

How Does the Brain Discriminate Familiar and Unfamiliar Faces?: A PET Study of Face Categorical Perception

Bruno Rossion^{1,2}, Christine Schiltz², Laurence Robaye²,
David Pirenne², and Marc Crommelinck²

Abstract

■ Where and how does the brain discriminate familiar and unfamiliar faces? This question has not been answered yet by neuroimaging studies partly because different tasks were performed on familiar and unfamiliar faces, or because familiar faces were associated with semantic and lexical information. Here eight subjects were trained during 3 days with a set of 30 faces. The familiarized faces were morphed with unfamiliar faces. Presented with continua of unfamiliar and familiar faces in a pilot experiment, a group of eight subjects presented a categorical perception of face familiarity: there was a sharp boundary in percentage of familiarity decisions between 40% and 60% faces. In the main experiment, subjects were scanned (PET) on the fourth day (after 3 days of training) in six conditions, all requiring a sex classification task. Completely novel faces (0%) were presented in Condition 1 and familiar faces (100%) in Condition 6, while faces of steps of 20% in the continuum of familiarity were presented in Conditions 2 to 5 (20% to 80%). A principal component analysis (PCA) indicated

that most variations in neural responses were related to the dissociation between faces perceived as familiar (60% to 100%) and faces perceived as unfamiliar (0 to 40%). Subtraction analyses did not disclose any increase of activation for faces perceived as familiar while there were large relative increases for faces perceived as unfamiliar in several regions of the right occipito-temporal visual pathway. These changes were all categorical and were observed mainly in the right middle occipital gyrus, the right posterior fusiform gyrus, and the right inferotemporal cortex. These results show that (1) the discrimination between familiar and unfamiliar faces is related to relative increases in the right ventral pathway to unfamiliar/novel faces; (2) familiar and unfamiliar faces are discriminated in an all-or-none fashion rather than proportionally to their resemblance to stored representations; and (3) categorical perception of faces is associated with abrupt changes of brain activity in the regions that discriminate the two extremes of the multidimensional continuum. ■

INTRODUCTION

The human brain is extremely efficient at discriminating familiar and unfamiliar faces, one of the most important biological and social brain function of primates and other species: even faces that have been seen once can be recognized, sometimes years later. Paradoxically, the neural mechanisms underlying the discrimination of familiar and unfamiliar faces are unclear at the current state of knowledge, and is one of the outstanding problems raised in a recent review on the neural systems involved in face processing: “do representations of familiar faces, as compared to novel faces, have a different distribution across regions that can be dissociated from the representations of biographical and autobiographical information associated with these faces?” (Haxby, Hoffman, & Gobbini, 2000).

Despite the numerous cellular recording studies in monkeys (e.g., Fujita, Tanaka, Ito, & Cheng, 1992; Gross, 1992; Rolls, 1992), the intracranial and scalp event-re-

lated potential (ERP) recordings in humans (e.g., Allison, Puce, Spencer, & McCarthy, 1999; Bentin, Allison, Puce, Perez, & McCarthy, 1996), and the growing interest of functional imaging studies unraveling the neural correlates of face processing over the last few years (e.g., Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Kanwisher, McDermott, & Chun, 1997; Sergent, Otha, & McDonald, 1992), the questions of where, when, and how the brain distinguishes familiar and unfamiliar face representations remain largely unanswered. This lack of knowledge is due in part because most brain imaging studies have focused their interest on other main theoretical issues such as the modularity of face perception (e.g., Gauthier, Skudlarski, Gore, & Anderson, 2000; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kanwisher et al., 1997; McCarthy, Puce, Gore, & Allison, 1997), the neural basis of facial expression processing (e.g., Morris et al., 1998) and the neural regions involved in explicit encoding and retrieval of learned faces (e.g., Leveroni et al., 2000; Wiser et al., 2000; Haxby et al., 1996) but also because there are several potential difficulties that prevent the interpretation of the differences in activation produced by familiar and unfamiliar faces.

¹ Brown University, ² Université Catholique de Louvain, Belgium

First, task and stimuli factors are often confounded. For instance, encoding tasks (Leveroni et al., 2000; Haxby et al., 1996), face matching (Haxby et al., 1996), or sex categorization tasks (Wiser et al., 2000; Kapur, Friston, Young, Frith, & Frackowiak, 1995; Sergent et al., 1992) are performed usually on novel faces, while recognition/retrieval tasks are made on familiar faces (either learned or famous: Leveroni et al., 2000; Wiser et al., 2000; Haxby et al., 1996; Kapur et al., 1995; Sergent et al., 1992). Similarly, comparing familiar and unfamiliar faces in a face recognition task, as some recent ERP (Bentin & Deouell, 2000, Experiments 2 and 3; Paller et al., 2000) and fMRI (e.g., Katanoda, Yoshikawa, & Sugishita, 2000) studies have done may not be appropriate because the decision response is obviously different for familiar and unfamiliar faces. Accordingly, the differences cannot be unambiguously related to the perceptual discrimination of familiar and unfamiliar faces or to the differential explicit memory processes or decision output. Using irrelevant task to face familiarity, scalp ERP studies have described late (>250 msec) central differences between familiar and unfamiliar faces (Bentin & Deouell, 2000; Eimer, 2000) but the brain regions involved remain completely unclear, insofar as intracranial recordings did not disclose any differences between familiar and unfamiliar faces in the ventral, lateral, and internal part of the occipito-temporal cortex (Puce, Allison, & McCarthy, 1999)

A second problem is that most studies used famous faces to be compared to novel faces (e.g., Bentin & Deouell, 2000; Leveroni et al., 2000; Gorno-Tempini et al., 1998; Kapur et al., 1995; Seeck et al., 1993; Sergent et al., 1992) but famous faces stimuli automatically activate a great deal of semantic, and even episodic, lexical and affective information about the persons, preventing one to sort out the activations related to each of these processes, to the sole difference between visual representations of familiar and unfamiliar faces. As a matter of fact, we failed to find any late ERP differences between unfamiliar faces and visually familiar (no semantic information) faces (Rossion et al., 1999).

To avoid these difficulties, one can (1) compare familiar and unfamiliar faces in the same task' preferentially a task that is independent of face familiarity; and (2) compare unfamiliar faces to faces that are visually familiarized for long-term, without providing any semantic information regarding these faces to the subjects tested. This is the first objective of the present PET study.

A second objective is to assess whether the brain responses differentiating familiar from unfamiliar faces vary according to the subjective perception of familiarity (what the subject perceives) or proportionally to the similarity between the presented face and the long-term face representation.

As for object recognition, functional models of face processing propose that a face is recognized as familiar if the perceptual representation extracted during percep-

tion matches a face representation stored in long-term memory (a so-called "face recognition unit" or FRU, Bruce & Young, 1986; Hay & Young, 1982). In one of the first models introduced in the literature, a recognition unit was conceived as a firing in an all-or-none, threshold manner when the current input bears sufficient resemblance to the stored representation, the firing corresponding to the recognition of the face (Hay & Young, 1982). However, according to the later and widely accepted face processing model of Bruce and Young (1986), a unit fires proportionally to the resemblance between the input and the stored representation, and the decision process of recognition is made by the general cognitive system, outside of the face processing system per se. Whether the activation of long-term face representations is all-or-none or proportional to the resemblance with the face presented to the perceiver has not been clarified yet by behavioral studies.

Here we used the phenomenon of face categorical perception to clarify this debate. A critical feature of the brain's perceptual system is to process continua of sensory information, such as color wavelength or speech, for instance. Psychological research indicates that such continua are perceived more or less categorically (Harnad, 1987): the color wavelength spectrum varies continuously, yet we perceive bands of color rather than a gradual continuum of color change (Bornstein & Korda, 1984). Recently, categorical perception effects have been extended to human faces. Using artificial continua of information created by morphing procedures, categorical perception of facial expressions (Etcoff & Magee, 1992) and identity (Beale & Keil, 1995) has been demonstrated. More precisely, different stimuli on a continuum of facial expressions (i.e., from happy to sad) are perceived as belonging to one or to the other category of expression, and pairs of faces that straddled category boundaries are discriminated more easily than within category pairs (Calder, Young, Perrett, Etcoff, & Rowland, 1996; Etcoff & Magee, 1992). The same phenomenon has been shown for the facial identity of known faces (Beale & Keil, 1995), unknown human faces of own- and other-race (Levin & Beale, 2000), for face gender (Campanella, Chrysocoos, & Bruyer, *In press*), and for the facial identity of animal faces (Campbell, Pascalis, Coleman, Wallace, & Benson, 1997). These observations suggest that categorical perception is not restricted to "innate" perceptual constraints or categories but represent a general dynamic on-line process that parses perceptual input in response to both long-term needs and task-specific constraints (Goldstone, 1994).

Although the phenomenon has been well documented in behavioral studies, the neural basis of categorical perception is yet unclear, and so is particularly the case for faces. A recent ERP study (Campanella, Hano-teau, et al., 2000) described a decrease of the right hemisphere N170 face-sensitive potential (e.g., Rossion, Gauthier, et al., 2000b; Bentin et al., 1996) when a face



Figure 1. Examples of the face stimuli used in the PET study. One continuum is presented here, 30 were used in the experiment. Subjects are familiarized with the face on the right (100%) that is morphed with a completely unknown face. During a scan, subjects are shown 10 faces only belonging to one step of the continuum, say 20%. The six conditions correspond to the six steps as defined on this continuum, ranging from 100% (familiar) to 0% (unfamiliar).

stimulus was presented following the presentation of a different face photograph but belonging to the same identity, as compared to the N170 obtained when a (perceived) novel identity was presented. In the two cases, the physical distance between the first and the second stimulus was equal, as controlled by a face morphing algorithm. This result suggests that categorical perception of faces may occur quite early in the right hemisphere, but does not provide any information regarding the brain structures involved and their response patterns to a continuum of sensory information.

