

Event-related brain potentials distinguish processing stages involved in face perception and recognition

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Accepted 15 October 1999

Abstract

Objectives: An event-related brain potential (ERP) study investigated how different processing stages involved in face identification are reflected by ERP modulations, and how stimulus repetitions and attentional set influence such effects.

Methods: ERPs were recorded in response to photographs of familiar faces, unfamiliar faces, and houses. In Part I, participants had to detect infrequently presented targets (hands), in Part II, attention was either directed towards or away from the pictorial stimuli.

Results: The face-specific N170 component elicited maximally at lateral temporal electrodes was not affected by face familiarity. When compared with unfamiliar faces, familiar faces elicited an enhanced negativity between 300 and 500 ms ('N400f') which was followed by an enhanced positivity beyond 500 ms post-stimulus ('P600f'). In contrast to the 'classical' N400, these effects were parietocentrally distributed. They were attenuated, but still reliable, for repeated presentations of familiar faces. When attention was directed to another demanding task, no 'N400f' was elicited, but the 'P600f' effect remained to be present.

Conclusions: While the N170 reflects the pre-categorical structural encoding of faces, the 'N400f' and 'P600f' are likely to indicate subsequent processes involved in face recognition. Impaired structural encoding can result in the disruption of face identification. This is illustrated by a neuropsychological case study, demonstrating the absence of the N170 and later ERP indicators of face recognition in a prosopagnosic patient. © 2000 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Face perception; Face recognition; Semantic processes; Attention; N400; Event-related brain potential

1. Introduction

The ability to recognise familiar faces is a complex achievement. Different lines of evidence suggest that face identification processes are qualitative different from processes underlying the identification of non-face objects. Face recognition is more impaired than object recognition when line drawings are presented instead of photographs (Davies et al., 1978), and is more affected by stimulus inversion (Yin, 1969; Valentine, 1988). According to Farah (1991), object recognition is primarily based on representations where objects are decomposed into constituent parts, whereas face recognition depends on 'holistic' representations. Findings from neurophysiology also suggest functional and anatomical differences between face and object recognition. Face-specific cells that respond strongly to faces, but not to other types of objects have been found in the macaque temporal cortex in the inferior temporal gyrus and on the banks and the floor of the superior temporal

sulcus (cf. Perrett et al., 1982). The configuration of face components is critical for many of these cells, as their activity is reduced when face components are rearranged, or only single face component are presented (Desimone et al., 1984). Based on fMRI recordings from human participants, Kanwisher et al. (1997) identified an area in the fusiform gyrus that was activated when faces were presented, but not in response to houses, scrambled faces, or hands. Perhaps the most convincing case for face-specific processing modules comes from double dissociations between face and object recognition. In prosopagnosia, face recognition is disproportionately impaired, so that in the most extreme cases, object recognition capabilities seem entirely unaffected (Sergent and Signoret, 1992; McNeil and Warrington, 1993). In contrast, other patients are unable to identify different types of non-face objects, while their face recognition ability is remarkably spared (McCarthy and Warrington, 1986; Moscovitch et al., 1997).

If the identification of faces is subserved by specialised processes, this should also be reflected in face-specific modulations of event-related brain potentials (ERPs). Allison et al. (1994) recorded ERPs intracranially to faces and

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non-face stimuli and found a face-specific negative potential with a latency of about 200 ms in the left and right fusiform and inferior temporal gyri. Electrical stimulation of these areas resulted in a temporary inability to name familiar faces. In a study by Bötzel et al. (1995), faces elicited a midline positivity and an increased negativity at lateral temporal electrodes (T5, T6) around 160 ms after stimulus presentation (see also George et al., 1996; Eimer, 1998, 2000, for similar results). Bentin et al. (1996) found that faces elicited a negative potential with a latency of 170 ms (N170) at lateral posterior temporal sites and a fronto-central positivity of slightly longer latency. No N170 was triggered by cars, hands, furniture, or by scrambled faces.

While these ERP results support the idea that the processing of face stimuli is based on specialised brain mechanisms, it is not clear which processing stages are reflected by these effects. In their influential model of face recognition, Bruce and Young (1986) distinguish between a perceptual structural encoding stage, where individual face features and their spatial configuration are analysed, and a subsequent recognition stage, where structural representations are compared with stored face representations (face recognition units). When these units are sufficiently activated due to their match with a structural representation, person identity nodes in semantic memory can be accessed, resulting in face identification.

Bentin et al. (1996) obtained the face-specific N170 components not only to intact upright faces, but also to inverted faces or isolated eyes (but see Eimer (1998)), and argued that the N170 is likely to reflect face-specific structural encoding processes prior to processing stages involved in face identification. Additional evidence for a link between the N170 and structural encoding of faces comes from a recent study by Eimer and McCarthy (1999), who recorded ERPs to face and non-face stimuli from a severely prosopagnosic patient (see Bentin et al. (1999), for a similar case). Patient PHD has a prosopagnosia affecting both levels of the face recognition system. He is impaired in the structural and perceptual analysis of faces and is also impaired in recognising and identifying familiar faces. He shows substantial prosopagnosic deficits in everyday life as well as in neuropsychological tests (see Eimer and McCarthy (1999), for details). He often fails to recognise highly familiar faces including those of his mother and partner, and needs contextual cues like the sound of a voice or the style of clothes to recognise people. In contrast, his identification of fragmented letters, of objects photographed from unusual views, schematic objects, or cars was found to be within the normal range. In this patient, the N170 component was entirely absent, reflecting the fact that his selective impairment in face recognition is at least in part caused by deficits in structural encoding processes.

If the N170 was elicited prior to the contact of structural representations of faces with semantic memory, this component should not be affected by the familiarity of a face. ERP modulations sensitive to face familiarity, reflecting electro-

physiological correlates of face identification processes, may however be present at longer latencies. Several previous ERP studies have employed familiar faces as stimuli, but were primarily interested in effects of immediate stimulus repetitions (Barrett et al., 1988; Barrett and Rugg, 1989; Bentin and McCarthy, 1994; Begleiter et al., 1995). Barrett et al. (1988) found an enlarged N400 component when a familiar face did not match the identity of its predecessor. In the Bentin and McCarthy (1994) study, the N400 elicited by immediate repetitions of familiar and unfamiliar faces was reduced in amplitude relative to the first presentation of these stimuli. Only one very recent study directly investigated ERP correlates of face recognition. Bentin and Deouell (2000) found an enhanced negativity for familiar relative to unfamiliar faces in the N400 time range which they tentatively interpreted as indicating the activity of face recognition and identification mechanisms. Notably, no effect of familiarity on the N170 component was found in this study, which led Bentin and Deouell (2000) to conclude that this component reflects perceptual stages of structural analysis that are not influenced by face identification processes. The aim of the present study was to provide further insight into which processing stages are reflected by ERP modulations sensitive to faces, when and how face identification processes affect ERP waveforms, and whether stimulus repetitions and attentional factors influence ERP effects related to the familiarity of face stimuli. ERPs were recorded to familiar faces, unfamiliar faces, and non-faces (houses). To determine whether participants were able to successfully identify the faces declared as familiar, a familiar face/unfamiliar face discrimination block was run at the end of the experiment.

