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Effect of Familiarity on the Processing of Human Faces

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Most brain imaging studies on face perception have investigated the processing of unknown faces and addressed mainly the question of specific face processing in the human brain. The goal of this study was to highlight the effects of familiarity on the visual processing of faces. Using [^{15}O]water 3D Positron Emission Tomography, regional cerebral blood flow distribution was measured in 11 human subjects performing an identical task (gender categorization) on both unknown and known faces. Subjects also performed two control tasks (a face recognition task and a visual pattern discrimination task). They were scanned after a training phase using videotapes during which they had been familiarized with and learned to recognize a set of faces. Two major results were obtained. On the one hand, we found bilateral activations of the fusiform gyri in the three face conditions, including the so-called fusiform-face area, a region in the right fusiform gyrus specifically devoted to face processing. This common activation suggests that different cognitive tasks performed on known and unknown faces require the involvement of this fusiform region. On the other hand, specific regional cerebral blood flow changes were related to the processing of known and unknown faces. The left amygdala, a structure involved in implicit learning of visual representations, was activated by the categorization task on unknown faces. The same task on known faces induced a relative decrease of activity in early visual areas. These differences between the two categorization tasks reveal that the human brain processes known and unknown faces differently. © 1999 Academic Press

Key Words: **positron emission tomography; cerebral blood flow; face processing; familiarity; gender categorization.**

INTRODUCTION

Face perception is an essential process in social life, allowing the evaluation of the degree of familiarity, the emotional state, the social status and the gender, as well as the identification of conspecifics. The importance of face perception is dramatically revealed when one loses the ability to recognise known faces. Numerous neuropsychological studies devoted to this face agnosia, or prosopagnosia (since Bodamer, 1947, 1990), have revealed that it is not an homogeneous syndrome (Tranel *et al.*, 1988; McCarthy and Warrington, 1990; Sergent and Signoret, 1992; Schweich and Bruyer, 1993). Such observations as well as behavioral data from experimental studies on normal subjects led Bruce and Young (1986) to propose a cognitive architecture of face processing (Fig. 1).

According to this model, a first structural encoding stage extracts a three-dimensional invariant representation from different views of the same face. This stage, common to all kinds of faces (e.g., known and unknown), is followed by two independent routes. The first route allows the recognition of the face and the person, whereas the second concerns visual operations which are not mandatory for the recognition process per se, but are made in parallel to it: lip-reading behavior, analysis of facial expression and extraction of semantic information from surface facial features (age, gender, race, etc.). Neuropsychological findings are in agreement with this dissociation (Sergent and Signoret, 1992; Schweich and Bruyer, 1993). For instance, double dissociations between face recognition and facial expression processing (Young *et al.*, 1993), or between face recognition and lip-reading abilities (Campbell *et al.*, 1986) have been described. However, no double dissociation between gender processing and recognition has yet been reported (Bredart and Bruyer, 1994). This negative result is in line with behavioral data showing a preferential processing of internal face features in the presence of familiar faces (Young *et al.*, 1985; Hosie *et al.*, 1988). Such an observation argues for the existence of an effect of familiarity on the visual processing of faces and thus contrasts with the independence of the two processes as predicted by the Bruce and Young model (1986).

Despite the fact that several imaging studies have investigated the specificity of face processing as compared to other objects (Puce *et al.*, 1996; Kanwisher *et al.*, 1997b; McCarthy *et al.*, 1997), the encoding and the recognition of faces (Kapur *et al.*, 1995; Haxby *et al.*,

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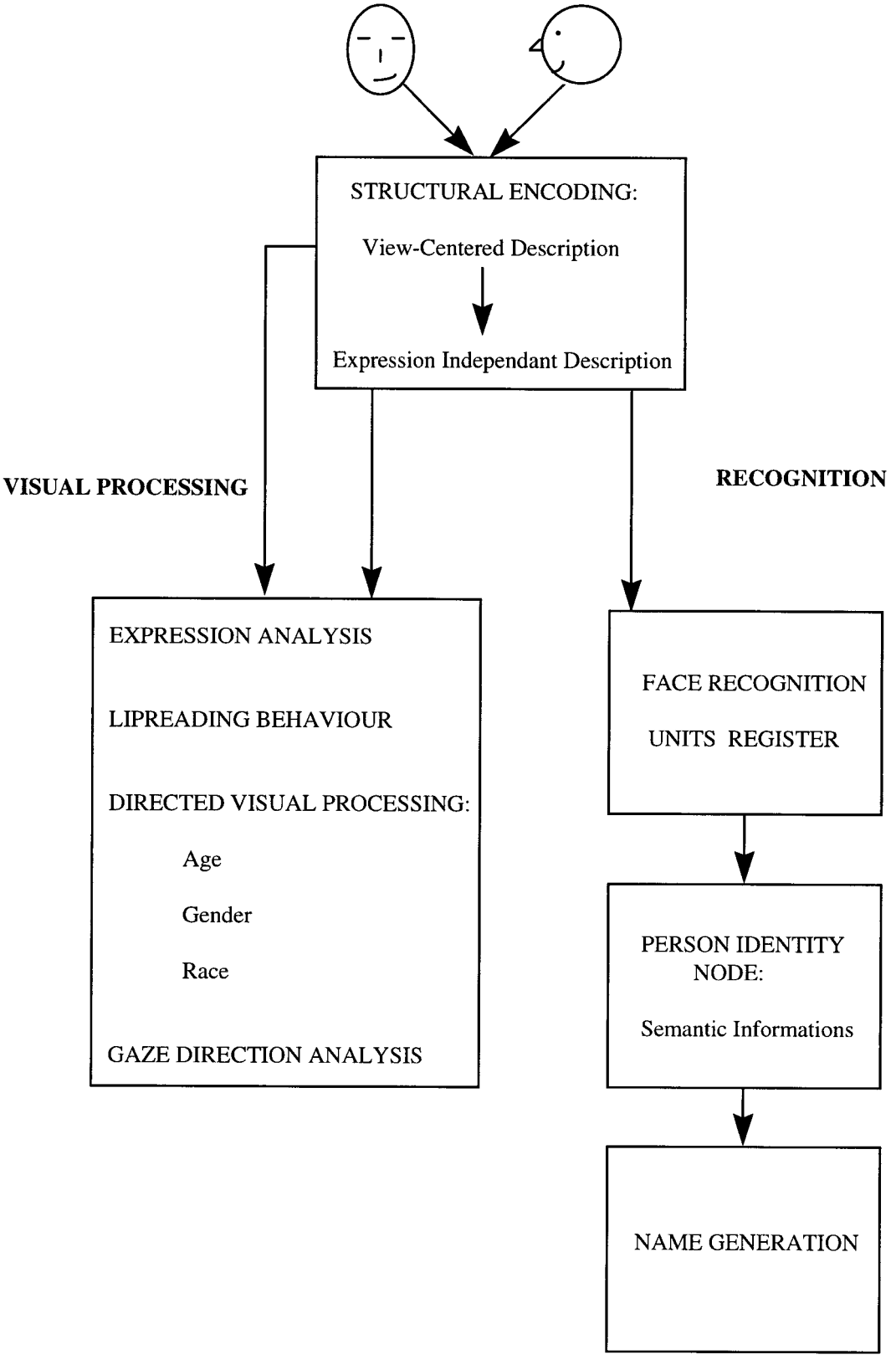

