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 localized 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 the 2 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° × 6°. 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 83% 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.
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.

**Results**

More than 2000 sites were recorded in 18 subjects in total, an average of 111 sites recorded simultaneously per subject. ERPs to famous faces recorded from these contacts constitute the basis of this study.

**ERP Identification**

A major aim of the present study was to identify the pattern of ERPs underlying the temporal processing of face recognition. We thus analyzed the ERPs region by region to identify those that met the 2 criteria: 1) exhibiting a similar waveform and latencies in the same region across and 2) being generated focally. Criteria for local generation were polarity reversal between adjacent contacts and/or steep voltage gradient and high voltage fluctuations between adjacent contacts (Halgren, Baudena, Heit, Clarke, Marinkovic 1994; Fernandez et al. 1999). A supplementary criterion was to reach a threshold of 5 subjects per region across our population of 18 patients in order to be able to perform statistical comparisons at least 5 subjects. ERPs corresponding to the criteria defined above were identified in 7 regions: the posterior fusiform gyrus (FG), the middle FG 1–2 cm anterior to the previous region, the posterior parahippocampal gyrus, the perirhinal cortex within the collateral sulcus, the medial temporal pole, the hippocampus (posterior and anterior), and the inferior frontal gyrus. Figure 2 depicts all brain regions explored and shows in black the 7 regions from which the focal ERPs reproducible across subjects were identified. Focal ERPs were recorded from other brain regions (shown in grey), for example, from the amygdala, the orbitofrontal cortex, the lateral temporal lobe (LTL) along the
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.

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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 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.** 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.** 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, visuopercepti
tive regions but also for middle and anterior regions that may be more involved in memory processing (e.g., posterior para-hippocampal 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 the 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,

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Figure 7. ERPs to (old) recognized abstract patterns. Same patients as in Figure 5. Left and right hemispheres combined.
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. 2000; Ishai 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
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 been previously hypothesized by other authors (Halgren, Baudena, Heit, Clarke, Marinkovic, Chauvel, 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 to our study criteria to report only ERPs that were simultaneously 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 familiar 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 component but is clearly divided into 2 subcomponents. A

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References


