Neural substrates for the recognition of newly learned faces: a functional MRI study

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Abstract

Face recognition is critical to the appreciation of our social and physical relations. Functional magnetic resonance imaging (fMRI) was used to identify brain regions involved in the recognition of newly learned faces. Two experiments were conducted. Experiment 1 contrasted a fixation control task with a face recognition task in which subjects were exposed solely to previously viewed faces (all-target). Experiment 2 compared a fixation control with another face recognition task in which subjects were presented with both novel and viewed faces (half-target). Compared to the fixation control, the all-target face recognition was associated with activation in the bilateral occipital and occipitotemporal regions, whereas the half-target face recognition produced activation in the right parietal and prefrontal regions, in addition to the occipital and occipitotemporal. The all-target minus half-target comparison revealed significant activation in the bilateral fusiform gyrus, suggesting stronger fusiform activity during the all-target than the half-target face recognition. The half-target minus all-target comparison showed significant activation in the superior and inferior parietal lobules and several regions in the right frontal lobe. These findings demonstrated that the bilateral fusiform gyrus is involved, not only in face perception, but in a certain aspect of face recognition memory and that this aspect is related to the actual recognition of previously viewed faces rather than the processing of novel ones, which results are consistent with previous lesion work. The right parietal and frontal regions, in contrast, are differentially more associated with the processes related to the detection of novel faces or retrieval effort. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Functional magnetic resonance imaging; Face recognition; Fusiform gyrus; Prefrontal cortex; Parietal cortex

1. Introduction

Despite the complexity of human facial features, we can often recognize people immediately even if we have seen their faces only once or twice. This kind of face recognition is critical to our appreciation of the social and physical environment. In addition, elderly people commonly complain of increasing difficulty in recognizing newly learned faces and significant age-related decrements in face recognition memory performance have been reported [7,10]. Research on the neural basis of face recognition will therefore not only help to elucidate the brain mechanisms underlying this important mnemonic function but also provide information regarding the deterioration of human cognitive abilities.

There have been several functional brain imaging studies examining the neural substrates for the recognition of previously viewed faces and multiple brain areas such as the right prefrontal cortex, the right or bilateral parietal cortex and the bilateral occipitotemporal cortex have been put forward as candidate cerebral regions involved in face recognition [1,14,16]. However, the specific roles of these regions in face recognition processes are still unknown. Face recognition memory involves many demands that can be separated broadly into processes related to memory search or retrieval
effort and processes related to retrieval success or actual recognition. The previous studies have provided no clear explanation as to which of these two processes the candidate brain regions are involved in.

Furthermore, there is one obstacle to the interpretation of the above findings. In the field of neuropsychology, face recognition memory has been generally evaluated by the tests in which previously studied (target) and un estudied (novel) faces are presented simultaneously or sequentially and subjects are required to distinguish between them. The above reports have also employed these kinds of tests as experimental tasks. What should be noted here is that subjects were exposed to novel faces as well as viewed ones while measuring regional cerebral blood flow (rCBF) associated with face recognition. It remains possible, therefore, that the observed activation responses represent the processes related to the detection of novel faces, in addition to, or instead of the processes related to the actual recognition of previously viewed faces. On the other hand, Clark et al. [5] used a random-stimulus fMRI method and examined differences between fMRI responses to novel faces and to memorized target faces. In their results, a large part of the bilateral fusiform gyrus responded to both novel and target faces. They interpreted this as the reflection of face perception. However, since their method did not subtract the effects of face perception from the whole process of face recognition, it is impossible to rule out the possibility that the observed fusiform activation reflected processes related to face recognition memory in addition to face perception. Thus, in functional brain imaging studies of face recognition, it is essential to control the inclusion of novel faces and to separate the effects of face perception.

