

View-independent coding of face identity in frontal and temporal cortices is modulated by familiarity: an event-related fMRI study

Gilles Pourtois,^a Sophie Schwartz,^a Mohamed L. Seghier,^{a,b}
François Lazeyras,^b and Patrik Vuilleumier^{a,c,*}

^aDepartment of Neurosciences, Neurology and Imaging of Cognition, Clinic of Neurology, University Hospital, University Medical Center, Switzerland

^bDepartment of Radiology, University Hospital, University of Geneva, Switzerland

^cDepartment of Psychology, University of Geneva, Switzerland

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Face recognition is a unique visual skill enabling us to recognize a large number of person identities, despite many differences in the visual image from one exposure to another due to changes in viewpoint, illumination, or simply passage of time. Previous familiarity with a face may facilitate recognition when visual changes are important. Using event-related fMRI in 13 healthy observers, we studied the brain systems involved in extracting face identity independent of modifications in visual appearance during a repetition priming paradigm in which two different photographs of the same face (either famous or unfamiliar) were repeated at varying delays. We found that functionally defined face-selective areas in the lateral fusiform cortex showed no repetition effects for faces across changes in image views, irrespective of pre-existing familiarity, suggesting that face representations formed in this region do not generalize across different visual images, even for well-known faces. Repetition of different but easily recognizable views of an unfamiliar face produced selective repetition decreases in a medial portion of the right fusiform gyrus, whereas distinct views of a famous face produced repetition decreases in left middle temporal and left inferior frontal cortex selectively, but no decreases in fusiform cortex. These findings reveal that different views of the same familiar face may not be integrated within a single representation at initial perceptual stages subserved by the fusiform face areas, but rather involve later processing stages where more abstract identity information is accessed.

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Introduction

We probably never see the same face twice with exactly the same view, yet we can readily recognize the same individual across changes in visual appearance. Little is known about brain systems responsible for such efficient recognition abilities across varying visual inputs. Focal brain lesions may selectively disrupt the recognition of familiar faces (prosopagnosia), while the ability to discriminate between two different faces may be spared even for unfamiliar faces (e.g., Ellis et al., 1989; Tranel et al., 1988), suggesting the existence of specific networks for recognizing the identity of well-known faces. Imaging studies in healthy subjects have also shown that familiarity may produce a differential response to seen faces in several brain regions (e.g., Haxby et al., 2000; Ishai et al., 2002), although there is a large variability across studies, including effects in the fusiform gyrus (George et al., 1999; Henson et al., 2000), left anterior middle temporal gyrus (Gorno-Tempini et al., 1998), right temporal pole (Nakamura et al., 2000), retrosplenial cortex (Shah et al., 2001), and left inferior frontal gyrus (Henson et al., 2003). This variability may partly relate to important differences in the nature or degree of face familiarity examined in these different studies (e.g., personal acquaintance, celebrities known through mass-media, pre-exposure, etc.).

An unresolved issue concerns the precise neuroanatomical substrates involved in the long-term storage of specific face identities, enabling the recognition of familiar faces associated with unique semantic information, as well as the acquisition of new representations for previously unfamiliar faces. It is still unknown how (and where in the brain) different images from the same face may converge onto a common identity representation, that is, whether different appearances of a familiar person may share a single view-invariant visual representation (i.e., in a “face recognition unit”, Bruce and Young, 1986), or rather involve different visual representations for each visual appearance, connected to some higher-level representation of the person in memory (i.e., in a “person-identity node”, Bruce and Young, 1986). In

* Corresponding author. Laboratory for Neurology and Imaging of Cognition, Department of Neuroscience and Clinic of Neurology, University Medical Centre (CMU), Bat. A, 7th floor, room 7042, 1 rue Michel-Servet, CH-1211 Geneva, Switzerland. Fax: +41 22 379 5402.

E-mail address: patrik.vuilleumier@medecine.unige.ch (P. Vuilleumier).

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behavioral studies using explicit recognition memory (e.g., Hancock et al., 1996; Otoole et al., 1994) or implicit repetition priming tasks (e.g., Goshen-Gottstein and Ganel, 2000; Roberts and Bruce, 1989), normal subjects were able to recognize unfamiliar faces even after a single encounter, sometimes across different visual appearances (Bruce, 1982; Burton et al., 2001; Moses et al., 1996), suggesting that some trace formed for a novel face can be retrieved when the same identity is repeated on a different occasion. However, the ability to recognize faces under different views is often strikingly limited when the faces are unfamiliar (Burton et al., 1999; Hancock et al., 2000), and generalization effects have often been obtained with relatively minor changes in facial structural information as compared with changes in real-life situations. Therefore, a critical question concerns the level within the recognition system at which different views of the same face identity are integrated, in order to support recognition across a wide range of visual appearances.

To address this question, we used event-related fMRI during a long-term repetition-priming paradigm (Henson and Rugg, 2003; Jemel et al., 2003a) in which familiar and unfamiliar faces were shown twice, but with a different appearance at each exposure. Priming involves a facilitation of processing for repeated stimuli as compared with initial exposure, reflecting a selective tuning of the stimulus representation (Wiggs and Martin, 1998), independent of explicit recollection (Schacter and Buckner, 1998; Tulving and Schacter, 1990). Recent fMRI studies have reported repetition-related effects for faces in visual areas such as the lateral occipital cortex (Grill-Spector et al., 1998) and lateral fusiform cortex (Gauthier et al., 2000; Huettel and McCarthy, 2001; Ishai et al., 2004; Vuilleumier et al., 2003a), including differential effects for familiar vs. unfamiliar faces in some cases (George et al., 1999; Henson et al., 2000, 2003; but see Ishai et al., 2002). However, these studies always repeated the same picture (Henson et al., 2000, 2003; Huettel and McCarthy, 2001) or the same view of faces (Eger et al., 2004; George et al., 1999; Vuilleumier et al., 2003a) on both presentations.

Here, in order to examine more abstract, view-independent, long-term representations of identity, rather than image-based or view-based representations, we systematically manipulated the appearance of both famous and unfamiliar faces using different photographs of the same person, with each identity being repeated once after an unpredictable interval, always with a different view. The different views of unfamiliar faces were chosen to be clearly recognizable as the same person.

