Spatio temporal Dynamics of Face Recognition

To better understand face recognition, it is necessary to identify not only which brain structures are implicated but also the dynamics of the neuronal activity in these structures. Latencies can then be compared to unravel the temporal dynamics of information processing at the distributed network level. To achieve high spatial and temporal resolution, we used intracerebral recordings in epileptic subjects while they performed a famous/unfamiliar face recognition task. The first components peaked at 110 ms in the fusiform gyrus (FG) and simultaneously in the inferior frontal gyrus, suggesting the early establishment of a large-scale network. This was followed by components peaking at 160 ms in 2 areas along the FG. Important stages of distributed parallel processes ensued at 240 and 360 ms involving up to 6 regions along the ventral visual pathway. The final components peaked at 480 ms in the hippocampus. These stages largely overlapped. Importantly, event-related potentials to famous faces differed from unfamiliar faces and control stimuli in all medial temporal lobe structures. The network was bilateral but more right sided. Thus, recognition of famous faces takes place through the establishment of a complex set of local and distributed processes that interact dynamically and may be an emergent property of these interactions.

Keywords: electrophysiology, epileptic patients, intracerebral recordings, model of face recognition, neural network

Introduction

Face recognition is a fundamental skill that has received considerable attention because of its importance for social interactions. Furthermore, the ability to recognize a face can be impaired in isolation suggesting that it relies on dedicated neural circuits (Charcot 1883; Wilbrand 1892; Bodamer 1947). Subsequent to the report of spatially and temporally localizable brain responses to faces (Allison, Ginter, et al., 1994), there has been an enormous interest in revealing the characteristics of these neural circuits via various functional neuroimaging and electrophysiological methods as well as neuropsychological case studies (De Renzi et al. 1994; Bentin et al. 1999; Haxby et al. 1999; McCarthy et al. 1999; Halgren et al. 2000; Itier and Taylor 2004a). Several brain areas have been identified as being involved in face processing, such as the inferior occipital gyrus, the posterior fusiform gyrus (FG), or the temporal poles (Sergent et al. 1992; Evans et al. 1995; Puce et al. 1995; Kanwisher et al. 1997). This has led to the proposal that face recognition relies on a distributed neural network (Haxby et al. 2000; Ishai et al. 2005). In the temporal domain, a negative component peaking around 170 ms (N170) is recorded on the scalp surface and has been shown to be consistently larger to face stimuli (Bentin et al. 1996; Itier and Taylor 2004b). This N170 is preceded by an earlier component (P1) that also shows some modulation by faces (Halgren et al. 2000; Taylor et al. 2001) and is followed by later responses around 250 and 400 ms that are modulated by face familiarity (Bentin and Deouell 2000; Schweinberger et al. 2002).

Despite progress in identification of the neural substrate and timing underlying face recognition, it has been difficult to relate both those dimensions because most investigation methods currently available allow satisfactory precision in either the spatial distribution (positron-emission tomography [PET], functional magnetic resonance imaging [fMRI]) or the temporal course of the information (scalp electroencephalography [EEG], magnetoencephalography), but not both simultaneously. However, precise knowledge of the temporal course of the neural activation in each brain area involved in face recognition is critical for any model of face recognition. It is only with this knowledge that how the different brain areas interact can be properly understood (Nowak and Bullier 1997; Bullier 2001; Bullier et al. 2001; Bar 2003). The aim of the present study was to analyze the temporal dynamics of the different brain areas involved in face recognition.

Precise measures of where and when activity occurs in the brain can be obtained with intracranial recordings. The classic studies by Allison, Ginter, et al. (1994), Allison, McCarthy, et al. (1994), Allison et al. (1999), McCarthy et al. (1999), and Puce et al. (1999) using grids on the cortical surface identified a series of components evoked by faces. A potential peaking at 200 ms specific to faces was found in the posterior FG as well as the posterior middle temporal gyrus regions. Other components such as a P350 were recorded in more widespread regions in the posterior (VP350) and anterior (AP350) ventral temporal surface as well as the posterior lateral temporal surface (LP350). Using intracerebral electrodes implanted within brain structures, Halgren, Baudena, Heit, Clarke, Marinkovic (1994) and Halgren, Baudena, Heit, Clarke, Marinkovic; Chauvel (1994) confirmed and extended these findings identifying a series of components evoked by a face recognition task with a first sequence of N130-P180-N240 followed by another of N310-N430-P630. These potentials did not have the same spatial distribution. Some were recorded in a limited set of brain areas, such as the 180 component in the ventral posterior temporal region, whereas others were recorded from different areas, such as the 130 and 240 components in the temporal, parietal, and frontal lobes. Using still a different intracerebral approach, with an electrode passing through the grand axis of the hippocampus, Trautner et al. (2004) and Dietl et al. (2005) focused on a potential peaking around 400 ms.
(facial anterior medial temporal lobe-N400) recorded in the depth of anterior subhippocampal structures and on a potential recorded within the hippocampus peaking around 600 ms (hippocampal P600).

