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Facial recognition reactivates the primary visual cortex: a functional magnetic resonance imaging study in humans

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Abstract

In order to investigate how the brain represents sensory-specific information during memory retrieval, we examined functional magnetic resonance imaging's during a face-recognition task. When compared with activation associated with viewing of novel faces, recognition of faces presented 5 min before scanning activated the primary visual cortex, consistent with the hypothesis that retrieved facial information is coded by the reactivation of the brain regions engaged during sensory perception. This reactivation was not observed 14 weeks following initial presentation of the faces despite no significant difference in recognition rate between the two intervals. This suggests that accessing of visual information during memory retrieval is associated with the primary visual cortex, and that its activation is time-dependent – probably related to the memory transformation or consolidation.

Keywords: Face recognition; Iconic memory; Pictorial code; Sensory-specific information; Primary visual cortex; Functional magnetic resonance imaging

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Human beings are able to remember past experiences, such as the appearance of a recently encountered face, with vivid sensory-specific representations. On the basis of human studies involving intraoperative recording [12], or single-unit studies in non-human primates [4,11], it has been hypothesized that rich sensory experiences associated with the process of retrieval are coded by the reactivation of the brain regions engaged during sensory-induced perceptions. Functional magnetic resonance imaging (fMRI) evidence appears to support this hypothesis. Recently, Wheeler et al. [15] found that recall of visual items memorized 1 day before scanning activated the visual association cortex. However, in the process of memory consolidation, multiple and geographically separate cortical regions that store the representation of a whole event, are considered to bind together gradually [1]. As such, the neural substrates of reactivation by retrieval may vary according to the phase of consolidation.

In this study, we hypothesized that at an earlier phase of the consolidation process (i.e. 5 min after encoding), the primary visual cortex may be reactivated during retrieval. As a control, we performed the same retrieval task 14 weeks later. This approach was taken on the basis of evidence that memory consolidation is complete by 14 weeks [16], and that performance on face recognition tasks is still high (60–100%, average 75%) after 3 months [14], thereby enabling the comparison of reactivation patterns at both ends of the consolidation process.

Eleven right-handed subjects (five males and six females with a mean age of 22.6 years) participated in the study. None of the subjects had any sign or history of neuropsychological disorder and MR images of their brains were normal. All subjects were informed as to the nature of the experiment and gave written consent. This study was approved by the ethical committee of Kyoto University

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School of Medicine. Stimuli were color pictures of human faces (18–70 years old, unknown to the subjects) presented using an Apple Macintosh computer. A video projector (XV-550 with a long lens; Sharp, Osaka, Japan) was used to project stimuli into the magnet bore space on a translucent screen. This setup allowed viewing of the stimuli with a visual angle of approximately 8° in both the horizontal and the vertical directions.

The procedure was as follows; firstly, 24 pictures of faces were consecutively presented to the subjects for 4 s each. Subjects were instructed to memorize the faces for the following recognition session. The time from the mid-encoding period to the mid-retrieval period was approximately 5 min. The recognition session consisted of two blocks; task and control. In the task block, both novel and memorized faces were pseudo-randomly presented with equal probability. A picture of a face was presented for 4 s followed by a fixation cross presented for 2 s. At this time subjects were required to respond with the right index finger if they thought the face they viewed had previously been memorized, or with the left index finger if the face was novel. In the control condition, a right or left arrow was presented for 4 s and subjects were instructed to respond with either index finger according to the direction of the arrow when the fixation cross appeared. Both the task and control blocks lasted 24 s and were repeated alternately six times each. Twelve faces were presented for each condition of novel or memorized face recognition. After the session, 12 face images, memorized but not displayed during the 5-min session, were presented again for 30 s per face in order to reinforce memorization. Fourteen weeks later, the same recognition task was performed using these 12 pictures together with images of 12 novel faces.