In Part I, photographs of familiar faces, unfamiliar faces, and houses were presented in random order, and participants had to respond to infrequently presented target stimuli (hands). ERPs elicited by familiar and unfamiliar faces and by non-faces were compared to find out if and how face-specific ERP modulations are affected by face familiarity. More specifically, it was studied whether familiarity would have no influence on the N170 component (as suggested by Bentin and Deouell (2000)), but would affect later parts of the ERP waveforms. Familiar and unfamiliar faces were presented repeatedly (immediate stimulus repetitions were not allowed), and separate averages were computed for the first and subsequent presentations of individual stimuli to find out whether ERP modulations related to familiarity are influenced by stimulus repetitions. If these ERP effects reflected semantic memory processes involved in the identification of familiar faces, these processes may be qualitatively different for the first and repeated presentations. Access to semantic memory and identification may be faster for previously encountered (primed) than for unprimed familiar faces (see Bentin and McCarthy (1994) for a discussion of ERP effects of stimulus repetitions related to semantic processing), and this may be reflected in ERP familiarity effects of shorter latency, smaller ampli-

tude, or even in the complete absence of such effects for repeated presentations of familiar faces.

In addition, Part I of the present experiment and the subsequent familiar face/unfamiliar face discrimination test was also delivered to the prosopagnosic patient PHD described by Eimer and McCarthy (1999). In their study, the absence of a face-specific N170 component for this patient was interpreted as evidence for impaired structural encoding processes. If structural encoding is impaired, subsequent face identification should also be disrupted due to the insufficient quality of structural representations. In this case, the absence of the N170 should be accompanied by the absence of any ERP familiarity effects in patient PHD.

Part II of the present study investigated whether ERP effects of face familiarity are affected by attentional factors. If face identification processes required focal attention, ERP familiarity effects should be attenuated or absent when a task demands attention to be engaged elsewhere. If such processes were triggered automatically whenever a familiar face is encountered on the visual field, familiarity effects on ERP waveforms should be present regardless of variations in attentional demands. To investigate this issue, photographs of familiar faces, unfamiliar faces, and houses were presented in Part II simultaneously with superimposed alphanumeric character strings. In the 'Detect Repetitions' condition, participants had to direct their attention to the pictorial stimuli in order to detect immediate repetitions of these stimuli. In the 'Detect Digits' condition, they had to ignore these photographs and to attend to the demanding task of detecting the presence of a digit within the character string. If face identification processes as reflected by ERP familiarity effects required focal attention, these effects should be present in the 'Detect Repetitions' condition, but not in the 'Detect Digits' condition. If they reflected a largely automatic response to face familiarity, similar familiarity effects should be elicited in both task conditions.

2. Subjects and methods

2.1. Participants

Twenty-six paid volunteers participated in the experiment. Two of them were excluded because their error rate exceeded 25% in the familiar-unfamiliar discrimination task delivered at the end of the experiment, so that 24 participants (13 female), aged 18–44 years (mean age: 27 years) remained in the sample. Twenty participants were right-handed, 4 were left-handed, and all had normal or corrected-to-normal vision.

Part I of the present experiment plus the subsequent familiar face/unfamiliar face discrimination task was also delivered to patient PHD. PHD is a 39-year-old left-handed man who sustained a closed head injury in a road traffic accident in 1977 and has significant cognitive deficits including prosopagnosia. On examination no sensory or

motor deficits were noted; his visual fields were full. MRI scanning showed moderate diffuse damage with an area of more focal injury in the left temporo-parietal region (see Eimer and McCarthy (1999) for neuropsychological details).

2.2. Stimuli and apparatus

Participants were seated in a dimly lit sound attenuated cabin, with response buttons under their left and right hands. A computer screen was placed 110 cm in front of the participant's eyes. The stimuli were photographs of familiar and unfamiliar faces, houses, and hands that were digitally scanned, processed by graphics software, and presented on a computer monitor in front of a white background. The familiar faces were photographs of well-known politicians, movie stars, musicians, and other celebrities. They were chosen out of a larger sample on the basis of the results of a pilot study where those face stimuli were most likely to be correctly identified. Fifty images of familiar faces, 50 images of unfamiliar faces and 32 images of houses were used in both experimental parts. In Part I, 4 images of left-pointing hands and 4 images of right-pointing hands were also presented. All face images showed a frontal view, with eyes positioned in the middle of the image. Face and house stimuli occupied a visual angle of approximately $4.5 \times 4^\circ$, and hand stimuli occupied a visual angle of about $5.5 \times 4^\circ$. All stimuli were presented for 300 ms at the centre of the screen, and successive stimulus presentations were separated by intertrial intervals of 1200 ms. In Part II, face and house stimuli were presented together with a 5-item string of red alphanumeric characters, centred at fixation, and occupying a visual angle of about $2.5 \times 0.5^\circ$.

2.3. Procedure

The experiment consisted of two successively delivered parts. Participants were instructed to respond as quickly and accurately as possible to the respective target stimuli, to withhold responses to all other stimuli, and to maintain central eye fixation during the trials. Part I consisted of 936 trials, where familiar and unfamiliar faces, houses, and hands were presented in random order, except that immediate stimulus repetitions were not allowed. After every 104 trials, a brief rest period was included, and participants could initiate the next run of trials by pressing the right button. Familiar and unfamiliar faces and houses were presented in 300 trials each, and houses were presented in 192 trials. Fifty different familiar faces, 50 unfamiliar faces and 32 houses were used, so that each individual face and house stimulus was presented on average 6 times. In 144 trials, left-pointing and right-pointing hands were presented with equal probability. Participants were instructed to respond with a left button press to hand stimuli pointing to the right side, and with a right button press to hands pointing to the left. Prior to the start of Part I, a brief training

block was delivered, where different face and house photographs were employed.