In addition to clarifying the neural substrates of familiar and unfamiliar face representations, the present study ought to clarify how the brain processes continua of facial identities. The pattern of activation observed should help us in understanding whether the brain discriminates familiar and unfamiliar faces in an all-or-none way, or if the visual regions are (de)activated proportionally to the similarity with previously stored representations.

Subjects were presented with continua of faces, each of them being made of a familiar and an unfamiliar face (Figure 1). At different steps of such a continuum, a face is perceived either as familiar or unfamiliar, in a roughly categorical way, even though the brain is presented with a continuum of sensory information. Does brain activity reflect the sharp boundary between category frontiers or does it decrease or increase linearly with the face familiarity continuum? In short, our purpose was to assess whether neural activity, as recorded by neuroimaging, was correlated with the subject's perceptual awareness of face familiarity (roughly categorical), or linearly with a continuum made from a familiar face to a novel face. Using this strategy, we hoped to extract some information about the automatic face recognition process per se: are familiar face representations activated in an all-or-none fashion (Hay & Young, 1982) or much proportionally to the resemblance between the input and the stored representation (Bruce & Young, 1986)?

In a pilot experiment, a group of control subjects was familiarized with a set of faces during 3 days and their familiarity response profiles to the continua between familiar and unfamiliar faces were recorded on the

fourth day. As expected, faces were perceived categorically, i.e., there was a sharper perception of face familiarity than the linear continuum made from the unfamiliar to the familiar face (see Methods and Figure 2). In the PET study, familiar faces were learned with the same procedure, and subjects were scanned on the fourth day. During scanning, subjects were presented with the same task (gender decision) in six conditions: from completely novel faces (0% of similarity to known faces) to 100% familiar faces, by steps of 20%. In other words, Condition 1 included faces that were completely unfamiliar to the subject (0%) while Condition 2 included faces saturated at 20% from familiar faces (80% novelty; see Figure 1). Faces saturated at 40% were presented during Condition 3, etc. Two rest scans were also made. The overall pattern of blood flow variation across conditions was first extracted by means of a principal component analysis (PCA). Then, the conditions for which control subjects mainly classified the faces as familiar (high subjective familiarity) were compared with those that were considered as novel faces (low subjective familiarity). Finally, the brain regions

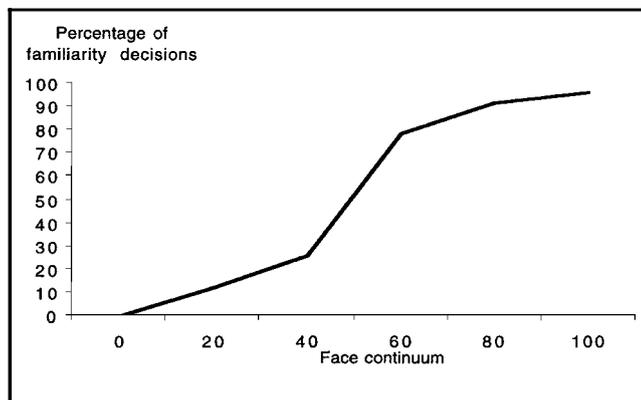


Figure 2. This graph indicates the percentage of familiarity decisions by an independent group of subjects who were presented with the faces at the different steps of the continuum. Although the distinction between familiar and unfamiliar decisions is not completely sharp, it is almost equal for 0%, 20%, and 40% faces on the one hand (faces perceived as unfamiliar) and for 60%, 80%, and 100% faces on the other hand (faces perceived as familiar).

where activity increases or decreases linearly with the percentage of familiarity of faces were determined using a linear contrast.

RESULTS

Behavioral Results

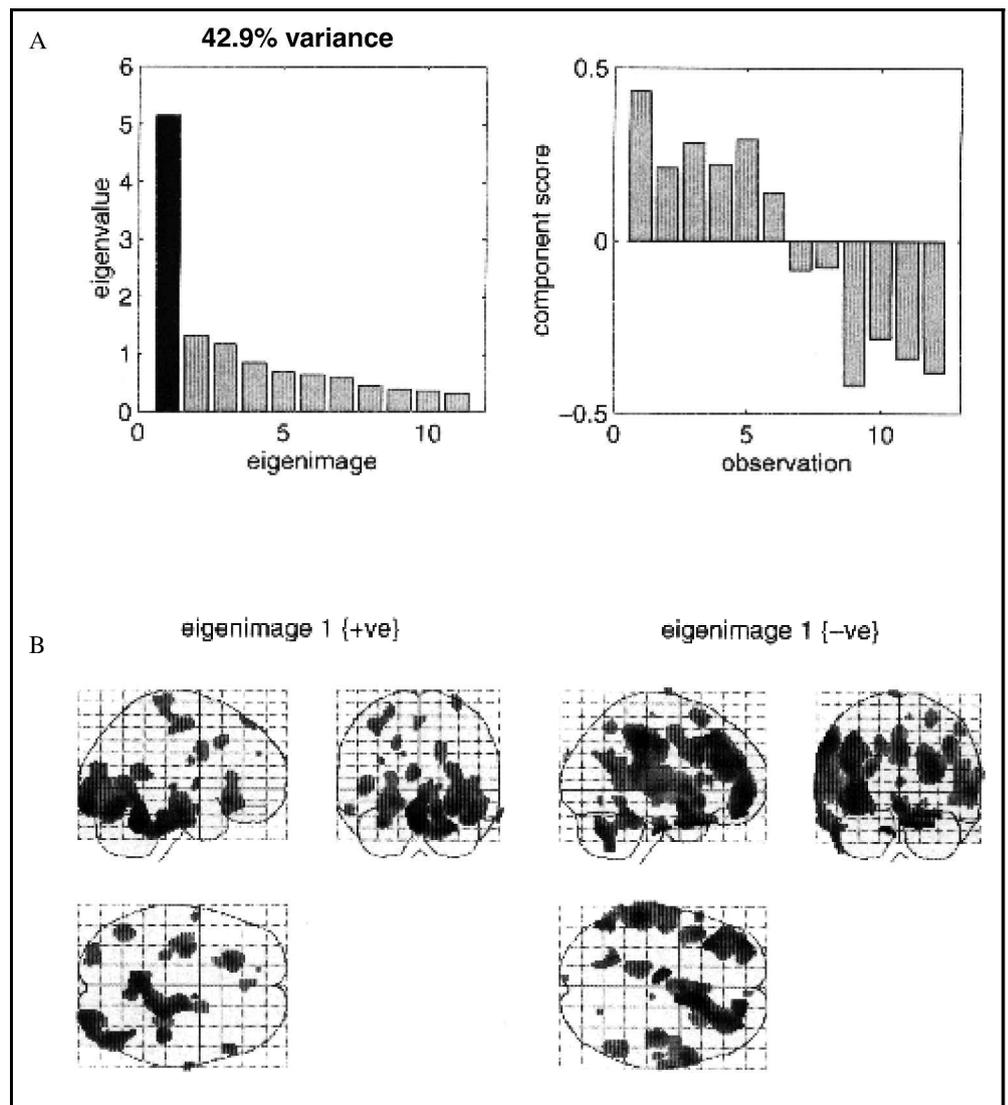
Performance rates were between 94.4% and 98% for the different conditions. Mean response times (RTs) were as follows: 0%: 1031 msec, 20%: 1028 msec, 40%: 1061 msec; 60%: 992 msec, 80%: 898 msec; 100%: 858 msec. A one-way ANOVA (repeated measures) on RTs showed a significant effect of condition [$F(1,7) = 4.383; p = .003$]. 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 ($p = .039$). Pairwise statistical contrasts showed significant differences between 0% and 80% (.022), 0% and

100% (.034), 20% and 80% (.049), 20% and 100% (.035), 40% and 80% (.032), 40% and 100% (.04), and 60% and 100% conditions (.018).

PET Results

The PCA was performed to characterize the patterns of brain activity related to the experimental conditions. Using this descriptive method, different factors were extracted, among which only one factor explained a high percentage (43%) of the variance of the data, while the second component accounted for only 11%. Figure 3A presents the principal component (PC) scores, reflecting their contributions to each experimental condition. The main component is prevalent in all scans of perceived unfamiliar faces with corresponding negative scores in each of the other scans (perceived familiar faces). In other words, despite the continuum of sensory information, the overall blood flow change observed in

Figure 3. PCA of the PET data recorded in the six face conditions. The principal factor explained 43% of the whole brain changes. It separated the overall blood flow changes in two parts related to the perception of face familiarity or novelty.



the present experiment for the face conditions was distributed between two poles corresponding to the two sets of faces: on the one hand, the faces perceived as unfamiliar, and on the other hand the faces perceived as familiar. The eigenimages corresponding to this main factor are shown on the right of Figure 3A. The positive eigenimage (Figure 3B) represents the functional network involved for faces perceived as unfamiliar: regional cerebral blood flow (rCBF) within these regions is highly correlated during the task performed on the unfamiliar faces (0%, 20%, and 40%). This functional network includes principally the lateral and superior part of the right middle occipital gyrus, and regions of the right ventral pathway. The negative eigenimage (Figure 3) shows the functional network involved for faces perceived as familiar. Its higher loadings are mainly in the left superior parietal and bilateral middle frontal gyrus.

Based on the behavioral observations and on the PCA analysis, the first inferential statistical analysis compared all the conditions in which the faces are mostly perceived as unfamiliar (0% + 20% + 40%) to the scans presenting faces perceived as familiar (60% + 80% + 100%). This comparison was masked by the contrast faces' rest. It revealed increases of activity in two regions of the right middle occipital gyrus (BA 18), and in two occipito-temporal regions of the right hemisphere: posteriorly in the lateral part of the right posterior fusiform gyrus (BA 19, see Figure 4), and more anteriorly, in the right inferotemporal cortex (BA 20). Table 1 shows the Z score and the Talairach coordinates of the maxima of

these regions, as well as the size of the regions (all voxels with a Z score > 3.09, size > 20 voxels). The opposite contrast, comparing visually familiar faces to novel faces, did not disclose any significant increase of brain activity.