Evidence from neurophysiological studies in the monkey suggests that single neurons in infero-temporal (IT) cortex and superior temporal sulcus (STS) may code complex multipart patterns such as faces using view-invariant processes (Rolls, 2000; Vogels et al., 2001), showing similar responses across various changes in visual appearance including size, contrast polarity, or spatial frequency content (Rolls et al., 1987). Such neurons therefore seem to encode view-independent properties of faces that can be useful in identification (Rolls, 2000). However, face-selective neurons have also been found to show view-dependent activity, with different responses to different views of the same face (Perrett et al., 1998; Wang et al., 1998). Some models have therefore proposed that different views of a given face might be mapped across neighboring neurons (or neighboring columns) within IT cortex, and that view-invariance in recognition might be achieved by pooling across different neurons or different columns each sensitive to particular views (Perrett et al., 1998; Wallis and Bulthoff, 1999).

In the present study, by using a repetition-priming paradigm, we aimed at determining whether the same neuronal population in visual cortex (or elsewhere in the brain) is activated by different pictures of the same familiar or the same unfamiliar person, even though these different populations might overlap in the same cortical region (e.g., see Grill-Spector and Malach, 2001). We predicted that repetition effects for famous faces seen with very different appearances should implicate neural systems essential for encoding person identity and related semantic knowledge (Gorno-Tempini and Price, 2001; Shah et al., 2001), whereas unfamiliar faces repeated with a varying appearance might preferentially implicate brain systems more concerned with the acquisition of new face representations (George et al., 1999; Henson et al., 2003; Vuilleumier et al., 2003a). A critical question was whether famous faces repeated with a different appearance would produce priming-related effects in visual areas encoding visual traits (such as the face-selective fusiform gyrus), or instead exclusively affect higher-level brain areas encoding more abstract identity information (such as temporal or frontal regions).

Materials and methods

Subjects

Participants were 13 healthy paid volunteers (8 males, mean age 26, range 20–35, all right-handed) who gave informed consent. All had a normal or corrected to normal vision, and no past of neurological or psychiatric history.

Stimuli and procedure

Stimuli were digitized color photographs of 48 different face identities (24 famous and 24 unfamiliar). Both famous and unfamiliar faces were taken from various views (Fig. 1) and

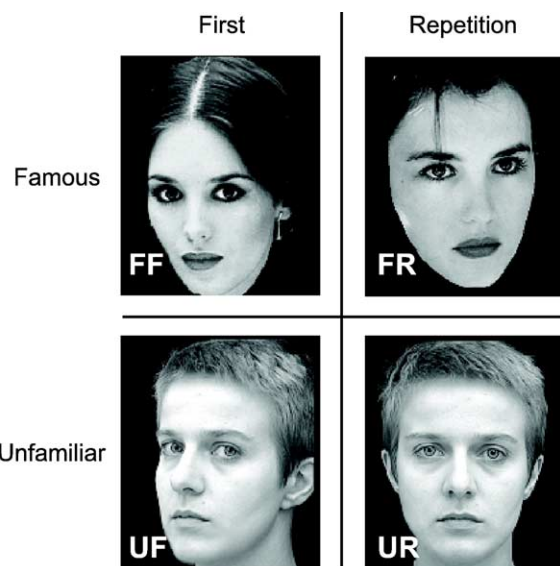


Fig. 1. Stimuli used in the repetition priming experiment. Each person identity ($N = 48$) was either famous or unfamiliar, and was repeated once under a different visual appearance at an unpredictable delay. This resulted in four possible event types (FF, famous first; FR, famous repeated; UF, unfamiliar first; UR, unfamiliar repeated).

depicted an equal number of women and men, all with a relatively neutral expression. The set of famous faces included 24 celebrities from the mass media, taken from different professional categories (e.g., politicians, actors, etc.). In a pilot experiment, all these faces were reliably rated as famous and highly familiar by a separate group of subjects who did not participate in the fMRI study. The set of unfamiliar faces included 24 different individuals, selected from those used by George et al. (2001), and from the AT&T database (Samaria and Harter, 1994). This set of unfamiliar faces was chosen in order to match the diversity in visual appearance and age of the famous face set.

Each of these 48 person identities was shown twice, with a second photograph depicting the face of the same person but seen from a different image (total 96 stimuli; see Fig. 1). For famous faces, each pair consisted of two different photographs of the same celebrity, for example, taken at different moments in time during his/her public career and with different poses (including changes in appearance and/or head orientation). These photographs were selected such that the two different views were visually quite distinct, but still clearly recognizable as the same famous face (see Fig. 1). However, major changes due to particular make-up or costumes (such as particular roles in different movies for actors), or important modifications in hairstyle (beard, moustache, etc.) were avoided. Similarly, for unfamiliar faces, each pair of photographs depicted the same person in two different views. These pairs of unfamiliar faces were chosen such that visual appearance was clearly distinct, while recognition of identity across the two views was still reliably above chance [$t(13) = 8.76$, $P < 0.001$] in a control experiment in which a different group of subjects ($N = 14$) performed an explicit memory task (>70% correct hits in a two-alternative forced choice recognition task with a randomized stimulus sequence). This allowed us to avoid image-based or view-dependent effects in the repetition of unfamiliar faces, while ensuring that these unfamiliar faces were generally recognizable across views, as were the famous faces. The number and type of full-front and three-quarter viewpoints, as well as the amount of changes between pairs of pictures of the same face were equally balanced across the famous and unfamiliar stimuli.

During the fMRI experiment, both famous and unfamiliar faces were presented in a continuous randomized sequence. For both face categories, each person identity was repeated once only, after an unpredictable lag and a varying number of other intervening faces (see below). This produced a total of four possible event types (Fig. 1): (1) famous face-first presentation (FF); (2) famous face-repeated presentation (FR); (3) unfamiliar face-first presentation (UF); and (4) unfamiliar face-repeated presentation (UR).

All images had the same size (457×511 pixels) and were presented against the same homogenous black background. During fMRI, these stimuli were back-projected onto a mirror mounted on the head coil (visual angle approximately $5.9 \times 6.8^\circ$). All 96 face stimuli were presented centrally (duration 400 ms each) in a pseudo-randomized order with a mean stimulus onset asynchrony of 4.8 s (randomly jittered between 2.7 and 6.8 s). Thirty null trials were also randomly intermixed with face stimuli in order to provide an appropriate baseline measure (Friston et al., 1999). Each face was preceded by a 500-ms fixation cross. The lags between the first and second occurrence of each face stimulus were calculated so that overall trial-ranks largely overlapped for the first and second presentation of the same person's face (respectively, range 1–112, median 49; range 6–126, median 72). To this aim, for each repetition condition, the pairs of faces were distributed into

two subsets, one in which the same face identity was repeated after relatively short lags, and the other in which the same face identity was repeated after longer lags (mean repetition lag $20 \pm \text{SD } 9.7$; see Vuilleumier et al., 2002), with these two sets being randomly mixed within a continuous stimulus sequence. This pseudo-randomization of trials does not completely eliminate the contribution of time effects associated with repetition effects, as is inherently the case for long-term repetition priming experiments (Henson and Rugg, 2003), but allowed us to minimize any confound of repetition and time, and to produce a non-predictive stimulus sequence with varying numbers of intervening stimuli between first presentations and repetitions (see Vuilleumier et al., 2002). This procedure also ensured that the average trial history preceding and following a given trial was equivalent for all trial types. Different stimuli lists were created according to this procedure and counterbalanced across participants.

