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The functionally defined right occipital and fusiform "face areas" discriminate novel from visually familiar faces

Bruno Rossion,*[,a,b,c] Christine Schiltz,[b] and Marc Crommelinck[b]

[a] *Unité de Neurosciences Cognitives, UCL, Belgium*
[b] *Laboratoire de Neurophysiologie, UCL, Belgium*
[c] *Department of Cognitive and Linguistic Science, Brown University, Providence, RI 02912; USA*

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Abstract

Neuroimaging (PET and fMRI) studies have identified a set of brain areas responding more to faces than to other object categories in the visual extrastriate cortex of humans. This network includes the middle lateral fusiform gyrus (the fusiform face area, or FFA) as well as the inferior occipital gyrus (occipital face area, OFA). The exact functions of these areas in face processing remain unclear although it has been argued that their primary function is to distinguish faces from nonface object categories—"face detection"—or also to discriminate among faces, irrespective of their visual familiarity to the observer. Here, we combined the data from two previous positron emission tomography (PET) studies to show that the functionally defined face areas are involved in the automatic discrimination between unfamiliar faces and familiar faces. Consistent with previous studies, a face localizer contrast (faces–objects) revealed bilateral activation in the middle lateral fusiform gyrus (FFA, BA37) and in the right inferior occipital cortex (OFA, BA19). Within all the regions of the right hemisphere, larger levels of activation were found for unfamiliar as compared to familiar faces. These results suggest that the very same areas involved in categorizing faces at the basic or individual level, play a role in differentiating familiar faces from new faces, showing an overlap between visual and presemantic mnesic representations of faces in the right hemisphere.

Keywords: Fusiform gyrus; Inferior occipital cortex; Face recognition; PET; Neuroimaging

Introduction

Understanding how the human brain perceives and recognizes faces has become one of the most exciting and debated areas of research in cognitive neuroscience (e.g., Kanwisher, 2000; Haxby et al., 2000; Tarr and Gauthier, 2000). Pursuing this general goal, neuroimaging studies have localized a set of brain areas in the human visual extrastriate cortex that respond more during the presentation of faces than to other object categories. These areas are located mainly in the middle lateral fusiform gyrus (the fusiform face area (FFA), Kanwisher et al., 1997), and in the inferior occipital gyrus (infOg, occipital face area (OFA), e.g., Halgren et al., 1999), with a right hemisphere advantage. Being located beyond the retinotopic striate and extrastriate visual cortices, the exact anatomical borders of these regions cannot be defined with respect to other visual areas (Halgren et al., 1999). Accordingly, their localization is based on functional criteria, i.e., a significantly larger response for pictures of faces than other objects (Kanwisher et al., 1997). An important and unresolved issue is whether the face areas are involved in perceptual aspects of face processing only, helping to discriminate between faces and other object categories ("face detection," Tong et al., 2000) or between different unfamiliar faces (Gauthier et al., 2000), or if they also contribute to presemantic face recognition, i.e., the discrimination between a face previously seen and a novel face. Despite the computational complexity of this task, humans are particularly efficient at it, even when the

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* Corresponding author. Unité de Neurosciences Cognitives (NESC), UCL, Place Cardinal Mercier, 10, 1348 Louvain La Neuve, Belgium. Fax: +32-10-47-37-74.

E-mail address: bruno.rossion@psp.ucl.ac.be. or Bruno_Rossion@brown.edu (B. Rossion).

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"familiar" face has been encountered just once, months or years ago (Bruce and Young, 1998). Because recognizing familiar faces and encoding new faces in memory appear to be the primary functions of the face processing system, it would be surprising that the areas forming the core of the face processing system (Haxby et al., 2000) do not play any role in these functions. In addition, the inability to recognize and encode faces in memory is exactly what defines *prosopagnosia*—a deficit usually observed following lesions of the occipitotemporal cortex—but these patients do not usually present difficulties at discriminating faces from other object categories (e.g., Bruyer et al., 1983).

