

Recognition of famous faces in the medial temporal lobe

An invasive ERP study

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Abstract—Objective: To investigate the involvement of the rhinal cortex and the hippocampus in the processing of famous faces in contrast to nonfamous faces using intracranial event-related potentials (ERPs), and to analyze repetition effects for famous and nonfamous faces. **Methods:** ERPs were elicited by pictures of famous and nonfamous faces and recorded from rhinal and hippocampal sites of intracranial electrodes in 10 presurgical patients with unilateral medial temporal lobe epilepsy. Famous and nonfamous faces were presented twice and mixed with distorted faces serving as targets. There was no instruction for an overt discrimination between famous and nonfamous faces. In contrast to nonfamous faces, famous faces stimulate processes related with access and retrieval of semantic memory. **Results:** All faces evoked anterior medial temporal lobe N400-like (AMTL-N400) potentials in the rhinal cortex and P600-like potentials in the hippocampus. The AMTL-N400 and the hippocampal P600 amplitudes were larger for famous faces than for nonfamous faces. Mean amplitudes of the first and second presentation of famous faces suggest a repetition effect for the rhinal sites; however, they are significant only in the later signal components. No repetition effect was found for nonfamous faces and for potentials from the hippocampus. **Conclusion:** The anterior medial temporal lobe N400 and the hippocampal P600 may be related to the access and retrieval of person-specific semantic memory.

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Bruce and Young proposed an influential model for the cognitive architecture of the recognition of a person by facial cues.^{1,2} According to this model, identifying a familiar person is achieved by a cascade of interacting sequential processing stages. An initial stage, during which the perceptual features of the individual face are encoded, is followed by a subsequent recognition stage, during which these structural representations of perceptual face features are matched with stored face representations (face recognition units). In case of a successful match, so-called person identity nodes (PINs) are accessed. These nodes provide person-specific semantic knowledge like biographical information retrieved from long-term memory. In a last (however, not obligatory) processing stage, the name of the perceived individual is retrieved.

This study concerns those memory processes (access to or retrieval of memory content) that are automatically initiated when famous faces are perceived. It can be assumed that famous faces trigger a cascade of fast and automatic processes in which the face is recognized as familiar and semantic and episodic information about this person is retrieved (e.g., biographical information, field in which the person is famous). Thus, famous faces may act as powerful

memory cues prompting the retrieval of stored person-specific information. Contrasting the processing of famous or known faces with the processing of unknown faces allows the analysis of the processes by which biographical information is associated with the perceived face.

The neurobiological processes revealed by EEG or fMRI measures may partly reflect the processing stages postulated by the Bruce and Young model. Several surface event-related potential (ERP) studies demonstrate differential processing of famous faces in contrast to nonfamous faces, which may be related to long-term memory access.^{3,4} For example, the N400 reflects access operations to semantic memory triggered by perceptual events.⁵ Two groups reported an enhancement of the N400 by the perceived famousness of a face.^{6,7} In one of these studies, another potential, the P600 component, was reported that also is enhanced by the perception of famous faces with a scalp topography similar to the N400.⁷ The authors concluded that the neural processes reflected by the N400 (and the P600) are related to recognition of familiarity and access to person-specific information. Interestingly, repetition of the famous faces in the course of the experiment resulted in a less-negative N400 component.

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In addition to N400 surface recordings, measurements with depth electrodes within the medial temporal lobe revealed an N400-like brain potential, the anterior medial temporal lobe N400 (AMTL-N400). The AMTL-N400 resembles the surface N400 with respect to latency, polarity, and in particular in its sensitivity to experimental manipulations. However, thus far, no firm data about a possible contribution of this AMTL-N400 to the surface-recorded N400 exist. The AMTL-N400 has been mainly investigated in object and word recognition tasks.⁸ Depth electrode recordings point to a generation of the AMTL-N400 anterior to the hippocampus in or near the rhinal cortex.⁹ Cognitive events that elicit an AMTL-N400 also generally evoke a positive hippocampal brain potential, the hippocampal P600 (late positive component [LPC]).

