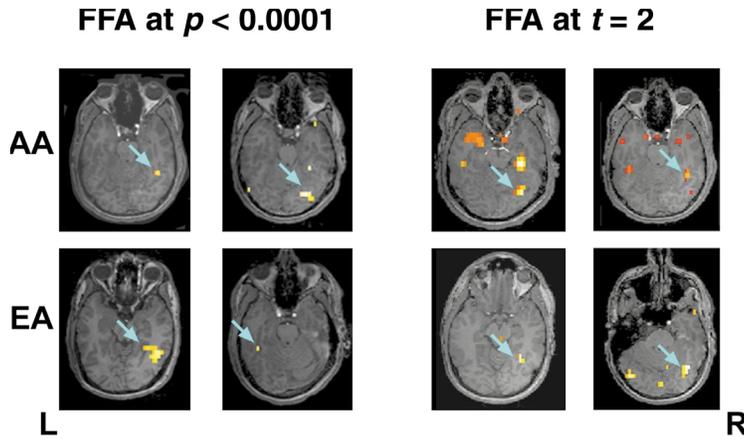
FFA at *p* < 0.0001

FFA at *t* = 2

Fig. 2. Representative activation maps from different participants demonstrating the functionally defined fusiform face area (FFA). Top, FFA regions (blue arrows) in four AA participants; bottom, FFA regions in four EA participants. Voxels more active while viewing faces of both races compared to radios that reached a statistical threshold of *p* < 0.0001 (left) or *t* = 2 (right) were defined as the face-responsive region of interest.

Activation correlations with memory differences

We investigated whether there was a correlation between the memory differences for same-race and other-race faces and brain activation differences to same-race and other-race faces. Memory score differences for same-race versus other-race faces were entered as a covariate in the same-race versus other-race contrast for the 19 participants with behavioral data. Superior memory for same-race versus other-race faces was significantly correlated with greater signal in the left fusiform gyrus for same-race versus other-race faces (**Fig. 3**). This analysis revealed a 10-voxel cluster with a maximum at –33, –39, –18 (Z = 2.51). Other areas demonstrating a significant correlation with superior memory for same-race faces were the right hippocampal and parahippocampal gyri (**Fig. 3**, **Table 1**).

DISCUSSION

In the present study, we used fMRI to study the neural basis of the same-race recognition advantage. Our behavioral results are in accord with many other studies showing superior recognition memory for same-race compared to other-race faces[1–4] and a greater effect for EA participants than for AA participants[2,21]. Compared to other-race faces, same-race faces were associated with greater activation in fusiform regions previously identified as areas of initial specialization for the perception of faces and modulated by expertise. Regardless of the method used to identify the FFA, this region was more active for same-race than for other-race faces in at least 84% of participants. Moreover, activation within the left fusiform was positively correlated with the magnitude of the same-race recognition advantage for individual participants.

These findings indicate that there may be two distinct processes mediated by different fusiform regions that promote superior memory for same-race versus other-race faces. One process is associated with individually defined FFAs that are found bilaterally, but more often in the right hemisphere[15–17,19,22]. In the present study, 15 of 19 participants had FFAs that were either exclusively or more prominently evident in the right hemisphere, and 16 of the 19 participants had greater FFA activity for same-race than for other-race faces. A second process is associated with the left fusiform cortex, where there was a positive correlation between activation differences and memory differences between same-race and other-race faces. This correlation occurred in a region that was common to all participants (it was not individually defined and varying in location like the FFA), and did not show an overall difference in response to same-race versus other-race faces. Rather, activation in this region was sensitive to the

direction and magnitude of individual participant's memory differences for faces of different races. These two distinct processes may be interpreted in terms of hemispheric asymmetry in visual processing. Left-hemisphere pathways may mediate categorical visual processes that maximize similarities among examples in a category, whereas right-hemisphere pathways may mediate coordinate visual processes that maximize individuation between examples in a category[23]. In the context of the present study, the FFA may be involved in the computation of precise metric information about faces that are essential for individuation of one face from another. The left fusiform cortex may be involved in segregating the faces into categories; in this experiment, the salient categories were AA and EA faces. Face perception may often reflect an interplay between such individuating and categorizing processes, and the present findings suggest that distinct fusiform regions mediate these two kinds of face processing.