To address these problems, two different experiments were performed in this study using functional magnetic resonance imaging (fMRI). In Experiment 1, an all-target face recognition task was employed, in which subjects were exposed solely to faces that had been viewed 25–30 min earlier and were not exposed to any novel faces. In Experiment 2, a conventional half-target face recognition task was employed, in which subjects were presented with both previously viewed faces and novel ones and were required to identify viewed ones. Experimental conditions of the two tasks (e.g. stimulus duration, frequency) were almost the same, except the proportion of novel and target faces presented during the fMRI scan. Our analyses included comparisons between the two kinds of face recognition tasks as well as those between each face recognition task and the fixation control. It was expected that these analyses would reveal brain regions involved in face recognition memory separated from face perception and that they would further clarify the specific roles of these regions.

2. Methods

2.1. Subjects

Subjects were 14 right-handed men, ranging in age from 20 to 32 (mean 22.9). All subjects had normal vision without corrective lenses or with contact lenses. None of the subjects reported any history of neurological or psychiatric diseases. The experimental procedures were approved by the Research Ethics Committee of the Faculty of Medicine, University of Tokyo and written informed consent was obtained from all the subjects. Two separate experiments were conducted. In Experiment 1, all 14 subjects were scanned and data from three subjects were omitted from analysis because of excessive motion. In Experiment 2, nine of the 14 subjects were scanned and all of their data were analyzed.

2.2. Task design

Stimuli for both Experiments 1 and 2 were black-and-white photographs of faces of various races balanced for gender and age, selected and scanned from American picture books. In Experiment 1, to examine brain activation involved in the actual recognition of previously viewed faces, not contaminated by the processing of novel faces, an all-target face recognition task was employed, in which subjects were exposed solely to target faces (i.e. previously studied faces) during the fMRI scan period. The experiment consisted of three separate sessions. In the pre-scan session, subjects were shown a set of 24 novel faces and asked to memorize them so that they could recognize them in the following fMRI scanning session. Later (25–30 min), subjects underwent the fMRI scanning session in which a sequential task-activation paradigm was employed, alternating between a control condition and an experimental condition for face recognition. During the control condition, subjects viewed a fixation presented in the center of the screen. During the experimental condition, the same set of 24 faces, as shown in the pre-scan session, were presented to the subjects one by one. Since the stimuli were displayed in a randomized order, the stimulus presentation order in the scanning session was different from that in the pre-scan session. Subjects were required to judge whether or not they recognized each face as previously viewed. It should be noted that no novel faces were presented to the subjects during the experimental condition of Experiment 1. In order to prevent the change of their mental state possibly caused by noticing this stimulus attributes during the scan, subjects were told in advance that all the stimuli presented during the experimental condition would be previously viewed faces. The subjects’ task during the experimental condition was thus to view the previously
studied faces again and to ascertain whether they remember them well or not. This is not in line with the typical face recognition paradigm, but according to the debriefing after the scan, subjects did not passively view the presented faces but actually recognized them engaging face recognition memory through the experimental condition. They also reported that they found some difficulty with this task since there were one or two faces that they could not recognize immediately. Each stimulus was displayed on the screen for 3.5 s, with a 0.5 s interstimulus interval. The control and experimental conditions were alternated every 32 s. Subjects performed the control task during the first, third and fifth time periods and the experimental task during the second, fourth and sixth time periods. The stimulus sequences were generated using a Macintosh computer and PsyScope software [6] and were back-projected on a translucent screen via a Panasonic liquid crystal projector TH-L592J. The post-scan session was started 20–25 min after the end of the fMRI scanning session. A yes/no decision face recognition test was performed to examine how well the subjects remembered the target faces. A new set of 24 novel faces was intermixed with the set of 24 faces presented in the pre-scan session. A total of 48 faces were presented one by one and subjects were asked to respond ‘yes’ or ‘no’ to indicate if they had viewed each face earlier in the experiment. Subjects were not told until the end of the fMRI scanning session that their memory would be tested later. The purpose of this was to decrease the likelihood that subjects might perform intentional encoding processes while they viewed the face stimuli during the fMRI scanning session.