FIG. 1. Functional architecture of face processing described by Bruce and Young (1986; with permission). After a common stage for all perceived faces, two separates series of cognitive operations can be executed in a parallel and independent way.

1996), the working memory for faces (Haxby *et al.*, 1995; Courtney *et al.*, 1996) and the processing of facial expressions (George *et al.*, 1993; Sergent *et al.*, 1994; Morris *et al.*, 1996, 1998a, 1998b) a precise attribution of brain regions to the different operations described by the cognitive model (Bruce and Young, 1986) has not yet been made. The seminal PET study of Sergent and colleagues (1992) described different patterns of activation related to the processing of known and unknown faces: a gender categorization on unknown faces activated mainly the ventral surface of the right occipito-temporal cortex, while an identification of famous faces activated a more anterior ventro-temporal region including the right parahippocampal gyrus. However, these results cannot be unequivocally attributed to the familiarity of faces as, in this study, both the tasks (gender categorization and recognition) and the faces (unknown and well-known) were different. Moreover, the use of well-known faces (celebrities) prevented the control of implicit access to semantic knowledge associated with these faces (Bruce, 1983; Bruce and Valentine, 1986).

The present PET study investigates the effect of familiarity on the processing of faces by the human brain. In our study, we consider familiarity as a feeling of "already-seen" when perceiving faces of known persons. Thus, it corresponds to the main impairment of prosopagnosia, i.e., an inability to experience a feeling of familiarity when viewing faces of known individuals (Sergent, 1991, 1994). To investigate this familiarity effect, the subjects performed one main task: a gender categorization task which was executed either on unknown (G_U) or on known faces (G_K). The two other tasks used in the study were a visuomotor discrimination task (Dis), which allowed to subtract away neural activity related to general sensory and motor operations, and a face recognition task (Rec), controlling for explicit recognition of the stimuli. To avoid an automatic semantic activation (as could occur in the presence of famous faces), we used a long-term visual face familiarization with videotapes showing persons in action. This procedure, during which subjects were not given any information about the presented persons, allowed us to produce purely visual long-term representation of faces. Two major hypotheses were made: first, we expected the activation of a common network in all face tasks. Indeed, according to Bruce and Young (1986), any face, known or unknown, initially proceeds through identical stages (i.e., the structural encoding stage). More precisely, among this common network, we expected the activation of the fusiform-face area (FFA), recently described by Kanwisher and colleagues (1997b), according to which this fusiform region is specifically dedicated to the processing of faces. Second, the study aimed to highlight possible processing differences between known and unknown faces while the task performed on both kinds of faces was matched and the familiarity of the faces was purely visual. Thus, regarding the importance of familiarity decisions on faces in our social life, we also expected processing differences between known and unknown faces in other brain regions such as the medial temporal lobe. Indeed, considerable evidence exists to support the hypothesis that medial temporal lobe structures are crucial for encoding novel information and visual recognition memory (Tulving *et al.*, 1994, 1997; Stern *et al.*, 1996).

MATERIAL AND METHODS

Subjects

Eleven right-handed normal male volunteers, between 18 and 28 years (mean 23 $\pm$ 3), took part in the study. All were drug-free, without any reported neurological disease, and showed no abnormality on their T1-weighted magnetic resonance images (MRI). Informed written consent was obtained from each subject. The experimental procedures were approved by the ethical committee of the Catholic University of Louvain. Seven of those subjects participated later on in a second experiment dealing with the processing of semantic and lexical knowledge associated with faces (paper in preparation).

Procedure and Equipments

The experiment comprised two phases, a training phase and an experimental phase, each using specific material and procedures.

1. Material and Procedure of the training phase. The training phase preceded the PET experiment and extended over three consecutive days. A videotape and a set of 40 printed photographs were used during this phase. The colored videotape lasted 14 min and presented 20 persons, 10 males and 10 females, appearing in an alternative order. All posers were young adults between 20 and 30 years old. They were instructed to come into an office, sit down on a chair, and write a letter at a desk. All were videotaped for 40 s during which they had to raise their head twice, showing right and left ¾ profile views to the camera. All photographs used during the training phase were printed in 16 grey-levels on paper sheets and represented faces of young adults oriented in ¾ profile. Half of these photographs represented unknown faces, the other half represented the faces of the persons appearing on the video.