During scanning, participants were asked to perform a gender categorization task on each face stimulus (male/female), by pressing one of two buttons with their dominant hand, with explicit instructions to privilege accuracy rather than speed. Participants were informed that some of the faces were from celebrities and that this was irrelevant to their task. To ensure that face identity would nonetheless be incidentally processed during gender judgments, we used pictures (see Fig. 1) that minimized gender cues from the external hair contours (see Goshen-Gottstein and Ganel, 2000).

After scanning, participants underwent a debriefing test in which they were shown again all face stimuli seen during the fMRI session, but now asked to categorize them as famous or unfamiliar. Famous faces judged as unknown, and unknown faces judged as famous, were all removed from the subsequent analysis of fMRI data for individual participants who made these errors (mean error rate of $6 \pm \text{SD } 5.6$).

We also performed a separate face-localizer scanning session (Gauthier et al., 2000; Grill-Spector et al., 2004; Kanwisher et al., 1997) to identify face-selective brain regions in each individual participant. In this fMRI session, a different set of photographs (72 faces and 72 houses) was presented in eight alternating blocks (4 face blocks and 4 house blocks). Each block comprised 18 stimuli from the same visual category. None of these faces and houses had been seen in the previous repetition-priming session, and faces were presented in a variety of head-orientations including a mixture of full-front and 3/4 views. Each stimulus was presented for 750 ms, with an inter-trial interval of 500 ms. Subjects performed a one-back repetition detection task, requiring them to press a button for any immediate repetition of the same image. During each of the four face-blocks and each of the four house-blocks, only one or two out of 18 stimuli were repeated. Participants correctly detected such immediate repetitions in >94% of trials for faces and in >87% of trials for houses [$t(12) = 1.8$, $P = 0.10$].

fMRI scanning

MRI data were acquired in a 1.5-T whole-body INTERA system (Philips Medical Systems), using the standard head coil configuration. For each participant, structural images were acquired with a 3D-GRE T1-weighted sequence (TR/TE/Flip = 15 ms/5.0 ms/30°, FOV = 250 mm, matrix = 256×256 , slice-thickness = 1.25 mm) and functional images with a GRE EPI sequence (TR/TE/Flip = 2400 ms/40 ms/80°, FOV = 250 mm,

matrix = 128×128). Each functional image comprised 27 contiguous 3 mm axial slices oriented parallel to the inferior edge of the occipital and temporal lobes (voxel size $3 \times 3 \times 3$ mm). For the main experiment, a total of 256 functional images were acquired in a single scanning run with an effective repetition time of 2.4 s. In the face-localizer scan, 85 images were acquired using identical imaging parameters.

Data analysis

Functional images were analyzed using the general linear model (Friston et al., 1998) for event-related designs using SPM99 (Wellcome Department of Cognitive Neurology, London, UK; <http://www.fil.ion.ucl.ac.uk/spm>). All images were realigned, corrected for slice timing, normalized to the MNI space, and spatially smoothed by an 8-mm full width at half-maximum (FWHM) Gaussian kernel. A high-pass frequency filter (cutoff 120 s) and corrections for auto-correlation between scans were applied to the time series.

Individual events were modeled by a standard synthetic hemodynamic response function (HRF). Five event types were defined, corresponding to each of the four critical stimulus conditions (see above) plus a fifth event type corresponding to faces incorrectly judged as famous or incorrectly judged as unknown during the explicit recognition task that took place in the debriefing session immediately post-scanning. Movement parameters derived from realignment corrections (3 translations, 3 rotations) were also entered as covariates of no interest. The general linear model was then used to generate parameter estimates of activity at each voxel for each condition and each participant. Statistical parametric maps of the t statistic ($SPM\{t\}$) generated from linear contrasts between different conditions were transformed to a normal distribution ($SPM\{Z\}$), in each participant. For each individual contrast, we then performed a random-effect group analysis (Friston et al., 1998). We concentrated on regions that survived $P < 0.05$ volume-corrected for regions showing a main effect of repetition (at $P < 0.001$ uncorrected) across the whole brain (Worsley et al., 1996), but for completeness, we also tabulated all regions of at least five contiguous voxels that survived $P < 0.001$ uncorrected (see Henson et al., 2003 for similar statistical approach).

Regions showing an activation for faces > house in the localizer scan were used to define several regions-of-interest (ROIs) with face-selective responses and to create an inclusive mask (thresholded at $P < 0.01$) that allowed us to examine the results from our main experimental scan (i.e., contrasts testing for familiarity and repetition-priming effects) more specifically for pre-defined regions within the face processing networks, in complement to the whole-brain SPM analysis.

Results

Behavioral results

Median reaction times (RTs) for correct responses during the gender decision task were analyzed using a repeated-measure analysis of variance (ANOVA) with two within-subject factors: Familiarity (unfamiliar faces vs. famous faces) and Repetition (first occurrence vs. second presentation). The ANOVA did not reveal significant effects [Familiarity, $F(1,12) < 1$; Repetition $F(1,12) =$

2.17, $P = 0.17$; Familiarity \times Repetition, $F(1,12) < 1$], despite responses being generally slightly faster on second than first presentation for both famous and unfamiliar faces (median RTs \pm SE, FF: 447 ± 55 ; FR: 423 ± 50 ; UF: 454 ± 46 ; UR: 446 ± 46). Accuracy for gender judgments was generally high (>92% correct), without any effects or interaction due to Familiarity or Repetition [all $F(1,12) < 2.96$, $P > 0.11$].