Experiment 2 was designed to parallel Experiment 1. A major difference was that in Experiment 2, a conventional half-target face recognition task was employed, in which subjects were exposed to both novel and previously viewed faces during the fMRI scan period. Subjects memorized a set of 24 novel faces in the pre-scan session and 25–30 min later, they underwent the fMRI scanning session in which a fixation control and an experimental condition were alternated. Unlike Experiment 1, a new set of novel faces were intermixed with the previous set of faces presented in the pre-scan session and subjects were presented with these novel and previously memorized faces one by one and required to judge whether they had viewed each face in the pre-scan session. The stimuli contained 12 target faces and 12 novel faces. The frequency and duration of the stimuli were the same as those in Experiment 1. Since we confirmed a high accuracy rate in the post-scan face recognition test in Experiment 1 (mean 98.8%), this session was omitted in Experiment 2. Debriefing the subjects after the scan showed that they identified all of the target and novel faces with confidence, except one or two. None of the subjects reported major differences in difficulty and attentional state between the two kinds of face recognition tasks in Experiments 1 and 2.

In both experiments, subjects were required to respond to the presented faces only internally, which made it difficult to assure their performance. However, the processing of human faces is a highly automatic process in the sense that it occurs even when subjects try not to do that [17], more generally see Ref. [11]. For example, one cannot avoid recognizing a presented face as previously viewed, if the face is well remembered. Since our subjects studied a relatively small number of faces a short time prior to the scan, it was presumed that they would remember them well and correctly recognize most of the presented faces during the scan. The debriefing results referred to above also supported this presumption.

We used a simple stimulus manipulation for the fMRI session, in which face recognition was compared with viewing fixation, rather than a complex task manipulation (e.g. face recognition compared with face categorization). The reason for this is also related to the above notion that face processing is difficult to bring under volitional control. For example, if a face recognition task and a face categorization task, in which subjects are asked to classify faces as male or female, are performed alternatively, it is virtually impossible to avoid carry-over effects between these two conditions. We considered that a combination of simple stimulus manipulations is more appropriate for localizing automatic mental processes than a complex task manipulation.

### 2.3. Image acquisition

The following methods for image acquisitions were employed in both Experiments 1 and 2. Imaging was performed on a 1.5 Tesla GE Signa Horizon system with a standard head coil. T2*-weighted time-series images depicting BOLD contrast [20] were acquired using a gradient-echo EPI sequence (TR = 4000 ms, TE = 50 ms, flip angle = 90°, FOV 24 × 24 cm and voxel dimensions 3.75 × 3.75 × 8 mm). Five sagittal contiguous 8-mm-thick slices in each hemisphere (ten slices in total) were collected. While slice placement varied by a few millimeters from subject to subject, brain tissue located between standard stereotaxic x coordinates [24] −50 and −20 in the left hemisphere, 25 and 55 in the right hemisphere was imaged in all subjects in both Experiments 1 and 2. The first three volumes of fMRI time-series were discarded to discount T1 saturation effects. Each epoch for the face recognition or the control condition lasted for eight volumes (32 s) and the two conditions were repeated alternately three times, thus, a total of 48 volumes were acquired for each subject. For anatomic localization and coregis-
tration of images across subjects, high resolution T1-weighted images of the entire brain were obtained during the same session using a spin echo sequence for contiguous 4-mm-thick sagittal slices including the same planes as the functional scan.

