An event-related brain potential study of explicit face recognition

Angela Gosling, Martin Eimer*

Department of Psychological Sciences, Birkbeck College, University of London, Malet Street, London WC1E 7HX, UK

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ABSTRACT

To determine the time course of face recognition and its links to face-sensitive event-related potential (ERP) components, ERPs elicited by faces of famous individuals and ERPs to non-famous control faces were compared in a task that required explicit judgements of facial identity. As expected, the face-selective N170 component was unaffected by the difference between famous and non-famous faces. In contrast, the occipito-temporal N250 component was linked to face recognition, as it was selectively triggered by famous faces. Importantly, this component was present for famous faces that were judged to be definitely known relative to famous faces that just appeared familiar, demonstrating that it is associated with the explicit identification of a particular face. The N250 is likely to reflect early perceptual stages of face recognition where long-term memory traces of familiar faces in ventral visual cortex are activated by matching on-line face representations. Famous faces also triggered a broadly distributed longer-latency positivity (P600f) that showed a left-hemisphere bias and was larger for definitely known faces, suggesting links between this component and name generation. These results show that successful face recognition is predicted by ERP components over face-specific visual areas that emerge within 230 ms after stimulus onset.

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1. Introduction

In everyday life, we encounter familiar and unfamiliar faces in many different contexts. Even though the recognition and identification of individual faces seems effortless, many behavioural and neuroscientific studies have demonstrated that face recognition is in fact a complex cognitive achievement that is mediated by a sequence of face-specific brain mechanisms. Cognitive-psychological models of face processing (e.g., Bruce & Young, 1986; Burton, Bruce, & Hancock, 1999) have described different stages that are involved in successful face recognition. These include perceptual processing stages such as the initial encoding of the visual properties of a face and the subsequent generation of an integrated representation of its configural and holistic features. Face recognition results when such perceptual face representations are successfully matched with stored memory traces of visual features of known familiar faces. Following this match, further semantic or episodic information about a particular individual can be retrieved from long-term memory.

ERP measures have been used in many studies to investigate the temporal organisation and neural basis of the component processes that underlie face recognition. The majority of these studies have focused on the face-sensitive N170 component. This component represents an enhanced negativity that is reliably triggered in response to faces as compared to non-face stimuli between 150 and 200 ms after stimulus onset over lateral occipito-temporal areas (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Bötzel, Schulze, & Stodieck, 1995; Eimer, 2000a, 2000b; Eimer, Kiss, & Nicholas, 2010; Rossion et al., 2000). The N170 is assumed to be generated in occipito-temporal cortex and posterior fusiform gyrus (Bötzel et al., 1995; Rossion, Joyce, Cottrell, & Tarr, 2003), and is usually interpreted as an electrophysiological marker for the structural encoding of faces and the activation of perceptual face representations that form the input for subsequent face recognition processes (Eimer, 2000b; Sagiv & Bentin, 2001).

It is important to note that face recognition and identification are unlikely to be directly reflected by the N170 component. Several studies have demonstrated that this component is not affected by the difference between famous and unknown faces (e.g., Bentin & Deouell, 2000; Eimer, 2000a), although evidence from face identity adaptation suggests that the construction of individual face representations might commence within 170 ms after stimulus onset (e.g., Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009). If the N170 reflects sensory-perceptual stages of face processing that precede the recognition of individual familiar faces, research that focuses on this component cannot be expected to yield direct insights into the time course and functional organisation of face recognition. Until now, only relatively few ERP studies have investigated face-specific ERP components beyond the N170 in order to determine whether and how these components are linked

* Corresponding author. Tel.: +44 020 7631 6538; fax: +44 020 7631 6312.
E-mail address: m.eimer@bbk.ac.uk (M. Eimer).

to face recognition and identification. In most of these studies, face repetition paradigms have been used as a tool to manipulate face familiarity. What was consistently found in these studies was that relative to previously unseen faces, repeated faces trigger an enhanced negativity at inferior occipito-temporal electrodes. This N250r component typically reaches its maximum between 230 ms and 280 ms after stimulus onset, and is often larger over the right hemisphere (e.g., Begleiter, Porjesz, & Wang, 1995; Schweinberger, Huddy, & Burton, 2004; Schweinberger, Pfütze, & Sommer, 1995). The repetition-sensitivity of the N250r suggests that unlike the N170, it reflects processes sensitive to the familiarity of faces that take place after their initial perceptual analysis. It has been suggested that the N250r is associated with face recognition, that is, with a successful match between a perceptual face representation and an episodic memory trace of a previously seen face (Schweinberger & Burton, 2003). Even though N250r components are triggered reliably by repetitions of unfamiliar faces (e.g., Itier & Taylor, 2004; Schweinberger et al., 1995), they are usually larger for familiar faces (e.g., Herzmann, Schweinberger, Sommer, & Jentzsch, 2004), which indicates that face-specific memory traces are activated more strongly by repetitions of faces that have pre-existing long-term representations than by repeated faces that are pre-experimentally unknown.

Results from a study by Tanaka, Curran, Porterfield, and Collins (2006) suggest that N250/N250r components reflect two different aspects of face recognition – the acquired short-term familiarity of a face that is repeated in an experimental context, and the activation of long-term representations of known familiar faces. Tanaka et al. (2006) asked participants to identify a previously studied but otherwise unknown target face that could appear in a sequentially presented series of distractor faces. One of these distractors was the participants' own face, the others were unfamiliar faces. Target faces triggered a right-hemisphere dominant occipito-temporal N250 that was similar in terms of its latency and scalp distribution to the N250r component described by Schweinberger et al. (1995, 2004). However, this N250 to target faces only emerged in the second half of the experiment, suggesting that an episodic representation of a previously unfamiliar target face builds up gradually (see also Kaufmann, Schweinberger, & Burton, 2009, for links between the N250 and the acquisition of new face representations, and Krigolson, Pierce, Holroyd, & Tanaka, 2009, for evidence that the N250 also develops during the acquisition of perceptual expertise with non-face objects). In contrast, participants' own faces elicited an N250 component throughout the experiment, which presumably reflects their long-term familiarity. Interestingly, there was no difference in N170 components in response to participants' own faces and unfamiliar faces, which underlines the conclusion that the N170 is not sensitive to face recognition.

