

STRUCTURAL ENCODING AND IDENTIFICATION IN FACE PROCESSING: ERP EVIDENCE FOR SEPARATE MECHANISMS

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The present study had two aims. The first aim was to explore the possible top-down effect of face-recognition and/or face-identification processes on the formation of structural representation of faces, as indexed by the N170 ERP component. The second aim was to examine possible ERP manifestations of face identification processes as an initial step for assessing their time course and functional neuroanatomy. Identical N170 potentials were elicited by famous and unfamiliar faces in Experiment 1, when both were irrelevant to the task, suggesting that face familiarity does not affect structural encoding processes. Small but significant differences were observed, however, during later-occurring epochs of the ERPs. In Experiment 2 the participants were instructed to count occasionally occurring portraits of famous politicians while rejecting faces of famous people who were not politicians and faces of unfamiliar people. Although an attempt to identify each face was required, no differences were found in the N170 elicited by faces of unfamiliar people and faces of familiar non-politicians. Famous faces, however, elicited a negative potential that was significantly larger than that elicited by unfamiliar faces between about 250 and 500msec from stimulus onset. This negative component was tentatively identified as an N400 analogue elicited by faces. Both the absence of an effect of familiarity on the N170 and the familiarity face-N400 effect were replicated in Experiment 3, in which the participants made speeded button-press responses in each trial, distinguishing among faces of politicians and faces of famous and unfamiliar non-politicians. In addition, ERP components later than the N400 were found to be associated with the speed of the response but not with face familiarity. We concluded that (1) although reflected by the N170, the structural encoding mechanism is not influenced by the face recognition and identification processes, and (2) the negative component modulated by face familiarity is associated with the semantic activity involved in the identification of familiar faces.

INTRODUCTION

Face recognition is an outstanding human visual ability. Despite the within-race overall physical similarity among faces, slight changes are sufficient to allow quick and unequivocal identification of a familiar face among tens and even hundreds of unfamiliar faces. Since this ability is not matched by

the ability to identify other visual stimuli that are similarly complex and even more frequently encountered, it has been suggested that face recognition is achieved by a special-purpose mechanism that probably uses different processing strategies than those used for the visual identification of most other objects or animals (e.g. Tanaka & Farah, 1993; see also Farah, 1990). Empirical evidence

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supporting this hypothesis was obtained in studies of monkeys and humans. In monkeys, single-unit recordings have revealed cells in the inferotemporal cortex that respond to monkey and human faces (Bruce, Desimone, & Gross, 1981; Desimone, 1991; Desimone, Albright, Gross, & Bruce, 1984; Perrett, Mistlin, & Chitty, 1987; Perrett et al., 1982; Young & Yamane, 1992) and face components (Perrett, Rolls, & Caan, 1982), but not to other complex stimuli such as snakes, spiders, or food (Baylis, Rolls, & Leonard, 1985; Desimone et al., 1984; Rolls & Baylis, 1986; Saito et al., 1986). In humans, the specificity of the face perception mechanism is suggested, for example, by the double dissociation between visual agnostic patients who cannot recognise objects while their ability to recognise faces is spared (e.g. Moscovitch, Behrmann, & Winocur, 1997) and prosopagnostic patients who cannot recognise familiar faces although they are able to identify other objects (Bentin, Deouell, & Soroker, 1999; for a recent review see De Renzi, 1997). In many cases, however, the impairment of the prosopagnostic patients was confined to the *identification* of faces (i.e. associating between a face and a person) whereas their ability to distinguish between faces and other visual stimuli and, in some cases, even to match between faces of the same individual seen from different angle, was significantly better or even intact (Benton & Van Allen, 1972; Malone, Morris, Kay, & Levin, 1982)¹. This pattern led to a further dissociation between a specific visual mechanism responsible for the structural encoding of faces, and a "higher level" mechanism responsible for associating the structural representation of a face with semantic information about the person to whom

the face belongs (e.g. Benton, 1980). A model for face recognition in which such a distinction is explicit was suggested by Bruce and Young (1986). According to this model an abstract tridimensional structural representation of the face is initially constructed by a face-specific visual encoding process. This structural representation is compared with a set of face recognition units; if a positive match results, the person's identity nodes are activated in semantic memory. A recent study of brain event-related potentials (ERPs) provided tentative support for the specificity of a structural encoding mechanism for faces (Bentin, Allison, Perez, Puce, & McCarthy, 1996; cf. George, Evans, Fiori, Davidoff, & Renault, 1996; Jeffreys, 1993)².