2.4. Image analysis

A set of five contiguous 8-mm-thick sagittal functional images were interpolated in each hemisphere to produce a new set of contiguous 4-mm-thick images. The data were then analyzed using statistical parametric mapping (SPM) technique (using the software SPM96 from the Department of Cognitive Neurology, Wellcome, London, UK) implemented in Matlab (Mathworks Inc, Sherborn, MA). The analysis involved the following steps. To correct for head movement between scans, the functional images from each subject were realigned to the first image using rigid body transformation. A mean image was created using the realigned volumes. The high resolution T1-weighted anatomical images were coregistered to this mean (T2*) images to ensure that the functional and anatomical images were spatially aligned. The anatomical images were then normalized into a standard space [24] by matching to a standardized MNI template (Montreal Neurological Institute, Quebec, Canada), using both linear and nonlinear three-dimensional transformations [12]. The transformation parameters determined here were also applied to the functional images. Finally, these normalized images were smoothed with a 5-mm (full width at half maximum) isotropic Gaussian kernel to accommodate intersubject differences in anatomy and to permit application of Gaussian random field theory to provide corrected statistical inference [13]. A multi-subject analysis was performed on the pooled data of Experiments 1 and 2 under the assumption that the error variance is homogeneous. A total of 960 volumes, 528 volumes from 11 subjects in Experiment 1 and 432 volumes from nine subjects in Experiment 2, were analyzed. Condition-specific effects and condition × experiment interaction were estimated using the general linear model and theory of Gaussian fields [13]. A high-pass filter with a cut-off frequency of 0.47 cycles per minute was applied to model and exclude low frequency confounding effects in the time series. A fixed response, box-car model was used to characterize condition effects, using linear contrasts to test hypothesis about regionally specific condition effects. Firstly, to identify brain regions involved in each of the two face recognition tasks (i.e. all-target and half-target), the within-experiment main effects of condition were assessed. The SPMs(Z) for the all-target face recognition minus fixation control comparison (for Experiment 1) and the half-target face recognition minus fixation comparison (for Experiment 2) were individually generated and thresholded at a Z value of 4.78. This Z threshold was determined by applying to our volume data a unified statistical theory proposed by Worsley et al. [26] so that the corresponding probability threshold would be $P < 0.05$ corrected for multiple comparisons. To identify common effects of the all-target and half-target face recognition tasks relative to the fixation control, conjunction analysis was also performed. Secondly, to examine differences between brain regions involved in the two different face recognition tasks the condition × experiment interaction was assessed. Here, the contrasts between the two kinds of face recognition tasks were modeled as an interaction between condition (face recognition and fixation) and experiment (1 and 2) and SPMs(Z) for the all-target minus half-target comparison and the half-target minus all-target comparison were generated. Activation revealed by these comparisons could be confounded with inter-session variability such as habituation, since all the subjects underwent Experiment 1 before Experiment 2. However, these two experiments employed totally different sets of face stimuli and the two experiments were conducted over a month apart. We considered, resting on several preliminary experiments, that comparisons between two experiments with such differences and intervals would be valid. Previous neuroimaging studies of face recognition [1,14,16] made us presume that activation related to face recognition memory would occur in the right prefrontal cortex, the bilateral parietal cortex and/or the bilateral occipitotemporal cortex. For these regions, SPMs produced by the comparisons between the all-target and half-target face recognition were thresholded at a Z value of 2.58 (voxel-wise $P < 0.005$, uncorrected) and a cluster size of eight voxels. For all other regions in these comparisons, significance was set at $Z > 4.78$ (corrected $P < 0.05$).