Brain-imaging results

Face-localizer

Face-selective regions were determined using the Face > House contrast from the localizer scan (Fig. 2A). This revealed several activations in temporal and occipital lobes of both hemispheres, larger on the right than left side (Table 1). Face-selective responses were primarily observed in the lateral part of the fusiform gyrus bilaterally, corresponding to the location of the “fusiform face area” (FFA, Kanwisher et al., 1997; see also Gauthier et al., 2000; Grill-Spector et al., 2004; Haxby et al., 2000; Puce et al., 1995). Additional activations were found in bilateral occipital gyri, corresponding to the putative “occipital face area” (OFA, Gauthier et al., 2000; see also Halgren et al., 1999; Haxby et al., 2000); plus in the right superior temporal sulcus (STS) and in left amygdala. All these regions have been shown to respond preferentially to faces than to other visual objects in previous fMRI studies (Grill-Spector et al., 2004; Halgren et al., 1999; Haxby et al., 2000; Kanwisher et al., 1997; Vuilleumier et al., 2001). These areas were used to create an inclusive mask of face-selective regions of interest (ROI, thresholded at $P < 0.01$), in order to examine in greater details the familiarity and repetition-priming effects obtained during our main experiment (see below).

The reverse contrast (House > Face, at $P < 0.001$) from the localizer scan revealed a distinct pattern of bilateral activation within the ventral visual stream, including the parahippocampal gyrus (peak coordinates, left: $-21x, -42y, -15z$; $T = 8.56$; right: $27x, -42y, -18z$; $T = 12.7$; see Epstein et al., 1999) and posterior lateral occipital regions (left: $-24x, -75y, -12z$; $T = 6.30$; right: $24x, -66y, -12z$; $T = 14.88$; see Grill-Spector et al., 1999).

Brain regions coding for face familiarity

In the repetition-priming experiment, we first examined the main effect of familiarity (i.e., famous versus unfamiliar faces), regardless of repetition (FF + FR > UF + UR), by performing linear SPM contrasts across the whole brain.

Whereas no region showed greater activation for unfamiliar faces relative to famous faces (even at a lower threshold of $P < 0.01$ uncorrected), the reverse contrast did reveal several brain areas showing greater responses to famous than unfamiliar faces (all at $P < 0.001$ voxelwise). These included the anterior fusiform gyrus in the left hemisphere (see Fig. 2D; 64 voxels, main peak at $-39x, -36y, -30z$; $T = 4.0$), a region partly overlapping with the face-selective ROI mask as determined by the localizer scan (Fig. 2A). Inspection of event-related activity in the left anterior fusiform gyrus across all conditions (Fig. 2D) confirmed that this region was mainly sensitive to the familiarity of previously known faces, but in addition also showed a modest trend for repetition-related decreases for both famous and unfamiliar faces (as indicated by a subsequent analysis testing for the main effect of First > Repeated; peak at $-42x, -39y, -27z$, $T = 2.98$, $P = 0.006$; with no significant interaction of familiarity \times repetition in this region).

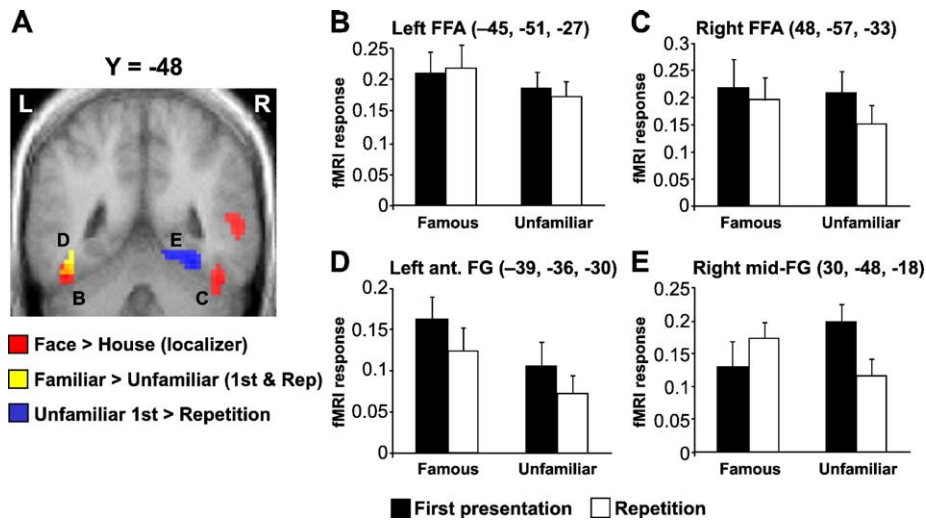


Fig. 2. (A) Face-selective areas in lateral fusiform gyrus (FFA) and right superior temporal sulcus, as determined the face > house contrast (in red); the left anterior fusiform area showing a main effect of familiarity (in yellow); and the right medial fusiform area showing repetition decreases for unfamiliar faces (in blue). Activations are overlaid on the mean anatomical scan of participants (SPMs thresholded at $P < 0.01$ for illustrative purpose). (B) Average parameter estimates of activity (\pm SE) in the left FFA show no reliable effect of face repetition, but a trend towards a main effect of familiarity. (C) Average parameter estimates of activity (\pm SE) in the right FFA show no reliable effect of face familiarity, but a small effect of repetition for unfamiliar faces. (D) Average parameter estimates of activity (\pm SE) in the left anterior fusiform gyrus showing a significant effect of familiarity, as well as repetition decreases in both conditions. This region partly overlapped with the left FFA. (E) Average parameter estimates of activity (\pm SE) in the right medial fusiform gyrus, showing repetition-related decreases for unfamiliar but not famous faces. This region was adjacent to, but did not overlap with the more lateral right FFA. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Other clusters showing a significant main effect of familiarity regardless of repetition were found in right temporal lobe, including the anterior right parahippocampal gyrus (52 voxels, main peak at $33x, -18y, -24z; T = 4.88$), the right middle temporal gyrus (7 voxels; Brodmann area 21; $60x, -3y, -18z; T = 3.95$), and the right temporal pole (10 voxels; Brodmann area 20/38; $27x, 12y, -39z; T = 3.95$). This pattern is consistent with previous neuroimaging results indicating that several areas within a distributed network are involved in the processing of famous relative to unfamiliar faces (Ishai et al., 2002), including the anterior fusiform gyrus (George et al., 1999; Henson et al., 2000), parahippocampal regions (Leveroni et al., 2000), as well as middle temporal gyrus (see Gorno-Tempini and Price, 2001). However, these regions did not overlap with the face-selective ROI mask as defined by the localizer scan.