Recording ERPs from the scalp of normal subjects, Bentin et al. (1996) found a negative potential peaking at about 170msec from stimulus onset (N170), which responded preferentially to human faces and isolated human eyes, but not to human hands, animal faces³, items of furniture, cars, or nonsense stimuli preserving the illumination level of the faces. The N170 was distributed over a relatively circumscribed region at the posterior-inferior aspects of the temporal lobes, and was greater at right than at left hemisphere sites. Extensive investigations aimed at unveiling the stimulus-related characteristics of the N170 showed that it is not significantly affected by altering the spatial organisation of the inner components or by face inversion (Bentin et al., 1996; Bentin, & McCarthy, 1999), manipulations that are known to hamper the identification of faces. On the basis of these characteristics, Bentin et al. (1996) suggested that the N170 is probably associated with a face-specific structural encoding mechanism that might not be

¹ In fact, such considerations have led some authors to suggest that prosopagnosia is not a face-specific syndrome but a mild form of visual agnosia (Humphreys & Riddoch, 1987), or that the basic deficit of these patients involves the identification of an exemplar within a semantic category whose members are very similar (Damasio, Damasio, & Van Hoesen, 1982). The latter hypothesis was undermined, however, by studies of prosopagnostic patients who were very good distinguishing among cars (Sergent & Signoret, 1992), faces of sheep (McNeil & Warrington, 1993), as well as members of other categories (Farah, Klein, & Levinson, 1995).

² Neurophysiological evidence for a specific for face perception has been amply provided by PET studies (e.g. Haxby et al. 1993; Sergent, Ohta, & MacDonald, 1992), fMRI studies (e.g. Clark et al., 1996; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Puce, Allison, Gore, & McCarthy, 1995), and intracranial ERP recordings (Allison et al., 1994a,b,c). These studies did not, however, address the dissociation between a structural encoding mechanism and a face identification mechanism.

³ Apes were excluded.

directly involved in face identification. This hypothesis was tested in the present study by examining the effects of face familiarity on the N170 and other ERP components.

GENERAL METHOD

Participants

The participants were 60 undergraduate students with normal or corrected-to-normal vision. They participated in the experiment for class credit or payment.

Stimuli

The stimuli were 150 different portraits and 30 butterflies of different kinds. All stimuli were scanned high-quality photographs. They were presented in black and white using a high-resolution monitor and graphic-board. The exposure time of each stimulus was 350msec. Among the portraits, 60 were of unfamiliar people, 60 were of famous movie stars, TV personalities, sportsmen and sports-women, and 30 were portraits of famous politicians. The familiarity of the photographed people was determined using the following procedure.

Photographs of 500 ostensibly known personalities from different professional fields were intermixed with 500 photographs of unknown people, and presented one-by-one on a computer screen to a random sample of 24 students from the same pool as the subjects in the present study. The participants in this pilot survey were instructed to judge the familiarity of each portrait by selecting one of four response categories: (1) Full recognition, including the name and the profession of the person; (2) Precise knowledge regarding who the person is, without remembering his or her name; (3) General feeling that the face is familiar without explicit knowledge of who the person is; and (4) Confident feeling that the face is unfamiliar. For the present study, we included in the "familiar faces" category only faces that were categorised in one of the first two categories by at least 85% of the subjects, and were not included in the fourth cate-

gory by any subject. "Unfamiliar faces" were those that were included in the fourth category by at least 90% of the subjects and were never included in the first two categories.

EEG Recording and Averaging

The EEG was recorded from 30 (Experiment 1) or 48 (Experiments 2 and 3) tin electrodes mounted on a custom-made cap (Fig. 1). The EOG was recorded with two electrodes, one located at the outer cantus of the right eye and the other at the infraorbital region of the same eye. The EEG and EOG were recorded with reference to the tip of the nose.