These studies confirmed that face recognition is carried out in different brain regions and helped reveal the underlying distributed network. The temporal dynamics of face recognition are also highlighted, with components found as early as 110 ms, up to 600 ms. However, except in a figure of ours (Halgren and Chauvel 1993), there has been little attempt to specifically compare the latencies of the intracerebral components recorded from different regions with one another. Such comparison can help in meeting our objective of providing a comprehensive framework of the spatiotemporal dynamics of face recognition at the whole-brain level.

In order to elicit potentials related to the recognition of faces, a famous face/unfamiliar face paradigm was used. To achieve simultaneous high spatial and temporal resolution, this paradigm was presented to subjects with drug-refractory epilepsy who had 6–10 depth electrodes implanted stereotaxically orthogonal to the interhemispheric plane. Each electrode contained 10–15 contacts along its length. It was thus possible to record from many different brain regions simultaneously, including some that had seldom been studied. We first investigated the spatiotemporal dynamics of the recognition of famous faces. We then investigated whether the recognition of faces differed from the recognition of another type of stimuli. Lastly, we analyzed the lateralization of face processing.

**Material and Methods**

**Stimuli and Tasks**

All subjects underwent a famous face/unfamiliar face recognition task using Eprime v1.1 (Psychology Software Tools Inc., Pittsburgh, PA). Accuracy of the delivery of the visual stimulus and the trigger recorded simultaneously with the EEG was controlled using a photodiode on the screen the subject was looking at. Famous faces (actors, singers, or politicians) and unknown faces (Fig. 1) were presented on the screen for 396 ms in a random order, and subjects had to indicate verbally whether they knew them. Note that our procedure was not intended to allow assessing how the patients recognized the faces (i.e., based on a feeling of familiarity, on semantic retrieval, or on naming). All photographs were gray scale and corresponded to an angular size of about $6^\circ \times 6^\circ$. Interstimulus interval (1992 ms) was filled by a fixation cross. Mean luminance of famous and unknown face photographs was equivalent. There were 48 pictures of each category of faces. Overall performance was 85% correct responses (detailed in Table 1). After correcting for errors (false alarms and omissions) and artifact rejection, the number of epochs per condition (famous faces correctly recognized and unfamiliar faces correctly rejected) was equated. Following these procedures, there were on average 38.1 (standard deviation = 7.8) epochs used to compute event-related potentials (ERPs) in each condition per patient.

In order to differentiate processes related to the recognition of faces from processes related to the recognition of other kinds of stimuli, patients also completed a visual recognition memory task in which trial-unique abstract patterns consisting of colorful clip arts (Fig. 1) were used as stimuli. In this task, subjects first had to learn a set of 15 stimuli and, after an interfering task of 3 min, had to recognize them among distracters in an old/new paradigm. Patients underwent several blocks according to their availability.

**Subjects and Recordings**

Eighteen patients who had drug-refractory epilepsy and were undergoing evaluation of possible surgical intervention were studied. Stereoelectroencephalographic (SEEG) recording was performed in order to define the epileptogenic zone (Talairach and Bancaud 1973). The choice of electrode location was based on pre-SEEG clinical and video-EEG recordings and made independently of the present study. This study did not add any invasive procedure to depth EEG recordings. All subjects were fully informed about the aim of investigation before giving consent. Subjects had from 6 to 10 intracerebral electrodes implanted stereotaxically orthogonal to the midline vertical plane. Each electrode was from 33.5- to 51-mm long, had a diameter of 0.8 mm, and contained from 10 to 15 contacts 2-mm long separated by 1.5 mm (Alcis, Besançon, France). Seventy-two to 126 intracerebral contacts were simultaneously recorded in each patient.