Taken together, these findings suggest that N250/N250r components are linked to early visual–perceptual stages of face recognition. These components may be generated when episodic memory traces in face-specific occipito-temporal cortex are activated by matching on-line perceptual face representations. If this interpretation was correct, N250 components should be observed not only in the context of face repetition paradigms, but also in experiments where ERPs elicited by well-known famous individuals and unfamiliar faces are directly compared. In two previous studies that used this procedure (Bentin & Deouell, 2000; Eimer, 2000a), consistent ERP modulations sensitive to the familiarity of faces were indeed obtained. Relative to unfamiliar faces, famous faces triggered an enhanced negativity that was maximal around 400 ms after stimulus onset (N400f). In contrast to the distinct lateral occipito-temporal focus of the N250/N250r component, this negativity to famous faces was much more broadly distributed, with a frontocentral maximum observed by Bentin and Deouell (2000), and a centroparietal maximum by Eimer (2000a). This

marked topographic difference suggests that the N250/N250r and N400f components reflect temporally and functionally separate processes. While the N250 is likely to reflect the activation of visual face memory in domain-specific ventral visual areas, the N400f is more plausibly associated with the subsequent activation of face-related episodic or semantic memory. This interpretation is supported by the fact that the semantic processing of linguistic material is associated with N400 components (e.g., Kutas & Hillyard, 1980). In addition, Bentin and Deouell (2000) and Eimer (2000a) found that the N400f was followed by an enhanced positivity to famous faces (P600f), which was again broadly distributed. The functional interpretation of this longer-latency component is not yet clear. It may reflect the generic reduction of uncertainty about facial identity that is associated with the explicit recognition of a particular individual, or could be linked more specifically to later stages of face recognition postulated by Bruce and Young (1986), such as the retrieval of a person's name.

In summary, ERP investigations of face recognition have not yet provided a clear picture of the links between face-specific ERP components and brain processes involved in recognizing and identifying familiar faces. For example, the question at what post-stimulus latency recognition-specific ERP components first emerge has not been conclusively answered. It seems clear that the N170 component is associated with perceptual stages of face processing that occur prior to the activation of identity-related information. However, evidence that face-specific occipito-temporal N250/N250r components are linked to face recognition has so far only been obtained in experiments that used face repetition paradigms, but not in studies that directly compared ERP responses to famous and unfamiliar faces. The interpretation of ERP differences that emerge from the contrast between repeated and non-repeated faces is complicated by the fact that these differences could reflect the activation of an episodic memory trace of a previously encountered face that is unrelated to its identity (a mere familiarity effect), or could be linked more directly to explicit face recognition, that is, to the activation of long-term representations of known faces.

The aim of the present experiment was to resolve these questions, and to provide new insights into the electrophysiological correlates of explicit face recognition. Participants were presented with a sequence of photographic images of famous and non-famous faces. Famous faces showed actors, politicians, musicians, sports personalities, and other celebrities well-known in the UK. These faces were selected from a larger sample because they were identified most consistently by participants in a pilot study. All faces were cropped and placed in oval frames (see Fig. 1). Famous and non-famous faces were matched with respect to their low-level visual properties. In contrast to previous studies that compared ERP components to famous and non-famous faces, where facial identity was either task-irrelevant (Bentin & Deouell, 2000, Exp. 1; Eimer, 2000a), or only relevant for a minority of target faces (politicians; Bentin & Deouell, 2000, Exp. 2 and 3), participants were instructed to categorise each individual face in terms of its identity on a four-point scale. Faces could be classified as definitely known, merely familiar, unfamiliar, or definitely unknown.

ERPs were computed for famous and non-famous faces, separately for each of the four response categories. One analysis contrasted ERPs to correctly classified famous faces (those judged to be definitely known or familiar) and correctly classified non-famous faces (those judged to be unfamiliar or unknown), in order to identify ERP correlates of face recognition. In line with earlier findings, the N170 component was expected to be unaffected by the difference between famous and non-famous faces. The critical question was whether famous faces would elicit an early N250 component with a distinct occipito-temporal distribution (as described by Schweinberger et al., 1995, 2004, and Tanaka et al., 2006, in

Famous faces

Non-famous faces

Fig. 1. Examples of famous faces (top) and non-famous faces (bottom) used in the present experiment. Matching famous and non-famous faces are shown in corresponding positions.

the context of face repetition procedures), or only later and more broadly distributed N400f and P600f components (as observed by Bentin & Deouell, 2000, and Eimer, 2000a). The presence of an N250 component to famous faces would provide new evidence for the rapid activation of long-term memory traces in ventral visual areas.

In previous face repetition experiments, it was difficult to distinguish ERP correlates of explicit face identification from effects associated with the identity-unspecific generic familiarity of repeated faces. To dissociate these two aspects of face recognition, a second analysis contrasted ERPs to famous faces that were explicitly recognized ("definitely known") and famous faces that were judged to be merely familiar. If the ERP differences between famous and non-famous faces identified in the first analysis were primarily driven by the explicit recognition of individual faces, similar effects should emerge in the contrast between ERPs to known as compared to just familiar famous faces. In contrast, if these differences reflected mere familiarity rather than explicit recognition, there should be no systematic differences between ERPs to known and just familiar famous faces. A final analysis contrasted ERPs to correctly classified non-famous faces and to famous faces that were incorrectly categorised as unfamiliar or unknown. This analysis was included to reveal possible ERP evidence for covert face recognition. An N250r to repeated famous faces has been observed when a competing high-load perceptual task was present during face encoding (e.g., Neumann & Schweinberger, 2008), that is, under conditions that have previously been linked to covert processing of facial identity (Jenkins, Burton, & Ellis, 2002). Covert face recognition also remains a controversial issue in the study of prosopagnosia (see Schweinberger & Burton, 2003), which makes it important to determine whether electrophysiological evidence for covert recognition might even be present in neurologically and functionally unimpaired participants.

2. Methods

2.1. Participants

Nineteen paid volunteers were tested, and informed consent was obtained from all of them. Three participants were excluded from analyses due to an insufficient number of trials after EEG artefact rejection. The remaining 16 participants (8 males; aged 21–37 years; mean age 27.3 years) had normal or corrected-to-normal vision. Fifteen were right-handed, one was left-handed.