On the first day, subjects were shown the videotape focusing on faces. Immediately after the presentation, a recognition test took place: subjects were given the set of 40 photographs of faces. Half of them corresponded to the persons presented on the videotape and the other half contained unknown distractor faces. Subjects had to categorize the photographs in two samples: the faces

previously seen in the videotape and the distractors. Whatever the subject's performance in this task, the videotape was then presented one more time. On the second day, subjects were first tested with the same set of 40 photographs, then watched the videotape again. On the third day, the test was presented a last time: all subjects recognized the 20 photographs corresponding to the persons shown on the videotape. At the end of the training phase, the persons appearing on the videotape (the known faces) had been seen three times on the video, each time during 40 s. The total exposure time for each face was thus 120 s. Additionally, each face had also been seen three times on paper sheet during the recognition tests.

2. Material and Procedure of the experimental phase. During the experimental phase, taking place on the fourth day, all subjects underwent 12 regional cerebral blood flow (rCBF) measurements with PET under four conditions. Each condition was repeated three times in a pseudo-random order. Stimuli were displayed in 16 grey-level using an Amiga Commodore A1200 computer. The monitor (Zenith) was positioned at the distance of 113 cm in front of the subjects so that stimuli did not exceed 4° of visual angle, which roughly corresponds to the size of the fovea. Such a display was used to avoid the occurrence of exploratory eye movements. Each stimulus was presented during 1 s with an interstimulus interval of 2 s (black screen), resulting in a presentation rate of one stimulus every 3 s. Each condition was composed of a sequence of 30 different stimuli and lasted 90 s. The mean luminance was identical in all conditions (7,5 Cd/m^2). Response accuracy and response times (RTs) were recorded by the computer. Three different sets of face photographs were used. All three sets contained 30 photographs representing young adults oriented ¾ profile. The first set (Set 1) consisted of unknown faces (these faces had never been seen by the subjects). The second set (Set 2) consisted of known faces (i.e., the faces of the persons seen on the videotape during the learning session). In these two sets, half of the faces were male, the other half female. Finally, the third set (Set 3) consisted of 15 known and 15 unknown faces (the unknown faces were different from those used in Set 1).

During the first control task, the discrimination task (Dis), subjects had to discriminate the presence of dots (one or two) on a visual pattern which had the same visual complexity as faces (Haxby *et al.*, 1994). Subjects were told to press the left or right mouse button (using the right hand), respectively, when one or two dots were presented. Half of the stimuli contained one dot and the other half contained two dots. In a second control task, the recognition task (Rec), Set 3 was presented and subjects had to decide whether the presented face was known or unknown. Response was given by pressing left (known) or right (unknown) mouse button using, respectively, the index or the middle finger. Finally, subjects performed a gender categorization task, which was made on known (G_K) and unknown (G_U) faces. In these two conditions, subjects had to press the left or right button according to the gender of the face (male or female, respectively). During the G_U task, Set 1 was presented, while during the G_K task, Set 2 was presented. Each of these four conditions was repeated three times. Thus, during scanning, each set of photographs was viewed three times by the subjects.

Data Acquisition, Image Reconstruction, and Analysis

Relative rCBF was measured by recording the distribution of cerebral radioactivity following the intravenous injection of $H_2^{15}O$. Twelve 60-s scans were obtained for each subject with an interscan interval of 12 min to allow decay of residual radioactivity between consecutive scans. Tasks started simultaneously with the injection and lasted for 90 s. The execution of the tasks outlasted the acquisition time to obtain additional behavioral data. The experiment was divided in three blocks during which the four tasks were executed in a random order. The head of each subject was fixed on the head holder by an elastic bandage and the position of the head was systematically controlled before each injection and readjusted if necessary.

Measurement of local radioactivity was carried out by scanning the whole brain with a Siemens CTI/ECAT Exact HR PET tomograph, which provides 47 slices equally spaced by 3.125 mm. Data were acquired in 3D mode (septa retracted) in a single 60-s frame following a bolus injection (10 s duration) of 8 mCi [^{15}O]water. Attenuation was corrected using measured transmission with three rotating rodsources loaded with 5 mCi ^{68}Ge. Since relative blood flow was measured, emission data were not corrected for scattered radiation. If one assumes similar scatter contribution in all conditions, this approach minimizes the variance of the individual relative blood flow measurements. Images were reconstructed in 3D using the Kinahan and Rogers (1990) reprojection algorithm. 47 slices were reconstructed with a Hann filter in both tomographic and axial resolution with a cut-off at 5.5 mm and an in-plane pixel size of 2 mm. This procedure allows to achieve an effective spatial resolution of 6 to 7 mm in the three directions. For eight subjects, T1-weighted MRI data were obtained from a 0.5 Tesla Philips Gyroscan imager. Data were acquired with a Fast Field Echo 3D protocol (repetition time = 30 ms, echo time = 13 ms, flip angle = 30°) and reconstructed with a voxel size of $0.86 \times 0.86 \times 2.0$ mm).

Image analysis was performed using the SPM software (Wellcome Department of Cognitive neurology) implemented in Matlab (Mathworks, Inc.). The results were displayed with an interactive image display software implemented in a home made IDL software

(Michel *et al.*, 1995). For each subject, images were first realigned to the first one, using a rigid body transformation; then a spatial normalization was executed to reorient and transform the images to fit the Talairach and Tournoux (1988) coordinate system (voxel size: $2 \times 2 \times 4$ mm). Finally, the images were smoothed using an isotropic Gaussian filter of 12 mm FWHM. The eight individual MRI were also spatially normalized using the same transformations as the corresponding PET images and then summed to allow the overlay of the obtained *Z*-map on this summed MRI. These preliminary steps were executed with SPM95. The following steps of the analysis were executed with the SPM96 version (Friston *et al.*, 1995). Between and within subjects differences in global blood flow were corrected using a voxel by voxel ANCOVA (Friston *et al.*, 1990). After correction for repetition effect, a voxel-by-voxel Student *t* test generated a map of spatially extended statistical processes (SPM$\{t\}$) that directly reflects the rCBF differences between conditions. The SPM$\{t\}$ values were then transformed to the unit Gaussian distribution using probability integral transform so that changes could be reported as *Z*-scores (SPM$\{Z\}$).