ERP recordings were part of the functional mapping procedure (language, memory, and vision depending on the epilepsy) carried out in each subject. Anticonvulsant therapy was reduced or withdrawn

![Figure 1. Examples of stimuli used in this study. Top: famous and unknown faces. Bottom: trial-unique abstract stimuli.](image-url)
during the SEEG exploration in order to facilitate seizures. However, no subject had seizures in the 12 h before ERP recordings. Signal was acquired using SynAmps amplifiers and Neuroscan software (Compumedics, El Paso, TX). The sampling frequency of EEG depth recording was 1000 Hz with an acquisition filter band-pass of 0.15 - 200 Hz. Reference was a surface electrode located in Fz. Implantation of electrodes, localization of epilepsy, and behavioral performance on the famous/unknown face recognition task are reported in Table 1. ERP Processing ERPs were computed off-line using Brainvision v1.05 (Brain Products GmbH, München, Germany) between 0 and 1500 ms with a prestimulus baseline of 150 ms. ERPs to famous faces and unknown faces as well as old/new abstract figures were computed after the rejection of omissions and false alarms (behavioral data were lost for 4 subjects due to a hard disk failure. In this case, all responses were considered correct, Table 1). Visual inspection of the EEG as well as artifact-rejection procedures enabled the rejection of periods with interictal activities. A filter with a high band pass of 0.53 Hz (time constant = 0.30, 12 dB/oct) and a low band pass of 40.00 Hz (12 dB/oct) was applied to the resulting ERPs. Statistical Analyses There were from 5 to 7 subjects’ data per brain area, so a nonparametric matched-paired signed-rank Wilcoxon test on individual averaged ERPs was used to assess significant differences. The Wilcoxon test was run on each millisecond in the 100 - 600 time windows. Performing tests on multiple time points increases the probability of a false positive. We therefore only considered differences significant that were present for at least 10 consecutive time points (Molholm et al. 2006). In contrast, gaps of less than 10 ms between adjacent periods were considered non-physiological and the periods were combined. Location of the Electrode Contacts Contact location has been described in detail elsewhere (Barbeau, Wendling, et al. 2005). Each electrode was inserted stereotaxically under general anesthesia. A routine postoperative computerized tomography (CT) scan without contrast was performed to check for the absence of bleeding and for the precise location of each contact. Magnetic resonance imaging (MRI) with 3-dimensional reconstruction was performed after the removal of the electrodes in order to locate the trace of each depth probe in the brain. The fusion of the postoperative CT scan with this MRI allowed precise anatomical localization of contacts. The distance from the midline vertical plane of a given contact could be calculated on the axial CT scan. After the trace of the electrode had been found on the postoperative axial MRI, the distance from the midline vertical plane could be determined and the position of the contact could then be viewed in the coronal or sagittal plane. After this procedure was completed, the anatomical structures in which contacts were located were identified using 3-dimensional verification.

Table 1

<table>
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<th>Subject</th>
<th>Sex</th>
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<th>Epileptic focus</th>
<th>Epilepsy</th>
<th>Number of electrodes</th>
<th>Number of contacts</th>
<th>Analyzed in this study</th>
<th>Task performance (%)</th>
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Note: R, right; L, left; A, ambidextrous; MTL, medial temporal lobe epilepsy; LTL, lateral temporal lobe epilepsy; PF, prefrontal lobe epilepsy; LOE, lateral occipital epilepsy; PA, parietal lobe epilepsy; pFG, posterior fusiform gyrus; rFG, middle fusiform gyrus; PG, posterior parahippocampal gyrus; PC, perirhinal cortex; TP, temporal pole; H, hippocampus; IFG, inferior frontal gyrus; r, right; l, left; CD, cortical dysplasia; OGD, olгодендроглиома; HS, hippocampal sclerosis; n/a, non available.
superior temporal sulcus, the anterior insula, or the dorsolateral frontal lobes, but did not fulfill the criteria mentioned above and so were not analyzed further.

**Spatiotemporal Dynamics of Face Recognition**

Figure 3 shows ERPs averaged across patients recorded from the posterior to anterior regions mentioned above in response to correctly recognized famous faces.

These results are also reported for a representative subject (subject 1) in whom most brain areas of interest in this study were recorded simultaneously, allowing an intrasubject comparison (Fig. 4). It demonstrates that the different components reported in the group analysis are robust as they can also be observed at the individual level.

The ERPs recorded from the posterior and middle FG were characterized by a N110-P160-N240 with a mean onset at ~80 ms. The N110, but not the P160, peaked slightly earlier in the posterior than the middle region. The P160 could be recorded from both the posterior and the middle FG simultaneously in some subjects and sometimes from the lateral occipitotemporal cortex, suggesting the involvement of several occipitotemporal brain areas.

A delayed N240-P300-N360 triphasic complex was recorded from mesial structures, notably from the posterior parahippocampal gyrus, the perirhinal cortex, and the medial temporal pole (Fig. 3). As shown in the intrasubject comparison, this complex was also recorded from other brain areas such as the lingual gyrus (Fig. 4), suggesting that it is a common complex that may concern more regions than those detailed in this study. Despite the similar morphology of this triphasic complex, differences in onset and amplitude were observed. The N240 was prominent in the perirhinal cortex and started earlier in this region, whereas the N360 was prominent in the temporal pole.