In healthy humans, the processing of familiar and unfamiliar faces has been compared in a number of imaging experiments (Haxby et al., 2000; Henson et al., 2000, 2002; George et al., 1999; Gorno-Tempini et al., 1998; Gorno-Tempini and Price, 2001; Katanoda et al., 2000; Leveroni et al., 2000; Rossion et al., 2001; Sergent et al., 1992; Wiser et al., 2000), but none of these studies tested the hypothesis that the *exact* same functional regions that respond more to faces than to other object categories, are *also* involved in familiar vs novel face discrimination. In addition, in the previous literature, there are a number of task and stimuli confounds that prevent a straightforward interpretation of activation differences produced by familiar and unfamiliar faces in visual areas (see Rossion et al., 2001).

Here, we tested the hypothesis that the functionally defined face areas differentiate between visually familiar and novel faces, using a multistudy analysis of the data of two previously reported PET experiments (Rossion et al., 2000a, 2001) carried out on the same eight male subjects. The data from the first study (Rossion et al., 2000a) were used to functionally define the areas responding significantly more to faces than to objects in this group of subjects, and these regions were then tested for familiar/unfamiliar face differences in the same subjects scanned later.

Materials and methods

Participants

Eight right-handed adult male subjects (age range: 22–25) took part in both PET studies, the two scanning sessions being performed at 4 to 6 weeks interval time.

Stimuli

Details of stimulation can be found in Rossion et al. (2000a) for the localizer task, and in Rossion et al. (2001) for the familiar/unfamiliar face comparisons. In the first study (localizer task), subjects underwent 12 scans, half of them with presentations of faces, and the other half with objects. In the second study, 30 novel photographs of visually familiar (learned) faces were morphed with 30 unknown faces and six images were extracted for each of the 30 face-pairs, at 20% increments of unfamiliar–familiar mixture (steps): 0%, 20%, 40%, 60%, 80%, 100% familiar.

General Procedure

In the first PET experiment, subjects were required to perform a delayed matching task on either faces or objects (central fixation cross 200 ms, ISI 250 ms, probe stimulus 1000 ms, ISI 500 ms, target stimulus 1000 ms; intertrial interval: 1600 ms of black screen). Before the second experiment, subjects underwent an extensive familiarization procedure (about 3 h total) with 30 photographs of faces during 2 days (see Rossion et al., 2001, for details) and performed a rapid test of familiarity decisions ("known–unknown") the third day (all scores between 28 and 30, mean RTs of 886 ms).

An independent group of subjects performed a "known–unknown" decision task on all the faces of the continua (30 × each step (i.e., six) = 180 faces), to show that the whole set of faces could be divided into two subsets: faces perceived as unfamiliar (0%, 20%, 40%), and faces perceived as familiar (60%, 80%, 100%; see Rossion et al., 2001).

Fourteen PET scans were recorded the day after training: two rest scans, six scans during which unfamiliar faces were presented (two scans for each step: 0%, 20%, 40%), and six scans during which familiar faces were presented (two scans for each step: 60%, 80%, 100%). For the experimental conditions, the images were selected as to avoid as much as possible the repetition of unfamiliar information. In addition, new photographs of the familiar faces were used during scanning. The order of the experimental scans was randomized across subjects. In each scan, 10 faces were presented (3 s on the screen, 2 s black screen interval). In order to maintain their attention on the faces throughout the scans, subjects were asked to press a right or left key of a response box according to the sex of the face. Half of the faces were male, the other half female in each scan.

PET scanning

Measurements of local radioactivity uptake were made using an ECAT EXACT-HR PET tomograph (CTI/Siemens), imaging 47 transaxial slices (thickness 3.125 mm) in 3D mode (effective resolution of 8 mm FWHM). rCBF measurement was performed using a 20 s bolus of oxygen-15-labeled water (8 mCi, 2.96 e+02 MBq). The task started 10 s after initiation of tracer injection, and PET data were acquired simultaneously. The integrated counts accumulated during 50 s scans (faces vs objects experiment) and 90 s (familiar vs unfamiliar faces) were used as an index of regional cerebral blood flow (rCBF). The time interval between successive scans was 13 min, which allowed decay of residual radioactivity. All images were reconstructed using standard software including scatter correction with both transaxial Hanning filter (cutoff frequency of 0.30) and axial Hanning filter (cutoff frequency of 0.50). For each subject, 3-D MRI anatomical data were also obtained on a 1.5 Tesla unit (GE) using the Spoiled Grass (SPGR) technique. T-1 weighted images (TR = 25 ms, TE = 6 ms, flip angle = 25°, slice thickness = 1.5 mm) were obtained in the bicommissural (AC–PC) orientation.