The second inferential statistical analysis used a parametric contrast, in which weights were assigned to each condition according to the proportion of unfamiliar or familiar face information (0% to 100%) in the stimuli. Within the regions activated in the contrast faces' rest, this analysis revealed only one subregion of the right middle occipital gyrus where activity was negatively linearly correlated with the continuum (increasing from 100% to 0%; $30, \cong 90, \cong 12$). This region was part of the larger activation observed when unfamiliar faces were compared to familiar faces in the categorical analysis (maxima: $32, \cong 90, \cong 14$). We observed no region where activity was positively correlated with the continuum (0% to 100%).

Plots of the adjusted correct responses (percentage of blood flow increase) in the four right occipito-temporal regions associated with face novelty are shown in Figure 5. The level of adjusted blood flow responses to the maxima of the right middle occipital region linearly correlated with the continuum was also included. Confirming the eigenimage description, all these graphs clearly indicate that brain activity changes were stepwise, at the boundary between face perceived as novel despite 40% of information from learned faces, and these stimuli perceived as familiar (60%) despite 40% of novel information (Figure 5).

Figure 4. The four right-hemisphere regions where larger responses were found to faces perceived as unfamiliar, as compared to familiar faces. *t* scores of these group changes obtained by PET are superimposed on a single subject MRI scan. The sagittal slice on the upper right shows the two foci in the right middle occipital gyrus. The lower region (BA 18) was the larger activation reported. It is also presented on the transverse and sagittal slices on the left part of the figure. The axes are in correspondence for the three other slices than the upper right figure. The activation in the posterior fusiform gyrus is presented on the transverse slice (lower left), while the inferotemporal activation is presented on the sagittal (lower right) and coronal (upper left) slices.

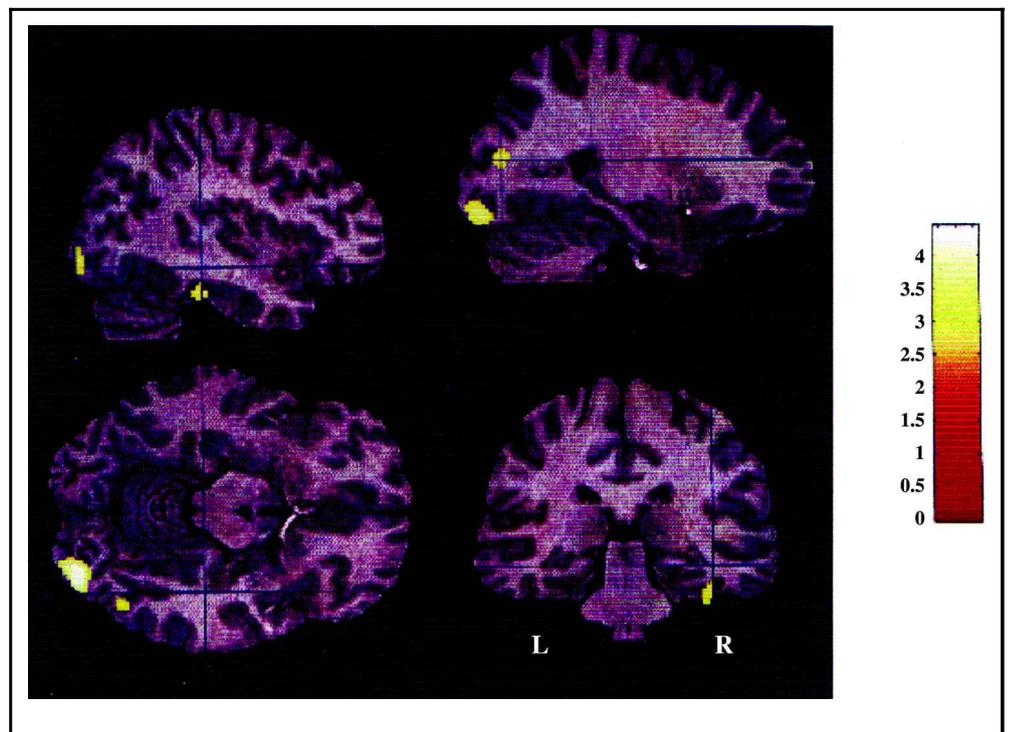


Table 1. Relative Increases of Brain Activity Associated with Unfamiliar Faces as Compared to Faces Perceived as Familiar

Region (Brodmann)	Side	Coordinates			Z Score	Size (N Voxels)
		x	y	z		
Middle occipital gyrus (18)	R	32	∠ 92	∠ 14	4.35	450
Middle occipital gyrus (18)	R	26	∠ 84	14	3.44	48
Posterior fusiform gyrus (19)	R	48	∠ 70	∠ 16	3.35	91
Inferotemporal cortex (20)	R	42	∠ 28	∠ 24	3.72	187

$p < .001$, uncorrected for multiple comparisons.

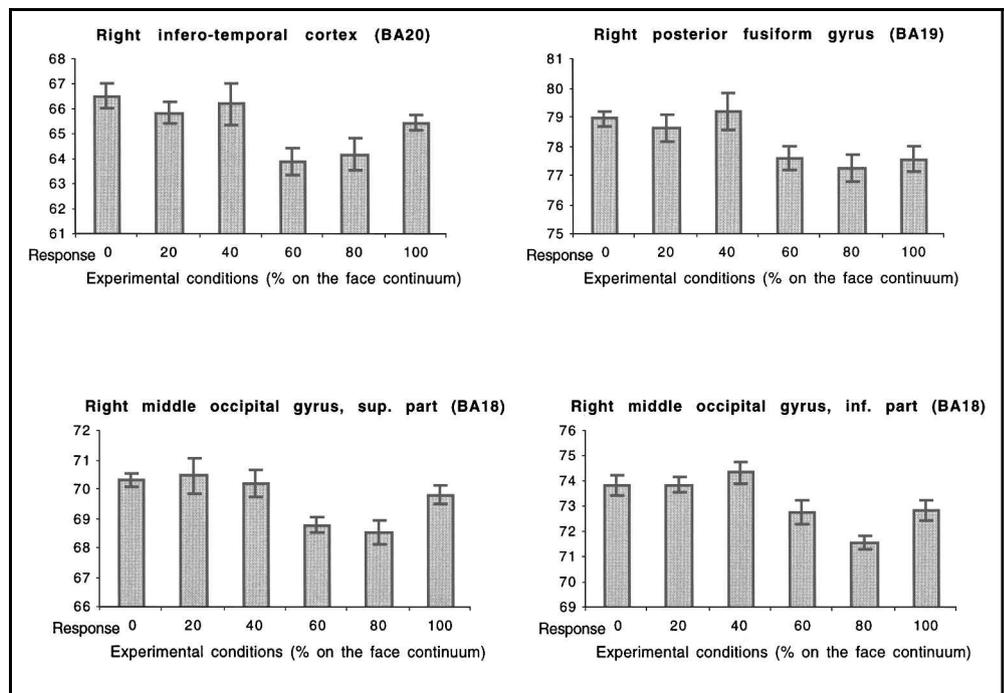
Coordinates (in standard stereotactic space; Talairach & Tournoux, 1988) refer to maximally activated foci as indicated by the highest Z score within an area of activation. x = distance (mm) to right (+) or left (∠) of the midsagittal line; y = distance anterior (+) or posterior (∠) to the vertical plane through the anterior commissure; z = distance above (+) or below (∠) the bicommissural (AC-PC) line.

In the right middle occipital gyrus (32, ∠ 90, ∠ 14, see Figures 4 and 5), a one-way ANOVA for repeated measures with the level on the continuum as factor and the adjusted correct responses computed over a 3-mm radius sphere centered on the maxima (Table 1), revealed a significant main effect of condition [$F(5,35) = 5.97$; $p < .001$]. Post hoc t tests indicated a significant difference between faces perceived as unknown and faces perceived as known [(0% + 20% + 40%) ∠ (60% + 80% + 100%): $p = .002$]. Pairwise contrasts showed significant differences or trends for the following comparisons: 0' 80 ($p = .001$); 20' 80 ($p = .003$); 40' 60 ($p = .006$); 40' 80 ($p = .002$); 40' 100 ($p = .01$). Thus, there was not any significant difference of blood flow changes within the category of faces perceived as novel or within

the category of faces perceived as familiar (except for a trend at 80' 100: $p = .081$; all other p 's $> .105$). The same results were found for (30, ∠ 90, ∠ 12): Effect of condition: $F(5,35) = 6.06$, $p < .001$; categorical contrast: $p = .003$; 0' 80: $p = 0.005$; 20' 80: $p = .004$; 40' 60: $p = .066$; 40' 80: $p = .002$; 40' 100: $p = .004$; 60' 80: $p = .06$, and 80' 100: $p = .037$.

In the superior part of the middle occipital gyrus (BA 18, see Figures 4 and 5), the ANOVA revealed a significant main effect of condition [$F(5,35) = 3.764$; $p = .008$]. Post hoc t tests indicated a significant difference between faces perceived as unknown and faces perceived as known [(0% + 20% + 40%) ∠ (60% + 80% + 100%): $p = .015$]. Pairwise contrasts showed significant differences or trends for the following comparisons: 0'

Figure 5. Plots of the corrected blood flow values (mean = 50) and standard errors in the four regions where larger responses were found to faces perceived as unfamiliar, as compared to familiar faces. These graphs clearly show the increases/decreases associated with the perception of unfamiliar/familiar faces (note the differences between 40 and 60 conditions).