ERPs to faces recorded from the hippocampus had a quite different waveform from the other structures, displaying a large and slow positive component starting at ~160 ms, peaking at 480 ms, and finishing around 750–800 ms. This distinct pattern suggests that the hippocampus plays a different role in face processing.

Finally, a low-amplitude negative component (~19 mV) peaking at 117 ms was recorded from the posterior inferior frontal gyrus and displayed an interesting analogy with the N110 recorded from the FG. They were recorded in both regions in 2 subjects. The N110 from the inferior frontal gyrus was slightly delayed compared with the N110 from the FG (Fig. 5). Also, the onset of the N240 recorded in the perirhinal cortex was found to coincide with the peak of the N110 in both the group study and the intrasubject comparison (Figs 3 and 4).

In summary, we demonstrated early components peaking at 110 ms poststimulus not only in the FG but also in the inferior frontal gyrus, a region not usually included in early visual processing. The N110 is followed by 2 stages of widespread parallel processing peaking at 240 and 360 ms. Given the limited spatial sampling of intracerebral electrodes, it is probable that still other regions participate in this network. The 240- and 360-ms stages involved many aspects of the visual ventral stream. In contrast, none of these components were recorded in the hippocampus indicating that this region is clearly involved in a different type of processing. These components do not index independent serial stages but largely overlap. The P160 is encompassed within the rise of the N240. Likewise, the N240 and N360 components are encompassed within the rise of the P480. These results suggest strong interactions between these stages and, together with the finding that an early N110 could be recorded in the inferior frontal gyrus, argue against sequential processing stages. Rather, they suggest that face recognition may be an emergent property of these interactions.

**Face Recognition**

In this section, we compare ERPs to famous and unfamiliar faces for each time point between 100- and 600-ms poststimulus onset using a nonparametric matched-pair signed-rank Wilcoxon test on individual averaged ERPs (Fig. 6). No difference between these conditions was found in the posterior or middle FGs or in the inferior frontal gyrus. However, significant differences ($P < 0.05$) were found in all medial temporal lobe (MTL) regions that were investigated, starting at 156 ms in the perirhinal cortex (156- to 216-ms poststimulus onset) followed by the posterior parahippocampal gyrus (220–248 and 268–326 ms), the medial temporal pole (315–426 and 450–510 ms), and the hippocampus (322–541 ms). This effect was prominent in the temporal pole and the hippocampus where 100% of the subjects showed a difference during some periods (338–406 ms, $n = 7$, in the temporal pole and 372–465 ms, $n = 6$, in the hippocampus). Famous faces
showed higher amplitudes in all these regions except in the posterior parahippocampal gyrus where unfamiliar rather than famous faces showed higher amplitude.

The difference between familiar and unfamiliar faces was found in the mesial structures for the components N240, N360, and P480. Together with the finding that the N240 and N360 reflect parallel processing in many different regions, this is a further indication that recognition may be a property of a network of activated brain regions rather than depend on a single region. All these medial structures play a well-known role in declarative memory, and the different responses in these regions probably reflect the various aspects of recognition such as familiarity detection and access to long-term semantic or episodic memory.

**Face Recognition versus Recognition of Other Stimuli**

These data demonstrate that a network of brain areas is involved in face recognition. The question we address in this section is whether this neural system is a general system involved in the recognition of any kind of stimulus. Thus, we compared the ERPs to the famous/unfamiliar faces with the ERPs to familiar and unfamiliar stimuli in a visual recognition memory task, in the same series of patients. In this task, the patients learned trial-unique abstract patterns (Fig. 1) during an encoding phase, followed a 3-min interfering phase, and then underwent a recognition phase. The patients had to recognize the familiar stimuli (learned during the encoding phase) and reject the unfamiliar stimuli (trial-unique distracters). We did not try to match faces and the abstract stimuli on any low-level visual characteristic, our goal in this section being to compare the recognition processes involved in the 2 tasks.

ERPs to recognized abstract targets are shown in Figure 7. Early components to familiar abstract patterns and famous faces are not compared as visual characteristics of the 2 sets of stimuli differ too much. However, note that the N110 and P160 are of strikingly similar amplitude in the middle FG indicating a similar level of activity. In contrast, the amplitude to abstract patterns was significantly lower in all MTL structures, whereas the difference did not reach significance in the inferior frontal gyrus.

Computing the difference between familiar and unfamiliar abstract patterns yielded very different results than for faces as
differences were mainly found in both regions of the FG during the N160 and N240 (matched-pair signed-rank Wilcoxon test, $P < 0.05$). On the other hand, no differences were found in the perirhinal cortex, hippocampus, and inferior frontal gyrus. Differences during relatively late periods were seen in the posterior parahippocampal gyrus (308–322 ms poststimulus) and medial temporal pole (443–495 ms).