PET analysis methods

PET images were realigned and coregistered to the subject's MRI using AIR 3.0 (Woods et al., 1992), spatially normalized, using SPM 96 [Wellcome Department of Cognitive Neurology], in the Talairach and Tournoux (1988) coordinate system with a cubic ($2\times2\times2$ mm) voxel size, smoothed using an isotropic Gaussian filter of 15 mm FWHM, and corrected for global activity by proportional scaling (Fox et al., 1988). All statistical analyses were performed in SPM 99 [Wellcome Department of Cognitive Neurology]. A multistudy design with replications and a covariate of noninterest was used. Two conditions (faces and objects) were included in the first study (six replications for each condition), and six conditions (0%, 20%, 40%, 60%, 80%, 100% familiar) in the second study. The covariate of noninterest modeled the effect of response times. In order to identify the regions showing significant rCBF changes, statistics were computed on a voxel-by-voxel basis, using the general linear model (Friston et al., 1995). All scans on faces were compared to all scans on objects in the first study, giving the localizer contrast. This contrast was used as a "mask" for the familiar and unfamiliar faces comparisons, such that only regions of voxels being more activated for faces than objects were tested further. The scans of the experimental conditions were grouped according to whether they contained faces perceived as unfamiliar (0%, 20%, 40%) or familiar (60%, 80%, 100%) and these two pools of conditions were subtracted from each other. A complementary analysis used a conjunction analysis (Price and Friston, 1997) between the localizer contrast (faces–objects) and the contrasts of interest (familiar–unfamiliar), showing the regions that are significantly activated ($P < 0.05$ corrected for multiple comparisons in the whole brain) in both of the orthogonal contrasts (faces–objects) and (familiar–unfamiliar).

Behavioral results

On average, subjects were equally efficient and quick to process faces (91%; 911 ms) and objects (94%; 932 ms) in the first experiment ($t_7 = 1.943$; $P > 0.05$). In the second experiment, performance rates ranged between 94% and 98% for the different conditions. Mean response times (ms) were as follow (from 0% to 100%): 1031; 1028; 1061; 992; 898; 858. An ANOVA1 for repeated measurements performed on these values showed a significant effect of condition ($F_{1,7}$: 4.383; $P = 0.003$). As described previously, subjects appeared to be quicker on faces perceived as familiar (60%, 80%, 100%) and this was confirmed by a post hoc *t* test comparing these conditions to the conditions in which faces are perceived as unfamiliar ($t_7 = 2.539$, $P = 0.04$).

PET results

The *faces–objects* comparison ($P < 0.0001$, uncorrected) revealed bilateral activation in the *middle fusiform gyrus* (FFA, right: 38 −44 −28; left: −42 −50 −26; BAs37) and in the *right occipital inferior gyrus* or *posterior lateral fusiform region* (OFA, 44 −76 −14; BA19), as previously described (Rossion et al., 2000a). Within the right FFA and right OFA, a larger level of activity was found for unfamiliar faces as compared to familiar faces. At a threshold of $P < 0.05$ (uncorrected) applied to the regions defined by the masking procedure, 48% of the face-specific contiguous voxels in the right FFA were more activated for unfamiliar faces than familiar faces (Fig. 1) (maxima: 40 −38 −28, $P = 0.004$), and 82% in the right OFA (maxima: 46 −80 −16, $P = 0.024$). Statistical analysis performed on the face-specific regions as volumes of interest (eight voxels box centered on the maxima of activation in the localizer contrast) showed that the right FFA was largely more responsive to novel than familiar faces ($P = 0.024$ corrected for multiple comparisons within a box of eight voxels; Table 1 and Fig. 2), and the right OFA was marginally significant ($P = 0.066$).

The conjunction analysis (*faces–objects and unfamiliar–familiar faces*) showed that the right middle fusiform region was activated in both cases (40 −36 −26, $P = 0.019$ corrected for multiple comparisons in the whole brain).