3. Results

3.1. Face recognition minus fixation control

The results of the comparisons between the face recognition tasks and the fixation control task are shown in Fig. 1 and Table 1 ($P < 0.05$, corrected). The all-target face recognition minus fixation comparison (Experiment 1) revealed significant activation in the occipital and occipitotemporal regions. This activation was bilateral, but slightly larger in the right hemisphere. As shown in Fig. 1, the right occipital activation involved a large part of the occipital lobe and extended superiorly into the parieto-occipital junction, while the left occipital activation was restricted to the middle occipital region. The right occipitotemporal activation involved a larger part of the fusiform gyrus than the left. It is notable that the activation revealed by the
all-target minus fixation was confined to the occipital and occipitotemporal regions and no significant activation was observed in the frontal and parietal regions. On the other hand, the half-target face recognition minus fixation comparison (Experiment 2) revealed significant activation in brain areas other than the occipital and occipitotemporal regions. The occipital and occipitotemporal regions were also activated in Experiment 2 and, as illustrated in Fig. 1, the activation pattern of these regions was very similar to that observed in Experiment 1. A marked difference was observed, however, in the frontal and parietal regions. Unlike Experiment 1, the face recognition (half-target) minus fixation comparison in Experiment 2 revealed significant activation in the right inferior frontal gyrus and the right superior and inferior parietal lobules. It is noteworthy that these loci of activation were seen in the right hemisphere only. The activation pattern of the conjunction between the all-target and half-target face recognition relative to the fixation was quite similar to that of the all-target minus fixation comparison illustrated in the upper row of Fig. 1. This indicates that the all-target and half-target face recognition tasks commonly activated the bilateral occipital and occipitotemporal regions relative to the fixation, as is also evident in the comparison of the upper and lower row of Fig. 1.

3.2. Comparisons between all-target face recognition and half-target face recognition

The results of the comparisons between two different face recognition tasks, namely, the all-target (Experiment 1) minus half-target (Experiment 2) and the half-target minus all-target comparisons are shown in Fig. 2.

Fig. 1. The activation maps revealed by the comparisons between the face recognition tasks and the fixation control in Experiments 1 and 2. The upper shows the results of Experiment 1 (all-target face recognition minus fixation) and the lower shows the results of Experiment 2 (half-target face recognition minus fixation). The SPMs were thresholded at $P < 0.05$ (corrected for multiple comparisons) superimposed onto T1 template images and presented as axial sections from inferior to superior. The right hemisphere appears on the left. The stereotaxic x coordinate is given on the upper left of each section. Probability values (corrected) for colored voxels are coded using the color bar at the bottom. Note that the activation patterns in the occipital and occipitotemporal regions are very similar between Experiments 1 and 2, whereas significant parietal and frontal activation was seen in Experiment 2 but not in Experiment 1.
Table 1
Stereotaxic coordinates of the brain regions with significant activation during face recognition compared to fixation\(^a\)

<table>
<thead>
<tr>
<th>Brain region</th>
<th>Anatomical location (Approximate BA)</th>
<th>Experiment1 (all-target)</th>
<th>Experiment2 (half-target)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x         y         z</td>
<td>Z-score</td>
<td>x         y         z</td>
</tr>
<tr>
<td>Occipital</td>
<td>Right IOG (BA 18,19)</td>
<td>32 -86 0 8.36</td>
<td>32 -86 0 8.31</td>
</tr>
<tr>
<td></td>
<td>MOG (BA 18)</td>
<td>40 -78 -6 7.47</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SOG (BA 19)</td>
<td>30 -64 -18 7.31</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Left MOG (BA 18,19)</td>
<td>-42 -76 -8 7.62</td>
<td>-32 -82 12 5.46</td>
</tr>
<tr>
<td></td>
<td></td>
<td>30 -86 6 5.07</td>
<td></td>
</tr>
<tr>
<td>Occipitotemporal</td>
<td>Right FG (BA 18,19)</td>
<td>26 -80 -14 8.68</td>
<td>28 -82 -14 8.58</td>
</tr>
<tr>
<td></td>
<td>Left FG (BA 18,19,37)</td>
<td>-32 -76 -20 8.75</td>
<td>-36 -74 -20 8.33</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-36 -60 -20 7.01</td>
<td>-34 -58 -18 7.20</td>
</tr>
<tr>
<td>Parietal</td>
<td>Right IPL (BA 39,40)</td>
<td>34 -66 50 7.10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SPL (BA 7)</td>
<td>42 -50 46 6.21</td>
<td></td>
</tr>
<tr>
<td>Frontal</td>
<td>Right IFG (BA 44)</td>
<td>46 12 26 6.26</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Significance level was set at \(P < 0.05\) (corrected for multiple comparisons). Abbreviations: BA, probable Brodmann’s area; IOG, inferior occipital gyrus; MOG, middle occipital gyrus; SOG, superior occipital gyrus; FG, fusiform gyrus; IPL, inferior parietal lobule; SPL, superior parietal lobule; IFG, inferior frontal gyrus.