2.2. Stimuli and procedure

Stimuli were presented on a CRT monitor at a viewing distance of 100 cm. E-Prime software (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation and behavioural response collection. The stimulus set contained 80 famous and 80 non-famous faces. The famous faces were selected from a larger sample of 129 faces. This selection was based on the results of a pilot experiment where each face was shown for 400 ms, and eight participants had to identify each face by naming the person and stating their profession. The 80 famous faces selected for inclusion in the main experiment were those faces that were explicitly identified by at least six of the eight pilot participants. They were celebrities widely known to the general public in the UK, and included actors/actresses, politicians, chefs, comedians, entrepreneurs, models, members of the royal family, sports personalities, and musicians. For each of the 80 famous faces, one non-famous face was selected from a larger sample to provide a match in terms of gender, approximate age, facial expression and low level visual attributes such as contrast and brightness (see Fig. 1 for examples of famous and matched non-famous faces). All face stimuli were converted to greyscale, resized, and cropped into an oval shape, thereby removing their outer contours. These image transformations were performed in Adobe Photoshop CS3. All face stimuli were presented at fixation in a full front view, with eye gaze straight ahead, against a light grey background (17.6 cd/m^2). They subtended a visual angle of 7.4° × 4.9°, and their average luminance was 21.9 cd/m^2.

The experiment consisted of eight blocks of 80 trials per block. In all blocks, famous and non-famous faces were presented with equal probability and in random order, so that each individual famous and non-famous face was shown four times throughout the experiment. Each face was presented at fixation for 400 ms, followed by a blank interstimulus interval of 1300 ms. Participants' task was to report on each trial whether they recognized a particular face by choosing one of four alternatives (definitely known – seems familiar – seems unfamiliar – definitely unknown). Response alternatives were mapped to four horizontally arranged response keys.

Participants were instructed to classify a face as definitely known only if they knew the person's name and profession, and to use the 'seems familiar' category if they felt that a particular face was familiar without being able to name the person or state their profession. Each response key was labelled with its response category, and was mapped to the index and middle fingers of the left and right hand. The assignment of keys and response categories was kept constant across all participants. A training block containing 20 different famous faces and 20 different non-famous faces was delivered prior to the first experimental block.

2.3. EEG recording and data analysis

EEG was DC-recorded with a BrainAmps DC amplifier (upper cut-off frequency 40 Hz, 500 Hz sampling rate) and Ag–AgCl electrodes mounted on an elastic cap from 23 scalp sites (Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO8, and Oz, according to the extended international 10–20 system). Horizontal electrooculogram (HEOG) was recorded bipolarly from the outer canthi of both eyes. An electrode placed on the left earlobe served as reference for online recording, and EEG was re-referenced off-line to the average of the left and right earlobe. Electrode impedances were kept below 5 kΩ. No additional off-line filters were applied. EEG was epoched offline from 100 ms before to 700 ms after stimulus onset. Epochs with activity exceeding ±30 μV in the HEOG channel (reflecting horizontal eye movements) or ±60 μV at Fpz (indicating eye blinks or vertical eye movements) were excluded from analysis, as were epochs with voltages exceeding ±80 μV at any other electrode.

Following artefact rejection, EEG waveforms were averaged for all combinations of face type (famous versus non-famous) and response category (known, familiar, unfamiliar, unknown), relative to a 100 ms pre-stimulus baseline. N170 amplitude was quantified as ERP mean amplitude obtained at lateral occipito-temporal electrodes P7/P8 in the 160–200 ms time interval after stimulus onset. N250 amplitude was measured as mean amplitudes in a 230–400 ms post-stimulus time window, for lateral posterior electrode pairs P7/8 and PO7/8. P600f mean amplitudes were measured during the subsequent 400–700 ms time window, at midline electrodes (Fz, Cz, Pz), and at lateral electrode pairs (F3/4, FC5/6, C3/4, P3/4). ERP mean amplitudes were also quantified during the 230–400 ms interval for the same midline and lateral electrodes. Repeated measures analyses of variance (ANOVAs) were performed on these mean amplitude values. Three sets of ERP analyses were conducted. The first set compared ERPs to correctly categorised famous faces (faces that were classified as known or familiar) and ERPs to non-famous faces that were correctly categorised as unfamiliar or unknown. The second set compared ERPs to famous faces as a function of whether they were classified as definitely known or merely familiar. 'Familiar' responses to famous faces were relatively infrequent (see Table 1). After artefact rejection, four participants retained ten trials or less where famous faces were judged as familiar. These were excluded from this set of analyses, which therefore only included data from the remaining twelve participants. The third set of analyses compared ERPs to famous and non-famous faces obtained in trials where they were both categorised as unfamiliar or unknown. For all analyses, Greenhouse–Geisser corrections to the degrees of freedom were performed where appropriate.

3. Results

3.1. Behavioural results

Table 1 shows the frequency with which participants chose one of the four alternative response categories, separately for famous and non-famous faces. Overall, face recognition performance was good, with more than 70% of all famous faces classified as definitely known, and nearly 75% of all non-famous faces categorised as unfamiliar or definitely not known, resulting in an overall d' value for the discrimination between famous and non-famous faces of 1.67. To test whether individual non-famous faces were more likely to be judged as known or familiar when they had been encountered before, accuracy data were quantified separately for the first to fourth presentation of each face. Ordinal position did not affect the probability of known or familiar classifications for non-famous faces ($F < 1$).

Table 1
Mean frequency (in percent) of each of the four alternative classification judgements in response to famous or non-famous faces.

	Definitely known	Familiar	Unfamiliar	Definitely unknown
Famous	71.77	9.80	9.08	9.32
Non-famous	12.54	12.91	38.57	35.96