Abstract patterns elicited clearly formed ERPs in all brain regions in which ERPs to faces were recorded (Fig. 7) with similar morphologies. Amplitude between the categories of stimuli was comparable in the middle FG and the inferior frontal gyrus. In this sense, the network involved in the recognition of faces is also involved in the recognition of abstract patterns.

However, significant amplitude differences were found in the posterior FG and all MTL structures, indicating a degree of specificity for faces possibly related to additional processes. For example, the posterior FG shows some early specificity to faces as areas in this region appear to be preferentially involved in the processing of faces over other kinds of stimuli (Puce et al. 1995; Kanwisher et al. 1997). Likewise, the amplitude differences found in MTL structures could be related to the fact that famous faces carry strong semantic content, whereas abstract

![Figure 4](image1.png)

**Figure 4.** Intrasubject comparison of ERPs to famous faces across regions (subject 1, right hemisphere). ERPs recorded in the lingual gyrus and lateral temporal pole are presented to demonstrate that the N240–P300–N360 complex and N360 may be even more common than reported in the group study.

![Figure 5](image2.png)

**Figure 5.** ERPs to famous faces recorded from the inferior frontal gyrus and the FG (posterior FG in subject 1, middle FG in subject 12). The N110 peaks slightly earlier in the FG. Note the different amplitude scales.
patterns were newly learned stimuli and carry little semantic content. In support of this hypothesis, a striking finding was that a recognition effect for faces was found in all MTL structures, whereas this effect was considerably smaller for abstract patterns. In contrast, a recognition effect was seen mainly in the FG for abstract patterns, whereas no such effect was found for faces. These results further indicate that recognition per se can rely on many brain regions and that this may differ with stimulus category and processes involved.

Hemispheric Asymmetries

In our previous sections, we combined data from both left and right hemispheres to focus on the general network underlying face recognition and because data per region were obtained from small samples (the fact that it was usually unilateral implantation and the small number of patients per group prevented direct right/left statistical comparisons). However, numerous studies have found greater activity for faces in the right hemisphere. In order to investigate this aspect, the same data were analyzed for each hemisphere.

As can be observed from Figure 8, both hemispheres are involved in face recognition. Further, the neuronal populations involved in face recognition perform comparable processes as ERPs with similar morphology can be found in both hemispheres. There are 2 notable exceptions, however. First, a large N240 was observed in the middle FG on the right, whereas this component was virtually absent on the left. An N240 larger in the right than in the left was also observed in the perirhinal cortex. Second, the N110 was very small in the left inferior frontal gyrus (in one patient, however) compared with the N110 in the right. Some areas thus appear to be more specific on the right than on the left. A notable exception was the finding that the ERP to famous faces showed higher amplitudes on the left than the on the right in the temporal pole.

Furthermore, 50% of the 18 patients included in this study had right-hemisphere implantation (left: 39%, bilateral: 11%). For all regions, we found more ERPs meeting our criteria (focal and similar morphology across subjects) on the right hemisphere than on the left, that is, the proportion of local ERPs retained for further analysis was higher on the right than expected by the number of right implantations (posterior and middle FG: 60%, posterior parahippocampal gyrus and perirhinal cortex: 67%, medial temporal pole: 57%, hippocampus: 67%, inferior frontal gyrus: 83%). This difference was maximal in the inferior frontal gyrus with 5 ERPs found in the right hemisphere for 1 ERP found in the left hemisphere.

Figure 6. ERPs to famous and unfamiliar faces. Asterisk indicates $P < 0.05$. For clarity, peak labels are indicated for some brain areas only.
Consistent with a large literature (Sergent et al. 1992; Allison, Ginter et al. 1994; Allison et al. 1999; Puce et al. 1996; Kanwisher et al. 1997; McCarthy et al. 1999; Haxby et al. 1999; Rossion et al. 2000; Ishai et al. 2005), these data demonstrate that face recognition relies on a bilateral network with a right dominance. This was true not only for posterior, visuoperceptiive regions but also for middle and anterior regions that may be more involved in memory processing (e.g., posterior parahippocampal gyrus, perirhinal cortex, and inferior frontal gyrus).

**Discussion**

The time course of face recognition processes has been studied extensively using surface electrophysiological methods. However, it has generally been difficult to relate these activities to precise brain regions due to the poor spatial resolution of these techniques. The brain areas involved in face recognition have been extensively studied using fMRI and PET, but these techniques have poor temporal resolution. Here, we meet these limitations using intracerebral recordings, allowing the assessment of the precise temporal course of the electrophysiological activity from ‘within’ the brain regions involved in face recognition. We recorded from a large sample of brain regions across a group of 18 patients and report only the electrophysiological activities that were similar in morphology and latency across patients. The brain regions and electrophysiological activities identified using this approach are thus hypothesized to be representative of the main regions and activities involved in face recognition in the general population.

