

Neural response to the visual familiarity of faces

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Abstract

Recognizing personally familiar faces is the result of a spatially distributed process that involves visual perceptual areas and areas that play a role in other cognitive and social functions, such as the anterior paracingulate cortex, the precuneus and the amygdala [M.I. Gobbini, E. Leibenluft, N. Santiago, J.V. Haxby, Social and emotional attachment in the neural representation of faces, *Neuroimage* 22 (2004) 1628–1635; M.I. Gobbini, J.V. Haxby, Neural systems for recognition of familiar faces, *Neuropsychologia*, in press; E. Leibenluft, M.I. Gobbini, T. Harrison, J.V. Haxby, Mothers' neural activation in response to pictures of their, and other, children, *Biol. Psychiatry* 56 (2004) 225–232]. In order to isolate the role of visual familiarity in face recognition, we used fMRI to measure the response to faces characterized by experimentally induced visual familiarity that carried no biographical information or emotional content. The fMRI results showed a stronger response in the precuneus to the visually familiar faces consistent with studies that implicate this region in the retrieval of information from long-term memory and imagery. Moreover, this finding supports the hypothesis of a key role for the precuneus in the acquisition of familiarity with faces [H. Kosaka, M. Omori, T. Iidaka, T. Murata, T. Shimoyama, T. Okada, N. Sadato, Y. Yonekura, Y. Wada, Neural substrates participating in acquisition of facial familiarity: an fMRI study, *Neuroimage* 20 (2003) 1734–1742]. By contrast, the visually familiar faces evoked a weaker response in the fusiform gyrus, which may reflect the development of a sparser encoding or a reduced attentional load when processing stimuli that are familiar. The visually familiar faces also evoked a weaker response in the amygdala, supporting the proposed role of this structure in mediating the guarded attitude when meeting someone new.

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1. Introduction

In two previous fMRI studies on familiar face recognition [12,23] we have suggested that recognizing someone we know is the result of a spatially distributed process that involves not only visual cortical areas but also areas that are involved in other social and cognitive functions such as the theory of mind areas (anterior paracingulate and posterior superior temporal sulcus) [10,11], the precuneus, the amygdala and the insula. We have hypothesized that different areas encode different types of information that support the successful recognition of a familiar individual [13]. While the precuneus and anterior temporal cortex [14,24,26,32] might be involved in retrieval of informa-

tion from long-term memory, the theory of mind areas might encode information about personality traits and mental states of a familiar individual [12,23]. The emotional response that we experience when seeing a familiar face plays an important role in successful recognition of that individual [1,12,23] and is reflected by changes in activity in the amygdala and the insula.

In our functional model on face perception [17], we grouped face responsive regions in two systems: the core system that includes areas involved with the visual analysis of a face and the extended system that includes areas that are involved in the extraction of other non-visual information.

We were interested in isolating the effect of simple visual familiarity in face recognition. With this purpose, neural activity was recorded with fMRI while participants viewed faces that were visually familiar, due to experimentally induced learning, with no associated semantic information.

Based on our previous findings, we hypothesized that visual familiarity would modulate activity in the “core system”, namely

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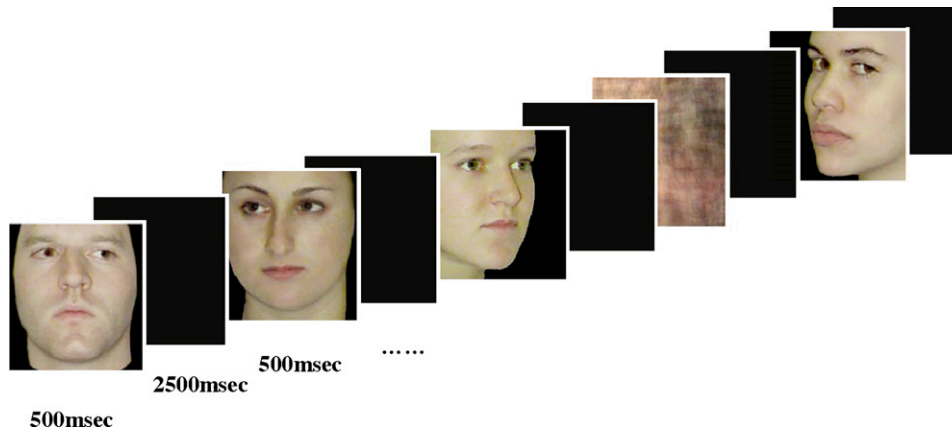