The correlational analysis also identified right parahippocampal and hippocampal gyri as being related to superior memory for same-race faces. This result converges with data from lesion[24,25], electrophysiologic[26,27] and functional imaging[28–30] studies that have shown involvement of right medial temporal lobe structures in memory for faces. The right medial temporal lobe structures and fusiform face processing regions may work in concert to perform processes essential to the encoding of faces into long-term memory.

Differential recruitment of face-processing areas in the fusiform region by faces of different races may be due to differences in perceptual expertise derived from long-term differences in exposure to same-race and other-race faces. There is converging evidence that the fusiform region mediates experience-dependent processes of visual expertise required to individuate members of large, visually similar populations, such as faces, birds, cars or artificially constructed objects[6,19,20,31]. Electrophysiological recordings in monkeys have found that the face-responsive homologue, the inferior temporal region[32], exhibits tuning of neurons in response to experience with faces[33] and non-face objects requiring subordinate-level discrimination[34]. From a young age, people usually have much more experience with faces from their own racial group[35]. Such variation in social experience may contribute importantly to the development of visual expertise with faces. How experience with faces alters the processes used in face identification is still unknown. It has been suggested, for instance, that there may be a greater reliance on the processing of isolated features, relative to configural processing, when encoding faces of other races[5,9].

The correlation between left fusiform signal and memory differences for same-race and other-race faces in the present study indicates that activation in the fusiform region is related to subsequent memory for faces. This is consistent with other studies finding a relationship between fusiform activity and memory for faces. One study found that the fusiform region is more active during intentional encoding of faces than passive viewing of faces[36]. In addition, as in
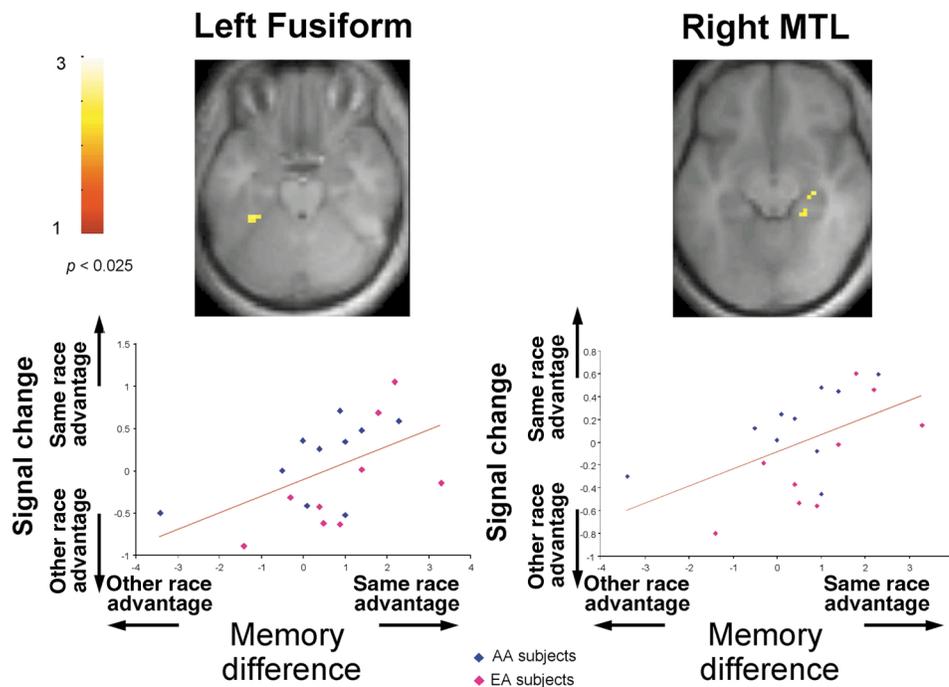
Fig. 3. Correlation between memory differences for same-race versus other-race faces with activations in response to same-race versus other-race faces. Axial slices with superimposed functional activation maps demonstrating voxels in the left fusiform (left) and right hippocampal and parahippocampal gyri (right) in which signal correlated with the relative difference in memory performance for same-race and other-race faces. Graphs demonstrate correlation between relative signal change and difference in memory score (d' same-race − d' other-race) for 19 participants.

the present study, activation in this region correlated with subsequent memory across participants. The fusiform is also preferentially engaged while viewing previously learned faces compared to novel faces[37]. Other evidence that fusiform activation and memory are associated is that experts demonstrate both enhanced fusiform activation in response to and superior memory for those stimuli with which they have expertise[19].