Part II consisted of 6 blocks with 108 trials each. Presentation conditions were similar to Part I, except that no hands were presented, and each photograph was presented simultaneously with an alphanumeric string superimposed on the centre of the image. In 3 blocks ('Detect Digits'), the participants' task was to respond with a left-hand button press whenever they detected a digit within this string. In 18 trials per block, one digit was presented together with 4 letters, and appeared equiprobably in one of the 5 serial positions within the string. These target strings were presented equally often in front of familiar faces, unfamiliar faces, and houses. In the remaining 90 non-target trials, the strings consisted exclusively of letters, and familiar faces, unfamiliar faces, and houses were presented with equal probability. Immediate stimulus repetitions were not allowed. In the other 3 blocks ('Detect Repetitions'), all images were presented together with a 5-item letter sequence, and participants' task was to respond with a left-hand button press whenever the image presented in the previous trial was immediately repeated. Repetitions occurred in 18 trials per block, and were equiprobable for familiar faces, unfamiliar faces, and houses. In the remaining 90 non-target trials per block, non-repeated familiar faces, unfamiliar faces, and houses were presented with equal probability. The 3 Detect Digits and Detect Repetition blocks were delivered in randomised order. Participants received a brief training block for each of the two task conditions prior to the start of Part II.

At the end of the experiment, a familiar face/unfamiliar face discrimination task was delivered where all 100 familiar and unfamiliar face stimuli employed before were presented in random order. Participants had to judge the familiarity of each face by classifying the images into one of 4 categories: (1) Definitely familiar face (name and profession known); (2) familiar face (name not known); (3) unfamiliar face (although vague feeling of familiarity); (4) definitely unfamiliar face. Categories 1 to 4 were mapped to button press responses with the left middle and index finger, and right index and middle finger, respectively. Each face stimulus remained on the screen until a classification response was made.

2.4. Recording and data analysis

EEG was recorded with Ag–AgCl electrodes from Fpz, Fz, Cz, Pz, T5, O1, T6, and O2 (according to the 10–20 system). EEG was measured relative to a reference electrode positioned on the tip of the nose. Electrode impedance was kept below 5 k Ω . The amplifier bandpass was 0.10–40 Hz. EEG and EOG were sampled with a digitisation rate of 200 Hz, and stored on disk. The latency of manual responses (if present) was measured on each trial. EEG was epoched off-line into periods of 900 ms, starting 100 ms prior to the onset of a stimulus, and ending 800 ms after stimulus onset.

Trials with eyeblinks (electrode Fpz exceeding 60 μ V in the 800 ms interval following imperative stimulus onset), muscular or other artefact (voltage on any recording electrode exceeding ± 80 μ V in the 800 ms interval following stimulus onset), or overt responses on non-target trials were excluded from further EEG analysis. ERPs were computed exclusively on the basis of non-target trials. For Part I, EEG was averaged separately for the 3 stimulus types (familiar face, unfamiliar face, house). To assess effects of stimulus repetition, separate averages were computed for the first and for each subsequent presentation of familiar faces, unfamiliar faces, and houses. For Part II, averages to familiar faces, unfamiliar faces, and houses were computed separately for the 'Detect Digits' and the 'Detect Repetitions' task.

Averaged waveforms were digitally low-pass filtered (20 Hz cut-off frequency) prior to statistical analysis. All measures were taken relative to the mean voltage of the 100 ms interval preceding stimulus onset. ERP effects of experimental variables were determined by conducting repeated-measures analyses of variance on ERP mean amplitude values. Repeated-measures ANOVAs were conducted separately for Part I, and for the 'Detect Digits' and 'Detect Repetitions' task of Part II, for the factors stimulus category (house vs. face, collapsed over familiar and unfamiliar faces), familiarity (familiar face vs. unfamiliar face), repetition (1st presentation vs. 2nd to 4th presentation vs. 5th and successive presentations of an individual stimulus, only for Part I), electrode location (temporal vs. occipital for lateral sites; frontal vs. central vs. parietal for midline sites), and recording side (left vs. right, for lateral sites). Greenhouse–Geisser adjustments to the degrees of freedom were performed when appropriate. To test specific effects or interactions, additional ANOVAs or paired *t* tests were employed.

3. Results

3.1. Performance in the familiar face/unfamiliar face discrimination task

Participants showed a very good ability to identify familiar faces and to discriminate between the familiar and unfamiliar faces used in this experiment. Only 3.3% of all familiar faces were incorrectly categorised as unfamiliar or definitely unfamiliar, while 91.6% of these faces were classified as definitely familiar (category 1). 15.6% of all unfamiliar faces were incorrectly classified as familiar (category 2), but only 1.8% of them were judged to be definitely familiar.

Patient PHD showed very poor performance on this task. He classified only 6 of the 50 familiar faces as definitely familiar (and a post-experimental interview revealed that he actually misidentified 3 of these 6 faces), and judged 38 familiar faces to be unfamiliar.

3.2. Part I

3.2.1. Behavioural performance

Mean reaction time (RT) was 555 ms in response to both left-pointing and right-pointing hands. Participants missed 1.4% of all target stimuli, and responded incorrectly on 3% of all target trials. The False Alarm rate to non-target stimuli was 0.05%.

3.2.2. N170

Fig. 1 shows ERPs elicited by familiar faces, unfamiliar faces, and houses in Part I (top), together with the resulting faces–houses and familiar faces–unfamiliar faces difference

waveforms (bottom). N170 was quantified as mean amplitude within the 140–190 ms post-stimulus latency window. When compared to houses, faces elicited a distinct N170 component at lateral posterior sites, as reflected by a highly significant main effect of stimulus category ($F(1, 23) = 40.24, P < 0.001$). A stimulus category \times electrode location interaction ($F(1, 23) = 6.88, P < 0.015$) indicated that this N170 effect was larger at temporal than at occipital electrodes (Fig. 1, bottom). The absence of any stimulus category \times repetition interaction ($F < 0.2$) showed that the N170 was entirely unaffected by stimulus repetitions. At midline electrodes, a stimulus category \times electrode location interaction ($F(2, 46) = 27.9; P < 0.001, \epsilon =$