Fig. 1. Example of the stimuli (faces and nonsense pictures) used for the experiment. Three faces to be learned with a behavioral training, three novel faces (repeated the same number of times as the faces to be learned), seldom-repeated faces and nonsense pictures were presented for 500 ms with a 2500 ms interval between the stimuli, in a pseudo-randomized order during the fMRI sessions.

the fusiform gyrus. We also predicted modulation of activity in parts of the extended system, such as in the precuneus, an area involved with the retrieval of episodic memories [3] and in the amygdala, a structure involved in detecting and processing unexpected or unfamiliar events with potential biological importance [5,7,12,22,23,31].

We did not expect any modulation of activity in areas involved with the retrieval of personal traits such as the anterior paracingulate cortex [12,23,25] or in areas associated with retrieval of biographical information such as the anterior temporal regions [14,24,26,30].

2. Methods

2.1. Subjects

Seven healthy right-handed volunteers with no history of neurological or psychiatric disease (four males and three females) participated in the experiment (mean age 30.7, range: 26–34). Subjects had normal or corrected-to-normal vision. All participants gave written informed consent.

2.2. Stimuli

Stimuli were faces and nonsense pictures (Fig. 1). Nonsense pictures were phase-scrambled images of the faces used in the study and matched the faces in terms of spatial frequencies and luminance.

Faces of 81 different, unfamiliar individuals were used. All the faces had the hair cropped. For nine of these individuals, pictures of 14 different views were used and three of these faces were selected randomly for each subject for familiarization (“learned” faces) during a session of behavioral training performed on

day 2 of the experiment. Three of the remaining highly repeated faces were used as control faces during the fMRI study on day 1, and the other three were used as control faces during the fMRI study on day 3 of the experiment. The learned faces and the highly repeated novel faces were presented the same number of times during each fMRI session. For the other 72 individuals, pictures of 3 different views were used. Thirty-six of these seldom-repeated faces were used as distracters on day 1, and the remaining 36 were used as distracters on day 3. The order in which faces were used was counterbalanced across subjects. Each picture portrayed the face either in three quarter profile, one-quarter profile or full view, with either a smiling or neutral expression.

For the behavioral training on day 2, stimuli were the three faces selected for familiarization and pictures of isolated features: the eyes, the mouth, the nose and the outline of the face with the other features removed (Fig. 2).

2.3. Task

The study consisted of three sessions on separate days: fMRI on day 1, behavioral training on day 2 and fMRI on day 3. The fMRI experiments on day 1 and day 3 had an identical design. The fMRI session on day 1 was performed to test whether the response to the faces to be subsequently learned was equivalent to the highly repeated and the seldom-repeated faces. The faces that were selected to be learned on day 2 were presented on both days 1 and 3, whereas all other stimuli were novel. The participants performed a one-back repetition detection task during the fMRI sessions. The fMRI study used an event-related design. Each stimulus was presented for 500 ms with an interstimulus interval of 2500 ms.

Faces and scrambled pictures were presented in a pseudo-randomized order with the frequency of stimulus repetition increased to 25%. Each learned face and each highly repeated control face were shown 96 times in each fMRI session. Each of the seldom-repeated faces and each scrambled picture were shown 5–6 times in each session. There were 192 presentations of seldom-repeated novel faces and 192 presentations of scrambled pictures.