Much of the previous discussion has concentrated on the effect of long-term practice on fusiform face processing regions, but attention and emotion also seem to flexibly modulate these regions. For example, activation within the FFA while viewing an array of faces and objects depends on whether attention is directed to the faces or the objects[38,39]. One interpretation of the studies showing activation of the FFA by perceptual expertise is that expertise effects may in part reflect the greater interest in and attention to the expert category[40]. It is possible that in the present study, greater attention was paid to same-race faces than to other-race faces, thereby leading to greater fusiform activation and superior memory for the same-race faces.

Responses to same-race and other-race faces can also be modulated by emotional factors. In one study of EA participants, the amygdala response to unfamiliar AA faces correlated with implicit measures of racial attitudes[41]. However, no such correlation was found when participants viewed faces of famous and positively regarded African Americans, emphasizing that individual knowledge and experience can modulate the amygdala response. In another study, the amygdala response to same-race faces habituated faster than the response to other-race faces for both EA and AA participants[42]. Given that the amygdala has been implicated in learned emotional responses, evaluation of social stimuli, and responses to social and emotional signals[43], both studies suggest that there are emotional responses to same-race and other-race faces that could affect perceptual processing. The amygdala is also associated with emotional memory, and activation in the amygdala has been found to correlate with subsequent memory for emotional stimuli[44,45].

There is also behavioral evidence suggesting that visual expertise or experience alone does not account for the same-race memory superiority. One study found that those participants with the poorest recognition for AA faces were paradoxically the best at picking out an AA face within an array of EA faces[10]. The conclusion reached is that the same-race advantage stems not from perceptual expertise differences developed over a long period, but from attentional or affective processes leading to the classification of other-race faces by race-specifying information rather than by individuating information. This hypothesis predicts that altering momentary attentional strategies could eliminate inferior memory for

Table 1. Brain regions correlated with memory differences for same-race versus other-race faces.

Area	Voxels	Talairach coordinates			Z-score
		x	y	z	
R parahippocampal gyrus	15	24	−35	−6	3.26
L fusiform gyrus	10	−33	−39	−24	2.51
R hippocampal gyrus	4	27	−27	−16	2.24

Cluster size, Talairach coordinates, and Z-scores of areas of which the activation in the same-race minus other-race conditions correlated with memory score differences for same-race minus other-race faces.

other-race faces. It remains unknown to what extent the response to same-race and other-race faces is the result of differences in bottom-up perceptual processing, dependent on long-term experience, versus a top-down, flexible modulation of existing face-processing systems by affective, attentional or other systems.

The present study concentrates primarily on commonalities between the AA and EA groups in their response to same-race and other-race faces. However, it is likely that there are also differences in the neural response to same-race and other-race faces between the two groups (and other racial groups). The two groups were similar in their greater FFA responses to same-race versus other-race faces and the correlation between left fusiform activation and subsequent memory superiority for same-race faces. However, superior memory for same-race faces was stronger in EA participants than in AA participants, as has been found before[2,21]. The two groups had equivalent memory for EA faces, but differed in their memory for AA faces (enhanced in AA participants and diminished in EA participants). The best memory performance in the study was for AA participants looking at AA faces. As a racial minority in the US, African Americans may have a stronger racial identity than do European Americans[46], and this may be associated with enhanced memory for same-race faces.

Social psychology and cognitive neuroscience have evolved as separate disciplines, but in reality, social experience must be important in brain functioning. The present finding shows that functional brain imaging can provide insights into how variation in social experience may guide the organization of neural systems that process faces encountered on a daily basis. The FFA is often viewed as an area involved in relatively early perceptual processing, the first stage of face-specific perception. Regardless of whether the effect presented in the present study derives from greater perceptual expertise with same-race faces or from modulation of the FFA by other processes, our results demonstrate that social factors can influence this initial perception of faces and people.

METHODS

Participants. Ten AA and ten EA right-handed males were recruited from San Francisco Bay Area colleges and universities. Participants were between the ages of 18 and 30 with normal or corrected-to-normal vision. Each participant gave written informed consent to participate in the study. The Medical Human Subjects Committee at Stanford University approved the study.