To test our first hypothesis, we delineated a common network for faces by using the contrast $\{(G_U + G_K + Rec) - 3Dis\}$ masked with the three contrasts $(G_U - Dis)$, $(G_K - Dis)$, and $(Rec - Dis)$. All contrasts were thresholded at $Z = 3.09$ ($P < 0.001$). This procedure allowed us to highlight those brain regions significantly more activated in the three face tasks than in the nonface task (Dis). The negative contrast $\{3Dis - (G_U + G_K + Rec)\}$ masked with $(Dis - G_U)$, $(Dis - G_K)$, and $(Dis - Rec)$ was also computed using the same thresholds as above.

To highlight the extent of processing differences existing between known and unknown faces (i.e., to test our second hypothesis), we directly compared the two categorization tasks. In order to categorize the results into face-related activations or deactivations, we again used a masking procedure. The contrast of interest $(G_U - G_K)$ was thus first masked with the contrast $(G_U - Dis)$, which allowed us to select among the pattern of regions more activated in G_U than in the baseline task, those that were also more active for the unknown faces (G_U) than known faces (G_K). The same contrast of interest $(G_U - G_K)$ was then masked with the contrast $(Dis - G_K)$, which allowed us to select among the pattern of regions less activated in G_K than in the baseline task, those that were also less active for the known faces (G_K) than unknown faces (G_U). Finally, the same masking procedure was applied to the second contrast of interest $(G_K - G_U)$ with the contrasts $(G_K - Dis)$ and $(Dis - G_U)$. All the contrasts used (both the contrasts of interest and the masks) were thresholded at $Z = 3.09$ ($P < 0.001$).

The SPM$\{Z\}$ were fused with the summed normalized MRI and displayed as volume images in three orthogonal projections to allow precise anatomical localization of the foci.

RESULTS

Behavioural Results

Response times (RTs) and response accuracy are presented in Table 1. The near maximal accuracy score obtained in all conditions revealed that subjects performed all tasks very efficiently. Regarding the mean response times (Dis = 812 ms, G_U = 660 ms, G_K = 617 ms, Rec = 749 ms), a task (4) × repetition (3) ANOVA (repeated measures) revealed a main effect of task ($F_{3,10} = 21.7$, $P < 0.001$) and repetition ($F_{2,10} = 5.937$, $P < 0.05$), but no interaction ($F_{6,10} = 0.73$), indicating that the repetition had no specific effects on particular tasks. Post-hoc *t* tests revealed a significant difference between the pattern discrimination task and the other (face) tasks ($P < 0.001$). Indeed RTs were higher in the Dis task than in the face tasks. Finally, there were also significant RT differences when comparing the tasks on faces to each other (G_K faster than G_U, $P < 0.05$; G_U and G_K faster than Rec, $P < 0.01$).

PET Results

Using the contrast $\{(G_U + G_K + Rec) - 3Dis\}$ masked with the three contrasts $(G_U - Dis)$, $(G_K - Dis)$, and $(Rec - Dis)$, we highlighted three regions which were activated in the three face tasks when compared to the nonface task (Dis). The results are presented in Table 2. Compared to the discrimination task, all face tasks significantly activated bilateral fusiform gyri, independently of the task performed and the familiarity of the faces (Fig. 2A). In the right fusiform gyrus, two different regions were activated, one was located in the posterior part of the fusiform gyrus, the other one 28 mm more anteriorly. A single focus of activity was detected in the posterior part of the left fusiform gyrus. The contrast $\{3Dis - (G_U + G_K + Rec)\}$ masked with $(Dis - G_U)$, $(Dis - G_K)$, and $(Dis - Rec)$ revealed activa-

TABLE 1

Response Times and Response Accuracies Obtained in the PET Session, during the Three Repetitions of the Four Tasks

	Response times				Percentage of correct responses			
	Dis	G_U	G_K	Rec	Dis	G_U	G_K	Rec
1	838	672	636	790	98.5	99.6	99.3	97.8
2	805	662	605	739	97.8	99.6	99.6	99.3
3	794	644	610	717	97.4	100	99.6	98.2
Mean	812 ms	660 ms	617 ms	749 ms	97.9%	99.7%	99.5%	98.4%

TABLE 2

Regions Having rCBF Increases in the Contrast $\{(G_U + G_K + Rec) - 3Dis\}$ Masked with the Contrasts $(G_U - Dis)$, $(G_K - Dis)$, and $(Rec - Dis)$

Region	Brodmann area	Talairach coordinates			*Z*-Score[a]	Size[b] (number of voxels)
R. Fusiform gyrus	19	40	−80	−16	5.97	32
	37	40	−52	−20	5.91	75
L. Fusiform gyrus	37	−40	−64	−20	4.82	37

Note. All contrasts are thresholded at $Z = 3.09$ ($P < 0.001$).

[a] *Z*-Scores of the local maxima in the main contrast $\{(G_U + G_K + Rec) - 3Dis\}$.

[b] Size of the regions surviving the masking procedure.

tions in bilateral middle occipital gyri as well as in the right superior parietal lobule (Table 3).