From these data, we propose a model of the electrophysiological activities indexing face recognition, with the particularity that they are detailed simultaneously in both time and space.

Figure 9 shows a schematic representation of this model, which confirms and extends the current knowledge on face recognition. 1) An early (110-ms poststimulus onset) electrophysiological activity can be recorded not only from the posterior regions but also from the inferior frontal gyrus. 2) Around 160 ms, there is activation in both the middle and posterior FGs. 3) A stage of massive parallel processing occurs around 240 ms poststimulus, involving different areas in the visual ventral stream and closely followed by a second stage of parallel processing around 360 ms. 4) Long-lasting electrophysiological activities are recorded from the hippocampus that appear unrelated to the activities recorded from the visual ventral stream. 5) There are strong interactions between these stages because some are encompassed in others, for example,
the N160 on the rise of the N240. 6) Recognition effects between famous and unfamiliar faces are found in all 4 MTL regions investigated, suggesting that these effects are distributed. On the other hand, recognition of abstract patterns mainly involved posterior regions where no such effect was found for faces. Overall, these data support the view that face recognition relies on a distributed network of brain areas, involving both hemispheres but more prominent in the right, and illustrate the dynamics of the information flow among these areas.

The finding that face recognition is mediated by a distributed network of brain structures is in accordance with several electrophysiological and fMRI studies (Puce et al. 1999; Leveroni et al. 2000; Paller et al. 2002, 2004, 2005; Ishai and Yago 2006). Leveroni et al. (2000) reported activations in parietal and frontal brain regions for newly learned faces compared with trial-unique faces. These authors also compared the recognition of famous faces with the recognition of these newly learned faces. They found an even larger network to the famous faces, including areas in the LTL and MTL, the frontal, and parietal lobes as well as in cingular and extrastriate structures. This network was found to be more prominent in the right hemisphere.

Figure 8. ERPs to famous faces recorded from the left and right hemispheres. For clarity, peak labels are indicated for some brain areas only.

Figure 9. Schematic model of the main electrophysiological activities underlying face recognition in different brain regions. Components' names are indicated on the abscissa. The rectangles indicate the main peaks of the components in each region. The horizontal lines provide an idea of the components' onsets. The rectangles in dark blue indicate the peaks during which a recognition effect was found.
hypothesized to reflect participation of these regions in long-term memory.

We identified a distributed cortical network of at least 7 structures involved in face recognition. These included the posterior and middle FGs, posterior parahippocampal gyrus, perirhinal cortex, medial temporal pole, hippocampus, and inferior frontal gyrus. Haxby et al. (2000) reported that face processing is mediated by a distributed neural system, which consists of a core and an extended system. The core system includes the inferior occipital gyrus and FG and the superior temporal sulcus. The FG is proposed to process invariant aspects of faces, whereas the superior temporal sulcus would process changeable aspects such as eye or mouth movements. The extended system comprises several regions depending on the information extracted from the face. Pertinent to the present work, person identification would depend on anterior temporal structures. The neural network identified in our study largely supports the model of Haxby et al. as it includes both the FG as well as anterior temporal lobe structures such as the perirhinal cortex and temporal pole, expected when subjects process famous faces. That the perirhinal cortex participates in face recognition has previously been hypothesized by other authors (Halgren, Baudena, Heit, Clarke, Marinkovic, 1994; Allison et al. 1999; Trautner et al. 2004). Our data confirm this assumption as they are the first direct recordings from this area. Components were also identified in the superior temporal sulcus in our study, but not reliably across subjects. This appears consistent with the fact that subjects did not have to process changeable aspects of the face to perform the task. In an fMRI study, Ishai et al. (2005) found that face perception is mediated, independently of the nature of the task, by a cortical network that includes the inferior occipital gyrus, FG, superior temporal sulcus, hippocampus, amygdala, inferior frontal gyrus, and orbitofrontal cortex. Interestingly, this study as well as others (Leveroni et al. 2000; Ishai et al. 2002) report on 2 brain structures, the hippocampus and the inferior frontal gyrus, which we also identified but which were not reported in the model of Haxby et al. On the other hand, anterior temporal lobe structures are not reported in Ishai’s study, which is probably related to the methodology used. These authors searched for areas activated through various face tasks, rather than exclusively tasks of face recognition. In contrast, our study confirms that anterior lobe structures are part of a complementary system specifically involved in face recognition. Note that Ishai et al. (2005) also reported on several brain areas that were not identified in our study (inferior occipito gyrus, amygdala, and orbitofrontal cortex). This discrepancy is probably related to our study criteria to report only ERPs that were comparable in at least 5 subjects and as such does not refute the possibility that these other brain regions may also contribute to the network involved in face recognition. It remains, however, to characterize the temporal course of the neuronal activity in these regions.