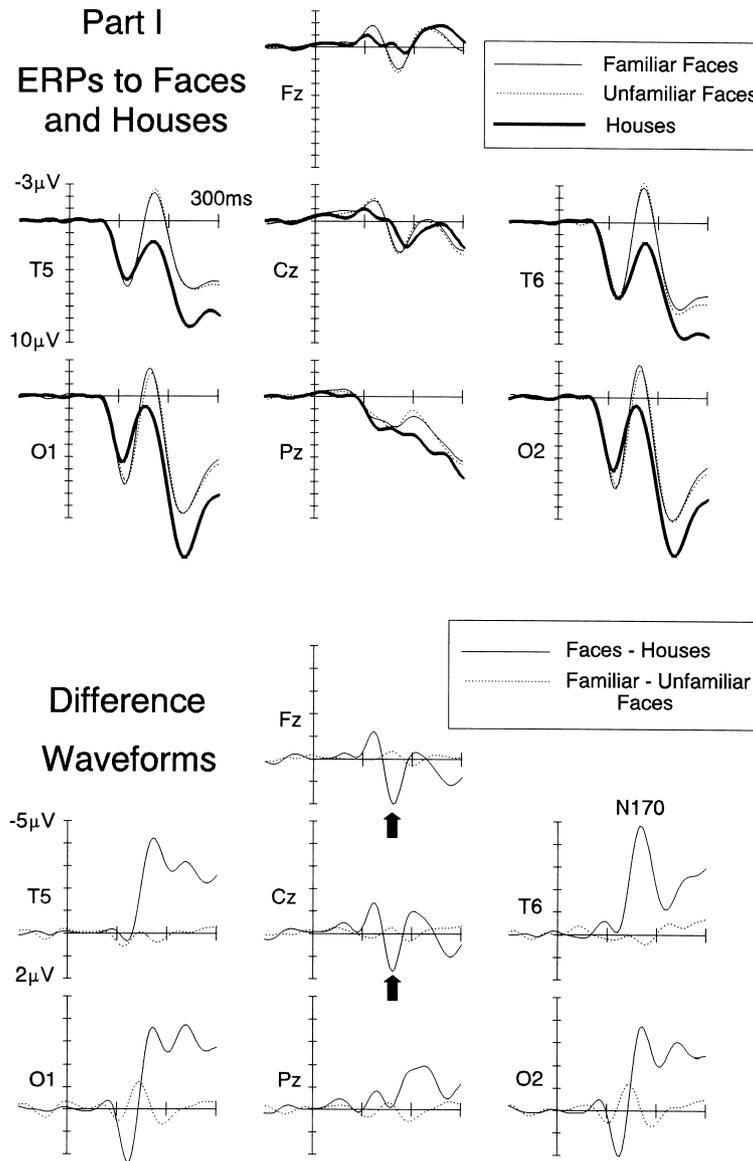


Fig. 1. (Top) Grand-averaged ERPs recorded at midline and lateral posterior electrodes in response to familiar faces (thin solid lines), unfamiliar faces (thin dashed lines), and houses (thick solid lines) in Part I. ERPs are averaged across all successive presentations of individual stimuli. (Bottom) Difference waveforms obtained by subtracting ERPs to houses from ERPs to faces (averaged across familiar and unfamiliar faces; solid lines) and by subtracting ERPs to unfamiliar faces from ERPs to familiar faces (dashed lines).

0.927) reflected a significantly enhanced positivity to faces as compared to houses at frontocentral sites (indicated in Fig. 1, bottom, by the black arrows).

As can be seen in Fig. 1, the difference between familiar and unfamiliar faces had no effect whatsoever on ERPs at midline and lateral posterior sites in the N170 time range (both $F < 0.2$). In addition, no familiarity \times repetition interactions were obtained.

3.2.3. ERP effects sensitive to face familiarity

Fig. 2 shows the ERPs to familiar and unfamiliar faces, collapsed across all repetitions of individual stimuli (top), together with the resulting familiar face–unfamiliar face difference waveforms (bottom). Two distinct effects of familiarity were present in the ERP waveforms. When

compared with unfamiliar faces, familiar faces elicited an enlarged negativity between 300 and 500 ms post-stimulus ('N400f') that was followed by an enhanced positivity beyond 500 ms ('P600f'). Both effects seem larger at midline electrodes than at lateral sites, and most pronounced at centroparietal electrodes. The reliability of these ERP modulations and effects of stimulus repetition were analysed within 4 time windows covering the 'N400f' and 'P600f' latency ranges (N400a: 320–400 ms; N400b: 400–480 ms; P600a: 500–600 ms; P600b: 600–750 ms).

Significant face familiarity effects were present in both N400 latency windows at midline electrodes (both $F(1, 23) > 11.5$, both $P < 0.002$) as well as at lateral posterior sites (both $F(1, 23) > 7.7$, both $P < 0.011$), reflecting enhanced negativities for familiar faces. At

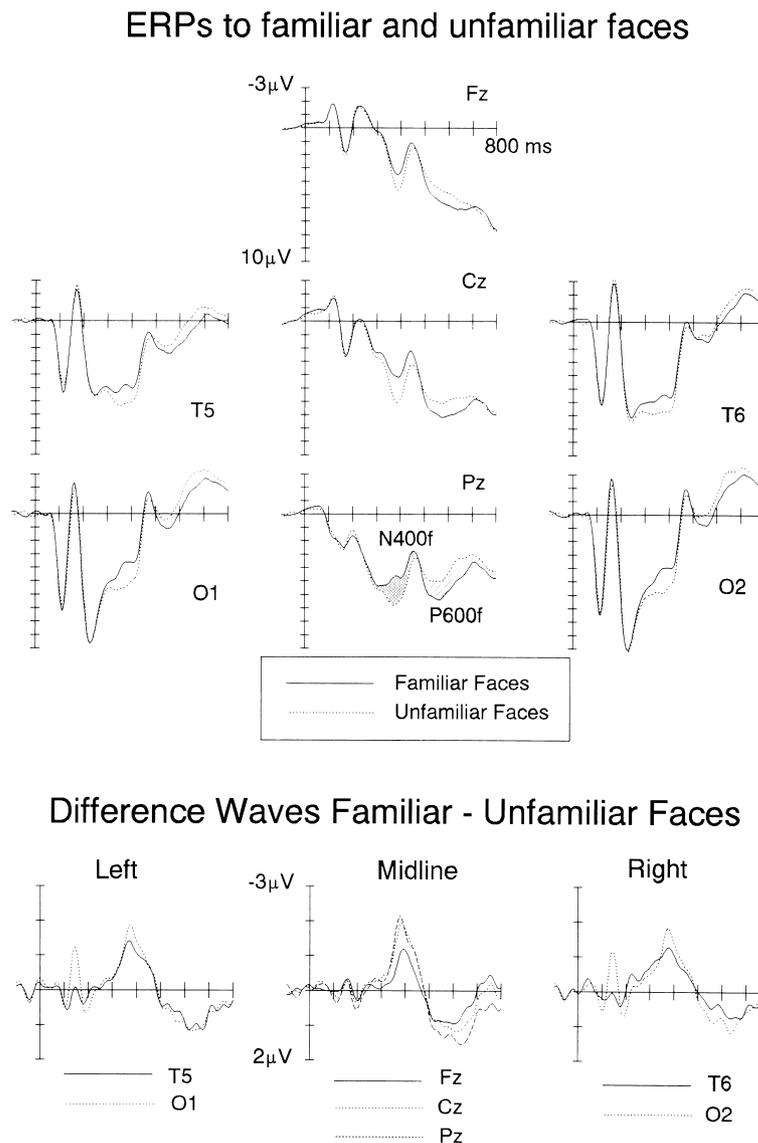


Fig. 2. (Top) Grand-averaged ERPs recorded at midline and lateral posterior electrodes in the response to familiar faces (solid lines) and unfamiliar faces (dashed lines) in Part I. ERPs are averaged across all successive presentations of individual stimuli. (Bottom) Difference waveforms obtained by subtracting ERPs to unfamiliar faces from ERPs to familiar faces at left, midline, and right recording sites.