Discussion

The main conclusion of our multistudy analysis is that the functionally defined right fusiform face area and also the right occipital face area, at a lower level, are involved in the discrimination of familiar from unfamiliar individual faces. These results complement our previous study (Rossion et al., 2001), in which we identified a network of visual areas activated by faces compared to a baseline resting condition and modulated by visual familiarity of the faces. In that study, the activations were restrained to the right hemisphere, i.e., the right middle occipital, the posterior fusiform, and the inferior temporal gyri. However, this last study left unanswered the question whether face-selective voxels located using a classical localizer task comparing faces vs objects (e.g., Gauthier et al., 1999, 2000; Kanwisher et al., 1997) were also sensitive to long-term visual face familiarity (Rossion et al., 2001). Consequently, the observation of a differential activation for unfamiliar and familiar faces in the right FFA and OFA in the present study is not a consequence of a less conservative threshold used in the analysis, but of the opportunity to run a conjunction analysis with the faces–objects and the familiar–new faces comparisons. In fact, the right OFA is part of an area of activation identified in our previous study, but it was unclear

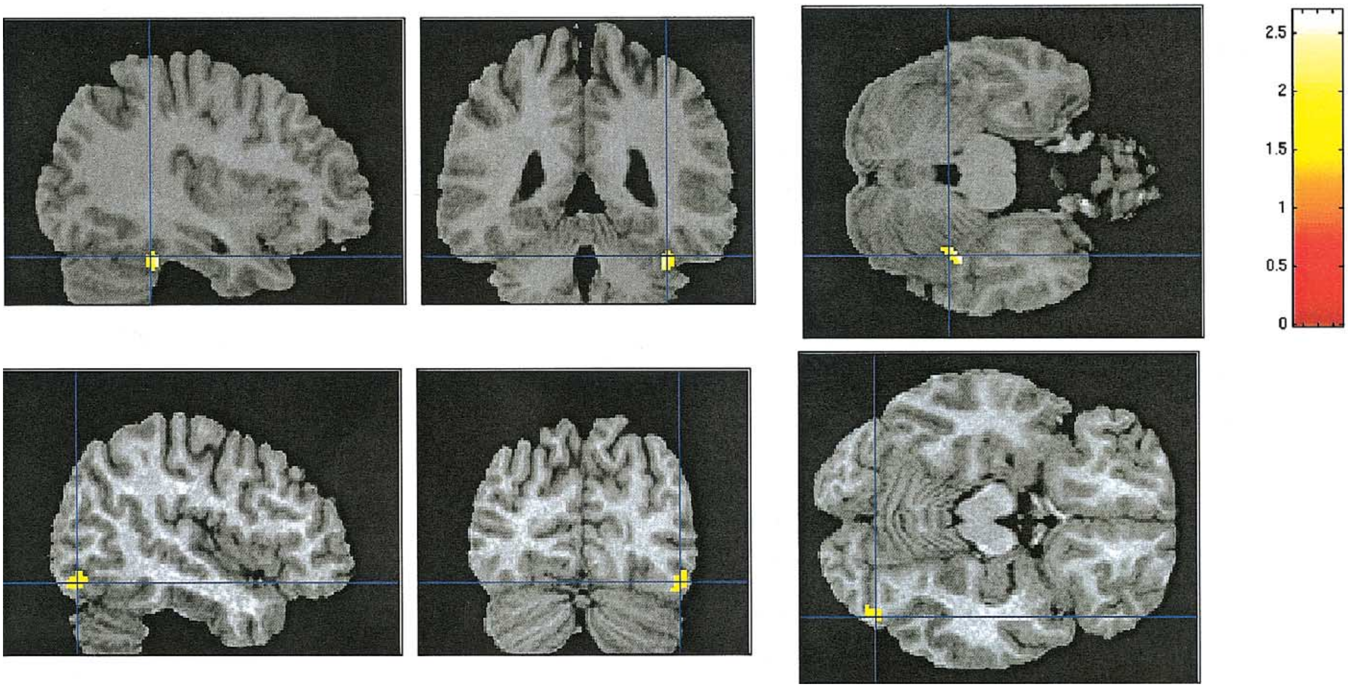

Fig. 1. The localization of the face-sensitive regions in the right middle fusiform gyrus (top) and the right inferior occipital cortex (bottom), where a larger response was observed for unfamiliar compared to familiar faces. The regions of activation in the group analysis have been superimposed on a segmented normalized MRI of a single subject of this study.

whether these voxels also played a role in face vs object discrimination. As for the FFA described in the present study, it was found to be larger for unfamiliar faces at a very conservative threshold ($P = 0.004$) in the masking procedure, given that the a priori hypothesis restricted the testing to three regions in the present analysis.