Repetition priming effects irrespective of familiarity

In a second step, we examined the main effect of face repetition by comparing activation to the First versus Repeated presentation of

each face identity, irrespective of familiarity ($FF + UF > FR + UR$). This contrast, performed across the whole brain, identified a number of cortical regions showing decreased activity when a face was repeated with a different appearance, relative to the face of the same person presented for the first time (Table 2). All these regions were located in the left hemisphere. The largest repetition-related decreases were found in the inferior frontal gyrus (Fig. 3A), including both an anterior cluster corresponding to Brodmann area 45/pars triangularis ($-45x, 27y, 18z; T = 5.97$) and a more dorsal cluster corresponding to Brodmann area 44/pars opercularis ($-42x, 6y, 12z; T = 4.58$). Such repetition-related decreases independent of familiarity were also found in the left middle temporal gyrus where repetition-related decreases were larger for famous than unfamiliar faces (Fig. 4B), left hippocampus (Fig. 4C) and adjacent parahippocampal gyrus, as well as retrosplenial/posterior cingulate cortex (see Table 2). Note that no main effect of repetition was found at the same statistical threshold ($P = 0.001$) in the more lateral fusiform regions where face-selective responses were seen in the localizer scan (see also next sections for face-selective ROI analyses).

The reverse contrast, testing for regions with repetition-related increases (i.e., greater responses to repeated faces than to first presentations) irrespective of face familiarity did not reveal any significant effect throughout the whole brain (even at a lower threshold of $P < 0.01$ uncorrected).

Repetition priming effects modulated by familiarity

In a third step, we examined if repetition-related effects were differentially modulated by previous familiarity with faces. To this aim, we performed two further statistical comparisons testing for view-independent repetition-related decreases (or increases) for unfamiliar and famous faces separately. In each condition, faces were always repeated with a different viewpoint as compared with their initial presentation, after an unpredictable delay.

Table 1

Brain regions activated by faces > houses (localizer scan)

Brain areas	Side	Coordinates			T	Cluster size
		x	y	z		
Amygdala	L	-21	-15	-12	5.18	11
Fusiform gyrus	R	48	-57	-33	4.65	22
Fusiform gyrus	L	-45	-51	-27	5.09	12
Middle occipital gyrus	R	54	-72	-3	5.06	15
Superior occipital gyrus	L	-54	-72	15	4.98	5
Superior temporal sulcus	R	51	-54	6	4.60	10

All $P < 0.001$ uncorrected (random-effect analysis).

Table 2
Brain regions showing repetition priming effects

Brain areas	Side	Coordinates			T	Cluster size	
		x	y	z			
<i>First > Repeated (all conditions)</i>							
Inferior frontal gyrus	BA45	L	-45	27	18	5.97*	141
	BA44		-42	6	12	4.58*	
Posterior cingulate cortex		L	-9	-36	21	5.25*	56
Hippocampus		L	-24	-18	-6	4.82	58
Middle temporal gyrus		L	-57	-12	-18	4.05	47
<i>First > Repeated (unfamiliar faces)</i>							
Medial fusiform gyrus		R	30	-48	-18	6.32*	59
Cuneus		R	9	-96	9	5.67	16
Middle occipital gyrus		R	24	93	12	4.79	17
Posterior cingulate cortex		R	6	-36	18	6.74*	50
Parahippocampal gyrus		R	15	-36	-15	4.84	12
Amygdala		R	27	3	-24	4.57*	27
Middle occipital gyrus		L	-51	-69	9	4.95	8
Lingual gyrus		L	-9	-60	-3	4.68	20
Amygdala		L	-18	3	-18	4.92	6
Inferior frontal gyrus	BA44	L	-45	3	12	8.43*	30
<i>First > Repeated (famous faces)</i>							
Middle temporal gyrus		L	-60	-24	-9	4.81	14
Inferior frontal gyrus	BA45	L	-45	24	18	4.30*	20

All $P < 0.001$ uncorrected (random-effect analysis).

* $P < 0.05$ volume-corrected (see Materials and methods).

For unfamiliar faces, the (UF > UR) contrast revealed significant repetition decreases in the right medial fusiform gyrus (Fig. 2E) and in several other bilateral visual areas (Table 2), including the lateral occipital cortex in both hemispheres and the left lingual gyrus. Such repetition effects in the right medial fusiform gyrus did not overlap with the more lateral right FFA (Fig. 2A) as defined by the localizer scan, although the right FFA peak

also showed a weak trend for repetition-related decreases with unfamiliar faces ($T = 1.99$, $P = 0.03$; see Fig. 2C and below). Inspection of event-related activity across all conditions revealed that repetition decreases in the right medial fusiform gyrus occurred selectively for unfamiliar faces, but not for famous faces (see Fig. 2E). This was confirmed by a formal test for an interaction of repetition \times familiarity across the whole brain

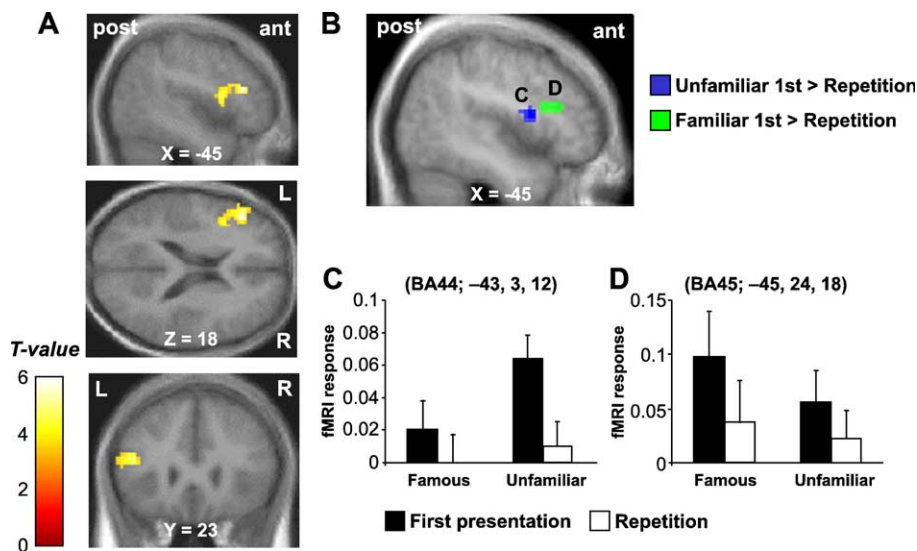


Fig. 3. (A) Main effect of repetition priming in left inferior frontal cortex (SPMs thresholded at $P < 0.001$) overlaid on the mean anatomical scan of participants. Distinct repetition priming effects arose in different subregions of the inferior frontal gyrus (IFG) as a function of familiarity. (B) Sagittal view showing both effects of repetition decreases for unfamiliar (blue) and familiar faces (green). (C) Average parameter estimates of activity (\pm SE) showing predominant repetition-related decreases for unfamiliar faces in the posterior IFG (blue area; Brodmann 44, pars opercularis). (D) Average parameter estimates of activity (\pm SE) showing predominant repetition-related decreases for famous faces in the anterior IFG (green area; Brodmann 45, pars triangularis). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