and Table 2 (voxel-wise \(P < 0.005\), uncorrected). Though most of the activation foci revealed in these two comparisons were not so sufficient to pass the correction for multiple comparisons, their results formed a sharp contrast to each other. The all-target minus half target comparison revealed bilateral activation centered in the fusiform gyrus. As shown in the upper images in Fig. 2, this activation was slightly greater in the left hemisphere than the right. It should be noted that the activation revealed by this comparison was confined to the fusiform gyrus. On the other hand, the half-target minus all-target comparison revealed activation in multiple brain areas in the right hemisphere including the superior and inferior parietal lobules, the middle frontal gyrus, the inferior occipital gyrus and the precentral gyrus. The most significant one was located in the inferior parietal lobule (42, -50, 46), which is shown in the lower images in Fig. 2. This activation focus was in the same position as observed in the half-target minus fixation comparison (Table 1). It should also be noted that half-target minus all-target comparison revealed many activation foci in the right frontal region.

3.3. Behavioral results

The results of the yes/no decision face recognition test performed in the post-scan session in Experiment 1 demonstrated that subjects were able to recognize the previously viewed faces with a high accuracy rate ranging from 91.7 to 100% (mean 98.8%). Together with the fact that subjects studied relatively few items a short time before the scan, this high performance indicates, although indirectly, that they also successfully recognized most of the presented faces during the scan.

4. Discussion

In this study two different kinds of fMRI experiments were conducted. In Experiment 1, the all-target face recognition task in which subjects were exposed solely to previously studied (target) faces was contrasted with the fixation control. In Experiment 2, the conventional half-target face recognition task, in which subjects were exposed to both target and unstudied (novel) faces, was contrasted with the fixation control. Our analyses included comparisons between the two kinds of face recognition tasks as well as those between each face recognition task and fixation control. The most striking result was the sharp contrast between comparisons of the all-target and half-target face recognition tasks, as illustrated in Fig. 2 and Table 2. The all-target minus half-target comparison revealed activation focused on the bilateral fusiform gyrus, whereas the half-target minus all-target comparison showed
right parietal and frontal activation. The comparisons with fixation control also produce different activation patterns between these two kinds of face recognition tasks. As shown in Fig. 1 and Table 1, all-target face recognition activates the occipital and occipitotemporal regions alone, while half-target face recognition activates the parietal and frontal regions in addition to the occipital and occipitotemporal. In the following sections, specific roles of these regions are discussed in relation to previous research.

4.1. Fusiform activation

In the literature of functional brain imaging studies, the fusiform gyrus has been consistently reported to be a candidate brain region responsible for the process of face perception [15,18,21]. However, there has not been universal agreement as to whether this region also plays a crucial role in facial memory, such as the recognition of previously viewed faces. Andreason et al. [1] contrasted the recognition of well-learned faces with the categorization of unknown faces and observed activation fairly focused on the bilateral fusiform gyrus. In contrast, Haxby’s group observed major activation in the right prefrontal and bilateral parietal regions during face recognition as compared to face perception and the inferior occipital region posterior to the fusiform gyrus showed relatively weak activation [14,16]. Due to the differences in task and subtraction designs between their experiments, it is difficult to explain why they observed different results. Furthermore, there is another obstacle to the interpretation of those results. They employed conventional face recognition tasks, in which previously studied faces and novel ones are pre-