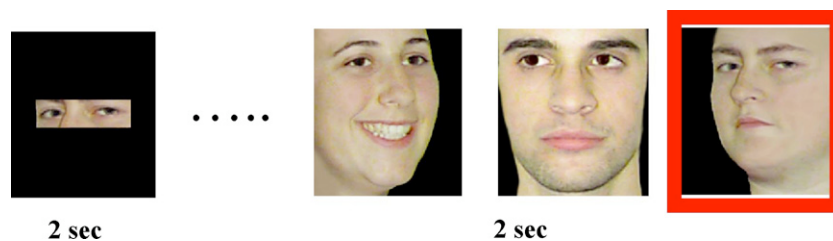


Fig. 2. Example of a trial from the behavioral training (delayed match to sample task). An isolated feature from one of the three faces to be learned was presented for 2000 ms, and then the three full faces were presented for 2000 ms. After the participants made their choice, feedback was provided by a red square highlighting the correct response.

A behavioral training task was administered to the subjects on day 2 of the study to induce learning of the visual appearance of the learned faces in detail. The behavioral training consisted of a delayed match-to-sample task in which the subject first saw a single isolated feature of one of the learned faces (eyes, nose, mouth, face outline) followed by presentation of all three learned faces. The task of the behavioral training was to indicate which of the three faces had that feature. The feature and the three learned faces were shown for 2 s (Fig. 2). After the subject's response, feedback was provided in the form of a red square that surrounded the correct answer. During the behavioral training, the participants performed 90 trials for each isolated feature.

Accuracy and reaction time were collected during the fMRI sessions on days 1 and 3 and for the behavioral training on day 2 of the experiment.

2.4. Imaging

High resolution T1-weighted spoiled gradient recall (SPGR) anatomical images (1241.2 mm thick sagittal images, field of view (FOV) = 24 cm, 256 × 256 matrix) were obtained for each subject.

Responses to different faces and scrambled pictures were measured using blood oxygen level dependent (BOLD) contrast fMRI with the acquisition of T2*-weighted gradient echo planar images in a 3T GE scanner (General Electric, Milwaukee, WI). In each time series, the whole brain volume was acquired 116 times, each volume consisting of 40 contiguous 3.5 mm thick sagittal slices (TR = 2.5 s, TE = 30 ms, flip angle 90, FOV = 24 cm).

Twelve time series were obtained in each fMRI session. Each time series began with 10 s of rest before the presentation of the stimuli. For each time series, two blocks of 40 stimuli were presented; the blocks were separated and followed by an interval of 15 s.

2.5. Statistics

Image data were analyzed with multiple regression [16]. Regressors of interest were used to model the hemodynamic response for each learned face, for each highly repeated novel face, for the seldom-repeated faces and for the scrambled pictures. The β -weight for each of these regressors was used as an index of the magnitude of response to the corresponding stimulus relative to rest.

An omnibus test of the combined significance of all regressors for responses to faces was calculated to identify voxels that were face-responsive.

A group analysis was performed to test the significance of the contrast, learned faces versus highly repeated novel faces. To perform the group analysis, the maps of response magnitudes for the comparison, visually familiar faces as compared to the highly repeated novel faces, for each subject were converted to Talairach space [34]. Conversion to Talairach space and *t*-tests were calculated using the Analysis of Functional Neuroimages software package (AFNI; <http://afni.nimh.nih.gov/afni/>). *t*-Tests are random effects tests in which each subject accounts for a single degree of freedom. Significant clusters were defined as contiguous voxels with $p < 0.01$ (uncorrected for multiple comparisons) and a minimum volume of 80 μ l. The maximum Z-score for each cluster is reported in Table 1. In the amygdala, smaller clusters of voxels were defined as significant because of the small volume of this structure and previous hypotheses about its role in face perception.