Stimuli. Stimuli consisted of color photographs of 42 AA and 42 EA males standardized for neutral facial expression and background illumination. Photographs included the head and neck only. Other stimuli included 42 antique radios and a fixation cross. All stimuli were ~150×200 pixels in size and were shown with a gray background. All photographs were obtained with consent.

Stimulus presentation and response collection. Stimuli were presented visually using a magnet-compatible back-projector (Resonance Technology, Van Nuys, California). A Macintosh computer with PsyScope[47] software generated visual stimuli and controlled experimental parameters. A custom finger switch response system was used to collect responses and reaction times.

Task design. A blocked design was used in which participants viewed the stimuli in six epochs. Each epoch contained four counterbalanced blocks; each block consisted of six AA faces, six EA faces, six radios or six fixation crosses. Stimuli were shown for 3,500 ms with an inter-stimulus interval of 500 ms. During the scan, participants pressed a button to indicate their attention to the stimuli. They were instructed to try to remember the stimuli for a subsequent memory test.

Following the scanned encoding session, an unscanned recognition memory test was administered. Participants were presented with 12 AA

faces, 12 EA faces and 12 radios; 6 of each were previously presented and 6 of each were foils, in random order. Participants evaluated whether or not each stimulus was previously seen and responded with a left/right button press.

Data acquisition. Participants were scanned using a 3T Signa LX Horizon Echospeed MRI system (General Electric, Milwaukee, Wisconsin) with a prototype birdcage headcoil. Foam padding around the head was used to minimize movement.

Whole-brain functional imaging was done using a single-interleave gradient echo spiral pulse sequence[48], imaging 31 contiguous coronal slices (6 mm thickness) at 2 s per image volume. In-plane spatial resolution was 3.75 mm; TR, 2,000 ms; TE, 40 ms; flip angle, 68°; field of view, 24 cm; matrix acquisition, 64×64.

T1-weighted spin echo images were acquired for all slices that received functional scans. These were used to verify proper slice selection before functional imaging and to correlate functional activation with anatomical structures. A three-dimensional SPGR volumetric scan was acquired for Talairach registration and reslicing along different planes.

Behavioral analysis. Memory for faces was evaluated using discriminability (d') scores. Statistical significance was evaluated using paired and unpaired one-tailed t-tests.

Data analysis. Following image reconstruction, motion correction in three dimensions was done using the six-parameter, rigid-body, least-squares realignment routine from SPM99 (Wellcome Department of Cognitive Neurology, London, UK). Functional data were spatially smoothed with an 8 mm FWHM Gaussian kernel.

Statistical analysis was done using SPM99. Analysis was first performed individually for each participant using data that were not normalized. Differences between stimulus conditions were examined using the general linear model, modeling stimulus-related activation as a delayed boxcar function and treating low-frequency signal components as nuisance covariates. Differences in global signal intensity were corrected using proportional scaling to a common mean. The individual statistical images were then subjected to region-of-interest analyses (outlined below).

Group analysis was performed on the contrast images derived from the single-participant analyses. The contrast images obtained from the single-participant analysis were normalized into common stereotaxic space[49] on the basis of the high-resolution volume images, allowing comparison of common regions across multiple participants. The normalized contrast images were entered into a mixed-effects general linear model, treating participants as a random effect and conditions as a fixed effect and thus allowing population inference. Contrast images were overlaid onto a group mean anatomy image created in SPM99 for viewing. Coordinates of activation were converted from the Montreal Neurological Institute (MNI) coordinates used by SPM to the Talairach coordinates using the mni2tal algorithm (M. Brett, Cambridge, Massachusetts).

The correlation analysis was done by calculating a memory score difference for same-race versus other-race faces. This d' difference score was entered into the SPM analysis as a regressor during the contrast of same-race to other-race faces.

The FFA was defined individually for each participant as those areas that were more active while viewing faces (both same race and other race) compared to radios. Voxels within activated clusters ($p < 0.0001$ or $t = 2$) in the fusiform area were assembled into ROIs for each participant. Signal change within these regions was calculated based on the adjusted mean image procedure within SPM99 using custom software in Interactive Data Language (Research Systems, Boulder, Colorado).

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