All images were acquired with a 1.5 Tesla MR scanner (Horizon; General Electronics, Milwaukee, WI). For functional images, a T2*-weighted, gradient echo, single-shot, echo planar imaging (EPI) sequence was used. Each volume consisted of 13 transaxial slices, and the slice thickness was 7 mm, with a 1-mm gap to cover the whole cerebral cortex. The interval between two successive acquisitions of the same image volume was 3 s. Echo time was 40 ms, and the field of view was 24 cm. The in-plane resolution was 64×64 pixels with a pixel dimension of 3.75×3.75 mm. Head motion was minimized by placing foam padding around the subject's head. The anatomical images were acquired with a T1-weighted, three-dimensional, inversion recovery, gradient echo sequence. The flip angle was 15°, echo time 2 ms, repetition time 30 ms, inversion time 300 ms, and field of view 24 cm. A total of 124 transaxial images were obtained. Matrix size was 256×256, slice thickness 1.5 mm, and pixel size 0.94×0.94 mm. The first four volumes of EPI images were discarded because of unsteady magnetization and the remaining 96 volumes used for the analysis. The data were analyzed by the use of SPM99 [8] on Matlab (Mathworks, Sherborn, MA). The anatomical and EPI images from each subject were realigned to the first EPI image and all EPI images were then spatially normalized [7] into the Montreal Neurological Institute stereotaxic space [5]. Spatial smoothing was performed with a Gaussian kernel of 10 mm full width at half maximum. The mean signal intensity of brain voxels in each image volume was scaled to 100 and signal changes slower than the period of 96 s were modeled and excluded to eliminate artifactual signal fluctuations. Hemodynamic responses for conditions of novel and memorized face recognition were modeled respectively in an event-related fashion, and regressed with the signal time-course for each and every brain voxels; yielding an average image of the signal changes for each condition per subject [9]. These averaged images were incorporated into the second level random effect model to evaluate the population inference. Differences were evaluated for memorized (M) minus novel (N) face conditions after 5 min (M5–N5) and 14 weeks (M14–N14) in order to find the neural substrates of the retrieval. The reverse contrasts were also tested. The resulting set of voxel values constituted a statistical parametric map of the t statistic, SPM$\{t\}$. The statistical threshold was set at $P < 0.005$ at the voxel level and $P < 0.05$ at the cluster level after correction for multiple comparisons. The abovementioned comparisons were performed within the areas of significant positive signal increase compared with the control condition.

The success rate of memorized face recognition (hit rate of the memorized faces) was 86.4 ± 10.7% (mean ± SD) after 5 min and 78.8 ± 16.4% after 14 weeks. The correct rejection rate of novel faces was 86.4 ± 5.62% after 5 min and 81.8 ± 12.3% after 14 weeks. There was no significant difference in either recognition or rejection rates between the two delay periods ($P = 0.26$ and $P = 0.38$, paired t-test, respectively), and no difference was detected between either recognition rates or rejection rates at the 5-min and 14-week delay periods ($P = 1$ and $P = 0.56$, paired t-test, respectively).

When the memorized face conditions were contrasted with novel face conditions, significant activation was observed in bilateral primary visual areas extending to the right lingular gyrus after 5 min (M5–N5, Fig. 1), but no significant reactivation was present after 14 weeks (Fig. 2). There was no significant activation when the novel face condition was compared with the memorized face condition after 5 min.

This study was designed so that visual input was identical between the two sessions (at 5 min and 14 weeks). We found no difference in activation of the primary visual cortex when the subjects viewed novel faces in the separate sessions. Furthermore, as the memorized and novel faces were presented within the same block in randomized fashion, the level of attention paid to the faces is considered to have been the same [13]. Moreover, the effect of priming (i.e. repeated exposure to a visual stimulus) does not affect the Blood Oxygen Level Dependent (BOLD) signal change of the primary visual cortex [3]. Hence, the present findings