In the direct comparison between the two categorization tasks $(G_U - G_K)$, masked with the contrast $(G_U - Dis)$, the left amygdala (−18, −8, −12) reached a *Z*-score of 4.07 (Fig. 2B and Table 4). Figure 3 illustrates activity profile in the left amygdala. In the direct comparison $(G_U - G_K)$ masked with the contrast $(Dis - G_K)$, the middle occipital gyrus (18, −100, 4), and the right calcarine sulcus (8, −100, −8) reached *Z*-scores of 3.45 and 3.39, respectively (Fig. 2C and Table 4). Figure 4 illustrates activity profile in the right calcarine sulcus.

The other contrast of interest $(G_K - G_U)$ masked with the contrast $(G_K - Dis)$ did not reveal any significant foci of activation. Similarly, the contrast $(G_K - G_U)$ was masked with the contrast $(Dis - G_U)$. Again, no significant activations were detected.

DISCUSSION

Two main results were obtained in the present study: first, a common set of brain regions was activated in the fusiform gyri when faces were presented, independently of the task performed and the familiarity of the faces. Second, in the two categorization conditions, two brain regions, the left amygdala and the right early visual areas, showed significant rCBF differences according to the familiarity of the perceived faces.

Common Network for Faces

The common network was highlighted by comparing all tasks performed on faces to the Dis task using masking. The Dis task was an active discrimination task performed on a visual pattern of equivalent complexity as faces (Haxby *et al.*, 1994). Its subtraction eliminated general visuomotor components related to visual discrimination tasks and revealed only those regions related to face processing. Since the pattern used during the baseline condition did not contain any shape features, the present subtraction might, however, also include regions involved in general shape analysis processes, irrespective whether such features belong to faces or any other objects. Bilateral posterior activations in the fusiform gyri and/or in the middle occipital gyri located at similar coordinates have been described in previous imaging studies when comparing rCBF distributions obtained in face matching tasks to those obtained in control tasks using the same pattern as in our study (Haxby *et al.*, 1994). Identical activations have also been reported when comparing different face tasks to control tasks requiring subjects to discriminate orientation of sine wave gratings (Sergent *et al.*, 1992, 1994). Nevertheless, other studies investigating shape analysis (Malach *et al.*, 1995; Martin *et al.*, 1996; Kanwisher *et al.*, 1997a) and object recognition (Kosslyn *et al.*, 1994) also found similar posterior activations. Therefore, in our three face tasks, the posterior activations in bilateral fusiform gyri could reflect the operations of a general object recognition system rather than a face processing system. More recently, McCarthy *et al.* (1997) demonstrated that bilateral regions of the fusiform gyrus were activated by faces viewed among nonobjects as compared to nonobjects presented alone, but only a focal right fusiform gyrus region was activated when faces were compared to other common objects. The same anterior right fusiform region has also been activated during passive viewing of faces when compared to different control tasks, during which subjects passively viewed various kinds of objects as well as body parts (Kanwisher *et al.*, 1997b). This region, labeled fusiform-face area or FFA (Kanwisher *et al.*, 1997b) is considered as a cerebral module dedicated to the processing of faces and automatically activated whenever a face is presented. The coordinates of the anterior right fusiform activation (40, −52, −20) in our study are very close to the mean coordinates of the FFA described by Kanwisher (40, −55, −10). Several other authors also reported activations around these coordinates during face processing tasks (Sergent *et al.*, 1992; Haxby *et al.*, 1994; McCarthy *et al.*, 1997).

Considering the above mentioned results obtained in studies on object and face processing, we propose that in our face tasks, the posterior bilateral activations are related to the extraction of simple visual features and therefore are not specifically related to the processing of faces. On the other hand, regarding the more recent findings of Kanwisher *et al.* (1997b) and McCarthy *et al.* (1997), we propose that the anterior right fusiform gyrus activation corresponds to the FFA and is therefore a specific brain region dedicated to face processing. As this region is not activated in the left hemisphere, we confirm the right hemisphere superiority in face processing as evidenced by functional imaging (Sergent *et al.*, 1992; McCarthy *et al.*, 1997), neuropsychology