Although in most of the above studies activations were observed in different brain regions, several pieces of information critical to characterize a network were missing. These include the notion of connectivity (is there a relation between the different brain areas?), the direction or causality between these areas, and the time when these relations occur. Fairhall and Ishai (2006) recently attempted to meet these issues using dynamic causal modeling on fMRI data while subjects processed emotional and famous faces. They found that the core system is mediated by a feed-forward architecture with the inferior occipital gyrus exerting influence on the FG and superior temporal sulcus. Furthermore, the FG was found to exert a strong causal influence on the orbitofrontal cortex when processing famous faces and on the amygdala and inferior frontal gyrus when processing emotional faces. However, the timing of the FG influence on other brain regions was not determined and could occur either during the N110, P160, or the N240, which can be recorded in this region. The present study identified an N110 in the FG; an N110 was also identified in the inferior frontal gyrus. However, it was shown that this component was slightly delayed compared with the N110 recorded in the posterior FG. It may be compatible with the notion that rapid feed forward from the FG occurs during this period, although an alternative is that a third region (i.e., the lateral occipital gyrus) projects to both simultaneously. The involvement of prefrontal cortex in face processing has already been reported in primates (Wilson et al. 1993) and humans in intracranial and fMRI studies (Halgren, Baudena, Heit, Clarke, Marinkovic, 1994; Allison et al. 1999; Vignal et al. 2000; Ishai et al. 2002, 2005). Marinkovic et al. (2000) described large ERPs selective to faces in the right anterior prefrontal region beginning 150 ms after stimulus onset. However, although an N110 recorded from the FG had already been reported (Halgren, Baudena, Heit, Clarke, Marinkovic, Chauvel, 1994; Allison et al. 1999), this is the first time that a component as early as 110 ms is reliably reported in the inferior frontal gyrus.

Besides the N110, the causal influence of the FG on other brain regions could also occur during the P160, which was recorded in several posterior regions. This component probably corresponds to the P180 recorded using intracerebral electrodes (Halgren, Baudena, Heit, Clarke, Marinkovic, 1994) or to the N200 recorded on the cortical surface (Allison, McCarthy, et al. 1994; Allison et al. 1999) as well as to the N170 recorded from the scalp surface. The polarity inversion between intracerebral and surface recordings is related to the fact that different sides of the generators are captured. The N110-P160-N240 intracerebral complex thus probably corresponds to the P1-N170-P2 components recorded from the brain surface. (Note, however, that the N240-P300-N360 that we also report is probably not polarity inverted and corresponds, at least partly, to the N400 recorded from the surface. In this case, it is the component (P350) reported by Allison et al. (1999) which was polarity inverted because they recorded from the temporal ventral surface and not from above the source (dipole) as we did or as is done with surface recordings.) The fact that the P160 was seen at several occipitotemporal regions is in agreement with previous studies which showed that this component could be recorded from a large area covering the ventral occipital and posterior temporal region (Allison, McCarthy, et al. 1994; Halgren, Baudena, Heit, Clarke, Marinkovic 1994; Allison et al. 1999), including simultaneously in different regions in the same subject. Interestingly, Klopp et al. (2000) showed that during 160- to 230-ms poststimulus onset, a face-selective increase in coherence was found between the FG and regions in the temporal, parietal, and frontal lobes. This mechanism may underlie the causal influence found by Fairhall and Ishai (2006). The fact that the fusiform P160 was encompassed in the rise of the N240 components found in different regions corroborates this analysis.
On the other hand, the N110 was also found to be synchronous with the onset of the N240 in the perirhinal cortex. These data suggest that the N110 could be a signal triggering further processing. Specifically, the frontal N110 could be a top-down signal on the visual ventral stream. Such a mechanism has been postulated to be necessary to allow more accurate and faster computation (Humphreys et al. 1997; Tomita et al. 1999; Adolphs 2002; Bar 2003; Bar et al. 2006). Bar (2003) proposed that low spatial frequencies of an image could be projected rapidly through the magnocellular pathway from occipital regions to the inferior frontal gyrus in order to trigger expectations about the identity of the image itself. This top-down modulation has been proposed to occur around 250 ms (Ishai et al. 2006), although the current data suggest that this can happen considerably earlier. This rapid activation could then have projections on the visual ventral stream, possibly on the perirhinal cortex, for early activations.