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**Fig. 2.** Three orthogonal views of the activation foci superimposed onto T1 template images, revealed by the comparisons between two different kinds of face recognition tasks in Experiment 1 and 2. The upper shows all-target (Experiment 1) minus half-target (Experiment 2) and the lower shows half-target minus all-target. Significance level of $P < 0.005$ (uncorrected for multiple comparisons) was applied for a priori set regions of interest. The right prefrontal, bilateral parietal and bilateral occipitotemporal regions and $P < 0.05$ (corrected) for other regions. Probability values (uncorrected) for colored voxels are coded using the color bar at the bottom. The right hemisphere appears on the left for axial and coronal images. The activation focus shown on the upper images ($-32, -74, 18$) is located in the left fusiform gyrus. Note that there is another activation locus in the right fusiform gyrus. The activation focus on the lower images ($42, -50, 46$) is located in the right inferior parietal lobule.
Table 2
Stereotaxic coordinates of the brain regions with significant activation revealed by comparisons between all-target and half-target face recognition tasks*  

<table>
<thead>
<tr>
<th>Brain region</th>
<th>Anatomical location (approximate BA)</th>
<th>All-target minus half-target</th>
<th>Half-target minus all-target</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>x   y         z      Z-score</td>
<td>x    y         z      Z-score</td>
<td></td>
</tr>
<tr>
<td>Occipitotemporal</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Right FG (BA 19)</td>
<td>24  -80  -14   2.91</td>
<td>32  -62   6     3.56</td>
<td></td>
</tr>
<tr>
<td>Left FG (BA 19)</td>
<td>-32 -74  -18   4.18</td>
<td>-42 -74  -14   3.60</td>
<td></td>
</tr>
<tr>
<td>Left LG (BA18)</td>
<td></td>
<td>24  -58   6     2.72</td>
<td></td>
</tr>
<tr>
<td>Parietal IPL (BA 40)</td>
<td></td>
<td>42  -50  46    5.04</td>
<td></td>
</tr>
<tr>
<td>Parietal SPL (BA 7)</td>
<td></td>
<td>30  -48  36    2.66</td>
<td></td>
</tr>
<tr>
<td>Frontal MFG (BA 9,10,46)</td>
<td></td>
<td>34  40   14    3.36</td>
<td></td>
</tr>
<tr>
<td>Frontal MFG (BA 6,8)</td>
<td></td>
<td>28  32   42    3.10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>36  38   28    3.04</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>32  6    54    3.57</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>34  6    46    2.83</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* We set the above regions a priori as regions of interest based on previous neuroimaging studies of face recognition memory. Uncorrected significance level of $P < 0.005$ was applied for these defined regions, and $P < 0.05$ (corrected) for other regions. Abbreviations: BA, probable Brodmann’s area; FG, fusiform gyrus; LG, lingual gyrus; IPL, inferior parietal lobule; SPL, superior parietal lobule; MFG, middle frontal gyrus.

sented simultaneously or sequentially and subjects are required to distinguish between them or to identify either of them. In these kinds of face recognition tasks, subjects are exposed to novel faces as well as target ones while their brain activity is being examined. It remains unclear, therefore, whether the observed activation responses represent the processes associated with the actual recognition of previously viewed faces, or they reflect the processes associated with the detection of novel faces. To address this problem, Clark et al. [5] used a random-stimulus fMRI method and examined differences between MRI responses to novel faces and to memorized target faces. In their results, a large part of the bilateral fusiform gyrus responded to both novel and target faces. However, since their method did not subtract the effects of face perception from the whole process of face recognition, it remains uncertain whether or not the observed fusiform activation reflected processes related to face recognition memory in addition to face perception.

Here in this study, to overcome those problems associated with the inclusion of novel items and the involvement of face perception, we employed a method in which two different face recognition tasks varying in the proportion of novel and target faces (i.e. all-target and half-target) were separately conducted and the brain activities involved in each of them were contrasted. With this method, we were able to demonstrate bilateral fusiform activation during the all-target face recognition task as compared to the half-target face recognition task. We also observed that when compared to the fixation control, both the all-target and half-target face recognition tasks produced large activation in the bilateral occipitotemporal region including the fusiform gyrus. These findings support the notion that the bilateral fusiform gyrus is involved not only in face perception but also in a certain aspect of face recognition memory and that this aspect is related to the actual recognition of previously viewed faces, not to the processing of novel faces.