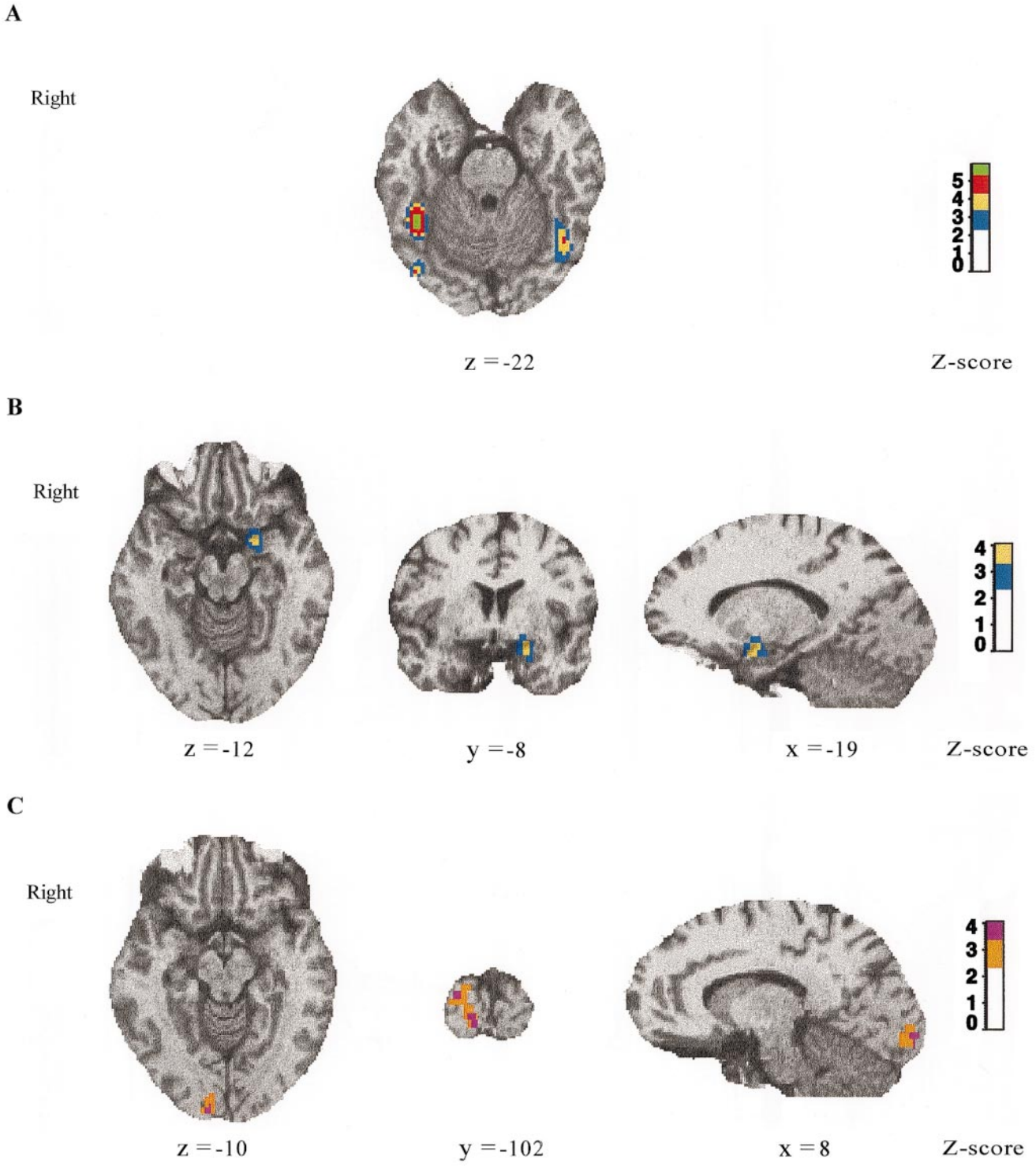

FIG. 2. Common network for faces and differential activations related to the processing of known and unknown faces. (A) Fusiform gyri ($z = -22$) activated in the three face tasks. The anterior peak in the right fusiform gyrus corresponds to the FFA described by Kanwhisher *et al.* (1997b). (B) Left amygdala ($x = -19$, $y = -8$, $z = -12$) more activated in the categorization task on unknown faces than in the same task on known faces. (C) Right calcarine sulcus ($x = 8$, $y = -102$, $z = -10$) less activated in the categorization task on known faces than in the same task on unknown faces. *Z*-scores are indicated by color-bars.

TABLE 3

Regions Having rCBF Increases in the Contrast {3Dis − (G_U + G_K + Rec)} Masked with the Contrasts (Dis − G_U), (Dis − G_K), and (Dis − Rec)

Region	Brodmann area	Talairach coordinates			Z-Score[a]	Size[b] (number of voxels)
R. Middle occipital gyrus	19	26	−90	4	6.75	214
L. Middle occipital gyrus	19	−30	−86	8	6.54	323
R. Superior parietal lobule	7	20	−70	40	5.51	53

Note. All contrasts are thresholded at $Z = 3.09$ ($P < 0.001$).
[a] Z-Scores of the local maxima in the main contrast {3Dis − (G_U + G_K + Rec)}.
[b] Size of the regions surviving the masking procedure.

(Michel *et al.*, 1989), and divided visual field techniques (Rhodes, 1993).

Considering the cognitive model for face processing (Bruce and Young, 1986), the activation of the FFA is a highly plausible candidate as the neuronal correlate to the structural encoding stage. Indeed, according to the model, this first processing step is mandatory for all presented faces and is, in the present study, the only cognitive component common to the three face conditions.

Processing Differences during the Categorization of Known and Unknown Faces

The direct comparisons between G_K and G_U revealed that each of the two categorization conditions, which differ only for the familiarity of the faces, induced rCBF changes in specific brain structures. First, the amygdala was significantly more activated for unknown than for known faces. This was an unexpected result since the gender categorization task on unknown faces has been explored in previous PET studies (Sergent *et al.*, 1992; Kapur *et al.*, 1995), but none of them reported an activation of the amygdala.

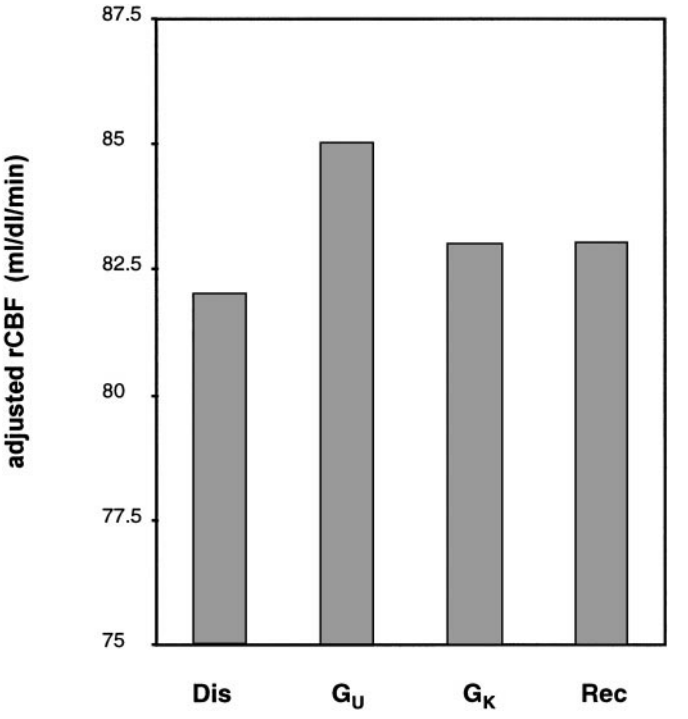

FIG. 3. Plots of rCBF values in the four experimental tasks ($x = -18$, $y = -8$, $z = -12$). rCBF increase in the left amygdala related to the categorization task on the unknown faces.