We wanted to evaluate how the response to the different categories changed over time during the fMRI sessions. With this aim, we drew anatomical regions of interest in the fusiform gyri and in the posterior cingulate/precuneus. Face responsive voxels were selected in these regions of interest and used as functional masks. The amount of habituation of the response to the highly repeated learned and novel faces was evaluated with the β -weights obtained with separate regres-

Table 1
Areas of significant activity ($p < 0.01$) for the contrast visually familiar faces (learned faces) versus highly repeated novel faces (Z score is reported for the maximum in each cluster)

Location	BA	R/L	x	y	z	Z score
Anterior cingulate	32	L	-3	-29	27	-4.064
Precentral gyrus	6	L	-50	-3	29	-4.266
		R	36	4	25	-3.979
Middle frontal gyrus	46	R	43	32	21	-3.5133
		R	46	18	24	-3.804
Inferior frontal gyrus	45	R	47	35	4	-3.6044
	47	L	-24	31	3	-4.0074
Supplementary motor area Insula	8	L	-4	18	45	-4.019
		R	31	27	4	-3.4821
		R	37	-6	8	-3.7486
Fusiform gyrus	37	L	-36	-49	-18	-4.048
	37	R	42	-46	-23	-3.791
	18	L	-31	-74	-6	-3.928
Lingual gyrus	18	L	-17	86	-5	-4.0053
	18	R	23	-87	-6	-4.2672
Middle occipital gyrus	18	R	29	-78	7	-3.457
	19	L	-32	-84	7	-3.5819
Superior temporal sulcus Intra-parietal sulcus	39	R	44	-66	16	-3.754
	7	R	25	-63	44	-3.8316
	40	L	-34	-48	46	-3.22
Precuneus	7	L	-1	-44	35	3.2717
Amygdala		R	16	-9	-14	-3.07
Corpus striatum		R	21	-11	5	-3.136
Corpus striatum		L	-26	-20	1	-3.418
Cerebellum		L	-22	-70	-30	-3.575
		L	-25	-59	-31	-4.0399
		L	-3	-56	-20	-3.3665
		L	-25	-65	-43	-3.7511
		L	-25	-65	-43	-3.7511

sors modeling the hemodynamic response to the first three presentations of the learned faces, to the first three presentation of the highly repeated novel faces, to all presentations of the same-seldom-repeated faces and to all presentations of the scrambled pictures.

For the learned faces and the novel highly repeated faces, additional regressors modeled the response to the presentations 4–6, 7–16, 17–36, 37–56, 57–76 and 77–96.

2.6. Anatomically defined volumes of interest (VOIs)

VOIs in each hemisphere were drawn on the high resolution anatomical images, defined by anatomical features and Talairach coordinates. The fusiform gyrus VOIs were defined laterally by the occipito-temporal sulcus and medially by the collateral sulcus, and bounded anteriorly by the plane 2 cm posterior to the anterior commissure and posteriorly by the plane 7 cm posterior to the anterior commissure. The posterior cingulate/precuneus was drawn in the coronal view of the high resolution anatomical dataset: the anterior border was identified by the ascending branch of the cingulate sulcus while the posterior boundary was identified by the parietal-occipital fissure.

3. Results

3.1. Behavioral results

Behavioral data from day 1 of the experiment did not show any difference in reaction time for the learned faces and the highly repeated novel faces (respectively, 457.5 ms, S.D. 195.4 versus 454.7 ms S.D. 189.7, $p = 0.8$).

The behavioral data from the training session on day 2 of the experiment demonstrated an improvement in performance through a faster reaction time (RT at the beginning of the training session = 1438.0 ms, S.D. 205.3 versus RT at the end of the training session = 285.4 ms, S.D. 60.5, $p < 0.0001$).

The behavioral data collected during fMRI on day 3 of the experiment showed an advantage in matching the learned faces compared to the highly repeated novel faces (292.02 ms, S.D. 113.5 versus 345.5 ms, S.D. 129.3, $p < 0.0001$).