midline sites, familiarity × electrode location interactions within both time windows ($F(2, 46) = 12.86$ and 6.09 , $P < 0.001$ and 0.016 , $\epsilon = 0.852$ and 0.602 , respectively) indicated that this effect was larger at Cz and Pz than at Fz (see Fig. 2, bottom). Subsequent analyses revealed that the ‘N400f’ effect was significant within both analysis windows at all midline sites, but that it was reliably larger at Cz and Pz than at Fz.

Highly significant effects of familiarity on midline ERP waveforms were also obtained for both ‘P600f’ latency windows (both $F(1, 23) > 15.7$, both $P < 0.001$), reflecting enhanced positivities for familiar as compared with unfamiliar stimuli. A highly significant familiarity × electrode

location was obtained in the P600b latency range ($F(2, 46) = 13.73$, $P < 0.001$, $\epsilon = 0.763$), and subsequent analyses showed that the familiarity effect was largest at Pz, and smallest at Fz (see Fig. 2, bottom). At lateral posterior sites, familiarity was significant only in the P600b latency range (600–750 ms; $F(1, 23) = 12.7$, $P < 0.002$), and approached significance in the earlier P600a window ($F(1, 23) = 3.35$, $P < 0.080$).

Fig. 3 (top) shows the ERPs elicited at midline electrodes for the first, 2nd–4th, and all subsequent presentations of individual familiar and unfamiliar faces, together with the resulting familiar–unfamiliar face difference waveforms for all recording sites (bottom). The ‘N400f’ appears to

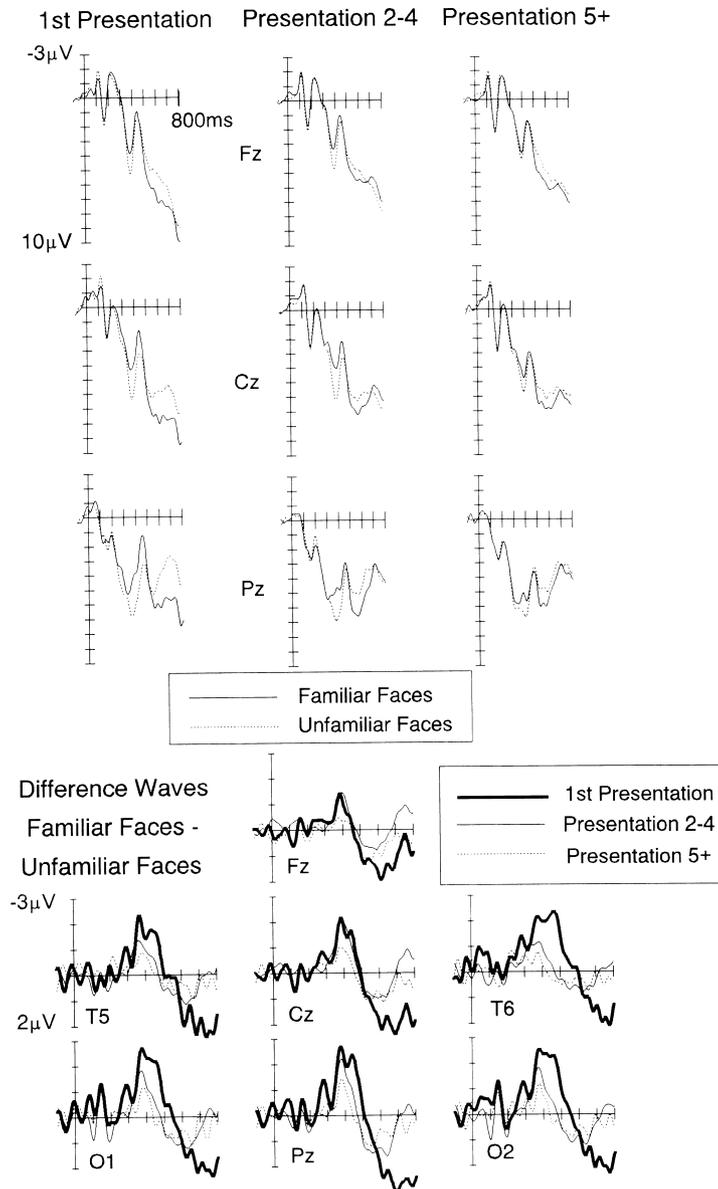


Fig. 3. (Top) Grand-averaged ERPs recorded at midline electrodes in response to familiar faces (solid lines) and unfamiliar faces (dashed lines) in Part I, displayed separately for the first presentation (left), the 2nd–4th presentation (middle), and the 5th plus all successive presentations (right). (Bottom) Difference waveforms obtained by subtracting ERPs to unfamiliar faces from ERPs to familiar faces at midline and lateral posterior electrodes, displayed separately for the first presentation (thick solid lines), 2nd–4th presentation (thin solid lines), and 5th plus subsequent presentations (thin dashed lines) of individual stimuli.

decrease in amplitude as a function of stimulus repetition. Significant familiarity \times repetition interactions were present in the N400b latency window (400–480 ms post-stimulus) at Pz as well as at lateral temporal and occipital electrodes (all $F(2, 46) > 6.2$, all $p > 0.004$, all $\epsilon > 0.938$). Follow-up analyses were conducted separately on the ERPs elicited by familiar and unfamiliar faces. Repetition effects were found for familiar faces at midline as well as lateral posterior sites in the N400b interval ($F(2, 46) = 3.37$ and 11.88 , $P < 0.049$ and 0.001 , $\epsilon = 0.899$ and 0.815 , respectively), reflecting a reduced negativity for repeated familiar faces. In contrast, stimulus repetition did not affect ERPs to unfamiliar faces (both $F < 1$). Despite its reduction with stimulus repetition, additional analyses performed exclusively for repeated presentations of faces showed significant effects of familiarity at all electrodes in the N400a interval, while this effect was significant only at Cz in the N400b interval.