60' 80 ($p = .014$); 0' 80 ($p = .002$); 20' 60 ($p = .029$); 20' 80 ($p = .07$); 40' 60 ($p = .05$); 40' 80 ($p = .018$); but also 60' 100 ($p = .015$) and 80' 100 ($p = .053$).

In the lateral part of the right fusiform gyrus (BA 19, see Figures 4 and 5), the ANOVA revealed a significant main effect of condition [$F(5,35) = 3.008$; $p = .023$]. Post hoc t tests indicated a significant difference between faces perceived as unknown and faces perceived as known [(0% + 20% + 40%) \cong (60% + 80% + 100%): $p = .002$]. Pairwise contrasts showed significant differences or trends for the following comparisons: 0' 60 ($p = .056$); 0' 80 ($p = .013$); 0' 100 ($p = .008$); 20' 60 ($p = .055$); 20' 80 ($p = .063$); 40' 60 ($p = .085$); 40' 80 ($p = .078$); 40' 100 ($p = .058$). None of the comparisons within the category of faces perceived as novel or within the category of faces perceived as familiar were significant (all $ps > .56$).

In the right inferotemporal cortex (BA 20, see Figures 4 and 5), the ANOVA revealed a significant main effect of condition [$F(5,35) = 3.131$; $p = .019$]. Post hoc t tests indicated a significant difference between faces perceived as unknown and faces perceived as known [(0% + 20% + 40%) \cong (60% + 80% + 100%): $p = .014$]. Pairwise contrasts showed significant differences or trends for the following comparisons: 0' 60 ($p = .012$); 0' 80 ($p = .061$); 20' 60 ($p = .026$); 20' 80 ($p = .071$); 40' 60 ($p = .087$); 40' 80 ($p = .091$). None of the comparisons within the category of faces perceived as novel or within the category of faces perceived as familiar were significant (all $ps > .455$).

Finally, RTs were entered as a covariate of interest in a last analysis to ensure that the differences observed between familiar and unfamiliar faces were not due to attentional factors, and because it turned out that face familiarity speeded gender decisions on faces (see Behavioral Results). There was neither a positive nor a negative correlation between RTs and rCBF in any of the regions that were found to be activated in the categorical analyses.¹

DISCUSSION

Two main findings were made in the present study. First, familiar faces do not involve the recruitment of specific (additional) brain regions as compared to novel faces, as long as the face does not evoke any semantic or lexical content, and the subject is not engaged in any explicit recognition task. Rather, familiarity with a face stimulus is associated with large decreases of activity (as compared to novel faces) in the right occipito-temporal regions. The second observation concerns the nature of these changes: they clearly correlate with the subject's perception of familiarity, not the proportion of physical similarity between a perceived face representation and a stored face representation. In other words, we described a neural correlate of face categorical perception in the right occipital and occipi-

to-temporal regions that differentiate familiar and unfamiliar faces.

Where and How Does the Brain Discriminate Familiar and Unfamiliar Faces?

The brain mechanisms for familiar and unfamiliar face discrimination in humans are not well understood. Most previous neuroimaging studies have described increases of activity for familiar as compared to novel faces, particularly in the more anterior and medial regions of the left and right temporal lobe (i.e., Leveroni et al., 2000; George et al., 1999; Gorno-Tempini et al., 1998; Sergent et al., 1992), but these activations are probably related to the retrieval of semantic knowledge about people rather than to the difference between familiar and unfamiliar face representations (Haxby et al., 2000). Other studies have reported the involvement of prefrontal and parietal structures as well as the posterior cingulate for familiar faces (i.e., Leveroni et al., 2000; Gorno-Tempini et al., 1998), but these increases were observed in explicit recognition tasks.

The present study did not evidence any increase of brain activity for familiar faces as compared to novel faces, suggesting that these stimuli may share similar neural representations. This finding is consistent with the two brain imaging studies that contrasted visually familiar and unfamiliar faces, controlling for task factors (Gauthier, Tarr, et al., 2000; Dubois et al., 1999). In a recent fMRI study (Gauthier, Tarr, et al., 2000) a decrease of activity for repeated face identities as compared to the presentation of different faces was observed in the "fusiform face area" (FFA, Kanwisher et al., 1997) and an occipital region also described as face-sensitive ("occipital face area," OFA; Gauthier, Tarr, et al., 2000). No increases were found for the faces repeated during the scanner testing. However, the faces were not learned in long-term memory and only a small part of the brain was tested in that study.

More important for our purpose, the present findings replicate a recent PET study that failed to describe any increase of activity for long-term familiar faces (Dubois et al., 1999). Rather, decreases of activity were described in the right middle occipital gyrus, including the primary visual cortex (V1) for familiar faces. Here the decrease of the right middle occipital gyrus was still observed (and larger), but it did not extend to V1. One reason for this difference might be that novel photographs of familiar faces were used in the present study, while the images presented during scanning in Dubois et al. (1999) had already been seen before. In the present study, not only novel photographs of unfamiliar and familiar faces were compared, but also the training procedure was longer and more intensive. Here, two different regions of the right middle occipital lobe underwent decreases when familiar facial identities were presented, and these decreases were also

observed in two regions of the right ventral pathway, in occipito-temporal sites (Figure 4, Table 1). Discriminating between familiar and unfamiliar faces thus appears to depend on decreases for familiar items as compared to novel ones in the right occipito-temporal pathway. The observation that both low- and high-level visual areas of the right hemisphere undergo such decreases for familiar faces is in agreement with the prevalent role of this hemisphere in face perception, as indicated by divided visual field studies in humans (Rhodes, 1993; Hillger & Koenig, 1991) and animals (Peirce, Leigh, & Kendrick, 2000), neuropsychological face perception impairments (Farah, 1990; Michel, Poncet, & Signoret, 1989) and neuroimaging studies (Kanwisher et al., 1997; McCarthy et al., 1997). However, the left hemisphere also plays a role in face perceptual processes, and face-selective activations have been nearly as often described in the left occipito-temporal regions of the fusiform gyrus (i.e., Rossion, de Gelder, et al., 2000; Gauthier et al., 1999; Haxby et al., 1999; Halgren et al., 1998; Puce, Allison, Asgari, Gore, & McCarthy, 1996). Our results suggest an even stronger lateralization bias in favor of the right hemisphere for face novelty/familiarity effects, and future studies must verify whether this lateralization is as strong or reversed for nonface objects and word stimuli. In any case, no strong claim can be made from the present PET study that these decreases to familiar stimuli are specific to faces. In particular, the decreases observed in the right middle occipital gyrus are certainly not specific to faces and we hypothesize they should be observed with any kind of familiar/novel comparison on visual items (maybe with a left lateralization for linguistic stimuli).

The Right Middle Occipital Gyrus

The different hypotheses that may account for the decreases to familiar faces in the right middle occipital gyrus have been previously discussed (see Dubois et al., 1999). One plausible explanation is that they are due to a modulation in the amount of attentional resources devoted to the early processing of familiar faces. RTs indicate that subjects were quicker at telling the sex of familiar than unfamiliar faces, despite the alleged independence of the task to familiar faces suggested by functional face processing models (Bruce & Young, 1986). Other behavioral studies indicate that perceptual judgments on faces are performed differently whether the faces are known or unknown: internal features are preferentially used for familiar faces (Hosie, Ellis, & Haig, 1988; Young, Hay, McWeeny, Flude, & Ellis, 1985), and matching faces from different viewpoints is performed quicker for familiar than unfamiliar faces (Young, McWeeny, Hay, & Ellis, 1986). Since faces were presented in blocks, subjects might have adopted a particular perceptual strategy to perform the task, that would have been different for familiar and unfamiliar faces

throughout the block. Comparing long-term familiar and unfamiliar faces in event-related fMRI paradigms (Dale & Buckner, 1997) may help to clarify this issue. A simpler explanation would be that familiar faces have been previously processed extensively and accordingly require a less detailed visual analysis than novel faces. However, there was no correlation between corrected blood flow values in the two regions of the right middle occipital gyrus and RTs, suggesting that a difference in strategy or in easiness may be insufficient to account for the whole difference between familiar and unfamiliar faces observed in this region.

The brain blood flow difference observed in the posterior part of the right middle occipital gyrus suggests that either familiar and unfamiliar faces are discriminated early in the right visual cortex, or that early visual areas can be modulated to reduce their level of activation to previously seen stimuli, by feedback from anterior regions. Scalp ERP studies and intracranial recordings indicate that early visual components (below 250 msec) are not influenced by face familiarity (Bentin & Deouell, 2000; Eimer, 2000; Paller et al., 2000; Puce et al., 1999; Rossion et al., 1999) and thus preferentially support this last hypothesis.

The Posterior Fusiform Gyrus

The more anterior regions that showed a difference of activation for novel and familiar faces were located in the right occipito-temporal pathway. One focus of activity (BA 19, see Figure 4) is part of the ventral lateral occipital (LO) complex (Malach et al., 1995). This large region is thought to be involved in shape extraction, but part of it definitely presents selective responses to faces (see Rossion, de Gelder, et al., 2000; Gauthier et al., 1999; Gauthier, Skudlarski, et al., 2000; Haxby et al., 1999; Halgren et al., 1998). Although the absence of object conditions in the present study does not ensure that the familiarity/novelty effects observed are specific to faces, the focus of the difference in brain activity in the posterior fusiform gyrus is nearly identical in location and size to the region that was found to be more activated for faces (as compared to objects) in a complementary study with the same PET camera (Rossion, de Gelder, et al., 2000). Coordinates of this region also corresponds to the occipital face area described by Gauthier, Tarr, et al. (2000), even though all the voxels reported here might not present a larger response for faces than for objects. This observation suggests that at least some of the regions that are involved in the perception of faces are also those regions that discriminate long-term familiar and unfamiliar faces.