Considering our previous findings and the current observations altogether, one has to conclude that familiar and unfamiliar faces are discriminated at the level of a network including visual extrastriate regions presenting a face-selective response, but also regions that do not present such a face-selectivity such as the right inferior temporal cortex (BA 20) and the right middle occipital gyrus (see Rossion et al., 2001). Our study does not test whether these effects of familiarity also stand for other object categories in these regions. It may even well be that the effects of long-term familiarity reported here would be found for other object categories, as recent fMRI evidence suggests that even within the face "selective" areas, there are small subsets of neurons responding to nonoptimal stimuli (nonface objects) which are also sensitive to adaptation (repetition, see Avidan et al., 2002).

Before discussing the theoretical implications of the present findings, a couple of methodological points should

Table 1
Faces–objects comparison

Region	Side	*x*	*y*	*z*	Faces–objects			Novel faces–familiar faces	
					Size (voxels)	*t* score	*P* (uncorr.)	*t* score	*P* (corr.)
Middle fusiform gyrus (rFFA)	R	38	−44	−28	99	4.67	$<10^{-4}$	2.69	0.024
Posterior fusiform gyrus (rOFA)	R	44	−76	−14	51	4.40	$<10^{-4}$	1.94	0.066
Middle fusiform gyrus (lFFA)	L	−42	−50	−26	31	4.27	$<10^{-4}$	—	—

Regions where relative increases in brain activity associated with face processing compared to visual object processing were found (face-selective regions, $P < 10^{-4}$ uncorrected for multiple comparisons), and their differential response to unfamiliar and familiar faces (P values corrected for multiple comparisons for the volume of interest, a 4 mm radius, i.e., eight voxels box centered on the coordinates of the most face-specific voxel). Coordinates (in standard stereotaxic space; Talairach and Tournoux, 1988) refer to maximally activated foci as indicated by the highest Z score within an area of activation. *x,* distance (mm) to right (+) or left (−) of the midsagittal line; *y,* distance anterior (+) or posterior (−) to the vertical plane through the anterior commissure; *z,* distance above (+) or below (−) the bicommissural (AC-PC) line.

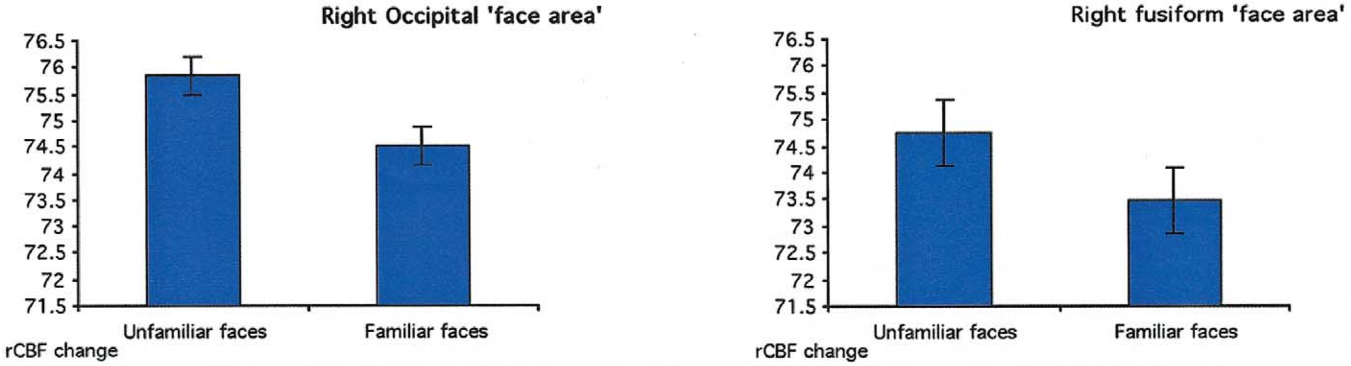

Fig. 2. Corrected blood flow values (mean = 50) and standard deviations for the conditions using familiar and unfamiliar faces in the two regions where larger responses were for faces than for objects.