No familiarity \times repetition interactions were found in the P600a latency range, but these interactions were clearly present in the P600b window ($F(2, 46) = 13.73$ and 4.28 , $P < 0.001$ and 0.024 , $\epsilon = 0.802$ and 0.902 , for midline and lateral central sites, respectively), reflecting a decreased ‘P600f’ effect with stimulus repetitions. Similar to the ‘N400f’, stimulus repetition affected the ERPs to familiar faces at midline and lateral posterior sites in the P600b time range ($F(2, 46) = 9.41$ and 6.60 , $P < 0.001$ and 0.003 , $\epsilon = 0.753$ and 0.588 , respectively), reflecting reduced positivities for repeated familiar faces. Again, no repetition effects were present for the ERPs to unfamiliar faces (both $F < 1$). Additional analyses conducted only for repeated presentations of faces showed significant familiarity effects at all

midline electrodes (except for Fz in the P600b interval) and for all lateral posterior sites in the P600b interval.

3.3. Part II

3.3.1. Behavioural performance

Mean RT was slower in the ‘Detect Digits’ task (570 ms) than in the ‘Detect Repetitions’ task (506 ms), which was reflected in a highly significant effect of task condition when the RT data obtained for both tasks were analysed together ($F(1, 23) = 36.69$, $P < 0.001$). Participants missed 11.5% of all targets in the ‘Detect Digits’ task, and 6.1% in the ‘Detect Repetitions’ task. The rate of False Alarms to non-target stimuli was 1.2% and 0.3% in these two tasks, respectively.

3.3.2. N170

Highly significant effects of stimulus category were again present at lateral posterior electrodes ($F(1, 23) = 74.79$ and 68.64 , both $P < 0.001$, for the Detect Digits and Detect Repetition tasks, respectively), reflecting the presence of a face-specific N170 component (not shown in Figures). As in Part I, face familiarity did not have any effect on N170 amplitudes ($F < 0.2$ in both tasks).

3.3.3. Later ERP effects related to face familiarity

Fig. 4 shows the midline ERPs elicited by familiar and unfamiliar faces in the ‘Detect Repetitions’ and ‘Detect Digits’ task together with the corresponding familiar–unfamiliar faces difference waveforms. In the ‘Detect Repetitions’ task, familiarity affected ERPs in the N400a and

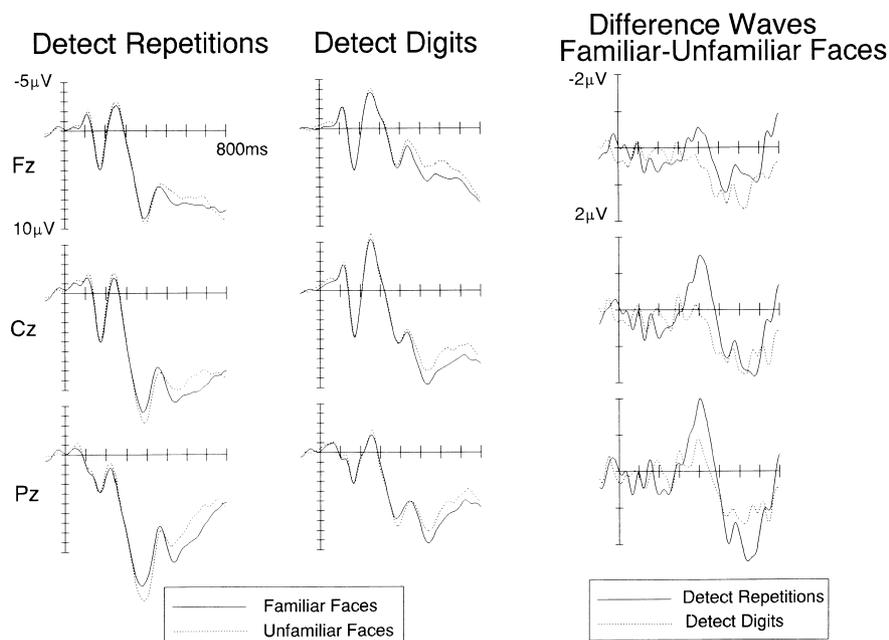


Fig. 4. Grand-averaged ERPs recorded at midline electrodes in response to familiar faces (solid lines) and unfamiliar faces (dashed lines) in the ‘Detect Repetitions’ task (left) and the ‘Detect Digits’ task (middle) of Part II. Right: difference waveforms obtained at midline electrodes by subtracting ERPs to unfamiliar faces from ERPs to familiar faces in the ‘Detect Repetitions’ task (solid lines) and the ‘Detect Digits’ task (dashed lines).

N400b latency windows ($F(1, 23) = 5.73$ and 7.35 , $P < 0.025$ and 0.012 , respectively), reflecting enhanced negativities for familiar faces. Familiarity \times electrode location interactions ($F(2, 46) = 9.06$ and 9.85 , both $P < 0.002$, $\epsilon = 0.771$ and 0.615 , for the N400a and N400b intervals, respectively) were obtained, and additional analyses showed that significantly enhanced negativities to familiar faces were present at Cz and Pz, but not at Fz (see Fig. 4, right). In contrast, no significant 'N400f' effect was elicited at midline sites in the 'Detect Digits' task (both $F < 0.3$).¹

As can be seen from Fig. 4, a 'P600f' effect similar to the effect observed in Part I, reflecting enhanced positivities to familiar faces beyond 500 ms post-stimulus, emerged in both experimental tasks at midline electrodes. This effect was statistically analysed within the 500–700 ms post-stimulus latency range. Significant effects of familiarity were obtained for the 'Detect Repetitions' task ($F(1, 23) = 14.0$, $P < 0.001$), but, notably, also for the 'Detect Digits' task ($F(1, 23) = 4.30$, $P < 0.005$). In the former task, a familiarity \times electrode interaction was present ($F(2, 46) = 19.38$, $P < 0.001$, $\epsilon = 0.618$), and subsequent analyses showed that the 'P600f' effect was largest at Pz, and smallest, although still significant, at Fz (see Fig. 4). No such interaction was present in the 'Detect Digits' task.²

3.4. Patient PHD (Part I)

Patient PHD responded correctly to left-pointing and right-pointing hands on 64% of all target trials. His mean RT was 823 ms. Fig. 5 (top) shows the ERPs recorded from PHD in response to faces (collapsed across familiar and unfamiliar faces) and houses, and Fig. 5 (bottom) compares ERPs to familiar and unfamiliar faces. Consistent with previous findings (Eimer and McCarthy, 1999), and in marked contrast to the results obtained for the neurologically unimpaired participants (Fig. 1), no face-specific N170 component was elicited. In fact, houses tended to elicit larger N170 components than faces (Fig. 5, top). A comparison of the ERPs elicited in response to familiar and unfamiliar faces for patient PHD to the effects of face familiarity shown in Fig. 2 for unimpaired participants showed that systematic ERP modulations related to face familiarity were entirely absent (Fig. 5, bottom).