This proposal is consistent with previous neuroimaging studies on word and object processing: several PET and fMRI studies have shown that the regions activated during word and object perception present reduced activations for repeated presentations (Blaxton et al.,

1996; Buckner et al., 1995; Squire et al., 1992; objects: Buckner et al., 1998; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). Usually, these observations are accompanied by better (or faster) performance at processing these stimuli, thus indicating the neural correlates of perceptual priming or implicit memory processing (repetition priming, see Buckner & Koutstaal, 1998; Wiggs & Martin, 1998, for reviews). In other words, these deactivations reflect a facilitation in neural computations when the same information is processed again. Such effects had not yet been described with faces, except in the recent work of Gauthier, Tarr, et al. (2000)² in the right occipital face area and in the more anterior middle FFA. The present study now shows that such reduced activations also hold for faces that have been familiarized during days before the experiment, indicating long-term effects of face perceptual learning. Furthermore, it suggests that these reductions of activity in BA 19 are exclusively right lateralized for faces learned extensively for days, and even when novel pictures of familiar identities are presented: the reduced activations are not due to repetition of the same images, but of the same facial identities. If these results could be replicated in the occipital face area defined precisely with localizer tasks, it would strongly support the hypothesis that not only face detection is performed in these regions, but also discrimination between faces, and face recognition. This is consistent with recent cellular recordings in the monkey inferotemporal cortex, showing that identical cells are involved in face detection and discrimination, albeit with a different response timing (Sugase et al., 1999).

The Right Inferotemporal Cortex

Finally, a significant difference between familiar and unfamiliar faces was found in a more medial and anterior region in the temporal lobe (BA 20, see Figure 4). Again, it is unclear from our study that this region is particularly dedicated to face processing, but several indications suggest that it actually plays a role in this function. The inferotemporal cortex in the primate brain is divided in posterior area TEO, which receives topographically organized inputs from areas V2, V3, and V4, and projects to the anterior area TE, and the temporal pole. Area TE projects in turn mainly to the inferotemporal pole, the parahippocampal gyrus and the superior temporal sulcus (Webster, Ungerleider, & Bachevalier, 1991). Area TE of the inferotemporal cortex encompasses portions of Brodmann's areas 20 and 21 (bordering in BA 36) and is functionally distinguished from the posterior inferotemporal cortex (TEO, BA 37) by associative and visual memory deficits following focal lesions (Cowey & Gross, 1970). Several studies have described cells in macaque area TE that responds to monkey faces (e.g., Fujita et al., 1992; see Tanaka, 1996), although the largest proportions of face-selective cells are found in

the inferior bank of the superior temporal sulcus, in subregions TEa and TEm of TE (see Rolls, 1992).

The activation reported here is located at the posterior part of BA 20, in the anterior part of TEO/posterior TE (see Figure 4). Surprisingly, BA 20 in the inferior temporal lobe is barely described as activated in fMRI studies (see Cabeza & Nyberg, 2000). However, activation of this region in the right hemisphere has been described in PET studies of face processing (Wiser et al., 2000; Kukowski & Pardo, 1999; Nakamura et al., 1999). An activation of this region in the right hemisphere has also been described in two studies that compared the presentation of completely novel faces to faces recently learned (Wiser et al., 2000), or unfamiliar faces unrepeated to repetition of the same faces throughout the scanner (Kukowski & Pardo, 1999). In this last study, the level of activation in this region was not correlated with memory performance on a recognition task following the PET experiment. Given the functional and anatomical features of this region, as well as the findings from these studies, the activation observed in the present study may be related to a real increase to novel faces, facilitating their implicit encoding in mnemonic circuits of the medial temporal lobe, with which BA 20 is highly connected. In other words, this region of the right inferotemporal cortex might be involved in novel face detection and encoding, being closely linked to occipito-temporal regions (BA 37) and to medial temporal lobe regions (BAs 36, 28, and 34) involved in memory encoding.

In favor of this interpretation also come the well-documented findings of cellular recording studies in behaving monkeys that IT cell responses to faces can be modulated by recent experience in delayed-matching from sample and habituation paradigms (Miller, Li, Desimone, 1993; Rolls, Baylis, Hasselmo, & Nalwa, 1989), and may also show longer term effects of experience (Miyashita, 1988). More precisely, Rolls et al. (1989) found that a large number of IT cells presents a higher mean response to the first presentation of a set of novel faces than to the subsequent presentations of faces. Miller et al. (1991, see also Riches, Wilson, & Brown, 1991) also observed that IT cell responses to incoming visual stimulus are attenuated if it matches a stimulus actively held in working memory. More to the point, responses of IT cells to novel stimuli decline as visual stimuli become familiar to the monkey, suggesting that the response of IT neurons to incoming visual stimuli carry information about the memories of past (short-term and long-term) stimuli. IT neurons are thus thought to be acting as adaptive mnemonic filters that seek to preferentially pass information about new or unexpected stimuli (Desimone, 1995; Miller et al., 1993).

All these findings concur with the observation of a higher activity in the right inferotemporal cortex for faces perceived as novel in the present PET study in humans, showing moreover that these novelty effects depend on what the subject perceives as novel or

familiar, and not on the amount of visual information that has been previously presented (see the next point).

It is worth noting that no changes of brain activity in the FFA (Kanwisher et al., 1997), nor in other face-sensitive regions such as the superior temporal sulcus (e.g., Haxby et al., 1999; Halgren et al., 1998; Kanwisher et al., 1997) were reported in the present study. This suggests, at first glance, that at least some of the regions involved in discriminating faces from other categories (what the factors of this specialization may be, see Kanwisher, 2000, and Tarr & Gauthier, 2000) would be different than the regions involved in discriminating familiar from unfamiliar faces. However, Gauthier, Tarr, et al. (2000) described effects of face identity repetition in the FFA, as in the occipital face area. The fusiform area is located in BA 37, somewhat in between the two occipito-temporal regions that were found to be sensitive to face familiarity in the present study. It cannot be excluded from the present study that future PET or fMRI studies using a simple localizer task (face' objects) and familiar and unfamiliar faces might disclose such long-term familiarity effects at the level of the FFA.

The Neural Correlates of Face Categorical Perception

The second objective of this PET study was less related to the localization of brain activity per se than to the nature of these changes: subjects were presented with continua of complex multidimensional sensory information, and changes of brain activity were not linearly related to these continua, but rather to the more categorical perception of the subjects (see Figures 2, 3, and 5). To our knowledge, this is the first neuroimaging study to identify a neural correlate of such a categorical perception effect.

Here the localization of these regions is not of particular importance: had we presented continua from one face expression to another (e.g., joy to fear), we would probably have observed differences in another set of brain regions (probably including the amygdala), insofar as these two emotions are clearly dissociated in the human brain (Morris et al., 1998). What is important here is that brain activity is correlated with the subject's perceptual awareness of a difference, rather than with the continuum of information. This is in line with cellular recordings and neuroimaging studies on binocular rivalry (Tong, Nakayama, Vaughan, & Kanwisher, 1998; Logothetis, Leopold, & Sheinberg, 1996) and rapid perceptual learning (Dolan et al., 1997; Tovee, Rolls, & Ramachandran, 1996). These studies show that neurons in low-level and (mainly) high-level visual areas correlate their activity with the subject's perception, being decreased when the face or object is not perceived from the image, either before learning (Dolan et al., 1997; Tovee et al., 1996), in binocular rivalry paradigms (Tong et al., 1998), or by short

presentations and backward masking (Grill-Spector, Kushnir, Hender, Malach, 2000).

The mechanisms underlying these all-or-none abrupt changes accompanying perceptual awareness are yet unknown. However, contrary to previous paradigms, the present study used more than two contrasted conditions (e.g., before/after learning), allowing a better description of the way changes of brain activity correlate with the subject's perception. Indeed, despite the amount of sensory information previously presented to the subject in the 40% images as compared to the 0% images, there was no difference between these two conditions, whereas the functional difference between 40% and 60%, albeit being physically smaller, was much more pronounced in several right occipito-temporal regions (see Figure 5). This neural correlate of face categorical perception is also in line with a recent ERP study in which we showed a decrease of the right N170 to the repetition of faces perceived as of the same identity, while there was not any such decrease when the repeated face was perceived as a different identity, despite the absolute difference on the continuum being equal in the two conditions (see Campanella, Hanoteau, et al., 2000). Together with the present observation, these findings clarify the spatio-temporal correlate of the face categorical perception effect: occipito-temporal regions of the right hemisphere rapidly and abruptly modify their level of activity when crossing a perceptual boundary. The exact mechanisms that allows these abrupt changes accompanying perceptual awareness must be clarified in future cellular recordings and neuroimaging studies. Moreover, our study helps to clarify an unresolved question regarding the way perceptual representations of face are matched to representations stored in long-term memory (FRU). Contrary to what was proposed by Bruce and Young (1986), our results, drawn from an activations/deactivations pattern in brain regions, support the hypothesis that an FRU activation' corresponding to face recognition' is made in an all-or-none fashion (Hay & Young, 1982) rather than proportionally to the resemblance between the two representations to be matched.

METHODS

Pilot Experiment

The aim of the pilot experiment was twofold. First, it was to ensure that subjects would easily discriminate familiar and unfamiliar faces after the face familiarization procedure. Second, we aimed to ensure that subjects perceive one part of the continuum as made-up of familiar faces and the other part as unfamiliar. Thus, although categorical effects have been clearly demonstrated on both familiar (Beale & Keil, 1995) and unfamiliar faces (Levin & Beale, 2000), we tested specifically whether exemplars coming from continua made up of a familiar and an

unfamiliar face would be perceived in a categorical way. We did not aim to extract the exact boundary value for each continuum and each subject, but we simply set the different conditions of the experiment at equidistant percentages on the continuums, from the unfamiliar to the familiar faces (0%, 20%, 40%, 60%, 80%, and 100%). The test of the pilot experiment was made to ensure that subjects roughly perceive faces from the three first sets as unfamiliar and from the three last sets as unfamiliar.³

Subjects

Eight right-handed adult subjects (four men, age range: 20–26) took part in the pilot behavioral experiment.