Furthermore, a N240--P300--N360 complex following the P160 was observed in different brain regions. In the perirhinal cortex and temporal pole, this complex may be equivalent to the facial AMTL-N400 described by Trautner et al. (2004) and Dietl et al. (2005). It has a comparable latency and polarity, a similar topography in anterior subhippocampal structures, elicits a component of higher amplitude to famous faces in the 300- to 600-ms time frame, and is composed of 2 subpeaks (see Fig. 1a in Dietl et al. 2005 for example). However, the data reported here indicate that the AMTL-N400 is not a single component but is clearly divided into 2 subcomponents. A further important finding of our study is that the N240 and the N360 were observed in different regions (>5 or 6) where they were generated locally, suggesting parallel processing. These regions were located in the visual ventral pathway (Ungerleider and Mishkin 1982; Ungerleider and Haxby 1994), although the term pathway is improper here because simultaneous, rather than serial, activation was observed. Therefore, along with feed-forward activations, phases of possible top-down signal and parallel processing are also identified in our study.

The recognition effects found in the present study were all in MTL structures. This is in accordance with a study that identified single neurons with invariant representations of famous faces in several regions of the human MTL including the amygdala, entorhinal cortex, parahippocampal gyrus, and hippocampus (Quian Quiroga et al. 2005). It is important to note that recognizing a face can mean different things: having a sense of familiarity with a face, activating semantic knowledge related to a person who has been recognized, or retrieving the name of that person. In this study, a sense of familiarity with the face was enough to perform the task, but complementary processing related to identification may have been performed. Along this line of thought, we hypothesize that the activities recorded in MTL structures primarily reflect access to different aspects of long-term memory. A putative model could be that the earliest signal from the perirhinal cortex during the N240 could signal that the stimulus is familiar, based mainly on the visual characteristics of the stimulus. This would be congruent with the role of this structure in visual processing and familiarity detection (Aggleton and Brown 1999; Murray and Bussey 1999; Barbeau, Felician, et al. 2005; Barense et al. 2005). The N360 amplitude to famous faces was higher than to unfamiliar faces in the temporal pole and, although seen bilaterally, was more prominent in the left hemisphere. It may indicate access to a distributed semantic system involving person identification and attempts to name the faces (Joubert et al. 2006). On the other hand, because the P480 recorded from the hippocampus showed a component unrelated to those of the visual ventral pathway, a possibility is that this component is related to a different system, for example, episodic (personal) memory. We also suggest that the MTL is where the major recognition effects are found as the unique nature of famous faces can trigger memory retrieval. In accordance with this hypothesis, we found that ERPs to famous faces showed higher amplitude than to recently learned abstract patterns. These control stimuli carry little semantic content or relation to episodic memory, which may explain why they elicit less neuronal activation in this brain region.

There is a continuing debate over the period during which recognition effects (i.e., differences between familiar and unfamiliar faces) can be found. The most robust effects are seen 250- to 500-ms poststimulus onset when comparing famous and unfamiliar faces in scalp recordings (Bentin and Deouell 2000; Eimer 2000; Jemel et al. 2003). The N170, in contrast, was not modulated, implying that posterior regions are relatively insensitive to the "famous" factor. In accordance with these studies, no difference between famous and unknown faces was observed during the P160 in our study in either the posterior or the middle FG. Indeed, the intracranial face-specific P160 has been shown to reflect a mandatory and invariant processing stage unaffected by passive viewing of faces, face familiarity, face habituation, or semantic priming (Puce et al. 1999). This led to the view that the surface N170 or its intracerebral counterpart may reflect operations carried out by a "structural encoding module" (Bruce and Young 1986) in charge of automatically processing physiognomic aspects of the faces (Bentin et al. 1996). However, recent findings using scalp recordings indicate that other kinds of familiar faces such as personally known faces (own face, family members' faces, or friends' faces) could evoke larger N170s (Caharel et al. 2006). The N170 has also been shown to be modulated by face repetition (Hiter and Taylor 2004a), and we further found in this study that the P160 was modulated by recently learned abstract patterns. These results emphasize the fact that the mechanisms underlying recognition could be different for famous faces than for other types of faces or other types of visual stimuli. In particular, recognition of repeated, newly learned, or personally known faces can easily rely on visual clues because they have been seen repeatedly and/or recently. On the other hand, the photographs of famous faces are usually seen for the first time during the experiments, implying that recognition may have to rely more on person's identification than on the visual characteristics of the face.

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Address correspondence to Emmanuel J. Barbeau, Centre de recherche Cerveau et Cognition, UMR 5549, Centre National de la Recherche Scientifique postdoctoral fellowship to E.B.
References