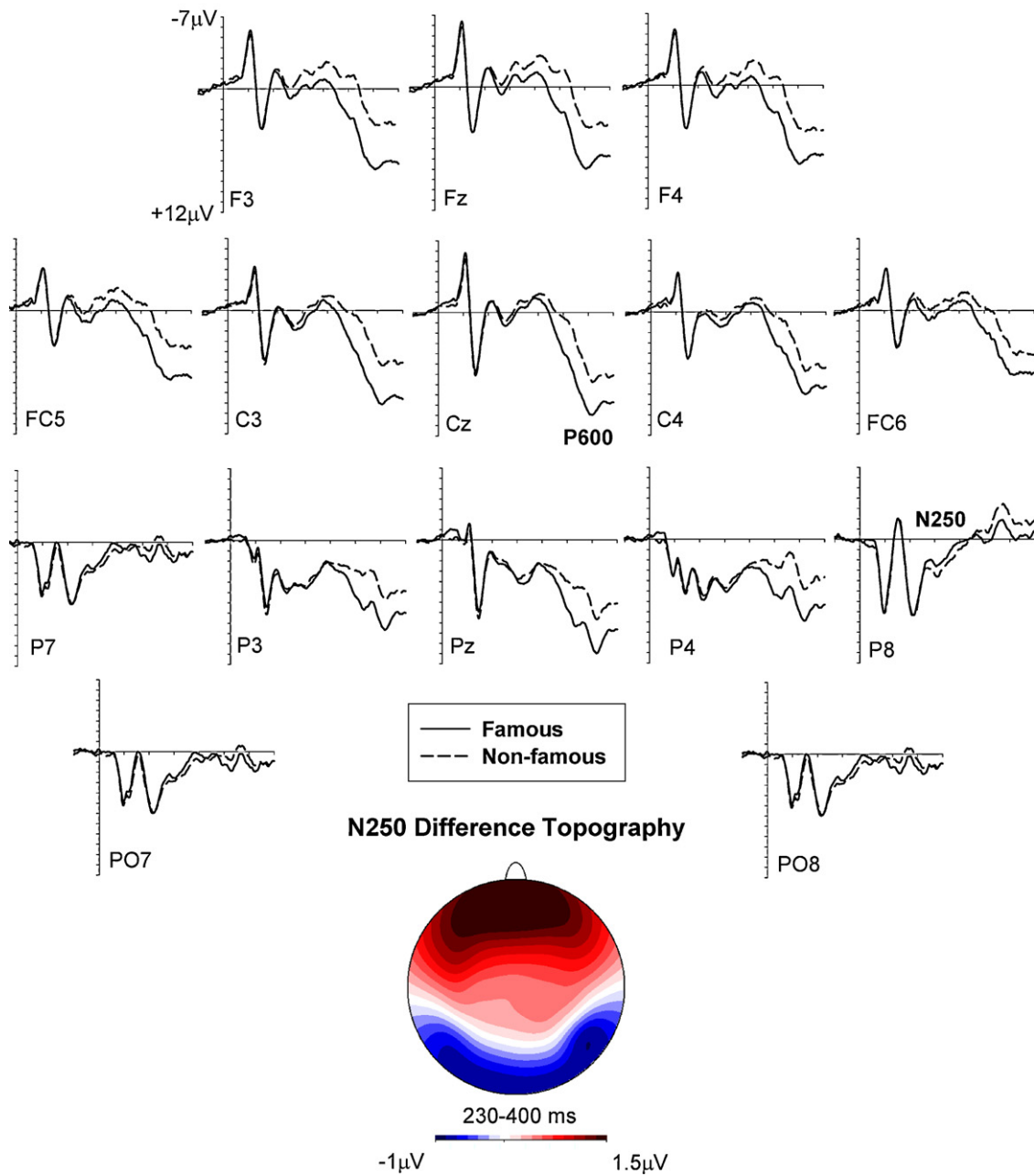## ERPs to correctly classified famous and non-famous faces

Fig. 2. Grand-averaged ERPs based on sixteen participants, obtained in the 700 ms interval after stimulus onset (relative to a 100 ms pre-stimulus baseline) in response to famous faces classified as definitely known or familiar (solid lines) and non-famous faces classified as unfamiliar or unknown (dashed lines). The topographic map was constructed by spherical spline interpolation (see Perrin, Pernier, Bertrand, & Echallier, 1989) and shows difference amplitudes obtained during the N250 time interval (230–400 ms post-stimulus) by subtracting ERP mean amplitudes in response to non-famous faces from mean amplitudes to famous faces. Enhanced negative amplitudes for famous faces are shown in blue, an enhanced positivity in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

Mean RT across all face and response categories was 912 ms. Participants were faster to respond to famous than non-famous faces (889 ms versus 936 ms; $t(15) = 3.23$; $p < .01$). The classification of famous faces as definitely known was faster (742 ms) than their categorisation as familiar, unfamiliar or definitely unknown (1011 ms, 943 ms, and 859 ms, respectively; all $t(15) > 3.7$; all $p < .02$). For non-famous faces, responses were faster when they were classified as definitely known or definitely unknown (866 ms for either category) relative to trials were they were judged to be familiar or unfamiliar (1040 and 972 ms; all $t(15) > 4.3$; all $p < .001$).

3.2. ERP results

3.2.1. ERPs to correctly classified famous and non-famous faces

Fig. 2 shows ERPs triggered in response to famous faces (collapsed across faces classified as definitely known or as merely familiar) and ERPs to non-famous faces that were classified as unfamiliar or unknown. As expected, there was no familiarity-related modulation of the N170 component. Differential ERP modulations linked to facial identity started approximately 230 ms after stimulus onset. At lateral occipito-temporal electrodes, an enhanced

negativity for famous as compared to unfamiliar faces (N250) was observed. At anterior electrodes, an enhanced positivity for famous faces started at approximately the same time. This positivity emerged later (around 400 ms post-stimulus) at more posterior electrode sites and remained present in a broadly distributed fashion throughout the 700 ms post-stimulus analysis window (P600f). The topographic map of ERP difference amplitudes triggered by famous versus non-famous faces in the N250 time window (Fig. 2, bottom) shows the presence of a lateral occipito-temporal negativity to famous faces (N250) that was accompanied by an enhanced positivity at frontocentral electrodes.

N170 component. There was no effect of face type (famous versus non-famous face) on N170 mean amplitude obtained in the 160–200 ms post-stimulus time window at P7/8, $F(1,15) < 1$, and no interaction between face type and hemisphere, $F(1,15) < 2.2$, demonstrating that the N170 component was not affected by face recognition.

N250 component. A significant effect of face type was obtained in the N250 time interval (230–400 ms post-stimulus) at occipito-temporal electrodes, $F(1,15) = 6.4$; $p < .03$, confirming the presence of an N250 component to famous faces. A three-way interaction (face type × electrode site × hemisphere; $F(1,15) = 7.7$; $p < .02$) was observed. Separate follow-up analyses confirmed a reliable main effect of face type at P7/8, $F(1,15) = 9.6$; $p < .01$. This effect was almost significant at PO7/8, $F(1,15) = 4.1$; $p < .07$. There were no reliable interactions between face type and hemisphere at either electrode pair.