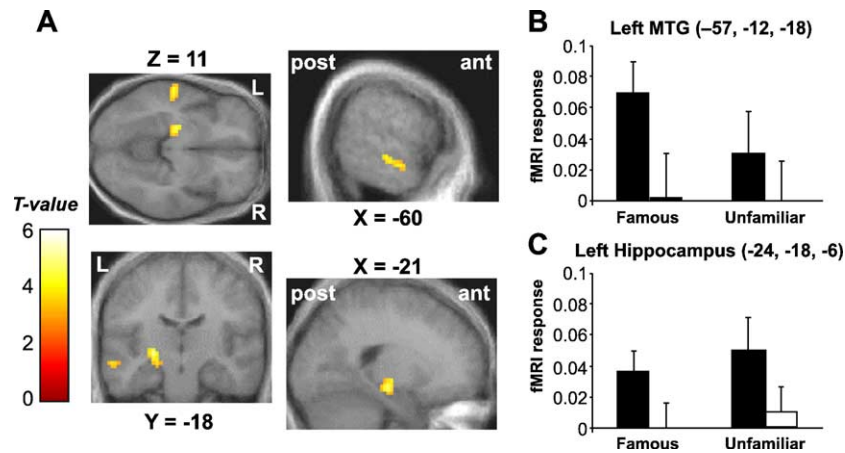


Fig. 4. (A) Main effect of repetition priming in the left MTG and left hippocampus overlaid on the mean anatomical scan of participants (SPMs thresholded at $P < 0.001$), upper sagittal view centered on left MTG and lower sagittal view centered on left hippocampus. (B) Average parameter estimates of activity (\pm SE) in the left MTG showing that repetition decreases arose irrespective of familiarity, but predominated for famous as compared with unfamiliar faces. (C) Average parameter estimates of activity (\pm SE) in the left hippocampus showing similar repetition-related decreases for unfamiliar and famous faces.

([UF > UR] > [FF > FR]), showing a peak in right medial fusiform (33x, -51y, -15z, $T = 4.63$, $P < 0.001$).

Additional repetition-related decreases for unfamiliar faces (UF > UR) were found in the right parahippocampal gyrus, right retrosplenial cortex, bilateral amygdala, and left inferior frontal gyrus (Table 2). These regions also showed a reliable differential effect for unfamiliar faces when formally testing the repetition \times familiarity interaction across the whole brain (right parahippocampal, 24x, -30y, -15z; $T = 4.57$, $P < 0.001$; left lingual gyrus, -12x, -57y, -6z; $T = 4.14$, $P = 0.001$; right amygdala, 30x, 0y, -24z; $T = 3.48$, $P = 0.002$; left amygdala, -18x, 6y, -21z; $T = 3.36$, $P = 0.003$). The left posterior inferior frontal gyrus (BA44) also showed strong repetition-related decreases for unfamiliar faces (-45x, 3y, 12z, $T = 8.43$, $P < 0.001$), but weaker decreases were found for famous faces in the same region (-45x, -9y, 12z, $T = 2.48$, $P = 0.01$; see Fig. 3C). Therefore, the repetition \times familiarity interaction did not reach significance in inferior frontal gyrus (see also below).

Overall, these results agree with repetition-related decreases found in both visual and frontotemporal areas in previous studies using unfamiliar faces (Huettel and McCarthy, 2001; Ishai et al., 2004; Soon et al., 2003; Vuilleumier et al., 2003a) or man-made objects (Grill-Spector et al., 1998; Koutstaal et al., 2001; Vuilleumier et al., 2002), although here our repetition effects arose even though the actual photographs and viewpoints were always different on the first and second presentation. This difference in pictorial format probably accounts for a predominance of repetition effects in medial fusiform gyrus (see George et al., 1999; Vuilleumier et al., 2003a), rather than in the more lateral face-selective areas of fusiform cortex (Henson et al., 2000; Kanwisher et al., 1997).

For famous faces, we next performed the (FF > FR) contrast to identify brain areas showing repetition decreases when the same well-known face identity was seen under two distinct visual appearances. This comparison revealed only two significant clusters, both in the left hemisphere (Table 2). The largest repetition decreases were found in the left middle temporal gyrus (MTG, Fig. 4B), as well as in the anterior part of the left inferior frontal gyrus (Fig. 3D), corresponding to the pars triangularis (Brodmann area 45).

Both the left inferior frontal gyrus (Fig. 3D) and left middle temporal gyrus (Fig. 4B) tended also to show some repetition effects for unfamiliar faces, although this was not significant when tested alone (using the UF > UR contrast) (see Table 2). Thus, there was a small repetition decrease in left MTG for unfamiliar faces (-63x, -18y, -15z; $T = 3.73$, $P < 0.01$), but a much stronger decrease for famous faces (-60x, -24y, -9z; $T = 4.81$, $P < 0.001$). Likewise, in the anterior inferior frontal gyrus (BA45), there were larger decreases for the repetition of famous faces (-45x, 24y, 18z, $T = 4.30$; $P < 0.001$) than for unfamiliar faces (-45x, 27y, 18z; $T = 2.43$, $P = 0.02$). Accordingly, when testing for any region showing a repetition \times familiarity interaction, that is, with repetition-related decreases arising selectively for famous but not unfamiliar faces ([FF > FR] > [UF > UR]), we did not find any significant cluster, even at a lower statistical threshold ($P < 0.01$). More critically, the (FF > FR) contrast did not show any significant cluster within visual areas even at a lower statistical threshold ($P < 0.05$), including within the face-selective ROI in bilateral fusiform gyrus as defined by the face localizer mask (see also below).

Finally, note that the peak of repetition-related decreases for famous faces in the left inferior frontal gyrus (-45x, 24y, 18z) did not overlap with that observed with unfamiliar faces (-45x, 3y, 12z). Inspection of event-related activity in left inferior frontal gyrus indicated that the former activation for famous faces was clearly more anterior and predominantly involved the pars triangularis (Brodmann area 45), whereas the latter activation for unfamiliar faces was more posterior and predominantly situated in the pars opercularis (Brodmann area 44). This difference is illustrated in Fig. 3.

Taken together, these results suggest that distinct views of the same famous face identity did not produce reliable repetition effects in visual cortical areas, but primarily affected higher-level areas within the frontal and temporal cortex.

Familiarity and repetition effects within the face selective regions

For completeness, we directly examined the face-selective peaks identified in lateral fusiform gyrus by the Face > House localizer (within the FFA coordinates; e.g., Kanwisher et al., 1997). Contrasts testing for the main effects of familiarity and for effects

of repetition were also performed for all other ROIs included in the face-selective mask defined by our localizer scan.