These findings of ERP components within the medial temporal lobe and their resemblance with the ERPs from surface recordings suggest that the rhinal cortex and the hippocampus are brain areas that may be involved in the differential processing of famous vs nonfamous faces. The specific relevance of the medial temporal system is stressed by a recent fMRI study that reports an activation of medial temporal brain structures during the processing of famous and familiar persons in contrast to unfamiliar persons.^{10,11}

We investigated the differential effect of famous faces compared with nonfamous faces on the AMTL-N400 and the hippocampal P600. The famous and nonfamous faces are repeated during the course of the experiment to analyze the modulation of the AMTL-N400 and the hippocampal P600 by stimulus repetition. We hypothesized that both ERP components on first presentation of the faces will be modulated by the factor famousness because the sole presentation of the faces will initiate semantic and episodic memory processes. These memory processes involve the rhinal cortex and the hippocampus manifesting in the AMTL-N400 and P600 potentials. Surface ERP studies reported an early positive ERP modulation (200 to 300 ms) and reduced N400 components with repetition of famous faces.^{4,12} This decrement in amplitude was proposed to reflect facilitated access to PINs and related person-specific semantic information.⁴ In a variety of experiments including stimulus repetition with objects and words as stimuli, the AMTL-N400 was reported to be reduced, and the hippocampal P600 was reported to be enhanced in amplitude.¹³ Previous reports have addressed ERP modulations of the N400 (or in the time range of the N400) elicited by the repetition of faces.^{7,14} This “ERP repetition effect” (old/new effect) most consistently reported is that repeated faces evoke less negativity (more positivity) in a time range typical for the N400. Therefore, we presented the faces repeatedly to analyze the “ERP repetition effect” for famous and nonfamous faces in the medial temporal lobe.¹⁵

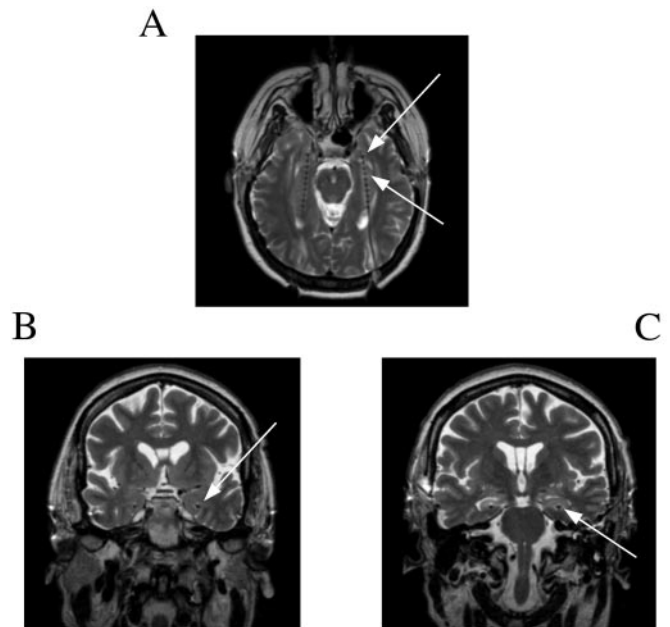


Figure 1. Verification of electrode positions in T2-weighted MRIs obtained with temporal angulation in a patient with right-sided hippocampal sclerosis. Top, (A) presentation of intrahippocampal multicontact depth electrodes in their longitudinal axis covering the rhinal cortex (anterior arrow) and the hippocampus (posterior arrow). Bottom, coronal T2-weighted slices identifying a rhinal (B) and hippocampal (C) electrode contact.

Methods and experimental design. *Participants.* Ten patients undergoing presurgical evaluation for medically intractable temporal lobe epilepsy with bilateral implanted depth electrodes participated in this study. In all cases, seizures proved to originate unilaterally; therefore, ERPs recorded in the hemisphere contralateral to the seizure origin are assumed to reflect brain activity from nonepileptogenic brain areas. Multicontact (10 contacts) electrodes were implanted bilaterally into the longitudinal axis of the hippocampus with the first contacts reaching medial temporal structures anterior to the amygdala. This allows recording ERPs from the rhinal cortex and the hippocampus.

All patients (five men, five women) gave informed consent. They were 19 to 55 years old (mean, 40 ± 12.8 years) with normal or corrected-to-normal vision. The temporal lobe was considered not affected by epilepsy on the right side in six subjects and on the left side in four subjects. The precise neuroanatomic position of the electrodes was obtained from axial and coronal 2 mm-sliced T2-weighted and 3 mm-sliced fluid-attenuated inversion recovery MRIs routinely acquired after electrode implantation (figure 1).