Early anterior positivity. As can be seen in Fig. 2, the enhanced positivity for famous as compared to non-famous faces emerged early at anterior, but not at more posterior electrodes. Significant face type × electrode site interactions were observed in the N250 time window (230–400 ms post-stimulus) at midline electrodes Fz, Cz, and Pz, $F(2,30) = 6.2$; $p < .02$; $\varepsilon = .698$, as well as at lateral electrode pairs, $F(3,45) = 9.9$; $p < .001$; $\varepsilon = .552$. Follow-up analyses revealed significant main effects of face type at frontocentral electrodes Fz, FC3/4, and FC5/6, all $F(1,15) > 7.1$; all $p < .02$, reflecting an enhanced positivity for famous faces at these anterior electrodes during the N250 time window. No reliable effects of face type were present at this time at more posterior electrodes (Cz, Pz, C3/4, P3/4).

P600f component. During the P600f time window (400–700 ms post-stimulus), highly significant main effects of face type were present at midline electrodes, $F(1,15) = 40.1$; $p < .001$, and at lateral electrode pairs, $F(1,15) = 44.6$; $p < .001$, reflecting a broadly distributed enhanced positivity for famous as compared to non-famous faces. This effect was also reliably present at occipito-temporal electrodes in the P600f time interval, $F(1,15) = 4.7$; $p < .05$. Interestingly, the P600f component was larger over the left than over the right hemisphere, and this was confirmed by a reliable face type × hemisphere interaction at lateral electrode pairs, $F(1,15) = 5.1$; $p < .04$. The same interaction approached significance at occipito-temporal electrodes, $F(1,15) = 3.3$; $p < .09$.

3.2.2. ERPs to famous faces classified as definitely known or just familiar

The ERP data to correctly classified famous faces shown in Fig. 2 include trials where these faces were classified as definitely known as well as trials where they just seemed familiar. It is therefore not possible to determine on the basis of these data whether the N250 and P600f components elicited in response to famous faces are linked to explicit recognition or to a more unspecific impression of familiarity. Fig. 3 shows ERP mean amplitude values obtained during the N250 and P600f time windows at electrodes P8 and Cz, respectively, for famous faces classified as known, famous faces classified as merely familiar, and correctly classified non-famous faces. Mean amplitudes to known famous faces were more negative
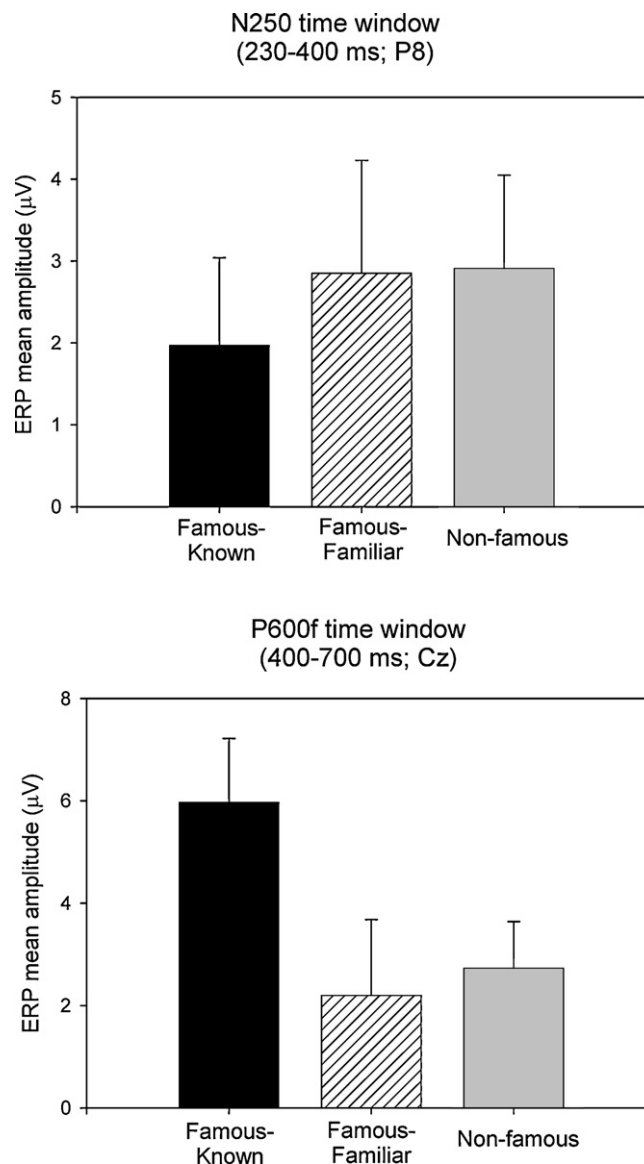

Fig. 3. ERP mean amplitude values (based on sixteen participants) obtained in the N250 and P600f time windows in response to famous faces that were classified as known, famous faces that were classified as familiar, and correctly classified non-famous faces. Error bars represent standard errors of the mean.

in the N250 time range, and more positive in the P600 time range than amplitudes to merely familiar famous faces and non-famous faces, which were very similar in size. These observations strongly suggest that N250 and P600f components are primarily linked to explicit face recognition, and not just to face familiarity.

To obtain formal statistical support for this conclusion, ERPs elicited by famous faces classified as definitely known or as merely familiar were computed for those twelve participants who had a sufficient number of trials on which famous faces were judged as merely familiar. These ERPs are shown in Fig. 4, and analyses were restricted to these twelve participants. There were systematic ERP differences for known versus merely familiar famous faces, and these differences resembled the differences observed when contrasting ERPs to correctly categorised famous and non-famous faces that were obtained for all sixteen participants (Fig. 2).

N170 component. There was no main effect of response category (known versus just familiar), $F(1,11) < 1$, and no response category × hemisphere interaction, $F(1,11) < 2$, for N170 mean amplitudes at P7/8, demonstrating that the N170 component was