The EEG was continuously sampled at 250Hz, amplified $\times 20,000$ with an analog band-pass filter of 0.1Hz to 33Hz, and stored for off-line analysis. For ERP averaging, the EEG was segmented into 1100msec epochs, starting 100msec before the stimulus. Epochs with EEG or EOG exceeding $\pm 100\mu\text{V}$ were excluded from the averaging. The baseline was adjusted by subtracting the mean amplitude of the pre-stimulus period of each ERP from all the data points in the epoch. Frequencies lower than 0.4Hz or higher than 19Hz (-3dB points) were digitally filtered out from the ERPs after averaging.

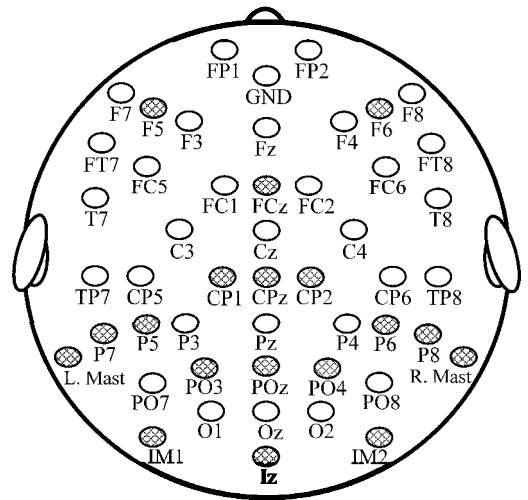


Fig. 1. The distribution of the electrode sites on the electrocaps. The electrodes added for Experiments 2 and 3 are shaded.

ERP Analysis

Averaged ERPs at each scalp site were used to calculate the overall scalp distribution of the electrophysiological activity presumably associated with face processing. On the basis of these topographies (and previous results), regions of interest were determined and the stimulus-type effects were statistically analysed only at these sites. ANOVAs were used to evaluate the statistical significance of the effects. Greenhouse–Geisser adjustment of degrees of freedom was applied whenever necessary.

EXPERIMENT 1

Previous results showed that the N170 is elicited by human faces regardless of whether or not the faces are relevant to the observer's task. In all the experiments reported by Bentin et al (1996), the participants' task was to silently count non-face targets while ignoring other stimulus types, including faces. The emergence of the N170 under these circumstances suggests that the face-processing mechanism with which the N170 is associated may be triggered automatically by the occurrence of a face in the visual field. However, automatic initiation does not imply that the process, once triggered, cannot be controlled, and that its activity cannot be shaped by top-down information. More specifically, as would be predicted by interactive-activation models of face recognition (e.g. Burton, Bruce, & Johnston, 1990; see also Burton, Bruce & Hancock, in press), it is possible that the construction of the structural representation of a face is facilitated by familiarity even if the face identity is not task-relevant. In addition, familiarity in general and face familiarity in particular may act as an exogenous, data-driven cue attracting attention to the face (for a comprehensive discussion of data-driven attention deployment, see Yantis, 1998). Experiment 1 was designed to explore this possibility by comparing the ERPs elicited by familiar faces with those elicited by unfamiliar faces while subjects were monitoring the screen for the occasional appearance of butterflies.

Method

Participants

The participants were 14 undergraduates (10 women), all right-handed according to self-report. One participant was excluded due to technical problems.

Stimuli

The stimuli were 60 unfamiliar faces, 60 faces of famous people (not including politicians), and 30 butterflies.

Task and Procedures

The participants were instructed to silently count the occasionally appearing butterflies and to ignore the faces. They were not told that some of the faces might be familiar to them. Following the application of the electrode-cap, the experiment was run within a single session lasting about 15 minutes. Two pauses were included, 1 every 50 trials. During the pause, the participants were asked how many butterflies they had seen up to that point, and were told to continue counting when the stimulus presentation resumed.

Results

Replicating previous results, faces elicited N170 potentials at the posterior temporal sites; at the same latency the butterflies elicited a much smaller negative-going deflection that did not cross the baseline (in order to see Plate 1 of the colour section, please click here).