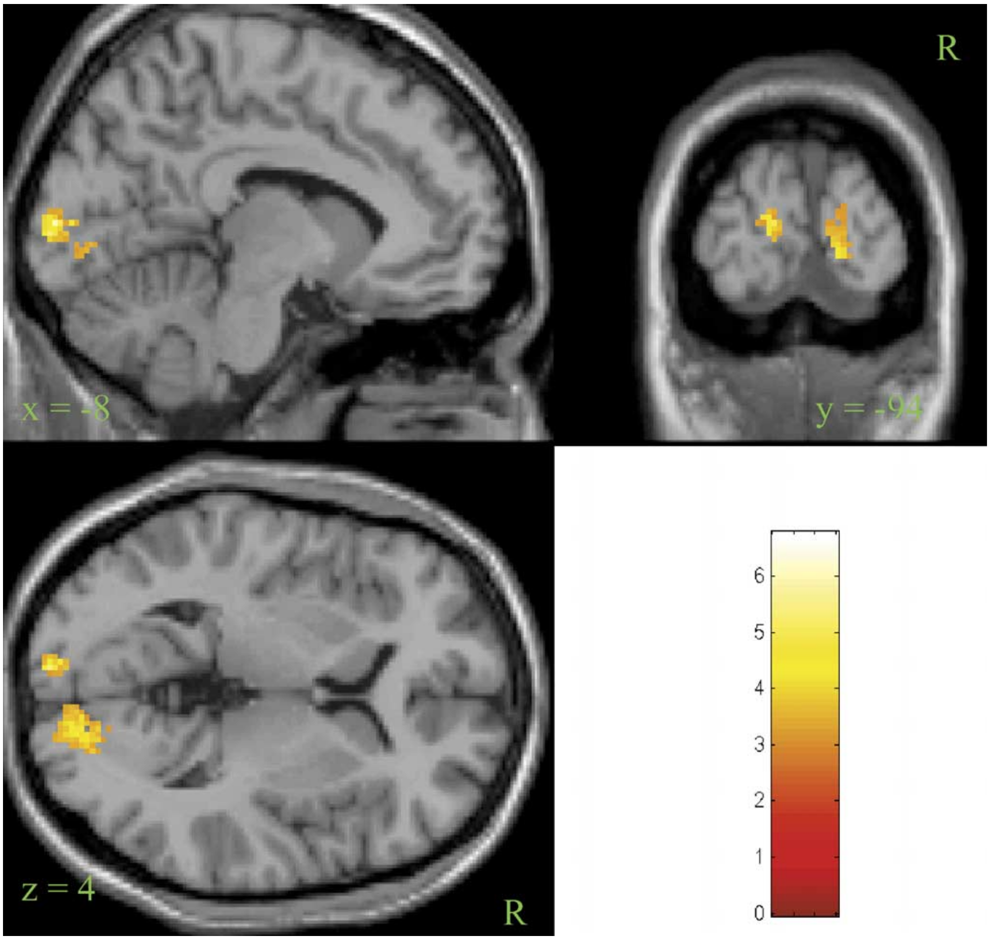

Fig. 1. A more prominent activation in the primary visual cortex was noted during face retrieval at 5 min post-encoding compared with viewing of novel faces. The focus of activation on a pseudocolor functional activation superimposed on a high-resolution anatomical MRI in the sagittal (upper left), coronal (upper right), and transaxial (lower left) planes, crossed at (−8, −94, 4) in MNI coordinates. Activity level is as indicated by the color bar; statistical significance of activation increasing from red to white. The statistical threshold was $P < 0.05$, corrected for multiple comparisons at the cluster level.

indicate that the primary visual cortex is most likely to be reactivated by retrieval of faces memorized 5 min before.

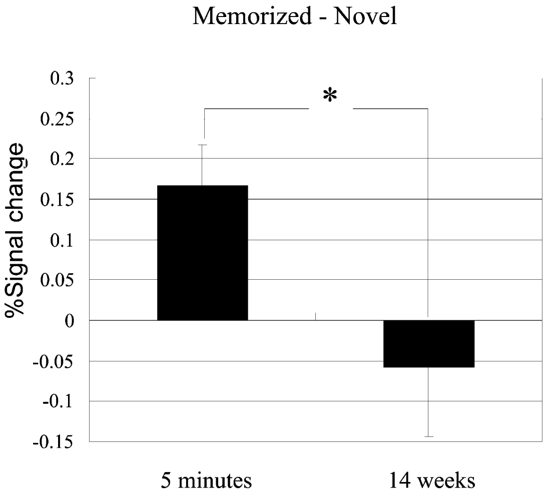

Fig. 2. Percent signal increase at the left primary visual cortex, (−6, −96, 4) in MNI coordinates during face retrieval compared with the perception of novel faces 5 min after (left) and 14 weeks after the encoding (right). $^*P < 0.005$, paired t test. The error bars indicate standard error of mean.

These results are concordant with those of the study of Wheeler et al. [15] showing that modality specific reactivation occurs during retrieval, and add further support to the reactivation hypothesis. Furthermore, it was found that with a shorter interval between encoding and retrieval (5 min in the present study compared with 1 day in Wheeler et al.), 'low-level' visual cortical areas (i.e. those engaged early in the visual processing sequence) were reactivated. This may be related to the perceptual characteristics of the encoded visual information.

As we used photographs of unfamiliar faces as stimuli, we consider that the information was encoded as pictorial code [2]. Pictorial code is a description of the static picture, i.e. specific and static face images containing details such as the lightning, grain, and flaws in a photograph, as well as the pose and expression it portrays. Pictorial code is a general code formed by any visual pattern or picture.

Area V1 is a topographically organized 'low-level' region that receives high-resolution information during bottom-up perception [6]. Visual imagery tasks that require one to visualize patterns that depict information such as length, width, orientation, and the amount of space between bars, have been shown to activate V1 in a functionally relevant way [10]. In this context, the present findings suggest that the stored pictorial code can evoke visual patterns in relatively low-level visual areas in a top-down fashion that promotes visual imagery and retrieval of pictorial code.

Retrieval of the faces that were encoded 14 weeks before did not show significant activation across the whole brain, whereas retrieval performance was fairly well maintained. This may be due to the fact that the encoding was repeated twice to reinforce memorization. Despite this, there was no significant activation in the primary visual cortex at 14 weeks. One possible explanation for this is the transformation of pictorial code into structural code [2]. The structural code contains the arrangement or configuration of facial features, important for everyday recognition of familiar faces, that seldom leads to the formation of an identical image on successive occasions [2]. The structural code, more abstract than the pictorial code, should be regarded as part of long-term memory that is supposedly stored in a distributed fashion within different cortical networks [1]. Although the exact mechanism is not presently known, it is conceivable that from pictorial codes, more abstract visual representation is established as structural codes, possibly during the consolidation period. Five min after initial perception, encoded sensory information might be held in the relatively restricted areas of the primary visual cortex. Fourteen weeks later, consolidation or the distributed storage of the abstract structural code is completed, and therefore reactivation may be too faint to be detected.

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