Stimuli. Eighty pictures of famous and nonfamous persons were presented on a black background in the center of a computer screen. All pictures were grayscale and were the same size. Famous pictures showed well-known celebrities like politicians, television stars, or actors. Photographs were taken from several public databases. Decision of famousness of the faces was based on the evaluations of 33 independent raters.¹²

The photos were presented for 300 ms with an interstimulus interval of 3,000 ms (± 50 ms). To focus the subjects' attention on the pictures, each photo was preceded by a fixation cross (“x” for 100 ms). In addition to famous and nonfamous faces, 44 pictures of nonfamous faces were presented that showed distortions created using graphic morphing software. The distortions could appear anywhere in the face with a different grade of distortion. This distortion-detection task aimed to facilitate a scrutinizing mode of perception. Because the distorted faces are difficult to identify, intense attention of the subjects is guaranteed. No particular hypothesis concerning the processing of distorted faces was formulated. All faces were repeated once; therefore, 160 famous, 160 nonfamous, and 88 distorted faces (overall, 408 presentations)

Table Mean amplitudes \pm SDs elicited from the four different conditions at rhinal and hippocampal sites

	Famous 1st	Famous 2nd	Nonfamous 1st	Nonfamous 2nd	Targets 1st	Targets 2nd
Rhinal						
300–600 ms	-50.6 ± 25.9	-40.0 ± 27.8	-37.9 ± 30.0	-39.3 ± 32.0	-39.9 ± 23.5	-43.1 ± 39.4
600–900 ms	-17.7 ± 17.3	-3.5 ± 12.5	-3.9 ± 18.6	-6.1 ± 14.8	-13.5 ± 37.2	-16.3 ± 23.0
300–900 ms	-34.2 ± 17.5	-21.7 ± 15.4	-20.9 ± 19.4	-22.7 ± 21.1	-26.7 ± 23.9	-29.7 ± 27.1
Hippocampal						
300–600 ms	7.1 ± 35.6	9.4 ± 29.1	-8.9 ± 28.1	-4.7 ± 38.0	4.6 ± 47.1	-10.7 ± 27.3
600–900 ms	43.1 ± 50.5	37.0 ± 39.9	23.6 ± 32.8	17.1 ± 56.0	15.6 ± 43.3	-3.8 ± 22.5
300–900 ms	25.1 ± 41.9	23.2 ± 33.6	7.4 ± 27.6	6.2 ± 46.4	10.1 ± 43.3	-7.2 ± 23.2

were presented. ERPs to the first and the second presentation of each stimulus were recorded. Pictures were repeated with a lag of 5 to 13 intervening stimuli. Faces were shown in a pseudorandomized sequence. No pictures of the same category followed each other.

Experimental procedure. Participants sat on a comfortable chair in front of a computer display at a 1-m distance. They were fully informed about the procedure and were instructed to press a button with the right hand if a distorted face was detected. No overt reaction had to be performed by the subjects concerning the discrimination of famous and nonfamous faces or repetition of the faces. The experiment lasted ~20 minutes.

Recording and data analysis. Data were recorded using the Harmonie digital system from Stellate (Montreal, Canada). Electrode impedance of depth electrodes was controlled to be <5 k Ω . The EEG was measured against a reference of left and right mastoid electrodes with a sampling rate of 200 Hz and a bandpass filter of 0.01 to 70 Hz.

For analysis only, EEG recordings from the medial temporal lobe of the hemisphere contralateral to seizure onset were selected. The recordings were inspected manually for contamination with epileptiform activity and other artifacts. Contaminated segments were rejected. MRI was used to identify the precise neuroanatomic position of the implanted electrodes. Electrode positions were taken from MRIs and classified into two groups: one group contained contacts located within the hippocampus, and the other group contained anterior extrahippocampal contacts located in the rhinal cortex. Two electrodes are usually used to cover the rhinal area, whereas three to five electrodes are used to represent the hippocampus, depending on individual characteristics.

EEG was segmented into periods of 1,500-ms duration, starting 200 ms before stimulus onset. The 200-ms interval before picture onset was assumed to represent brain background activity and therefore was used for baseline correction. For further analysis, only trials were selected with correct responses within a time window of 100 ms to 2,500 ms. Correct responses include a button press for distorted faces and no button press in all other cases. Averaging was performed separately for six conditions (i.e., famous faces, nonfamous faces, targets, each first and second presentation). For all conditions, grand averages were calculated for the datasets of the 10 participants and separately for the two anatomic regions (hippocampus and rhinal cortex). For each subject, only one MRI-verified electrode for each anatomic region was included into the average. For the rhinal leads, the contact with the largest AMTL-N400 was selected, and for the hippocampal leads, the contact with the largest P600 to the first presentation of famous faces was selected.