Stimuli

Photographic face quality images of 90 students (45 men and 45 women, age 18–30), without glasses, facial hair, and make-up, were taken with a digital camera. These photographs were divided in three sets of 30 facial identities each: A, B, and C. Set A was divided in two parts: A1 and A2. A1 served for extensive training. There were three photographs (full front, left and right 3/4 profiles) for each identity in Set A1. Set A2 was made up of another pool of full-front photographs of the same faces. Set B was made-up of 30 unknown full front faces that were used for the test of familiarity (third day, see below). Set C contained the unknown full front faces that were morphed with the familiarized faces (A2). All sets and subsets of faces always contained half male and half female faces. All face photographs were edited in Adobe Photoshop 4.0 to remove backgrounds and haircut, and everything below the chin (see Figure 1). They were all of neutral facial expression. The resolution of all face photographs was of $155 \cong 188$ pixels at 72 dpi. Each of 30 full front faces from Set A2 was paired with one of the 30 full front faces of Set C, giving 30 pairs of faces (only male–male and female–female morphs were made). Thirty continuums were generated from these pairs using a ‘morph– program (Morph™) that, given any two images as endpoints, can produce a linear continuum of images between the two end images (see Beale & Keil, 1995). Using this program, six images were extracted for each of the 30 face-pairs, at 20% increments: 0% familiar, 20%, 40%, 60%, 80%, 100%. All of these 180 images (extracted from Sets A2 and C) were shown only after the training procedure (see next section), that is either during the testing (pilot experiment) or the PET data acquisition.

Procedure: Learning Phase

This phase took part two consecutive days before testing. The first day, subjects were familiarized with the faces (Set A1) during about 100 min, and the second day

during 60 min. On each day of training, subjects were familiarized with manually presented photographs, and computer exercises. First, subjects were given 90 photographs of the 30 faces (A1): full front, 3/4 right profile, 3/4 left profile. All faces were mixed and subjects had to find the three faces belonging to the same person (making 30 triplets), with no time limit. On average, subjects completed the task in 51 min, with only two errors for four out of eight subjects. Then, subjects were familiarized again with the faces presented on the computer by means of various tasks: passive viewing at the faces (full front faces, 3/4 faces, original full front photographs), checking for face repetition within a sequence, judging whether full front and 3/4 faces were ‘nice– or ‘not so nice– persons, matching faces across viewpoint changes.

Procedure: Testing

The third day, subjects performed a simple face recognition task, as a control to test that they had learned the faces properly. Sixty full front faces were presented successively on the computer screen (2000 msec, ISI: 2000 msec): the 30 faces of Set A1 and 30 novel faces of Set B. Subjects had to press one of two keys depending on whether they knew the face or not. This testing of face familiarity was well performed by all subjects, with only four subjects responding unknown to one of the familiarized face (different item for each subject).

Procedure: Detection and Categorization Tasks

On the fourth day of the pilot experiment, subjects performed two tasks, a categorization task and a detection task. In the categorization task, 20 continua were used. Three stimuli were extracted from each continuum, in a way that 10 stimuli of each step (0%, 20%, 40%, 60%, 80%, and 100%) were presented to the subjects (60 stimuli). Each face was presented for 2000 msec as in the testing stage (Day 3), and subjects had to decide whether the face presented was a known or unknown face. The results indicated that subjects indeed perceived the continua in a categorical way, with a sharp difference in the percentage of the familiarity decisions between the 40% images (perceived as unknown) and the 60% images (perceived as known). The percentages of ‘familiar– decision for each of the steps in the continuum were as follow: 0%, 12.5%, 26.5%, 78.75%, 91.25%, and 96.25% for the conditions 0%, 20%, 40%, 60%, 80%, and 100%, respectively. These percentages are similar to what has been demonstrated in previous behavioral studies (e.g., Campanella, Chrysocoos, et al., In press; Calder et al., 1996; Beale & Keil, 1995): there is a sudden change in the decisions made at the boundary (around 50%), although this is not as sharp as a complete categorical perception would be (see Figure 2). The detection task was similar to the discrimination

task that was used with some variations in previous behavioral studies (Campanella, Chrysocoos, et al., In press; Beale & Keil, 1995). That is, it aimed at showing a better discrimination of two faces crossing the perceptual boundary than two faces on the same side of this boundary (even if the physical distance between the pairs is kept equal). The remaining 10 continua (extracted from A2 and C) were used for this task, and 24 pairs were extracted from each continuum, giving 240 trials in amount. Each trial was made-up of a consecutive presentation of two faces, each presented for 400 msec (delay between pairs: 500 msec, ISI: 2000 msec). There were 120 identical trials, and all the other trials were pairs of very similar but different face photographs: 40 pairs of 5%' 25%; 40 pairs of 40%' 60%; and 40 pairs of 65%' 85%. The subjects' task was to press a key when they detected that the two faces were different. This task was very difficult since the two faces look very similar and subjects were asked only to press the key when they were sure of their response, but as expected subjects pressed more often the key when the two faces were of the 40%' 60% pair than (5%' 25%) and (65%' 85%) pairs, although the number of difference detection was very low: 19.5/40 for 40%/60% pairs; 16/40 (65%/85%); 13.5/40 (5%/25%). Nevertheless, these differences were significant [one-way ANOVA for repeated measurements: $F(1,7) = 15.414$, $p < .001$] and post hoc t tests confirmed that the detection was better when the two faces of a pair were on different sides of the perceptual boundary: 40%/60% versus 5%/25% ($p < .005$), 40%/60% versus 65%/85% ($p < .005$), 65%/85% versus 5%/25% (ns).

PET Experiment

Subjects

Eight male right-handed adult volunteers (age range: 22' 25) provided written consent according to institutional guidelines.

Stimuli

The same stimuli were used as in the pilot study. Set C was introduced during the PET experiment, together with the new full front faces of Set A (A2).

Procedure

The training and testing procedure (first 3 days) were exactly identical to the pilot experiment. Overall, subjects recognized 96.25% of the faces (all subjects between 28 and 30), with mean reaction times of 885.5 msec.⁴

The PET study took place on the fourth day. Fourteen PET scans were recorded: two rest scans (eyes closed) and two scans of each condition (0%, 20%, 40%, 60%, 80%, and 100%). Rest scans were always the first and last one of the 14 scans. For the experimental conditions,

the images were selected as to avoid as much as possible the repetition of unfamiliar information. The 30 continua were divided in three groups. In the first set of six experimental scans, 0% and 100% images were extracted from Group 1, 20% and 60% images from Pool 2, 40% and 80% images from Pool 3. For the second set of scans, 0% and 100% images were extracted from Group 2, 20% and 60% images from Pool 3, 40% and 80% images from Pool 1. The order of the first six experimental scans was randomized, with this order reversed for the second repetition of six scans. In the experimental conditions, subjects saw a succession of 10 faces presented at the rate of 5 sec per face (3 sec for the face on the screen, 2 sec black screen interval) on a black computer screen (MacIntosh 17AV, 110 cm from the subject). Subjects' responses were recorded when pressing the right or the left key of a response box with the index or the medius of the left hand, depending on whether the stimulus was a male or a female face. Half of the faces were male, the other half female, in all conditions. Correct response latencies and error rates were recorded during scanning sessions.

Measurements of local radioactivity uptake were made using an ECAT EXACT-HR PET tomograph (CTI/Siemens), which allows simultaneous imaging of 47 transaxial slices in three-dimensional (3-D, septa retracted) mode, with an effective resolution of 8 mm full width half maximum (FWHM) (Wienhard et al., 1994) and a slice thickness of 3.125 mm. 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). Positioning of the subject in the gantry was accomplished by aligning two sets of low power laser beams with the canthomeatal line and the sagittal line, respectively. Head-restraining adhesive bands were used. A 22-gauge catheter was then placed in the antecubital vein of the right arm for radiotracer injection. Prior to tracer administration, each subject underwent a 15-min transmission scan performed with retractable germanium-68 rotating rod sources, allowing the subsequent correction of emission images for attenuation. Cerebral blood flow measurement was then performed using a 20s bolus of oxygen-15-labeled water (8 mCi, 2.96 e + 02 MBq). Beginning 10 sec after initiation of tracer injection, the related task was started and PET data were acquired simultaneously. The integrated counts accumulated during 50-sec scans were used as an index of rCBF (Mazziotta & Phelps, 1986). The time interval between successive emission scans was 13 min, which allowed decay of residual radioactivity. For each subject, 3-D MRI anatomical data were also obtained on a 1.5-T unit (General Electric Signa) using the Spoiled Grass (SPGR) technique. T-1 weighted images (TR = 25 msec, TE = 6 msec, flip angle = 25°, slice thickness = 1.5 mm) were obtained in the bicommissural (AC' PC) orientation.

Data Analysis

PET images were realigned to correct for interscan movements and coregistered to the subject's MRI using AIR 3.0 (Woods, Grafton, Holmes, Cherry, & Mazziotta, 1998). The resulting matching brain images were spatially normalized, using SPM 96 Wellcome Department of Cognitive Neurology, in the Talairach and Tournoux (1988) coordinate system with a cubic ($2 \cong 2 \cong 2$ mm) voxel size. The accuracy of realignment and normalization procedures were assessed with an interactive homemade image display software (Michel et al., 1995) implemented in IDL language (IDL Research System). PET images were further smoothed using an isotropic Gaussian filter of 15 mm FWHM and corrected for global activity by proportional scaling (Fox, Mintun, Reiman, & Raichle, 1988). Two kinds of statistical analyses were performed.