The N170 potentials elicited by familiar and unfamiliar faces were similar in their scalp distribution and amplitude ($-6.1\mu\text{V}$ and $-6.0\mu\text{V}$, respectively; see Plate 1). For both type of faces the N170 recorded over right hemisphere sites were apparently larger ($-6.8\mu\text{V}$) than those recorded over the left hemisphere sites ($-5.3\mu\text{V}$). The statistical validity of these observations was tested by a three-way ANOVA. The factors were Familiarity (familiar, unfamiliar), Site (P7/8, PO7/8), and Hemisphere (left, right). The ANOVA showed that there was neither effect of familiarity [$F(1,12) < 1.00$] nor of site [$F(1,12) < 1.00$]. The hemisphere

effect was conspicuous but failed to reach significance [$F(1,12) = 3.1, P < 10$].

In contrast to the absence of a familiarity effect on the N170, the ERPs elicited by familiar and unfamiliar faces seemed to diverge at most electrode sites during a later epoch of the waveform, starting at about 350msec. The two ERPs converged again at about 800msec from stimulus onset. The ERPs elicited by the familiar faces were more negative than these elicited by unfamiliar faces

between 350 and 550msec, and more positive between 550 and 800msec, resulting in bi-phasic difference waveforms (Fig. 2)⁴. The latency of the negative peak in the difference waveform was at about 450msec, roughly corresponding with the peak of the N400 potential observed for faces (Bentin & McCarthy, 1994). The scalp-distribution of the difference, however, extended more posteriorly than the distribution of the "classical" N400 (Kutas & Hillyard, 1980). The positive