However, recent imaging studies have shown the involvement of this structure in the processing of facial expression. Thus, Morris *et al.* (1996, 1998a) reported activation of the left amygdala during the processing of fearful faces. Moreover, it has been shown that the left amygdala is involved in emotional learning (Morris *et al.*, 1998b) and more particularly, in the acquisition and extinction phases of conditioning using aversive or threatening stimuli (Buchel *et al.*, 1998; Labar *et al.*, 1998). Regarding these results, we suggest that the activation of the left amygdala in our G_U task is related to the relatively aversive status of the unknown faces compared to the known faces. Indeed, the known faces can be considered as nonthreatening since, during the training phase, they have been extensively presented (on the videotape and on photographs) without any negative consequences. On the contrary, the unknown faces, when seen for the first time during the G_U task, can potentially represent a danger or a threat. Another important property of the amygdala is the rapid habituation of its responses during repeated presentations of fearful and neutral faces (Breiter *et al.*, 1996). In our study, the differential activation of this structure could be therefore related to this characteristic. Thus, the

TABLE 4

Regions Having rCBF Increase in the Contrast of Interest (G_U − G_K) Masked with the Contrast (G_U − Dis) (Top) and (G_U − G_K) Masked with the Contrast (Dis − G_K) (Bottom)

Region	Brodmann area	Talairach coordinates			Z-Score[a]	Size[b] (number of voxels)
		G_U − G_K				
Left amygdala		−18	−8	−12	4.07	52
		G_U − G_K				
R. Middle occipital gyrus	19	18	−100	4	3.45	28
R. Calcarine sulcus	17/18	8	−100	−8	3.39	

Note. All contrasts are thresholded at $Z = 3.09$ ($P < 0.001$).
[a] Z-Scores of the local maxima in the contrast of interest.
[b] Size of the regions surviving the masking procedure.

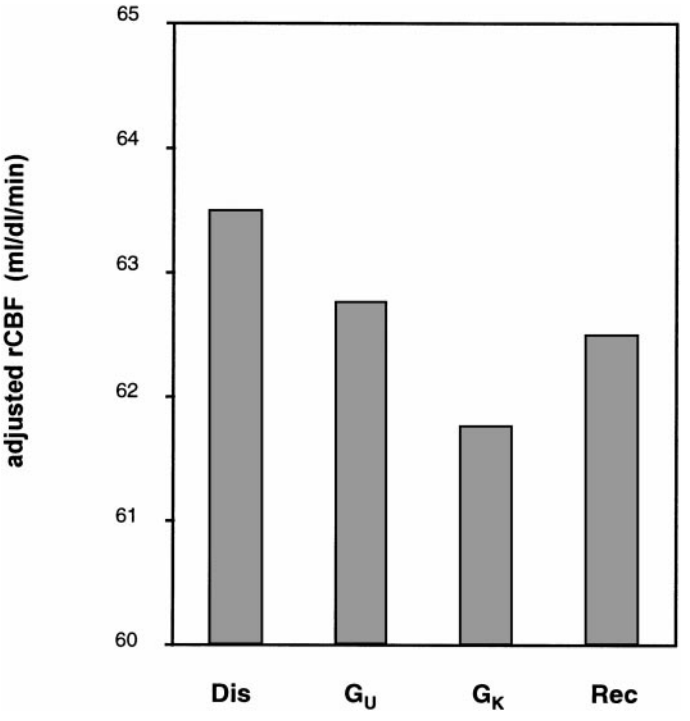

FIG. 4. Plots of rCBF values in the four experimental tasks ($x = 8, y = -100, z = -8$). rCBF decrease in the right calcarine sulcus related to the categorization task on the known faces.

familiar faces presented in G_K had been repeatedly presented during the training phase, whereas the unfamiliar faces were presented for the first time during the scanning session.

An alternative explanation for the present result can be proposed when considering neuropsychological observations (Young *et al.*, 1995; Bechara *et al.*, 1995) and intracranial recordings in humans (Seeck *et al.*, 1995). Young *et al.* (1995) described a patient with a partial bilateral amygdalotomy who suffered from a very peculiar deficit in face processing. After surgery, this patient was still able to recognise familiar faces learned preoperatively, but despite the fact that she was able to match simultaneously unfamiliar faces (visual processing), her ability to recognise faces learned postoperatively was severely impaired. Moreover, this failure was specific to faces: person recognition from names was unimpaired. These authors concluded that the amygdala may play a role in learning new faces. According to Bechara *et al.* (1995), the role of the amygdala in memory encoding may be largely implicit. Indeed, the authors described a double dissociation between the memory function of amygdalar and hippocampal structures: a patient with hippocampal lesions was severely impaired in acquiring new declarative knowledge (explicit encoding) about visual stimuli but was able to associate a physiological response with identical stimuli (implicit encoding). Another patient with amygdalar lesions showed the inverse pattern (implicit encoding deficit). Finally, a third patient with amygdalar and hippocampal lesions was severely impaired in the two types of encoding (explicit and implicit). Our results are also compatible with single cell recordings in humans since Seeck *et al.* (1995) have demonstrated modulation of amygdalar activity with the degree of face familiarity in epileptic patients. In the present study, subjects were not explicitly required to perform any other task on the unknown faces than categorize them according to their gender, but they could, however, implicitly encode these unknown faces. It could therefore be suggested that the activation of the amygdala is related to this automatic processes occurring in the presence of new, unfamiliar faces.

The second difference between the two categorization conditions was a significant rCBF decrease in the posterior part of the calcarine sulcus (which corresponds to the foveal representations in the areas V1 and/or V2) during the processing of the known faces. rCBF was also decreased in the right middle occipital gyrus, a region previously identified as area V3 (Van Oostende *et al.*, 1996; Orban *et al.*, 1997).