1. PCA: Principal components or eigenimages of the covariance matrix were extracted from the experimental data and maps of functional networks corresponding to significant components were obtained using SPM96 (see Friston et al., 1995).

2. Statistical parametric mapping: categorical and parametric analyses: 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). The resulting voxel sets of each contrast constitute a statistical parametric map of the t statistic $SPM\{t\}$, which is then transformed to the unit normal distribution $SPM\{Z\}$. This allows the overlay of the obtained Z maps on each spatially normalized MRI. First, a subtractive design was used. Three inferential analyses were performed. (1) The scans of the experimental conditions were grouped according to whether they contained mainly faces perceived as unfamiliar (0%, 20%, and 40%) or familiar (60%, 80%, and 100%) and these two pools of conditions were subtracted from each other. (2) An ANCOVA model was fitted to the data at each voxel, with the percentage of the morph images (0% to 100%) as covariate of interest. In this parametric contrast, weights were assigned to each condition according to the proportion of familiar (or unfamiliar) face in the stimuli. This covariate analysis (masked by the contrast faces-rest) identified the regions in which brain activity either increased or decreased linearly with the covariate of interest (i.e., percentages of the morph images). (3) An ANCOVA analysis was performed with the mean RTs for each condition as covariate of interest, in order to assess which brain regions underwent activity changes related to task difficulty. For all comparisons, only voxels significantly activated at $p < .001$ (uncorrected for multiple comparisons) were considered.

3. Analyses on functional ROIs: Finally, values of corrected blood flow were extracted in the each subject in the regions activated in the categorical and parametric

contrasts performed on the group analysis. These values were computed over a sphere of 3-mm radius, centered on the maxima identified by the SPM analyses. Statistical tests were then performed on these values using Systat 5.1.

Acknowledgments

The authors wish to thank D. Labar and C. Semal for help in isotope preparation, A. Devolder for help in data acquisition, A. Coppens, M. Sibomana, and A. Bol from the computer science staff, and R. Bausart for technical assistance. B.R. is supported by the National Fund for Scientific Research (Belgium). This work was supported by grant FRSM 3.4520.98.

Reprint requests should be sent to Bruno Rossion, Department of Cognitive and Linguistic Sciences, Brown University, 190 Thayer Street, Providence, RI 02912, USA, or via e-mail: Bruno_Rossion@brown.edu.

Notes

1. rCBF in regions of the right and left orbital gyri (9), the right superior parietal gyrus (7), and the left precuneus (7) had positive correlation with RTs while rCBF in numerous regions was negatively correlated with RTs, including the left superior temporal gyrus (22), the anterior cingulate (24), and the right superior frontal gyrus (6).

2. Henson et al. (1999) also reported right fusiform modulation during face repetition. Decreases were observed for repetition of familiar faces while repetition of unfamiliar faces increased the responses. However, these changes concerned the short-term repetition of faces and how they are qualified with long-term familiarity. They were reported in a clearly distinct region (middle fusiform gyrus) than the ones where changes were reported here.

3. This procedure slightly differs from what is classically done on behavioral categorical perception experiments for the following reasons. First, different subjects were used in the PET and pilot experiments, so that extracting the exact boundary value for each subject was of no purpose for the present experiment. Second, the perceived mean boundary value is usually around 50% for a set of continuums in a group of subjects, and should be closer to this 50% value (with a lower variance) the more continuums and subjects are used in the study. Given that the number of continuums was very high in the present study (30) as compared to previous behavioral studies that used only a few (between 2 and 6), the mean boundary value is likely to be around 50% in the present study. Third, and more importantly, we aimed at having the different conditions in the PET study to be of equal distance from each other, and clearly on one or another side of the boundary, so that using steps of 20% from 0% to 100% was the ideal solution for the PET experiment.

4. The incorrect categorization of familiar faces as unfamiliar were due to errors in the choice of the response keys, but when the faces were shown to subjects again, they easily and quickly recognized all of them.

REFERENCES

- Allison, T., Puce, A., Spencer, D. D., & McCarthy, G. (1999). Electrophysiological studies of human face perception: I. Potentials generated in occipitotemporal cortex by face and non-face stimuli. *Cerebral Cortex*, *9*, 415–430.

- Beale, J. M., & Keil, F. C. (1995). Categorical effects in the perception of faces. *Cognition*, *57*, 217–239.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, *8*, 551–565.
- Bentin S., & Deouell, L. Y. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cognitive Neuropsychology*, *17*, 35–54.
- Blaxton, T. A., Zeffiro, T. A., Gabrieli, J. D. E., Bookheimer, S. Y., Carrillo, M. C., Theodore, W. H., & Disterhoft, J. F. (1996). Functional mapping of human learning: A positron emission tomography activation study of eyeblink conditioning. *Journal of Neuroscience*, *16*, 4032–4040.
- Bornstein, M. H., & Korda, N. O. (1984). Discrimination and matching within and between hues measured by reaction times: Some implications for categorical perception and levels of information processing. *Psychological Research*, *46*, 207–222.
- Bruce, V., & Young, A. W. (1986). Understanding face recognition. *British Journal of Psychology*, *77*, 305–327.
- Buckner, R. L., Goodman, J., Burock, M., Rotte, M., Koutstaal, W., Schacter, D., Rosen, B., & Dale, A. M. (1998). Functional-anatomic correlates of object priming in humans revealed by rapid presentation event-related fMRI. *Neuron*, *20*, 285–296.
- Buckner, R. L., & Koutstaal, W. (1998). Functional neuroimaging studies of encoding, priming, and explicit memory retrieval. *Proceedings of the National Academy of Sciences, U.S.A.*, *95*, 891–898.
- Buckner, R. L., Petersen, S. E., Ojemann, J. G., Miezin, F. M., Squire, L. R., & Raichle, M. E. (1995). Functional anatomical studies of explicit and implicit memory retrieval tasks. *Journal of Neuroscience*, *15*, 12–29.
- Cabeza, R., & Nyberg, L. (2000). Imaging cognition: II. An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, *12*, 1–47.
- Calder, A. J., Young, A. W., Perrett, D. I., Ectoff, N. L., & Rowland, D. (1996). Categorical perception of morphed facial expressions. *Visual Cognition*, *3*, 81–117.
- Campanella, S., Chrysocoos, A., & Bruyer, R. (In press). Categorical perception of facial gender information: Behavioural evidence and the face-space metaphor. *Visual Cognition*.
- Campanella, S., Hanoteau, C., Depy, D., Rossion, B., Bruyer, & R., Guerit, J.-M. (2000). Right N170 modulation in a face discrimination task: An account for categorical perception of familiar faces. *Psychophysiology*, *37*, 796–806.
- Campbell, R., Pascalis, O., Coleman, M., Wallace, S. B., & Benson, P. J. (1997). Are faces of different species perceived categorically by human observers? *Proceedings of the Royal Society of London: Series B, Biological Sciences*, *264*, 1429–1434.
- Cowey, A., & Gross, C. G. (1970). Effects of foveal prestriate and inferotemporal lesions on visual discrimination by rhesus monkeys. *Experimental Brain Research*, *11*, 128–144.
- Dolan, R. J., Fink, G. R., Rolls, E., Booth, M., Holmes, A., Frackowiak, R. S., & Friston, K. J. (1997). How the brain learns to see objects and faces in an impoverished context. *Nature*, *389*, 596–599.
- Dubois, S., Rossion, B., Schiltz, C., Bodart, J.-M., Michel, C., Bruyer, R., & Crommelinck, M. (1999). Effect of familiarity on the processing of human faces. *Neuroimage*, *9*, 278–289.
- Eimer, M. (2000). Event-related potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology*, *111*, 694–705.
- Ectoff, N. L., & Magee, J. J. (1992). Categorical perception of facial expressions. *Cognition*, *44*, 227–240.
- Fox, P. T., Mintun, M. A., Reiman, E. M., & Raichle, M. E. (1988). Enhanced detection of focal brain response using intersubject averaging and change–distribution analysis of subtracted PET images. *Journal of Cerebral Blood Flow Metabolism*, *8*, 642–653.
- Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J.-P., Frith, C. D., & Frackowiak, R. S. J. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, *2*, 89–210.
- Fujita, I., Tanaka, K., Ito, M., & Cheng, K. (1992). Columns for visual features of objects in monkey inferotemporal cortex. *Nature*, *360*, 343–346.
- Gauthier, I., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience*, *3*, 191–197.
- Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P., & Gore, J. C. (1999). Activation of the middle fusiform–face area–increases with expertise in recognizing novel objects. *Nature Neuroscience*, *2*, 568–573.
- Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusiform–face area– is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience*, *12*, 495–504.
- George, N., Dolan, R. J., Fink, G. R., Baylis, G. C., Russel, C., & Driver, J. (1999). Contrast polarity and face recognition in the human fusiform gyrus. *Nature Neuroscience*, *2*, 574–580.
- Goldstone, R. (1994). Influence of categorization on perceptual discrimination. *Journal of Experimental Psychology: General*, *123*, 178–200.
- Gorno-Tempini, M. L., Price, C. J., Josephs, O., Vandenberghe, R., Cappa, S. F., Kapur, N., Frackowiak, R. S., & Tempini, M. L. (1998). The neural systems sustaining face and proper-name processing. *Brain*, *121*, 2103–2118.
- Grill-Spector, K., Kushnir, T., Hendler, T., & Malach, R. (2000). The dynamics of object-selective activation correlate with recognition performance in humans. *Nature Neuroscience*, *3*, 837–843.
- Gross, C. G. (1992). Representation of visual stimuli in inferior temporal cortex. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *335*, 3–10.
- Halgren, E., Dale, A. M., Sereno, M. I., Tootell, R. B. H., Marinkovic, K., & Rosen, B. (1998). Location of human face-selective cortex with respect to retinotopic areas. *Human Brain Mapping*, *7*, 29–37.
- Harnad, S., ed. (1987). *Categorical perception: The groundwork of cognition*. Cambridge: Cambridge University Press.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*, 223–233.
- Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*, *22*, 189–199.
- Haxby, J. V., Ungerleider, L. G., Horwitz, B., Maisog, J. M., Rapoport, S. I., & Grady, C. L. (1996). Face encoding and recognition in the human brain. *Proceedings of the National Academy of Sciences, U.S.A.*, *93*, 922–927.
- Hillger, L. A., & Koenig, O. (1991). Separable mechanisms in face processing: Evidence from hemispheric specialization. *Journal of Cognitive Neuroscience*, *3*, 42–58.
- Hosie, J. A., Ellis, H. D., & Haig, N. D. (1988). The effect of feature displacement on the perception of well-known faces. *Perception*, *17*, 461–474.
- Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences, U.S.A.*, *96*, 9379–9384.
- Kanwisher, N. (2000). Domain-specificity in face perception. *Nature Neuroscience*, *3*, 758–763.
- Kanwisher, N., McDermott, J., & Chun, M. (1997). The fusiform