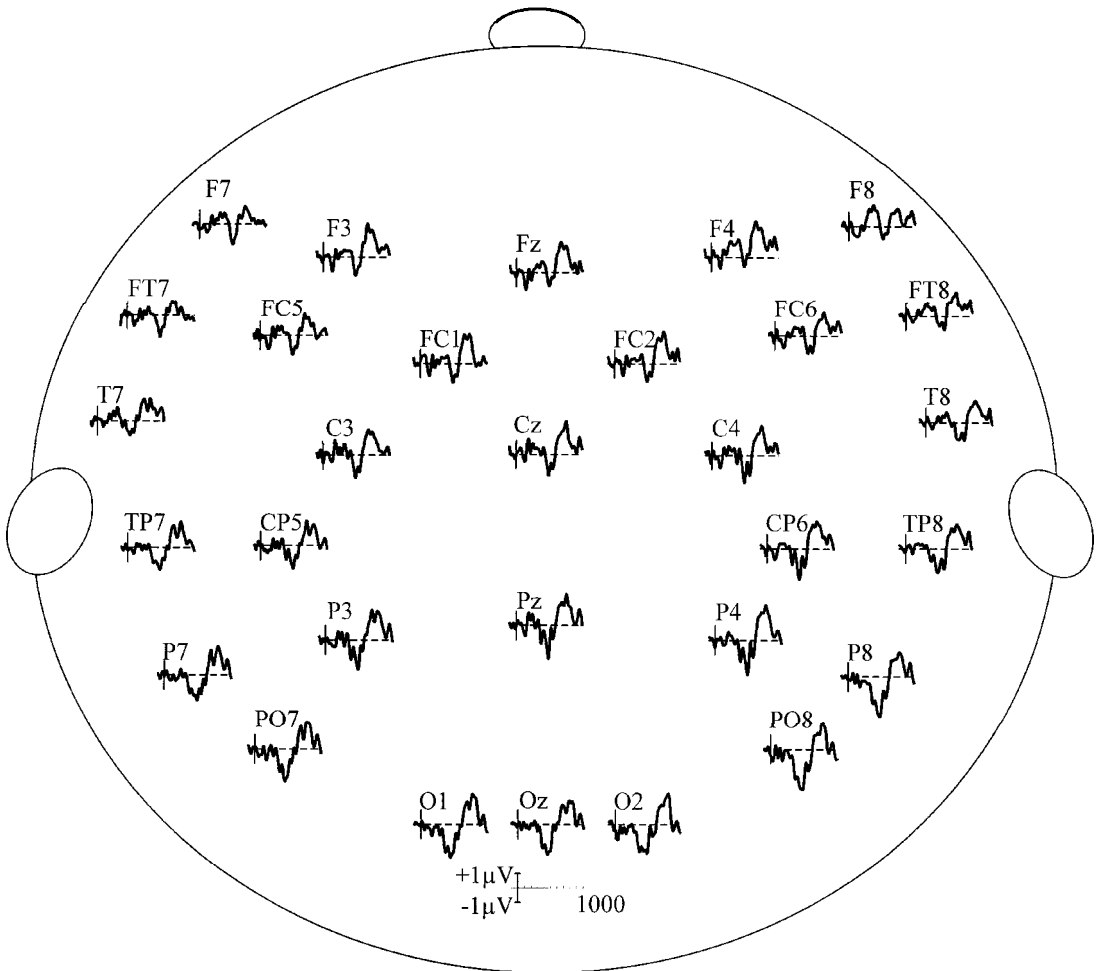


Fig. 2. The difference waveforms (familiar-unfamiliar) at the different scalp locations in Experiment 1.

⁴ For clarity, only difference waveforms are presented.

peak in the difference waveforms corresponded to a vertex-maximal positive peak elicited by nontargets at around 700msec.

The statistical validity of the negative difference was assessed by comparing the mean amplitude of the ERPs elicited by familiar faces and unfamiliar faces separately between 350 and 550msec, and between 550 and 800msec. The analysis of the first period showed that, across all sites⁵, the mean amplitude elicited by familiar faces was significantly more negative ($-0.70\mu\text{V}$) than that elicited by unfamiliar faces (which was, in fact, positive; $0.12\mu\text{V}$) [$F(1,12) = 10.2, P < .01$]. There was no effect of hemisphere [$F(1,12) < 1.0$], and none of the interactions were significant. The analysis of the differences observed during the second phase showed a similar pattern. The ERPs elicited by familiar faces between 550 and 800msec were significantly more positive ($2.1\mu\text{V}$) than these elicited by unfamiliar faces ($1.4\mu\text{V}$) [$F(1,12) = 6.63, P < .05$]. The hemisphere effect and all the interactions were not significant ($F < 1.00$ for all comparisons). A more detailed analysis of the familiarity effect on the later components was deferred to the next experiment.

Discussion

The most important result of this experiment was that familiarity with a particular face did not influence the N170. This result supports the hypothesis that the N170 is associated with an early visual mechanism which, although specific for face processing, is not influenced by processes that are directly associated with face identification. Such a mechanism could be the "structural encoder" suggested by Bruce and Young (1986). The structural encoding process is the final stage of the visual analysis and its product is an abstract sensory representation of the face, a representation that is independent of context or viewpoint, corresponding approximately with a 3-D representation in Marr's model (1982). According to Bruce and Young's model, the familiarity of the face is determined by a

different process, one of matching the structural representation with a set of face recognition units. Inasmuch as the N170 is associated with the formation of a sensory representation, the current data suggest that the flow of information between the structural encoding and the face recognition processes is uni-directional, that is, there is no top-down influence on the structural encoding.

It is possible that this hypothesis should, however, be constrained to the conditions of the present experiment, in which face identity was irrelevant for task completion. Indeed, the distinction between the ERPs elicited by familiar and unfamiliar faces found around the N400 latency suggests that, despite being task-irrelevant, face familiarity was probably noticed or, at the very least, implicitly processed. Nonetheless the task-irrelevant distinction between familiar and unfamiliar faces was inconsequential for the N170. Top-down influences on N170 might be evident, however, when the face identity is deliberately processed. Experiment 2 was designed to explore this hypothesis and examine the characteristics of the later differences between the ERPs elicited by familiar and unfamiliar faces.