3.2. Neuroimaging results

An omnibus test of the significance of all regressors for the response to faces revealed a distributed set of areas that was highly similar for days 1 and 3 (Fig. 3). Activated areas included the perceptual areas of the core system (fusiform gyrus, superior temporal sulcus and inferior occipital gyrus) as well as areas in the extended system, including the precuneus, amygdala, inferior frontal gyrus and intra-parietal sulcus [17,21].

The group analysis performed on the data collected from the fMRI session during the third day of the experiment showed a stronger response to the “learned” faces in the left precuneus (maximum $Z = 3.27$, $p < 0.001$, see Table 1) and weaker responses in the left fusiform gyrus (maximum $Z = -4.048$, $p < 0.001$), the right superior temporal sulcus (maximum $Z = -3.75$, $p < 0.001$), the right middle frontal gyrus (maximum $Z = -3.8$, $p < 0.001$), the right intra-parietal sulcus (maximum $Z = -3.83$, $p < 0.001$), the left anterior cingulate (maximum $Z = -4.064$, $p < 0.001$), the left supplementary motor area (maximum $Z = -4.019$, $p < 0.001$) and the right insula (maximum $Z = -3.75$, $p < 0.001$). A weaker response to the visually

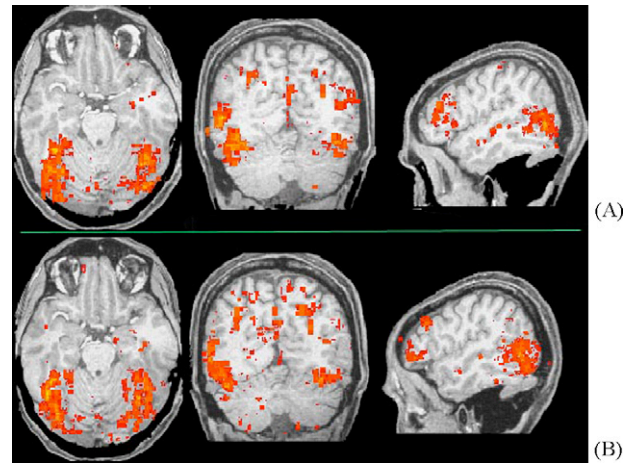


Fig. 3. (A) Statistical map of the group result for the omnibus test of the combined regressors for faces on day 1 of the experiment (thresholded at $p < 10^{-11}$). The neural activity in response to faces revealed a distributed set of areas encompassing both the perceptual areas (core system) and areas that are part of the extended system. (B) Statistical map of the group result for the omnibus test of the combined regressors for faces on day 3 of the experiment (thresholded at $p < 10^{-11}$). The pattern of the hemodynamic response to faces was very similar to the one recorded during day 1 of the experiment. The right side of the brain is on the left side of each image (radiological convention).

familiar faces also was detected in the right amygdala (maximum $Z = -3.07$, $p < 0.01$) (Fig. 4). (See Table 1 for all cortical and subcortical loci that showed a response difference.)

The group analysis also was performed on the data collected during the first fMRI session (day 1 of the experiment, see Section 2), and we found no differences between the response to be learned and highly repeated control faces.

Repetition of stimuli during the first fMRI session (day 1 of the experiment) did not show any significant difference in the adaptation of the hemodynamic response among the different categories. During the second fMRI session (day 3 of the experiment) repetition of stimuli induced adaptation with different time courses based on category (learned faces, highly repeated and seldom-repeated control faces, and scrambled images) in the fusiform gyrus and in the precuneus (Figs. 5 and 6).