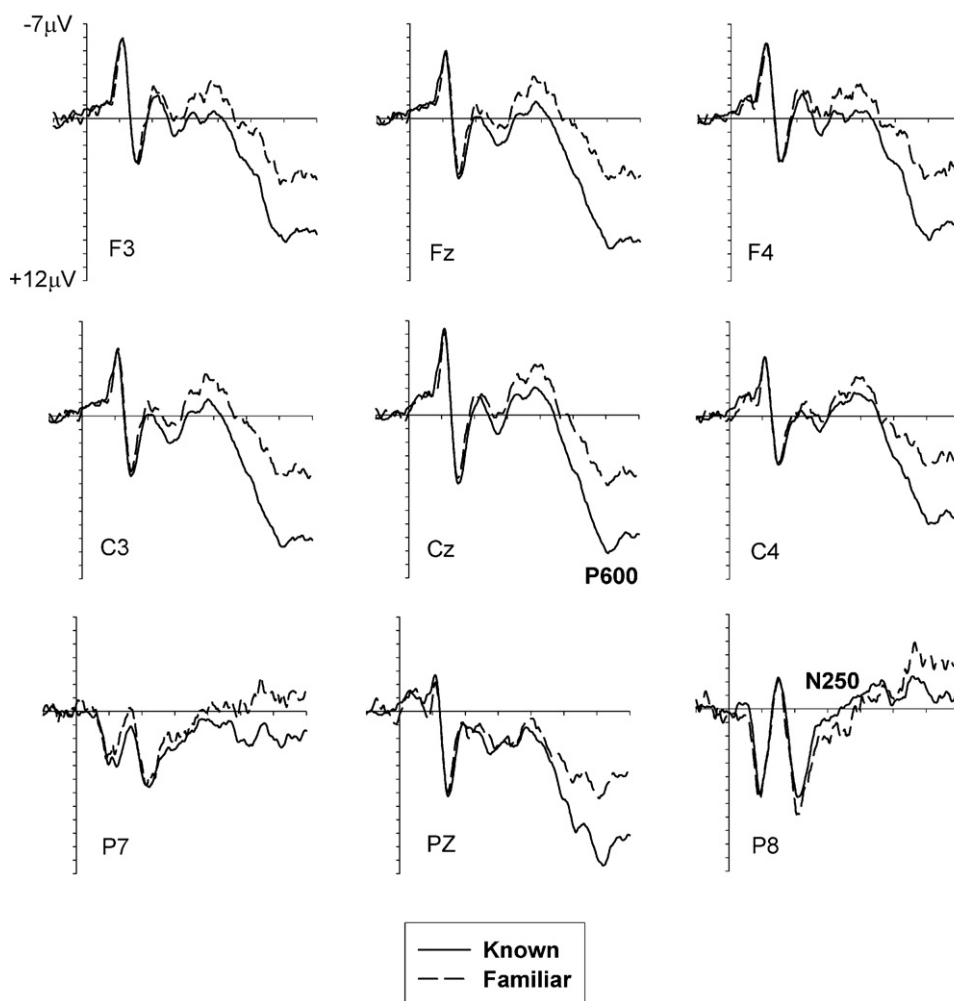## ERPs to famous faces classified as known or just familiar

Fig. 4. Grand-averaged ERPs elicited in the 700 ms interval after stimulus onset in response to famous faces that were classified as definitely known (solid lines) or were judged to be merely familiar (dashed lines). These ERPs include data from those twelve participants with a sufficient number of trials where famous faces were classified as familiar.

unaffected by the difference between known and just familiar famous faces.

N250 component. During the N250 time window (230–400 ms post-stimulus), a highly significant response category × hemisphere interaction was present at occipito-temporal electrodes, $F(1,11) = 23.0$; $p < .001$. Follow-up analyses revealed a reliable N250 component to definitely known as compared to merely familiar famous faces at right-hemisphere site P8, $F(1,11) = 5.9$; $p < .04$. The N250 was not significant at PO8, $F(1,11) = 2.4$; $p = .15$, and there were no effects of response category at left-hemisphere electrodes P7 and PO7, both $F(1,11) < 1$.[1]

Early anterior positivity. Analogous to the pattern of results observed for famous versus non-famous faces, an early enhanced positivity was triggered by explicitly recognized famous faces as compared to famous faces that only appeared to be familiar at anterior, but not at more posterior electrodes (Fig. 4). This was reflected by response category × electrode site interactions observed in the 230–400 ms post-stimulus interval at midline electrode sites, $F(2,22) = 5.8$; $p < .02$, $\varepsilon = .798$, and at lateral electrode pairs, $F(3,33) = 4.8$; $p < .04$, $\varepsilon = .448$. Follow-up analyses found a reliably enhanced positivity for known as compared to merely familiar famous faces within this time window at Fz, F3/4, and FC5/6, all $F(1,11) > 7.5$; all $p < .02$, but not at more posterior sites (Cz, Pz, C3/4, P3/4).

P600f. In the P600f time window (400–700 ms post-stimulus), significant effects of response category were observed at midline electrodes, $F(1,11) = 14.4$; $p < .01$, as well as at lateral sites,

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[1] As famous faces were much more often classified as definitely known than as just familiar (see Table 1), ERPs to definitely known famous faces were based on many more trials than ERPs to familiar famous faces, resulting in a higher signal-to-noise ratio for the former ERPs. As differences in noise levels between the two conditions could have been responsible for the presence of an N250 to known as compared to merely familiar famous faces, an additional analysis was conducted. ERPs to known famous faces were now based on a randomly drawn sub-sample of all trials, with the number of trials included identical to the number of trials used to compute ERPs to merely familiar famous faces for each participant. Results obtained for the N250 time window (230–400 ms post-stimulus) were very similar to the results obtained in the original analysis, thus confirming that these were not an artefact of unequal signal-

to-noise ratios. There was a significant response category × hemisphere interaction, $F(1,11) = 13.3$; $p < .01$, and follow-up analyses revealed a reliable N250 component to definitely known as compared to merely familiar famous faces at P8 as well as at PO8, both $F(1,11) > 9.9$; both $p < .01$, but not at left-hemisphere electrodes P7 and PO7, both $F(1,11) < 1$.

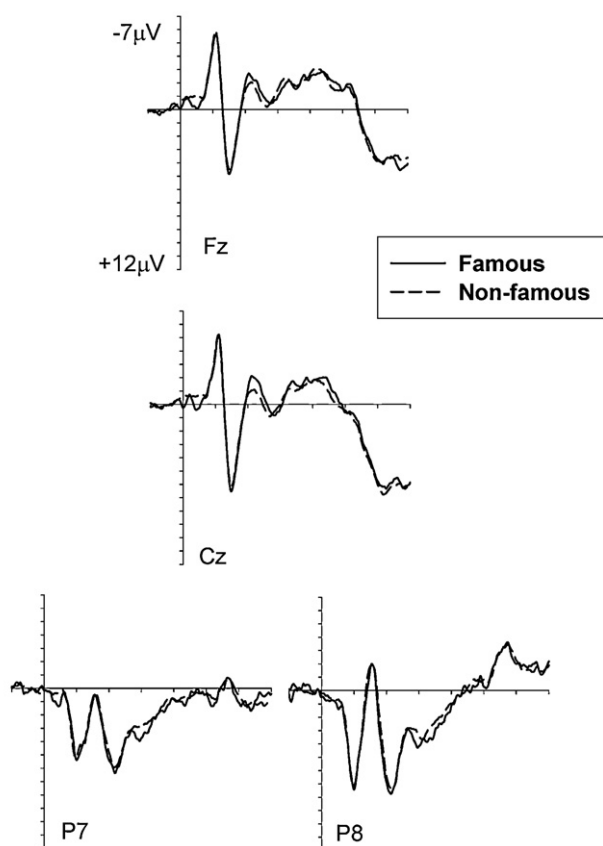## ERPs to famous and non-famous faces classified as unfamiliar/unknown