This analysis confirmed that the FFA peaks in both hemispheres (left: $-45x, -51y, -27z$; right: $48x, -57y, -33z$) did not disclose any consistent effects of either familiarity or repetition priming. The left FFA exhibited somewhat greater activation for famous than unfamiliar faces ($T = 2.06, P = 0.03$), in keeping with the significant familiarity effect found in anterior left fusiform by the whole-brain analysis above. The right FFA was not modulated by familiarity ($T = 1.08, P > 0.05$), whereas it showed a weak repetition decrease for unfamiliar faces ($T = 1.99, P = 0.03$), but not for famous faces ($T = 0.67, P > 0.05$), consistent with repetition effects found in the right medial fusiform cortex above (see Fig. 2C).

A similar detailed ROI analysis was performed on other face-selective regions identified by the localizer scan (Table 1), including the left amygdala, right STS, right middle occipital gyrus (MOG), and left superior occipital gyrus (SOG). Repetition-related decreases were only seen in the left amygdala for unfamiliar faces ($T = 3.83, P = 0.001$), consistent with the outcome of the UF > UR contrast performed above using a whole-brain analysis. There was no effect of familiarity (Famous > Unfamiliar) in this region ($T = 0.65, n.s.$). None of the other regions showed a significant effect at $P < 0.001$ of either repetition (STS, $T = 0.95$; MOG, $T = 0.61$; SOG, $T = 3.10$) or familiarity (STS, $T = 0.54$; MOG, $T = 0.08$; SOG, $T = 2.01$).

Discussion

In this study, we used event-related fMRI to compare repetition priming effects for famous vs. unfamiliar faces. Unlike previous studies (e.g., Henson et al., 2003), our participants were shown two different photographs of the same person, either unknown or famous (as assessed by a debriefing test post-scanning). This procedure ensured that the critical dimension equally repeated for both famous and unfamiliar faces was not the picture itself, but the more abstract face identity information.

Our results reveal a functional segregation in the neural systems supporting the recognition of well-known and unfamiliar faces, but also disclose some partial overlap. While repetition effects for famous faces seen with different visual appearance occurred primarily within temporal and frontal regions of the left hemisphere, repetition effects for unfamiliar faces were primarily found in posterior extrastriate visual areas, including the right medial fusiform gyrus. This pattern is consistent with previous imaging studies of face processing and repetition priming (Henson et al., 2000, 2003; Vuilleumier et al., 2003a; see also Buckner et al., 2000; George et al., 1999), but in addition reveals a significant modulation of face repetition effects as a function of familiarity and visual appearance. Whereas many fMRI studies have shown *decreased* responses in visual areas for the repetition of unfamiliar faces (e.g., see Eger et al., 2004; Gauthier et al., 2000; Huettel and McCarthy, 2001; Ishai et al., 2004; Soon et al., 2003; Vuilleumier et al., 2003a), using either the same pictures or the same frontal view of faces, two other studies (George et al., 1999; Henson et al., 2000) reported repetition *increases* in left fusiform for unfamiliar faces, in contrast to repetition decreases for famous faces only (Henson et al., 2000). Here, we did not observe any repetition increases, even at low statistical threshold ($P < 0.05$ uncorrected). However, numerous differences in task and stimulus characteristics

between the previous experiments might account for these apparent discrepancies (including unequal novelty effects as a function of familiarity in Henson et al., 2000; and increased face recognizability due to priming in George et al., 1999).

More generally, our data provide new support for behavioral findings that implicit memory for unfamiliar faces (e.g., in indirect tests such as repetition priming) is primarily based on perceptual representations, whereas recognition of famous faces may rely more on abstract/semantic description of identity (Burton et al., 1999). Our findings are also consistent with single-cell recordings in the monkey indicating that many face-selective neurons in IT cortex are modulated by face viewpoint (Perrett et al., 1998; Wang et al., 1998), although some invariance for changes in picture format is sometimes also observed (Rolls, 2000).

Thus, a crucial new result in our study was that repeating faces from either famous or unknown people with changing views did not produce any reliable repetition-decreases for face-selective areas in the lateral fusiform gyrus (FFA), independently defined by a standard localizer procedure (Gauthier et al., 2000; Kanwisher et al., 1997). Moreover, the bilateral FFA did not show any main effect of familiarity, except for a weak trend in left anterior fusiform cortex. These data suggest that the FFA may primarily hold view-dependent representations of faces. Although some findings indicate that the FFA may encode structural face information specific for a given identity (Gauthier et al., 2000; Grill-Spector et al., 2004; Henson et al., 2000), this information might not be sufficient to support a generalization to any other views of the same face, and hence would not distinguish between two faces from two different persons or two different views of the same person. Our results therefore suggest that repetition effects previously observed in the FFA for famous (Henson et al., 2003) or unknown faces (Huettel and McCarthy, 2001; Ishai et al., 2004) might reflect view-dependent processes engaged by the repetition of the same pictures or same views, rather than more abstract view-independent representations. Note that even in recent studies where pictorial format was changed (e.g. frequency filtered, see Eger et al., 2004; Vuilleumier et al., 2003a), the specific viewpoint and configuration of face traits was kept identical across repetitions.

Nevertheless, a distinct right medial fusiform region, adjacent to the functionally defined FFA, did show significant decreases when unfamiliar faces were repeated with a slightly different viewpoint. Similarly, a *medial* rather than lateral fusiform region was also found in two previous fMRI studies where unfamiliar faces were repeated with the same viewpoint but a different pictorial format, such as contrast polarity reversal (George et al., 1999) or spatial filtering (Vuilleumier et al., 2003a). Taken together, these data suggest that the medial part of right fusiform may hold face representations that are less sensitive to pictorial cues than the more laterally situated FFA, and thus more susceptible to afford some generalization across different views. In terms of the classical recognition model proposed by Bruce and Young (1986), it follows that if “face recognition units” are the depository of invariant facial traits for previously seen faces, then these are more likely to reside in medial rather than lateral fusiform cortex, unlike previously thought (e.g., Henson et al., 2000).