EXPERIMENT 2

The present experiment was designed to resemble Experiment 1 as much as possible except for using a task that required explicit identification of the faces. For this purpose, faces of famous politicians substituted for the butterflies, and the participants were instructed to silently count the number of politicians. Hence, all the stimuli in this experiment were faces, therefore assumed to generate the N170. The important comparison, however, was between the ERPs elicited by familiar and unfamiliar non-politicians. These two type of faces were equivalent in regard to their task relevance and were included in the same response category. Yet, because the process of matching the sensory representations with the face recognition units may be different for familiar and unfamiliar faces, and in

⁵The midline electrodes were excluded from this analysis to allow possible interhemispheric differences to emerge.

addition familiar faces should be able to activate specific semantic information whereas unfamiliar faces cannot, we expected conspicuous differences between the ERPs elicited by these two face categories. In particular, we predicted that they would differ during a latency period consistent with the N400—a potential that has been associated with the activation of semantic information (for a review see Kutas & Van Petten, 1988), as well as by faces (Barrett & Rugg, 1989; Bentin & McCarthy, 1994).

To summarise the questions addressed in this experiment were: (1) Would the difference between processing familiar and unfamiliar faces be reflected in the N170, suggesting top-down influence on the process of structural encoding when face identity is task-relevant? (2) Would the need to identify the faces enhance the difference observed in Experiment 1 between the N400 component elicited by familiar and unfamiliar faces?

Method

Participants

The participants were 24 undergraduates (15 women) who had not participated in the previous experiment. Four of the women were left-handed, by self-report.

Stimuli

The nontarget stimuli were the same faces used in Experiment 1. The familiar faces were media and sport celebrities and movie stars. The target stimuli were faces of politicians.

Task and Procedures

The subjects were instructed to identify and count the politicians. It was assumed that in order to perform this task the subjects would have to attempt to identify each face. The procedures were identical to those used in Experiment 1, except that the EEG was recorded from 48 rather than 30 scalp sites.

Results

The participants' ability to recognise politicians was good, but not perfect. On the average, the participants' count was about 92% accurate. In this experiment, however, we could not efficiently monitor the participants' ability to recognise the politicians because the reported counts might have included not only omissions but also false alarms. Nonetheless, the ERP pattern was mostly clear and consistent across subjects.

Adding recording sites, we obtained a finer grid, which showed that the regions where N170 was most evident extended more posteriorly and laterally than P8 and P7, including the mastoids, the IM locations (midway between theinion and the mastoids), and the parieto-occipital sites (PO7, PO3, PO8, and PO4). At all these sites, the N170 appeared to be larger over the right than the left hemisphere and almost the same for unfamiliar faces and familiar non-politicians (Fig. 3).

This observation was statistically validated by a Familiarity (familiar, unfamiliar) \times Site (PO3/4, P7/8, L/R Mast, PO7/8, IM1/2) \times Hemisphere (left, right) ANOVA. The dependent variable was the amplitude of the N170, assessed as the most negative amplitude between 140 to 210 msec from stimulus onset. Of course, the ERPs elicited by faces of politicians (target stimuli) were not included in this analysis. The ANOVA showed a significant effect of site [$F(4,92) = 11.0$, $P < .001$ G-G Epsilon = 0.47], and a significant effect of hemisphere, revealing that the N170 was larger over right ($-5.2\mu\text{V}$) than over left ($-3.6\mu\text{V}$) hemisphere sites [$F(1,23) = 9.9$, $P < .01$]. The effect of familiarity was not significant [$F(1,23) = 3.0$, $P = .09$], and there were no significant interactions. A post hoc analysis of the site effect showed that the N170 was largest at the lateral parieto-occipital (PO7 and PO8) and mastoid sites and smallest at the medial parieto-occipital sites (PO3 and PO4). The possible effect of attention to face identity was directly examined by comparing the N170 amplitudes in Experiment 1, in which face identity was irrelevant to the task, with those in the present experiment, in which attention had to be allocated to face identity. This analysis was based on a mixed