¹ This presence of a 'N400f' effect in the 'Detect Repetitions' task, and its absence in the 'Detect Digits' task was reflected in a familiarity \times task condition interaction ($F(1, 23) = 5.69$, $P < 0.026$) for the N400b interval when the data from both tasks were analyzed together. This interaction failed to reach significance for the N400a interval ($P < 0.20$).

² A similar pattern of effects was obtained at lateral posterior electrodes (not shown in Figures). Enhanced negativities to familiar stimuli were elicited in the N400a and N400b latency windows in the 'Detect Repetitions' tasks (both $F(1, 23) > 5.39$, both $P < 0.029$), but not in the 'Detect Digits' task. Between 500 ms and 700 ms post-stimulus, familiar faces elicited an enhanced positivity at lateral posterior sites in the 'Detect Repetitions' task ($F(1, 23) = 7.69$, $P < 0.011$), but this effect failed to reach significance in the 'Detect Digits' task ($F(1, 23) = 2.86$, $P < 0.104$).

4. Discussion

The aim of this study was to investigate which stages in the processing of faces are reflected by face-selective ERP effects. More specifically, it was studied how face identification processes would modulate ERP waveforms, and whether stimulus repetition or attentional manipulations can influence such effects. ERPs to familiar faces were compared to ERPs to unfamiliar faces and non-faces (houses), separately for the first and subsequent presentations of individual images (Part I), and under conditions where attention was either directed to or away from these pictorial stimuli (Part II).

In both experimental parts, a distinct N170 component was elicited by faces relative to non-face (house) stimuli at lateral posterior sites which was maximal at lateral temporal electrodes. Consistent with previous findings (Bötzel et al., 1995; Bentin et al., 1996; Eimer, 1998, 2000), a frontocentral positivity for faces relative to houses was observed in the same latency range.³ As can be seen in Fig. 1 (bottom), face familiarity had no effect whatsoever on the face-specific N170 component. This finding, which was replicated in Part II, thus confirms the observation of Bentin and Deouell (2000) that the N170 is not influenced by the familiarity of faces, and their conclusion that this component reflects the structural encoding of faces prior to a comparison of structural descriptions with representations stored in semantic memory. In the present study, the N170 component was also unaffected by stimulus repetition, which suggests that it indicates early visual processes that are elicited automatically by the presentation of any face, and are not subject to priming from previous stimulus presentation episodes.

While the N170 was unaffected by face familiarity and stimulus repetition, systematic and reliable differences between ERPs elicited by familiar and unfamiliar faces were found at longer latencies. When compared to unfamiliar faces, familiar faces elicited an enhanced negativity between 300 ms and 500 ms ('N400f') which was followed by an enhanced positivity beyond 500 ms post-stimulus ('P600f'). The 'N400f' may reflect similar processes as the 'classical' N400 component, which was initially attributed to the processing of semantically incongruous words (Kutas and Hillyard, 1980). Because N400 components have also been found in response to non-word stimuli (Barrett and Rugg, 1989; Bentin and McCarthy, 1994), it may more generally reflect the access to and activity within semantic memory. Bentin and Deouell (2000) also reported

³ The question whether the N170 and the frontocentral positivity reflect a single underlying generator process is still debated. Based on dipole analyses, Bötzel et al. (1995) suggested that the midline positivity reflected hippocampal activity, while the lateral temporal negativity was generated in the fusiform and lingual gyri. In contrast, George et al. (1996) argued that these effects are caused by a single neural generator in the parahippocampal and fusiform gyri oriented such as to produce a polarity reversal at the scalp surface between T5/T6 and Cz.

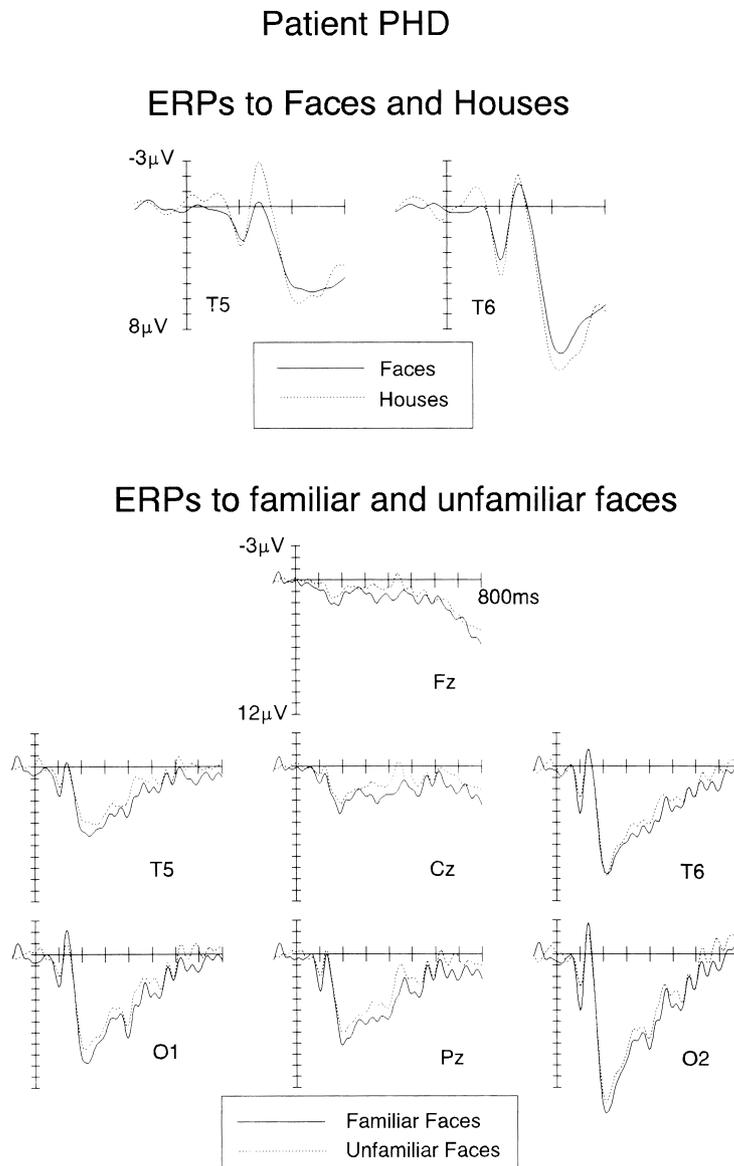


Fig. 5. (Top) Averaged ERPs recorded at lateral temporal electrodes in response to faces (solid lines) and houses (dashed lines) for patient PHD. No face-specific N170 component is elicited. (Bottom) Averaged ERPs recorded at midline and lateral posterior electrodes in the response to familiar faces (solid lines) and unfamiliar faces (dashed lines) for patient PHD. ERPs are averaged across all successive presentations of individual stimuli.