A second major finding of our study was that the repetition of well-known famous faces across different visual appearances did not produce significant priming-related effects in this right medial fusiform area, indicating that different views of the same familiar person may not activate the same neuronal population in this region. This finding provides a negative answer to the question of

whether the face of people known under different visual appearance may be represented within a single abstract visual template at perceptual stages. Even though we found that some view-independent traces were formed in the right medial fusiform for unfamiliar faces, these were not sufficient to generalize across the different appearances of famous faces used in our study. Note that such repetition decreases found in right medial fusiform for different images of unfamiliar faces is consistent with visual changes being relatively less important between pairs of unfamiliar faces than between pairs of famous faces used here, since our stimuli were deliberately chosen to make unfamiliar faces still recognizable across the different images (see Materials and methods). Behavioral studies show that even small changes in pictures (e.g., illumination direction) can severely impair recognition of unfamiliar faces (Braje et al., 1998), whereas recognizing familiar faces in degraded images is still very good (Burton et al., 1999).

Our results therefore go beyond previous imaging studies suggesting that long-term repetition effects for familiar and unfamiliar faces may arise in similar fusiform regions, when the exact same picture or viewpoint is used at each exposure (Eger et al., 2004; George et al., 1999; Henson et al., 2003; Vuilleumier et al., 2003a). Here, we show that view-independent coding of identity may occur in the right medial fusiform gyrus for novel faces, when different views are relatively similar and recognizable, whereas distinct face appearances of well-known people do not produce repetition effects in fusiform but in lateral temporal and inferior frontal cortex, where different views of the same person may be connected by a more abstract, non-visual representation of identity. These findings converge with evoked potential results from a long-term repetition priming paradigm (Jemel et al., 2003a) showing that famous faces repeated with different photographs modulate a late semantic component (N400), unlike the repetition of unfamiliar faces (see also Jemel et al., 2003b).

We note however that a region in left anterior fusiform cortex showed greater activation to famous than unfamiliar faces, irrespective of repetition. This is unlikely to reflect an attentional modulation (see Vuilleumier et al., 2001; Wojciulik et al., 1998) since the task made no demands on explicit identity recognition, RTs showed no difference between famous and unfamiliar faces, and any attentional modulation would not easily account for the selective left-lateralization of this familiarity effect. Therefore, our data corroborate previous results suggesting a differential response to face familiarity in left fusiform and parahippocampal gyri (Henson et al., 2000; Leveroni et al., 2000; Sergent et al., 1992), not found in a few other studies (Gorno-Tempini and Price, 2001; Shah et al., 2001). Moreover, a left anterior fusiform activation was previously observed for varied meaningful objects beyond faces (Bar et al., 2001; Ishai et al., 1999; Koutstaal et al., 2001; Vuilleumier et al., 2002), suggesting that this area may have a more general role in linking seen objects with pre-existing representations or semantic information about familiar visual stimuli (Buckner et al., 2000; Damasio et al., 1996).

Importantly, we found repetition decreases for famous faces in left lateral temporal and inferior frontal cortex, confirming a preferential activation of left hemispheric regions for famous faces relative to unfamiliar faces (Gorno-Tempini and Price, 2001; Gorno-Tempini et al., 1998; Henson et al., 2000), although bilateral temporal activations have also been reported (Leveroni et al., 2000; Sergent et al., 1992). In particular, our findings support a critical role of the left middle temporal gyrus, presumably

subserving the access to person-related semantic knowledge (Gorno-Tempini and Price, 2001; Vuilleumier et al., 2003b). Activation of personal semantic information from seen faces may occur even in situations where face identification is kept implicit, for example, in repetition priming experiments as used here (Ellis et al., 1990; Goshen-Gottstein and Ganel, 2000). Moreover, some degree of semantic activation may also occur with unfamiliar faces since these can covertly evoke an incomplete or fragmented semantic representation (Bruce and Young, 1986; Hancock et al., 2000), sometimes leading to false feelings of familiarity in normal subjects (Burton et al., 1991; Young et al., 1985) or false recognition in patients with left temporal lesions (Vuilleumier et al., 2003b). This covert activation of semantic associations might account for the fact that unfamiliar faces tended to produce similar, albeit smaller repetition effects in the left middle temporal gyrus, while famous faces produced much stronger effects.

Another striking result in our study was a dissociation within the left inferior frontal gyrus between its anterior (pars triangularis) and posterior (pars opercularis) sections, where repetition decreases occurred predominantly for famous versus unfamiliar faces, respectively (see Fig. 3). The left inferior frontal gyrus (e.g., BA 44/45) has often been involved in repetition priming (with faces, see Henson et al., 2003; with objects, see Koutstaal et al., 2001; Simons et al., 2003; Vuilleumier et al., 2002; with words, Buckner et al., 2000; Wagner et al., 2000). The more anterior/dorsal region might primarily be engaged during the activation of semantic information from memory (see Simons et al., 2003; Wagner et al., 2001), and therefore show greater activation for famous than unfamiliar faces only during their first presentation. Conversely, the more posterior region might be involved in encoding new stimuli, including unfamiliar faces, as shown for memory tasks (Haxby et al., 1996). Such encoding activity in left frontal cortex were paralleled by repetition effects in the left hippocampal/parahippocampal region, suggesting that memory processes can be engaged during incidental encoding of faces (Haxby et al., 1996; Leveroni et al., 2000), irrespective of previous familiarity.

Finally, we found repetition decreases selective for unfamiliar faces in several right hemisphere areas, including right parahippocampal and right retrosplenial cortex, as well as bilateral amygdala. All these regions are presumably involved in the initial response to novel faces (Schwartz et al., 2003) and may participate in the acquisition of new face representations (see Kosaka et al., 2003). Amygdala and retrosplenial activations may also reflect covert emotional appraisal of seen faces, modulated by previous familiarity or repetition. Retrosplenial activation might not be specific to faces but also sensitive to other social signals such as voices (Shah et al., 2001).

Our findings highlight the complex nature of neural systems involved in face processing (Haxby et al., 2001), encompassing several different processing stages from perception to memory. Whereas the functionally defined FFA showed only marginal effects of face familiarity and no reliable generalization across different face images, priming-related decreases for unfamiliar face identities occurred in medial fusiform and limbic areas of the right hemisphere, while famous face identities predominantly engaged temporal and frontal areas in the left hemisphere. Familiarity is a fundamental dimension in face recognition, with many neuropsychological distinctions established for famous vs. unfamiliar face processing (Bruce and Young, 1986; Burton et al., 1990; Ellis et al., 1990; Hancock et al., 2000). Further, changes in visual

appearance constitute a major challenge for the recognition system, since the face of a well-known person may take different aspects over time and across views. Our fMRI results suggest that recognition of known faces may involve more than just visual processing within abstract “face recognition units”, by demonstrating that the neural correlates of repetition effects for famous faces seen in different views involve higher-level semantic systems within frontotemporal cortex rather than perceptual systems in fusiform.

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