Fig. 5. Grand-averaged ERPs elicited in the 700 ms interval after stimulus onset in response to famous faces reported to be unfamiliar or unknown (solid lines) and correctly classified non-famous faces (dashed lines).

$F(1,11) = 8.9$; $p < .02$, reflecting a broadly distributed P600f component to definitely known famous faces. This effect approached significance at occipito-temporal electrodes, $F(1,11) = 3.9$; $p < .08$. Interestingly, the P600f component was again larger over the left hemisphere (see Fig. 4), and this was confirmed by response category × hemisphere interactions for lateral electrodes, $F(1,11) = 11.7$; $p < .01$, as well as for occipito-temporal electrode pairs, $F(1,11) = 6.6$; $p < .03$.

3.2.3. ERPs to non-recognized famous and non-famous faces

Fig. 5 compares ERPs to non-famous faces correctly categorised as unfamiliar or unknown and ERPs to famous faces that were not recognized but reported to be unfamiliar/unknown. Covert recognition of at least some of these faces should be mirrored by ERP differences between famous and non-famous faces that are similar to those seen in Figs. 2 and 4. As is evident from Fig. 4, no such differential ERP modulations were elicited at all. This was confirmed by statistical analyses that found no reliable effects of face type (famous versus non-famous) or interactions involving this factor for any analysis window.

4. Discussion

The aim of this study was to obtain new insights into the time course of face recognition and its electrophysiological correlates. ERPs triggered by faces of famous individuals were compared to ERPs to non-famous control faces in a task that required explicit judgements about facial identity. One question was which face-

specific components would be sensitive to face recognition, and when the earliest recognition-specific ERP modulations would emerge. A second question was whether differential ERP responses to famous as compared to non-famous faces are directly linked to the explicit recognition of individual famous faces, or merely reflect the generic familiarity of faces regardless of whether they are successfully identified.

As predicted on the basis of previous findings (Bentin & Deouell, 2000; Eimer, 2000a), the face-sensitive N170 component was insensitive to the difference between famous and non-famous faces (Fig. 2). There was also no differential N170 modulation in response to known versus merely familiar famous faces (Fig. 4). This is fully in line with the hypothesis that the N170 component is linked to pre-categorical perceptual stages of face processing, such as the structural encoding of facial features and the generation of configural and/or holistic face representations (e.g., Eimer, 2000b; Sagiv & Bentin, 2001; see also Eimer et al., 2010; Eimer, Gosling, Nicholas, & Kiss, 2011, for recent studies of the response profile of the N170 using rapid neural adaptation procedures).

While N170 amplitudes did not distinguish between famous and non-famous faces, the subsequent N250 component was sensitive to face recognition. A reliably enhanced negativity was elicited at lateral occipito-temporal electrodes in the N250 time interval (230–400 ms after stimulus onset) by correctly classified famous faces relative to non-famous faces that were judged to be unfamiliar or unknown. This difference was maximal at electrodes P7/P8, which are typically located close to posterior regions of the inferior temporal gyrus. As illustrated by difference topography shown in Fig. 2, the scalp distribution of the N250 component triggered in the present study by famous faces is very similar to the topography of N250/N250r components observed in previous studies (e.g., Schweinberger et al., 2004; Tanaka et al., 2006), which strongly suggests that they represent functionally and anatomically similar brain processes. The occipito-temporal focus of the N250 to famous faces is very much in line with the hypothesis that this component is associated with an activation of long-term memory traces in face-specific areas of ventral visual cortex that is triggered by their match with perceptual representations of famous faces. In other words, the N250 component is likely to reflect an early visual–perceptual stage of face recognition where on-line visual information is brought into contact with stored representations of visual features of known faces. A successful match between on-line and stored face representations will in turn activate subsequent modality-unspecific aspects of face recognition, such as the retrieval of semantic or episodic information about a specific individual (e.g., Bruce & Young, 1986).

In previous studies of face recognition that contrasted ERPs to famous and non-famous faces (Bentin & Deouell, 2000; Eimer, 2000a), the earliest identity-specific ERP modulations started substantially later (about 300–350 ms after stimulus onset). The N400f component observed in these experiments was broadly distributed, without clear evidence for a posterior occipito-temporal focus that was prominent for the N250 component observed in the present study. These topographic and latency differences strongly suggest that in contrast to the N250, the N400f component is not linked to visual–perceptual stages of face recognition, but is instead associated with the later activation of semantic or episodic memory. Why did electrophysiological correlates of face recognition emerge early and over face-specific visual areas in the present study, but not in previous studies that compared ERPs to famous and non-famous faces? This difference may be linked to the task-relevance of explicit face recognition and identification. In the present study, participants had to make speeded judgements with respect to the identity of a specific face on each trial, which required them to rapidly and efficiently match currently seen faces with stored representations of known faces. In previous ERP studies, the identity of specific faces

was either completely task-irrelevant (Bentin & Deouell, 2000, Exp. 1; Eimer, 2000a), or only relevant on infrequent target trials (Bentin & Deouell, 2000, Exp. 2 and Exp. 3). It is possible that reliable early ERP correlates of perceptual matches between on-line visual and mnemonic face representations are only triggered when task conditions place high demands on face recognition. A related issue concerns the absence of a distinct N400f component to famous faces in the present experiment. In the Bentin and Deouell (2000) and Eimer (2000a) studies, full face images that included external features were used, whereas the faces used in this experiment did not contain external features (Fig. 1). This difference may have delayed identity-sensitive processes that are reflected by the N400f component, resulting in an overlap between the N400f and the subsequent P600f component (see Henson et al., 2003, for an analogous argument).