In the fusiform gyrus the overall response to the novel faces was significantly stronger as compared to the visually familiar faces (learned faces), and with repeated presentations the responses to stimuli from both categories decreased over time

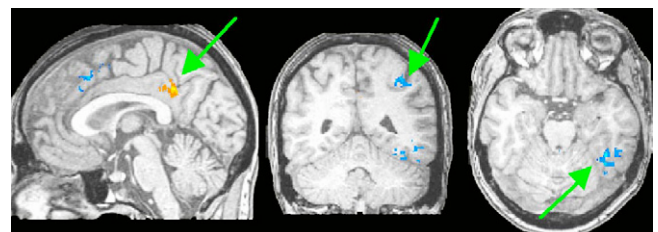


Fig. 4. Areas of activation for the contrast visually familiar faces (learned faces) as compared to novel faces: the learned faces evoked a stronger response in the precuneus ($p < 0.001$) and a weaker response in the fusiform gyrus and in the intra-parietal sulcus ($p < 0.001$). The right side of the brain is on the left side of each image (radiological convention).

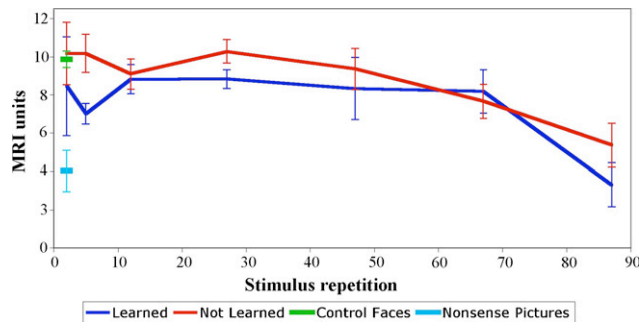


Fig. 5. Curve of adaptation to repetition of stimuli in the fusiform gyrus from day 3 of the experiment. Repetitions of stimuli over time induced a decrease in the hemodynamic response for both categories ($p < 0.02$).

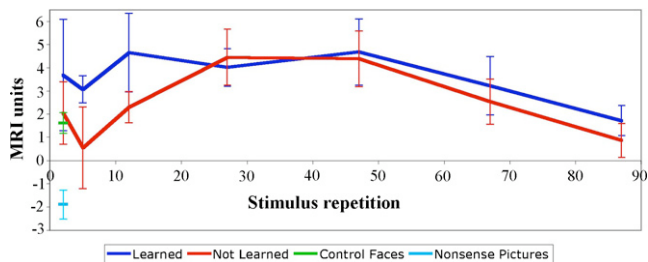


Fig. 6. Curve of adaptation to repetition of stimuli in the precuneus from day 3 of the experiment. Repetition of novel faces induced an increase in the hemodynamic response during the first 20 presentations as compared to the visually familiar faces ($p < 0.03$). The subsequent presentations induced a progressive decrease in the hemodynamic response with no significant difference between the two categories.

with a similar trend ($p < 0.02$) (Fig. 5). In the precuneus, by contrast, the response to novel faces was weaker than the response to the visually familiar faces for the first 20 presentations ($p < 0.03$) (Fig. 6). Over the course of these first 20 presentations, the response to novel faces increased to the level of response to the visually familiar faces after which similar rates of decrease were observed for both categories.

4. Discussion

Facial appearance is only one aspect of how we recognize known individuals. In two previous studies, we have demonstrated that recognizing familiar faces activates a distributed network of areas that involves not only the visual perceptual areas but also areas engaged in emotional response, such as the amygdala and the insula, and areas that are involved with social behavior and “theory of mind” [12,13,23]. According to our model of face perception [17], recognizing a face is the result of a process that is distributed among multiple areas. To differentiate the role of visual familiarity in the recognition of familiar individuals from the role of person knowledge, we designed an experiment in which the participants became familiar with the visual appearance of the faces of three strangers. The faces were “learned” visually with no associated biographical or other type of semantic information.

The visually familiar faces, as compared to novel faces, induced a stronger response in the precuneus and weaker

responses in the fusiform gyrus, in the right amygdala and in areas that have been associated with working memory and attention such as the intra-parietal sulci and the middle and inferior frontal gyri.

No modulation of response was detected in areas associated with personal traits and detection of intention such as the anterior paracingulate cortex [25] and the posterior superior temporal sulcus [36].