Results. Behavioral data. On average, patients detected 70% of the distorted faces. However, they also pressed the button in 12.6% of the nontargets. This substantially lower false alarm than hit rate suggests that the patients processed the faces in some detail. Trials of famous or nonfamous faces with erroneous button press were rejected.

Targets. Targets (distorted faces) evoked N400-like potentials similar to those evoked by nontargets. No significant

repetition effect was observed for target stimuli. At hippocampal leads, no clear potential was found (for ERP mean amplitudes and SD see the table).

Famous and nonfamous faces. Figure 2 depicts the grand average ERP waveforms of the four conditions of interest (famous and nonfamous faces, first and second presentation) for rhinal (A) and hippocampal (B) electrode sites.

Distinct potentials are obtained from rhinal and hippocampal leads: as a general pattern, at the rhinal electrodes, a negative component with an amplitude of ~ 45 μ V starting ~ 200 ms after stimulus onset (see figure 2A) is obtained. This negative component lasts ~ 500 ms and strongly resembles the AMTL-N400 elicited by words and pictures. At ~ 700 ms after stimulus onset, a long-lasting broad positive component is obtained. This positive component has not fully declined even 2 seconds after stimulus onset.

In contrast, at hippocampal leads, no distinct potential is observed in the early time range from 0 to 400 ms (see figure 2B). However, ~ 500 ms after stimulus onset, a positive potential arises. In terms of latency and configuration, this potential corresponds to the hippocampal positive potential elicited by words and pictures (P600, LPC).

For statistical analysis, a two-way repeated measures analysis of variance (ANOVA) with the factors “famousness” (famous vs nonfamous faces) and “repetition” (first presentation vs second presentation) was used. The significance of group differences was tested with the Newman-Keuls post hoc test.

The AMTL-N400 at rhinal contacts was expected in the time range between 300 and 600 ms, and the hippocampal P600 was expected in a time interval from 600 to 900 ms. However, because the AMTL-N400 and the P600 (LPC) were prominent in both time windows and the initial time windows did not appear to segment these potentials plausibly, we will present the results of the statistical analysis for the total time window from 300 to 900 ms in addition to the smaller time windows from 300 to 600 ms and from 600 to 900 ms. Detailed information about mean amplitudes and SDs is given in the table.

Rhinal contacts. At rhinal contacts, the grand average waveforms show a more negative potential for famous faces than for nonfamous faces: in the early time window (300 to 600 ms), a main effect was found for “famousness” ($F[1,9] = 5.764$; $p < 0.05$, no significant interactions). In the second time window (600 to 900 ms), an interaction effect between “famousness” and “repetition” was found