A difference in general arousal between the G_K condition and the other face conditions could induce rCBF modifications at an early visual level. However, this seems an implausible explanation for the decreases in the present study. Indeed, the G_K task did not reveal any additional rCBF decreases in brain regions thought to be involved in the regulation of the general

arousal state such as the right frontal lobe (Posner and Raichle, 1997) and more particularly the inferior part of the right precentral gyrus (Giard *et al.*, 1990; Tzourio *et al.*, 1997; Petit et al., (submitted)). Moreover, it is well known (Fuster, 1957; Lansing *et al.*, 1959) that a lowering of the level of general arousal induces a decrease in performance. Therefore, a lower general arousal level in G_K should have produced a decrease in the performance level. This is however not the case in the present study. To the contrary, as shown by the very high percentage of correct responses and also by the decreased RT in the G_K condition, the behavioral measurements reveal an improvement in performance when the categorization was performed on the known faces. Thus, a decrease in general arousal cannot explain the rCBF decrease in the primary and secondary visual areas.

The rCBF decreases could represent a modulation in the amount of attentional resources devoted to the early processing of the known faces. Indeed, during the debriefing following the PET session, subjects reported that, in the G_K task, they quickly noticed whether the 20 faces that had to be categorized according to their gender were all known or all unknown. This observation leads us to suggest that the rCBF decreases could be related to a "cognitive set" adopted by the subjects. In other words, since the faces were all known or unknown within a bloc, it was possible to adopt a particular strategy to extract the facial information. It has indeed been shown that, while performing perceptual judgements on unknown faces, the external and internal features of the faces are equally processed. When the same tasks are performed on known faces, on the contrary, subjects preferentially process the internal features (Young *et al.*, 1985; Hosie *et al.*, 1988). Thus, in the latter case, less information is processed and, hypothetically, the visuospatial attentional focus is limited to the central part of the face.

An alternative hypothesis explaining the present result would be a stimulus driven hypothesis that suggests that the processing of each known face is modified by the prior exposures of this face during the training phase, whether the face is presented in isolation or in a bloc. Such an item-specific effect could on the one hand correspond to a priming effect. Indeed, according to Squire *et al.* (1993) and Ungerleider (1995), priming refers to the improved ability—often measured as RT decrease—to detect or identify perceptual stimuli based on previous experience with them. According to the same authors, this type of memory is thought to involve changes in sensory processing areas. In our study, RTs were shorter in G_K than and in G_U and we also observed modifications of the visual processing in V1, V2, and V3. Therefore, one could argue that the effect revealing itself in the G_K task corresponds to priming. However, our paradigm has been constructed to produce purely visual, long-term face representations. The present design thus clearly went beyond the production of an exclusively implicit memory of the faces based on short exposures, as they are typically used in priming studies. Moreover, according to Ellis *et al.* (1990), who investigated the repetition priming of familiar faces in normal subjects, priming does not occur during gender categorization of faces.

On the other hand, the item-specific effect could result from the reactivation of the long-term face representations stored in memory, each time a familiar face is presented. Indeed, as explained above, the goal of the extensive training phase was precisely to produce such representations. Their automatic reactivation during the G_K task could then modify the processing of known faces as compared to the unknown faces. The recognition could thus, for example, induce, probably by using feed-back projections on earlier visual areas, a preferential processing of internal face features.

In the cognitive set hypothesis, the presentation of 20 familiar faces in a bloc could produce a shrinking of the attentional focus on internal face features. In the stimulus-driven hypothesis, each reactivation of the long-term face representation could also induce a preferential processing of the internal features of each individual known face. Indeed, by studying exploratory eye movements, a differential processing of face features of known and unknown faces has been reported (Rizzo *et al.*, 1987). However, in our study, both the foveal size and the presentation time (1 s) minimize the occurrence of large saccade. Nevertheless, as we did not control for eye movements, we cannot definitively rule out the observed activity reduction in terms of differential eye movement patterns.

Finally, another explanation for these rCBF decreases could be an influence of the amygdalar activity on the early visual processing of faces. In a recent paper, Morris *et al.* (1998a) showed that, first, the activation of the amygdala was proportional to the degree of threat vehiculated by the perceived faces and second, that the amygdala modulated itself the activity in extrastriate cortex. Given the potential involvement of the amygdala in threat evaluation, it is therefore possible that, in our study, the activity of striate and extrastriate visual areas depends on the level of activation of the amygdala. Indeed, Amaral *et al.* (1992) and Rolls (1992) suggested that the amygdala sends neuromodulatory projections to several visual areas.

Regarding the different results obtained in the G_U–G_K comparison, it appears that the brain processes known and unknown faces differently. On one hand, the larger activation of the amygdala during G_U than in G_K suggests that the unknown faces could be detected as a potential threat. On the other hand, the rCBF decrease in the earliest stages of the cortical visual system in G_K reveal that the familiarity of faces influences their

early visual processing. Therefore, these results argue against a strict independence of the two routes (visual processing and recognition) as it is described in the Bruce and Young model (1986). The lack of double dissociations between gender processing and recognition, as well as data from behavioral studies (Young *et al.*, 1985; Hosie *et al.*, 1988) already questioned this model. Now, our results clearly demonstrate, at the neurophysiological level, the influence of familiarity on gender categorization of faces. These results do not imply that the two kinds of operations are not performed in a parallel way but they clearly argue against a strict independence between them.

In summary, we have shown that, on one hand, the FFA is commonly activated in different cognitive tasks performed on known and unknown faces. On the other hand, the differences in activation patterns between the two categorization tasks reveal the involvement of specific processes during gender categorization, depending on the familiarity of the presented faces.

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