In addition to the N250 component over lateral occipito-temporal areas, the contrast of ERPs to correctly classified famous and non-famous faces also revealed a more broadly distributed enhanced positivity for famous faces. Similar effects have been observed in previous ERP studies (Bentin & Deouell, 2000; Eimer, 2000a) at longer post-stimulus latencies ('P600f'), and also in intracranial recordings from electrodes in the hippocampus (Barbeau et al., 2008; Dietl et al., 2005). However, an enhanced positivity for famous faces emerged much earlier in the present study. As shown by the topographic map in Fig. 2, this positivity started at anterior (but not at more posterior) electrodes in the same time window as the occipito-temporal N250 component. It is likely that the anterior positivity for famous faces that was triggered simultaneously with the lateral posterior N250 is not an independent phenomenon, but does in fact reflect the positive counterpart of the N250. Previous face repetition studies (e.g., Schweinberger et al., 2004) have demonstrated that the occipito-temporally enhanced negativity to repeated faces (N250r) is accompanied by a frontocentral positivity in the same latency range. This dipolar scalp topography is consistent with an underlying neural generator of the N250r in face-specific regions of fusiform gyrus (Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002).

The presence of an N250 component to famous as compared to non-famous faces demonstrates that ERP evidence for the rapid activation of memory traces in face-specific visual areas that has so far only been observed in face repetition studies (e.g., Schweinberger et al., 1995, 2004) can also be found in the context of standard face recognition experiments where observers are presented with previously known and unfamiliar faces. The latency of this N250 effect is in line with results from intracranial EEG recordings (Barbeau et al., 2008), where the earliest differential responses to famous as compared to unknown faces in medial temporal areas also emerged around 240 ms after stimulus onset. Previous N250/N250r research has not resolved the question whether these components mark an early stage of face recognition that ultimately results in the identification of a known individual, or whether they are associated with a more unspecific registration of face familiarity that is not necessarily followed by face identification. In fact, previous results from Tanaka et al. (2006) suggest that the N250 component can reflect the activation of short-term memory traces of a particular unknown face that has been encountered before in the same experiment (i.e., mere familiarity without identification), but also the activation of long-term representations of a previously known face (in their experiment, the participant's own face).

In order to ascertain that the ERP differences between famous and non-famous faces observed in the present study are associated with the explicit recognition of famous faces, rather than with a more unspecific impression of familiarity, ERPs triggered by famous faces were compared as a function of whether these faces were classified as definitely known or as merely familiar (Fig. 4). This comparison yielded a pattern of ERP differences in the N250 time

range that was analogous to the differential pattern observed for correctly categorised famous versus non-famous faces (Fig. 2). Relative to famous faces judged to be merely familiar, known famous faces triggered a reliably enhanced negativity over right occipito-temporal cortex that was accompanied by an enhanced anterior positivity. This strongly suggests that these ERP effects were driven by the explicit recognition of famous faces, and not just by their generic familiarity. The N250 component may be linked to the activation of visual–perceptual traces of previously encountered faces in long-term memory that ultimately results in the identification of a particular individual. In addition, the presence of an enhanced early anterior positivity for known as compared to merely familiar famous faces in the N250 time range would be expected if this anterior positivity and the posterior N250 reflected the same underlying neural generator processes, and if the N250 component was driven by processes that result in the explicit recognition of famous faces. More generally, these findings demonstrate that the successful recognition of famous faces can be predicted on the basis of differential ERP modulations over face-specific visual cortex that emerge within 230 ms after stimulus onset.

The conclusion that the N250 component is linked to explicit face recognition may seem inconsistent with previous observations that the N250r to repeated famous faces is preserved when the perceptual load of a competing task is high (Neumann & Schweinberger, 2008), as high perceptual load during face encoding impairs subsequent explicit recognition memory (Jenkins et al., 2002). One possibility that could be investigated in future research is that such load manipulations affect not so much the on-line recognition of famous faces, but instead their retention in episodic long-term memory.

During the 400–700 ms time window, a broadly distributed enhanced positivity for famous as compared to non-famous faces (P600f) was present, in line with previous results (Bentin & Deouell, 2000; Eimer, 2000a). The new finding of the current study was that similar to the N250 component, this longer-latency positivity for famous faces was associated not with mere familiarity, but with explicit face identification. This was demonstrated by the fact that very similar P600f components were observed when comparing ERPs to famous and non-famous faces and when contrasting ERPs to definitely known versus merely familiar famous faces. Another potentially interesting new observation concerns the laterality of this effect. Although P600f components were present over both hemispheres, they were reliably larger over the left side. The fact that this left-hemisphere advantage emerged when comparing ERPs to famous and non-famous faces, as well as in the contrast between known and merely familiar famous faces, underlines the reliability of this asymmetry. The left-hemisphere bias of the P600f might point to links between this component and verbal processing, that is, the retrieval and activation of the names of known individual faces. As the famous faces used in the present study were those of individuals whose names feature prominently in the public domain, associations between their faces and names should have been easily accessible, and may even have been activated automatically. The suggestion that the P600f component may be linked to name generation, which is identified as a separate component process in the face processing model of Bruce and Young (1986), must remain speculative at present, but could be tested in future experiments.

The final analysis contrasted ERPs to famous and non-famous faces on trials were both were judged to be unfamiliar or unknown, in order to uncover potential ERP correlates of covert face recognition. As is obvious from Fig. 4, these two sets of ERP waveforms were virtually identical, which indicates that there were no cortical processing differences between famous and non-famous faces when participants did not recognize a particular face as known or familiar. In other words, participants' face recognition judge-

ments were valid, and did not conceal any residual uncertainty with respect to the status of specific famous faces. It should be interesting to contrast this result with findings obtained under similar circumstances with acquired or developmental prosopagnosics, as the question whether covert face recognition is an important feature in prosopagnosia remains controversial (see Schweinberger & Burton, 2003).

In summary, the present study has uncovered new evidence for links between the explicit recognition of famous faces and face-specific ERP components. Even though the face-selective N170 component is not sensitive to the difference between famous and non-famous faces, the subsequent N250 component that is triggered over occipito-temporal areas within 230 ms after stimulus onset has emerged as a reliable marker of early perceptual stages of face recognition. This component may reflect the activation of stored long-term representations of previously known faces in ventral visual face processing areas that is triggered when they match on-line perceptual representations of a famous face. The N250 does not just reflect an unspecific registration of face familiarity, but is directly linked to processes that lead to the explicit identification of a particular face.

Acknowledgements

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