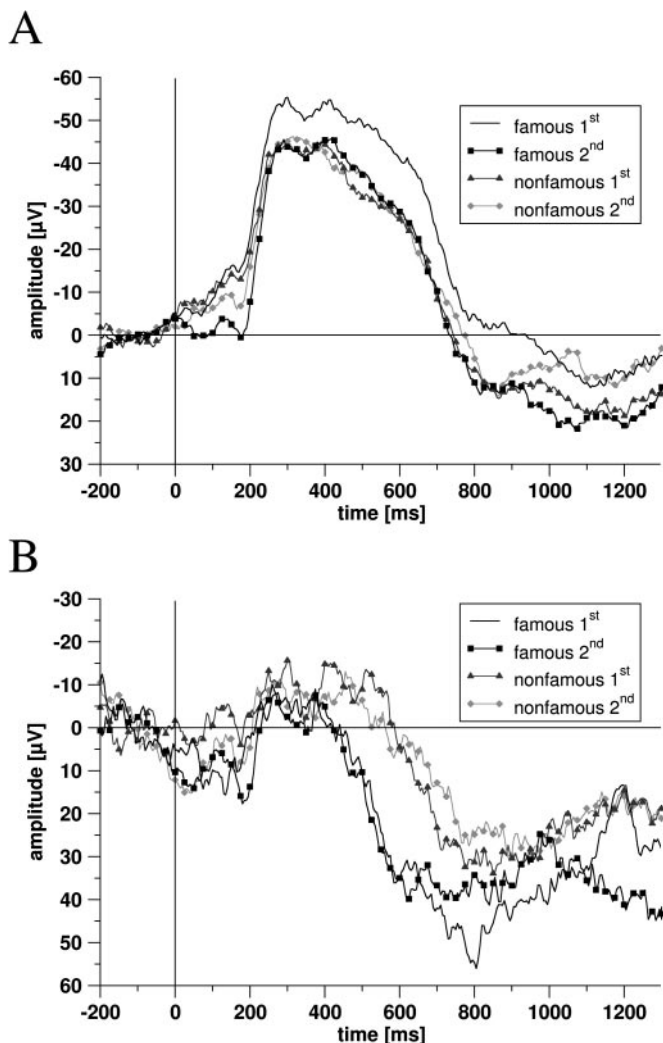


Figure 2. Grand average event-related potentials (ERPs) for all single conditions (famous and nonfamous faces, first and second presentation each). In (A), potentials elicited from rhinal leads and in (B) from hippocampal leads. At rhinal leads (A), an anterior medial temporal lobe (AMTL)-N400 potential is observed, with the potential of the first presentation of famous faces showing a higher negativity. At hippocampal leads (B), a P600 potential is observed, which is more pronounced for famous faces. No distinct difference between first and second presentation is observed.

($F[1,9] = 9.245$; $p < 0.05$). Post hoc tests indicated that the potential elicited by the first presentation of famous faces was significantly more negative than the potentials in the other conditions. Considering the entire time interval from 300 to 900 ms, two-way ANOVA yielded an interaction between “famousness” and “repetition” ($F[1,9] = 6.730$; $p < 0.05$). Post hoc tests again indicated that the first presentation of the famous faces elicited a more negative potential than the other three conditions (see figure 2A).

Hippocampal contacts. Analysis of the main effects revealed significant effects of “famousness” for all time windows and no significant effects for “repetition.” No significant interactions were found. For the famous faces, a more positive P600 (LPC) is observed for the 300- to 600-ms time window ($F[1,9] = 26.990$; $p < 0.005$) and for

the 600- to 900-ms time window ($F[1,9] = 15.569$; $p < 0.005$) and the total time window from 300 to 900 ms ($F[1,9] = 32.691$; $p < 0.001$). Thus, the hippocampal electrodes show an effect of “famousness” but not of “repetition.”

In summary, pictures of faces evoke potentials in the rhinal cortex and hippocampus. In the rhinal cortex, faces elicit N400-like potentials of the AMTL-N400 family. This facial AMTL-N400 is modulated by famousness of the perceived face and stimulus repetition in the current experiment. The first presentation of famous faces especially elicits a more negative potential than all other conditions. No distinct difference is observed between the potentials from second presentation of famous faces and first and second presentation of nonfamous faces. By this, there was a repetition effect for famous but not for nonfamous faces. Based on the large AMTL-N400 for first presentations of famous faces, it can be concluded that this group of stimuli particularly activates the rhinal cortex. In the hippocampus, a P600 (LPC) is induced. This potential is only modulated by the factor famousness. For hippocampal potentials, no interaction between famousness and repetition was found. Analysis of the main effects showed significant differences for potentials regarding famousness and no significant differences for repetition.

Discussion. The two potentials (AMTL-N400 and hippocampal P600) observed in the present study have also been found in previous studies using objects or words as stimuli.¹³ The fact that comparable potential components are observed across paradigms with different stimulus material is in line with the current interpretation of the medial temporal lobe memory system as part of a general multipurpose network for encoding, recognition, and retrieval. Other studies with intrahippocampal depth electrodes focused on other facets of face processing and therefore are not directly comparable with the present study.¹⁶⁻¹⁸

Famous faces elicit a more negative AMTL-N400 in rhinal electrode sites compared with nonfamous faces. This applies particularly for the first presentation of famous faces compared with the stimuli in all other conditions (second presentation famous faces, nonfamous faces). In studies concerning the surface N400 potential, related observations have been described. The N400 and the P600 were found to be larger for famous than for nonfamous faces.⁷ Other groups reported similar ERP patterns; however, the difference between famous and nonfamous faces started earlier (at ~250 ms) and was accentuated more frontally.⁶ The authors proposed that the more negative going potential for famous faces in the time window of the N400 is related to the access of PINs. Another study investigated recognition by contrasting unknown faces with newly learned faces.¹⁹ These artificially familiarized stimuli evoked a more positive potential in the typical (N400) time window (300 to 600 ms) compared with nonfamiliar faces. This discrepancy might be caused by a different experimental approach because artificially familiarized faces were used instead of faces of universally known

celebrities. There may be a difference in the semantic content of the two types of stimuli. This could possibly stem from different representations in long-term memory for celebrities, who were learned in a lifetime and which are continuously updated, and artificial biographies, which have been studied by the participants during a restricted period.