- face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
- Kapur, N., Friston, K. J., Young, A., Frith, C. D., & Frackowiak, R. S. J. (1995). Activation of human hippocampal formation during memory for faces: A PET study. *Cortex*, *31*, 99–108.
- Katanoda, K., Yoshikawa, K., & Sugishita, M. (2000). Neural substrates for the recognition of newly learned faces: A functional MRI study. *Neuropsychologia*, *38*, 1616–1625.
- Kuskowski, M. A., & Pardo, J. V. (1999). The role of the fusiform gyrus in successful encoding of face stimuli. *NeuroImage*, *9*, 599–610.
- Leveroni, C. L., Seidenberg, M., Mayer, A. R., Mead, L. A., Binder, J. R., & Rao, S. M. (2000). Neural systems underlying the recognition of familiar and newly learned faces. *Journal of Neuroscience*, *20*, 878–886.
- Levin, D. T., & Beale, J. M. (2000). Categorical perception occurs in newly learned faces, other-race faces, and inverted faces. *Perception and Psychophysics*, *62*, 386–401.
- Logothetis, N. K., Leopold, D. A., & Sheinberg, D. L. (1996). What is rivaling during binocular rivalry? *Nature*, *18*, 621–624.
- Malach, R., Reppas, J. B., Benson, R. R., Kwong, K. K., Jiang, H., Kennedy, W. A., Ledden, P. J., Brady, T. J., Rosen, B. R., & Tootell, R. B. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proceedings of the National Academy of Sciences, U.S.A.*, *92*, 8135–8139.
- Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L., & Ungerleider, L. G. (1995). Discrete cortical regions associated with knowledge of color and knowledge of action. *Science*, *270*, 102–105.
- Mazziotta, J. C., & Phelps, M. E. (1986). Positron emission tomography studies of the brain. In: M. E. Phelps, J. Mazziotta, & H. Schelbert (Eds.), *Positron emission tomography and autoradiography: Principles and applications for the brain and heart* (pp. 493–579). New York: Raven Press.
- McCarthy, G., Puce, A., Gore, J. C., & Allison, T. (1997). Face-specific processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience*, *9*, 605–610.
- Michel, C., Sibomana, M., Bodart, J.-M., Grandin, C., Coppens, A., Bol, A., De Volder, A., Warscotte, V., Thiran, J.-P., & Macq, B. (1995). Interactive delineation of brain sulci and their merging into functional PET images. *IEEE Medical Imaging Conference Record*, 1480–1484.
- Michel, F., Poncet, M., & Signoret, J.-L. (1989). Les lésions responsables de la prosopagnosie sont-elles toujours bilatérales? *Revue de Neurologie*, *145*, 764–770.
- Miller, E. K., Li, L., & Desimone, R. (1993). Activity of neurons in anterior inferior temporal cortex during a short-term memory task. *Journal of Neuroscience*, *13*, 1460–1478.
- Miyashita, Y. (1988). Neuronal correlate of visual associative long-term memory in the primate temporal cortex. *Nature*, *335*, 817–820.
- Morris, J. S., Friston, K. J., Buchel, C., Frith, C. D., Young, A. W., Calder, A. J., & Dolan, R. J. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, *121*, 47–57.
- Nakamura, K., Kawashima, R., Ito, K., Sugiura, M., Kato, T., Nakamura, A., Hatano, K., Nagumo, S., Kubota, K., Fukuda, H., & Kojima, S. (1999). Activation of the right inferior frontal cortex during assessment of facial emotion. *Journal of Neurophysiology*, *82*, 1610–1614.
- Pearce, J. W., Leigh, A. E., & Kendrick, K. M. (2000). Configurational coding, familiarity and the right hemisphere advantage for face recognition in sheep. *Neuropsychologia*, *38*, 475–483.
- Puce, A., Allison, T., Asgari, M., Gore, J. C., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letterstrings, and textures: A functional magnetic resonance imaging study. *Journal of Neuroscience*, *16*, 5205–5215.
- Puce, A., Allison, T., McCarthy, G. (1999). Electrophysiological studies of human face perception: III. Effects of top-down processing on face-specific potentials. *Cerebral Cortex*, *9*, 445–458.
- Rhodes, G. (1993). Configurational coding, expertise, and the right hemisphere advantage for face recognition. *Brain and Cognition*, *22*, 19–41.
- Riches, I. P., Wilson, F. A., Brown, M. W. (1991). The effects of visual stimulation and memory on neurons of the hippocampal formation and the neighboring parahippocampal gyrus and inferior temporal cortex of the primate. *Journal of Neuroscience*, *11*, 1763–1779.
- Rolls, E. T., Baylis, G. C., Hasselmo, M. E., & Nalwa, V. (1989). The effect of learning on the face selective responses of neurons in the cortex in the superior temporal sulcus of the monkey. *Experimental Brain Research*, *76*, 153–164.
- Rossion, B., Campanella, S., Gomez, C. M., Delinte, A., Debattiste, D., Liard, L., Dubois, S., Bruyer, R., Crommelinck, M., & Guerit, J. M. (1999). Task modulation of brain activity related to familiar and unfamiliar face processing: An ERP study. *Clinical Neurophysiology*, *110*, 449–462.
- Rossion, B., de Gelder, B., Dricot, L., Zoontjes, R., Bodart, J. M., Devolder, A., & Crommelinck, M. (2000). Hemispheric asymmetries for whole-based and part-based face processing in the human-brain. *Journal of Cognitive Neuroscience*, *12*, 793–802.
- Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., & Crommelinck, M. (2000b). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: An electrophysiological account of face-specific processes in the human brain. *NeuroReport*, *11*, 69–74.
- Seeck, M., Mainwaring, N., Ives, J., Blume, H., Dubuisson, D., Cosgrove, R., Mesulam, M. M., & Schomer, D. L. (1993). Differential neural activity in the human temporal lobe evoked by faces of family members and friends. *Annals of Neurology*, *34*, 369–372.
- Sergent, J., Otha, S., & MacDonald, B. (1992). Functional neuroanatomy of face and object processing. A positron emission tomography study. *Brain*, *115*, 15–36.
- Squire, L. R., Ojemann, J. G., Miezin, F. M., Petersen, S. J., Videen, T. O., & Raichle, M. E. (1992). Activation of the hippocampus in normal humans: A functional anatomical study of memory. *Proceedings of the National Academy of Sciences, U.S.A.*, *89*, 1837–1841.
- Talairach, J., & Tournoux, P. (1988) *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.
- Tanaka, K. (1996). Inferotemporal cortex and object vision. *Annual Review of Neuroscience*, *19*, 109–139.
- Tarr, M. J., & Gauthier, I. (2000). FFA: A flexible fusiform area for subordinate-level visual processing automatized by expertise. *Nature Neuroscience*, *3*, 764–769.
- Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron*, *21*, 753–759.
- Tovee, M. J., Rolls, E. T., & Ramachandran, V. S. (1996). Rapid visual learning in neurones of the primate temporal visual cortex. *NeuroReport*, *7*, 2757–2760.
- Webster, M. J., Ungerleider, L. G., & Bachevalier, J. (1991). Connections of inferior temporal areas TE and TEO with medial temporal-lobe structures in infant and adult monkeys. *Journal of Neuroscience*, *11*, 1095–1116.
- Wienhard, K., Dahlbom, M., Eriksson, L., Michel, C., Bruck-

- bauer, T., Pietrzyk, U., & Heiss, W. D. (1994). The ECAT EXACT HR— Performance of a new high resolution positron scanner. *Journal of Computer-Assisted Tomography*, *18*, 110–118.
- Wiggs, C. L., & Martin, A. (1998). Properties and mechanisms of perceptual priming. *Current Opinion in Neurobiology*, *8*, 227–233.
- Wiser, A. K., Andreasen, N., O'Leary, D. S., Crespo-Facorro, B., Boles-Ponto, L. L., Watkins, G. L., & Hichwa, R. D. (2000). Novel vs. well-learned memory for faces: A positron emission tomography study. *Journal of Cognitive Neuroscience*, *12*, 255–266.
- Woods, R. P., Grafton, S. T., Holmes, C. J., Cherry, S. R., & Mazziotta, J. C. (1998). Automated image registration: I. General methods and intrasubject, intramodality validation. *Journal of Computer-Assisted Tomography*, *22*, 139–152.
- Young, A. W., Hay, D. C., McWeeny, K. H., Flude, B. M., & Ellis, A. W. (1985). Matching familiar and unfamiliar faces on internal and external features. *Perception*, *14*, 737–746.
- Young, A. W., McWeeny, K. H., Hay, D. C., & Ellis, A. W. (1986). Matching familiar and unfamiliar faces on identity and expression. *Psychological Research*, *48*, 63–68.