an enhanced negativity for familiar as compared to unfamiliar faces in the N400 latency range, and attributed this effect to the activation of 'person identity nodes' by structural representations of familiar faces. While this effect tended to be frontocentrally distributed in the Bentin and Deouell (2000) study (although not consistently so across experiments), it showed a distinct parietocentral distribution in the present experiment. This fact distinguishes the 'N400f' found in this study from the N400 associated with the semantic processing of words, which is usually frontocentrally distributed. Although further experiments with more dense electrode arrays are needed to investigate in more detail scalp distribution differences between N400 and 'N400f,' the present data may suggest that word and

face recognition tasks activate at least partially distinct brain systems.

The 'N400f' was largest for the first presentation of a familiar face, and decreased in amplitude for subsequent presentations (Fig. 3). This reduction of the 'N400f' was due to the fact that ERPs to familiar faces were affected by stimulus repetition in the N400b time range. Less negativity was elicited for repeated familiar faces, although a reliable 'N400f' remained to be present for repeated familiar faces in Part I, and even in the 'Detect Repetitions' task of Part II (see below). If the 'N400f' reflected activation processes within face-specific semantic memory elicited by familiar faces, this pattern of results suggests that such processes are activated most strongly when a particular

image is first encountered, but will still be triggered, albeit in an attenuated fashion, after several repetitions of a specific familiar face. ERPs to unfamiliar faces were not affected by stimulus repetition, indicating that stimulus repetition selectively influenced the semantic processing of familiar faces.⁴ The effects of stimulus repetition on familiar faces and the absence of such effects for unfamiliar faces are comparable to ERP results obtained for repeated word stimuli. When compared to first presentations, ERPs elicited by repeated words show an enlarged positivity starting beyond 300 ms post-stimulus. These word repetition effects are larger for words than for orthographically legal non-words (Rugg, 1987), and larger for orthographically legal non-words than for illegal non-words (Rugg and Nagy, 1987), presumably reflecting differences in the access of these items to lexical memory.

In Part II, RT was longer and error rates higher in the 'Detect Digits' task than in the 'Detect Repetitions' task, which confirms that digit detection was a demanding task that required focal attention. The 'N400f' was present in the 'Detect Repetition' task where pictorial images were relevant, and absent in the 'Detect Digits' task, where these images had to be ignored. This suggests that the processes responsible for the 'N400f' will not be triggered automatically in response to the presence of a familiar face in the visual field, but depend upon attentional processing.

The 'P600f' effect, which followed the 'N400f' effect, was also reliably observed in both experimental parts. The fact that this effect showed a similar scalp distribution as the 'N400f,' and was similarly affected by stimulus repetitions of familiar faces in Part I (attenuated, but still reliable 'P600f' effects for repeated familiar faces; no effects of stimulus repetition for unfamiliar faces) may suggest that both effects reflect similar underlying mechanisms. It is notable that familiarity \times repetition interactions were observed for the later parts (N400b, P600b), but not for the earlier parts (N400a, P600a) of these effects. This pattern could indicate a reduction in the duration of face identification processes with stimulus repetitions, due to priming from previous presentations. A dissociation between the 'N400f' and 'P600f', however, was observed in Part II. While the 'N400f' effect was restricted to the 'Detect Repetitions' condition, significant 'P600f' effects were also observed in the 'Detect Digits' task, where attention was directed away from the pictorial stimuli. It is possible that the processes underlying the 'N400f' and 'P600f' differ in their attentional requirements, in that the former will only be elicited under focal attention conditions, while the latter are triggered independently from the current attentional set. Such a dissociation would provide strong evidence that these two effects reflected functionally differ-

ent processes. Additional studies are needed to investigate if and how the 'P600f' is linked to processes involved in face identification, and whether it can be reliably dissociated from the 'N400f'.

Overall, the present study demonstrated that different face-specific ERP modulations can be linked to different processes involved in the identification of faces. While the N170 reflects the pre-categorical structural encoding of face stimuli, longer-latency ERP components ('N400f,' 'P600f') are likely to indicate processes involved in the recognition and identification of faces. Based on the Bruce and Young (1986) model, these effects may be caused by the activation of stored representations of familiar faces and the subsequent activation of representations in semantic memory. The fact that the N170 component was not affected by familiarity does however not imply that the perceptual encoding processes as reflected by the N170 are irrelevant for subsequent face identification processes. Impairments in structural encoding are likely to disrupt subsequent face identification processes. This was illustrated by the ERP results obtained for a prosopagnosic patient (PHD). As in a previous study, (Eimer and McCarthy, 1999), no face-specific N170 component was elicited in this patient. In addition, no systematic ERP effects of face familiarity were present at longer latencies. The absence of any ERP indication of face identification processes in PHD is mirrored by his poor performance in the familiar face/unfamiliar face discrimination task. The lack of a face-specific N170 component together with the absence of an electrophysiological correlate of familiarity detection in PHD indicates that impaired structural encoding processes will affect face identification processes, and that prosopagnosia can at least in part be caused by deficits prior to face identification. ERPs may thus be used as markers for the selective impairment of different processing stages involved in face identification. For patients with deficits restricted to the recognition of familiar faces (prosopagnosics), intact structural encoding processes should be reflected by the presence of face-specific N170 components, while later ERP effects sensitive to face familiarity should be attenuated or absent.

Acknowledgements

This research was supported by a grant from the Human Frontier Science Program (HFSP). The author thanks Thomas Kress, Roz McCarthy, Kate Parmenter and Friederike Schlaghecken for their contributions to this study.

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⁴ This finding differs from the result of Bentin and McCarthy (1994), who found equivalent repetition effects on ERPs to familiar and unfamiliar faces. In contrast to the present experiment, stimuli were repeated immediately in the Bentin and McCarthy (1994) study.

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