In a recent study, surface ERPs were analyzed using the same stimuli and a similar paradigm in a more complex experimental setup.¹² In contrast to the results of previous studies,^{6,7,20} this group observed a more positive going waveform elicited by famous faces compared with nonfamous faces. An early, broadly distributed effect (200 to 300 ms after stimulus onset) was followed by a more frontally accentuated effect of famousness between 300 and 450 ms (famous first compared with nonfamous first). However, a direct comparison of the surface ERP data reported in that study and the present data is complicated by the fact that the main focus of the former study was on semantic familiarity, and by this only a subgroup of the famous faces was analyzed. In the present study, the modulation of the AMTL-N400 and the hippocampal P600 by the factors famousness and repetition was the major goal. Therefore, contacts with the largest AMTL-N400 and hippocampal P600 potentials in the respective anatomic sites have been selected. Further studies should aim to relate depth-recorded ERP components with surface ERPs to disentangle complex surface ERP patterns in their component structures and generators.

The differential responses to the first and second presentations of famous faces in our data may correspond to the repetition effects described for famous faces in surface electrodes.^{7,20-22} The most consistent finding in the surface N400 literature on the processing of famous faces is that repeated faces evoke less negativity in the range of 300 to 600 ms at centroparietal locations.²⁰ In agreement with our data, this repetition effect is prominent mainly for famous faces. In depth recordings with a comparable setting as in the present study, the repetition of items as objects and words results in a reduced AMTL-N400.⁸ According to an influential hypothesis, this ERP repetition effect may reflect a neurophysiologic correlate of a facilitated access to PINs and associated semantic information for repeated items.⁵ Alternatively, attenuations of a more frontally distributed N400 by repetitions have been associated with familiarity, a noncontextual form of memory that underlies explicit recognition memory judgments.^{23,24}

Consistent with the present data, the study using scalp-recorded ERPs found more positive going ERPs for second as compared with first presentations of famous faces.¹² This latter effect started earlier, but it extends in the N400 time range. This functional and temporal resemblance between the present intracranial effects and the scalp-recorded effects suggests that the rhinal cortex contributes to the scalp ERP effects.

In the present study, the AMTL-N400 waveform elicited by the first presentation of the famous faces is different from the waveform elicited in any other condition. In these other conditions (famous faces second presentations, first and second presentation of nonfamous faces), the AMTL-N400 waveforms are well comparable. This suggests a particular mode of processing for the first presentation of famous faces. The processing of nonfamous faces also may be more strongly related to perceptual analysis outside the medial temporal lobe. This may explain the absence of medial temporal repetition effects to nonfamous faces, especially because there is a lack of semantic information in these stimuli.

What neurocognitive processes in the recognition of famous faces may be reflected by the modulation of the face-related AMTL-N400 and the hippocampal P600? Current cognitive models of the N400 (and the AMTL-N400) propose that this component reflects the access to semantic memory stores.⁵ If we assume that the knowledge about famous faces is stored as a mosaic of features in the semantic long-term memory, this could imply that activation of these pieces of information sums up to an enlarged AMTL-N400 (or surface N400). In case of nonfamous faces or the repetition of a famous face, fewer long-term memory entries are activated. The more associative connections a face can activate, the larger the AMTL-N400 (and N400).

In contrast to the AMTL-N400, comparably less is known about the cognitive brain processes reflected by the hippocampal P600. In experiments with words and objects, the hippocampal P600 increases with stimulus repetition.^{8,15} The hippocampal P600 is particularly modulated by tasks that demand explicit memory processes.²⁵ This latter view might also explain why the P600 was not modulated by the repetition factor in the present experiment. Because the subjects were engaged in the detection of target faces, the repetition itself was not task relevant. Although subjects may have been aware of repetitions, we assume that the absence of the instruction to detect stimulus repetitions contributed to missing repetition effects in the hippocampus.

If the increased hippocampal P600 to famous faces is related to memory retrieval, this potential component could be related to the inflow transmission of information from neocortical long-term memory stores into the hippocampus. The hippocampus generally is linked to the retrieval of information distributed in neocortical association areas. Hippocampal activation was reported in fMRI studies contrasting the processing of famous and nonfamous faces.^{10,19} Hippocampal involvement was found during the processing of famous faces in older PET studies.^{26,27} The hippocampus has particularly been implicated in the retrieval of items from autobiographic memory.²⁸ Alternatively, the increased AMTL-N400 and P600 could indicate more efficient encoding processes of famous faces in long-term memory.

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