be added. First, it is important to note that these effects are not related to a simple *image familiarization;* none of the pictures presented during the PET experiment had actually been presented during training (see Rossion et al., 2001). Second, it should be noted that the procedure used to functionally localize the FFA and OFA in PET is identical to previous fMRI studies, although here these regions were functionally defined in a group analysis only, not individually. This was mandatory, due to the lower signal-to-noise ratio of PET compared to fMRI, where more repetitions of the same conditions can be performed in the same subject. Accordingly, the individual data were spatially smoothed with a larger kernel than in fMRI studies and averaged across subjects. This gives regions of interest of a larger number of voxels than the usually described FFAs and OFAs defined in individual subjects. Nevertheless, it is worth noting that the overall size of the FFA and OFA defined in our group is roughly similar to what is usually found in fMRI studies, due to the smaller size of the voxels in our study (3 × 3 × 3 mm) compared to previous fMRI studies (e.g., Kanwisher et al., 1997; Gauthier et al., 2000). Thus, even if functional images obtained by PET and fMRI differ in their spatial resolutions and signal-to-noise ratios, by running the same subjects in the two PET studies, we ensured in the present report that *all* the voxels that are tested for face familiarity effects show a statistically significant increase for pictures of faces compared to pictures of objects. This would have been impossible by simply using the coordinates reported in the literature.

Combined with previous findings (Gauthier et al., 2000; Tong et al., 2000), the present findings suggest that several basic functions of the face processing system—namely face detection, individual discrimination, and presemantic recognition—are carried out by an overlapping set of brain areas rather than by distinct networks, or differently localized brain regions. These findings are consistent with lesion studies of prosopagnosia because the prosopagnosic deficit is best characterized by the inability to distinguish between previously seen and novel faces, usually following a bilateral or right-sided occipitotemporal lesion (e.g., Barton et al., 2003; Damasio et al., 1982; Landis et al., 1988). Provided that an adequate testing of visual functions is performed, several pieces of evidence indicate that this inability to recognize faces is due to perceptual deficits at the level of face discrimination, even in the case of "associative" (prosop)agnosia (Barton et al., 2003; Farah, 1990). In short, both the perceptual and mnesic aspects of face processing appear to be impaired in prosopagnosia, following lesions of the fusiform gyrus.

However, discrimination of faces and objects on the one hand, and of between familiar and unfamiliar faces on the other hand, may occur at different time- scales in these overlapping brain areas. For instance, signal information processing analysis of face-selective cells in the inferior temporal cortex of monkeys have shown that identical single neurons can convey at least two different types of information about faces in their firing patterns (Sugase et al., 1999), coding for both face–object differences and individual face differences at different (short) time scales. Consistent with this suggestion, event-related potential (ERPs) recordings in humans indicate that the discrimination of faces and objects occurs between 100 and 170 ms in occipitotemporal cortex (e.g., Bentin et al., 1996; Rossion et al., 2000b), whereas familiar/unfamiliar face differences do not appear before 250 ms in the electrophysiological responses (e.g., Eimer, 2000). This suggests that the overlapping brain regions discriminating faces from objects, and familiar from unfamiliar faces, may indeed be involved at different time scales. Intracranial recordings are also consistent with this view (Puce et al., 1999).