The posterior cingulate and the precuneus are activated by a wide variety of familiar stimuli as compared to novel stimuli, irrespective of input modality. For example, a stronger response to familiar faces and familiar voices has been found in this area [14,24,27,33]. The precuneus is activated by tasks that require long-term memory [3] and by tasks that require imagery [9,19]. In a study by Fink et al. [8] the retrosplenial cortex was activated when the subjects listened to autobiographical memories. A recent study also [22] reported a progressively increased response in the precuneus to the repetition of the faces stimuli during an fMRI experiment.

In two previous studies on recognition of familiar individuals, we found that the strength of the response to faces in the precuneus was modulated by the degree of familiarity. The faces of individuals that had a richer representation, such as the faces of friends or family members or the faces of one’s own child, evoked a stronger response in the precuneus than less familiar faces, such as celebrities or the friends of one’s child, which in turn evoked a stronger response than the faces of strangers [12,23].

In the present study, we found a stronger response in the precuneus to the visually familiar faces as compared to the novel highly repeated faces. Moreover, we found that the course of habituation of responses to the visually learned and the highly repeated novel faces differed. The responses to novel highly repeated faces (similar to what has been reported by Kosaka et al. [22]), increased over time while the responses to visually familiar faces were stronger and more stable. These findings support the hypothesis that the precuneus might play an important role in the acquisition of familiarity [22].

When a stimulus is presented repeatedly, it is processed faster and more accurately (priming)[35] (for a more recent review on this topic see ref. [15]). Single unit recordings in monkeys [6] and imaging studies in humans have shown that the neural correlate of priming is a decrease in the neural response to repetitions of the same stimulus (‘repetition suppression’ effect) [18].

Reports on the effect of familiarity on neural responses to faces in the fusiform gyrus have not been consistent. Some studies have reported a stronger response to familiar faces [18,24], other studies a weaker response [7,29] or no modulation at all [14]. These discrepancies could be due to the different sets of stimuli defined as ‘familiar’ and to different tasks that have different requirements on memory or attention. In our previous experiments on the effect of familiarity in face perception, we used the same task (one-back repetition detection), and we compared different types of familiar faces. In those experiments, we did not find a simple modulation by familiarity in the ventral occipito-temporal regions [12,23]. The lack of a simple modulation of the response based on the type of familiarity could be

due to feedback from other areas [28]. In the current experiment, we found a weaker response to the learned faces in areas that are usually involved with attention and working memory [4], such as the intra-parietal sulcus and the middle and inferior frontal gyri. These findings suggest that processing of visually familiar faces, as compared to novel faces, required less attention, perhaps due to facilitated access to stored visual representations [2]. The slower reaction time to novel faces corroborates this interpretation. Moreover, the curves for the response to the repeated presentations of the two sets of faces demonstrated a similar trend of habituation in the fusiform gyrus. Our findings are in agreement with the data reported by Kosaka et al. [22], who found an increased hemodynamic response to repetition of novel stimuli (repetition enhancement) in the precuneus but not in the fusiform gyrus (but see [18]). Ishai et al. [19] reported similar decreases of the responses to repeated faces in the visual extrastriate areas, the amygdala and inferior frontal/insular cortex but did not report any increase in the precuneus [20]. In their study, however, repeated stimuli were targets for behavioral responses and were repeated only three times. In our study, by contrast, we used an implicit task and response enhancement in the precuneus was first seen with more than 10 repetitions.

We and others have reported that the amygdala responds more strongly to novel faces as compared to familiar faces. In the current study, we also found that novel faces evoked a stronger response than did visually familiar faces in this structure. The results of this experiment support the hypothesis that the amygdala is sensitive to unexpected or unfamiliar events with potential biological importance [5,31].

In contrast to our previous studies of familiar face recognition [12,23], we found that simple visual familiarity alone did not modulate activity in the anterior paracingulate cortex or superior temporal sulcus, areas associated with person knowledge and theory of mind. This finding supports our hypothesis that more than simple visual familiarity is necessary to evoke activity in these areas.

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