Lesion studies have also provided evidence for the involvement of the fusiform gyrus in face recognition memory. There have been many studies describing patients with damage to the right or bilateral occipitotemporal region including the fusiform gyrus who show selective impairment in facial memory [8,9,22,23]. The memory deficit typically described in those studies is called prosopagnosia, defined as an inability to visually recognize faces that were well-known before the cerebral damage (e.g. their family, famous people) which is generally accompanied by an impairment in recognizing faces that are frequently encountered after the brain injury (e.g. members of the clinical staff) [3]. The latter type of impairments is not discussed here, since it is possibly associated with defective encoding of newly encountered faces as well as a failure in later recognition. The recognition of well-known faces, on the other hand, can be discussed in the context of our study. Strictly speaking, this kind of face recognition is also different from the face recognition examined in this study: the former is, unlike the latter, closely associated with access to semantic information of the person seen.
4.2. Right parietal and frontal activation

In recent years, parietal and prefrontal activation have been repeatedly found in functional brain imaging studies of episodic memory (for review see Ref. [4]). With regard to face recognition, studies from Haxby’s group have suggested that the bilateral parietal and right prefrontal regions are involved in the recognition of previously viewed faces [14,16]. As discussed in the previous section, however, Andreasen et al. [1] did not observe activation in those regions associated with the recognition of well-learned faces and lesion studies have supported the involvement of the fusiform gyrus rather than the parietal and frontal regions in the production of face recognition memory deficits [8,9,22,23]. Moreover, due to the problem of the inclusion of novel faces, it has been unclear whether or not these regions are associated with the actual recognition of viewed faces. In our results, the parietal region and some discrete regions in the frontal lobe on the right hemisphere showed activation in the half-target minus all-target comparison, but not in the opposite comparison. These results demonstrate that the right parietal and frontal regions participate not in the actual recognition of previously viewed faces but in other aspects of face recognition. One simple interpretation is that these regions are involved in the processing of novel faces such as novelty detection, since the half-target face recognition task included both novel target faces, while the all-target task included target faces alone. Another possibility is that the right parietal and frontal regions are associated with retrieval effort. Since subjects were presented with target faces alone during the all-target task, it is possible that the task did not require so much retrieval effort as the half-target task. In a PET study of verbal recognition memory, the right prefrontal and parietal regions showed activation related to retrieval attempt rather than to actual recognition of previously encountered items [19]. These regions may be involved in retrieval effort regardless of the type of information to be retrieved.

In contrast, the random-stimulus fMRI study referred to above [5], has reported different results. They have observed bilateral parietal and frontal activation evoked by target faces, not by novel ones, suggesting that these regions are more associated with the actual recognition of previously viewed faces than with the detection of novel faces or retrieval effort. Another PET study of auditory recognition memory also suggests that the right prefrontal and bilateral parietal regions are associated with the actual recognition of previously encountered items [25]. The discrepancy between these studies and ours is difficult to explain, since those studies including ours considerably vary both in the proportion of novel and target items and in the subjects’ performance in recognition tests. Further studies that control these factors will be needed to elucidate the functional roles of the parietal and prefrontal regions in recognition memory.

5. Conclusions

This study has demonstrated that the activation in the bilateral fusiform gyrus is associated not only with face perception but also with face recognition memory. It has also been revealed that this region subserves the processes related to the actual recognition of previously viewed faces rather than the processing of novel ones. These findings are consistent with previous studies of facial memory deficits. The activation in the right parietal and frontal regions, in contrast, is considered to reflect the processes associated with the detection of novel faces or retrieval effort.

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References