Neuroimaging studies also support the hypothesis that perceptual and mnesic aspects of face processing are associated with largely overlapping neural substrates in the ventral occipital and occipitotemporal cortex. For instance, forming a mental image of a familiar face has been shown to increase the activation of the FFA (O'Craven and Kanwisher, 2000). A number of previous neuroimaging studies have also found differences at different locations in the fusiform gyrus during the processing of familiar and unfamiliar faces, albeit without using a *faces–objects* localizer to identify the face areas. Some have described greater activation for familiar than unfamiliar faces (e.g., Henson et al., 2000; Katanoda et al., 2000) or decreases for familiar faces (Dubois et al., 1999; Rossion et al., 2001). Yet others, however, have not described any differences (Leveroni et al., 2000; Nakamura et al., 2000). The comparison across these studies is difficult because they used different paradigms, tasks, and stimuli, and different regions were analyzed. Nevertheless, it is worth noting that most studies that found an increase for familiar faces usually used an explicit face recognition task (e.g., Katanoda et al., 2000; Sergent et al., 1992; Henson et al., 2002), which does not give an equal status to familiar and unfamiliar faces, whereas decreases to familiar faces were more systematically found in studies using an indirect task (Dubois et al., 1999; Henson et al., 2000; Rossion et al., 2001). Using such a task, Henson et al. (2000) found that repetition of familiar faces was associated with a reduced response in the right lateral fusiform region, whereas the same region increased its activation following the repetition of unfamiliar faces. The reduced response for familiar faces was attributed to lowered thresholds for activating perceptual representations of familiar faces, consistent with behavioral studies of perceptual priming (e.g., Ellis et al., 1990), whereas the enhanced response for unfamiliar faces was attributed to the gradual formation of new perceptual representations (Henson et al., 2000). This proposal would be a reasonable functional explanation of our findings at the level of the face areas.

Because it has been reported that visual attention directed to faces can increase the response of the right fusiform area (Wojciulik et al., 1998), one might argue that less attentional resources may have been devoted to the processing of familiar faces during the scanning. However, the covariate of noninterest modeling response times extracted the variance related to the different processing durations in the gender discrimination task. Consequently, the significant regions reported in the contrast (unfamiliar –familiar faces) appear to be related to the different degrees of familiarity of the presented faces. There is only one alternative explanation for the differences between familiar and unfamiliar faces in these regions observed in the present study, which we cannot rule out. Because faces were presented in blocks, the subjects might have adopted different perceptual strategies for familiar and unfamiliar faces throughout each block (Rossion et al., 2001). Thus, we cannot exclude the possibility that subjects used different visual strategies to perform the task on familiar and unfamiliar faces (e.g., Hosie et al., 1988), leading to differential activations in regions specialized to analyze faces. Using localizer tasks in event-related fMRI studies may help clarify this point. This latter explanation assumes that the reduction/increase of neural activation for visually familiar/unfamiliar faces is mainly a consequence of their recognition as familiar or unfamiliar faces, and arises from feedback originating for instance in more anterior regions of the temporal lobe involved in famous face processing (e.g., Gorno-Tempini et al., 1998; Leveroni et al., 2000). However, in the present design, familiar faces were not associated with any semantic information, in contrast to famous faces, and thus did not lead to any increase of activation in the anterior temporal cortex, consistent with previous observations (Leveroni et al., 2000). Consequently, in agreement with the existing neuropsychological, behavioral, neurophysiological, and neuroimaging literature, as discussed above, we propose that the differences of activation found in face-sensitive areas between familiar and unfamiliar faces during the visual processing of these stimuli play a direct role in the discrimination of familiar and unfamiliar faces. Accordingly, we hypothesize that in an event-related fMRI study, differential activity related to novel and familiar faces should be observed in the functionally localized right fusiform face area.

An observation that is also in agreement with lesion, electrophyiological, and behavioral studies is the dominant role of the right hemisphere in both the perceptual analysis and the recognition of faces (e.g. Landis et al., 1988; Bentin et al., 1996; Hillger and Koenig, 1991). When the whole brain is tested in neuroimaging studies, a larger number of voxels in the right hemisphere (RH) present a higher response to faces than to objects (Kanwisher et al., 1997; McCarthy et al., 1997; Rossion et al., 2000a). However, even more strikingly, within this subset of regions involved in face processing, our study shows that there is an additional large right hemispheric bias for the discrimination of familiar and unfamiliar faces; all the effects of face familiarity are found in the right occipital and occipitotemporal cortex. This suggests that the RH is dominant, almost in an additive way and in overlapping regions of the visual cortex, for both the visual categorization of faces and their discrimination based on previous experience.

Finally, the observation that the activity of highly specialized visual areas in the occipital and occipitotemporal cortex can be modified by a few hours of training should be pinpointed. Previous neuroimaging studies have shown that extensive training at processing nonface objects led to modulations of activation in the fusiform face areas (Gauthier et al., 1999). The present study goes a step beyond these findings by showing that these modulations of the level of neural activity in highly specialized regions can be found even for the visual category for which these visual areas are the most selective for (i.e., faces).

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