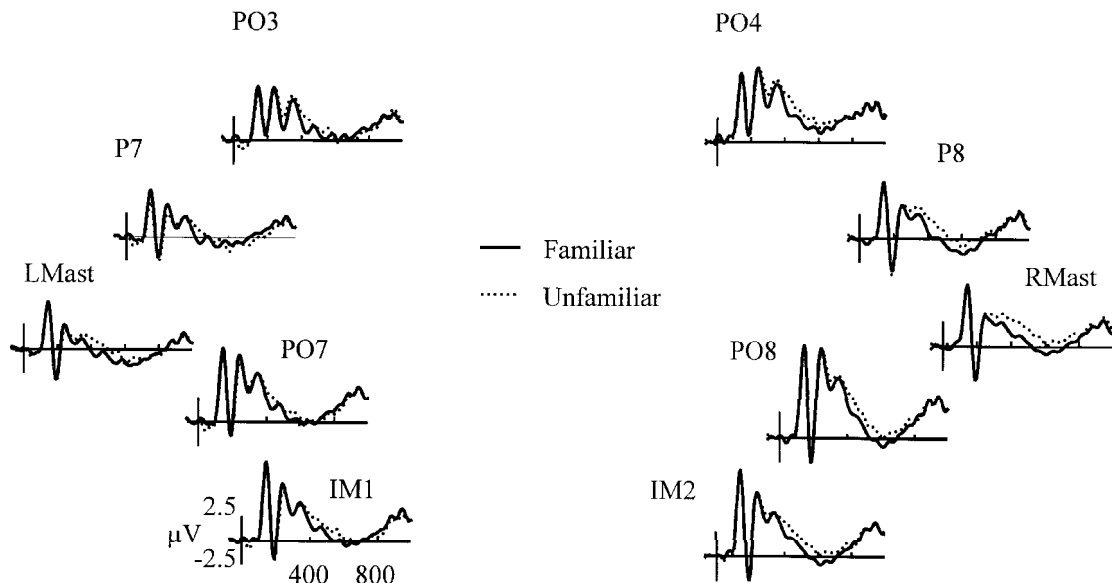


Fig. 3. The N170 potential at the parieto-temporo-occipital scalp locations in Experiment 2. Larger N170 were recorded over the right than over the left hemisphere, and there was no effect of familiarity.

model ANOVA in which the Experiment was a between-subjects factor. The results of the ANOVA showed that the N170 was almost the same in both experiments [$F(1,35) < 1.00$], and that the experiment factor did not interact with any of the other factors.

Following the N170, the ERPs elicited by faces of familiar non-politicians differed from those elicited by unfamiliar faces. In contrast to Experiment 1, however, the difference began earlier, at about 250msec, and ended at about 500msec from stimulus onset. During this period the ERPs elicited by familiar faces were more negative than those elicited by unfamiliar faces (Fig. 4). Furthermore, as evident in Fig. 4, the difference between the two conditions was more conspicuous at the central and centro-frontal sites, a distribution more consistent with the distribution of the N400.

The negative potential elicited by familiar faces during the epoch of interest (250–500msec from stimulus onset) included (at least at some sites) 2 distinctive peaks, one at about 300msec and the second at about 425msec from stimulus onset. However, spline interpolations of the potential

scalp distribution and the calculation of the scalp current densities (SCD) at the each of these peaks showed similar patterns. Therefore, the statistical significance of the observed differences was assessed comparing the mean amplitudes of the ERPs elicited by familiar and unfamiliar faces during 250 to 500msec from stimulus onset.

First, in an attempt to reduce the data to a manageable size, the mean averages at the 48 recording sites were collapsed into 4 quadrants: Posterior-right (IM2, O2, PO8, RMast, PO4, P8, P6, P4), Posterior-left (IM1, O1, PO7, LMast, PO3, P7, P5, P3), Anterior-right (TP8, CP6, CP2, T8, C4, FT8, FC6, FC2, F8, F6, F4), and Anterior-left (TP7, CP5, CP1, T7, C3, FT7, FC5, FC1, FT7, F7, F5, F3). These data were analysed by Familiarity (familiar, unfamiliar) \times Anterior/Posterior Distribution (anterior, posterior) \times Hemisphere (left, right). This analysis revealed that, across all sites, the average amplitude elicited by familiar faces between 250 and 500msec ($-0.14\mu\text{V}$) was significantly more negative than that elicited by unfamiliar faces (which was, in fact, positive; $0.47\mu\text{V}$) [$F(1,23) = 11.8, P < .001$] and that the familiarity

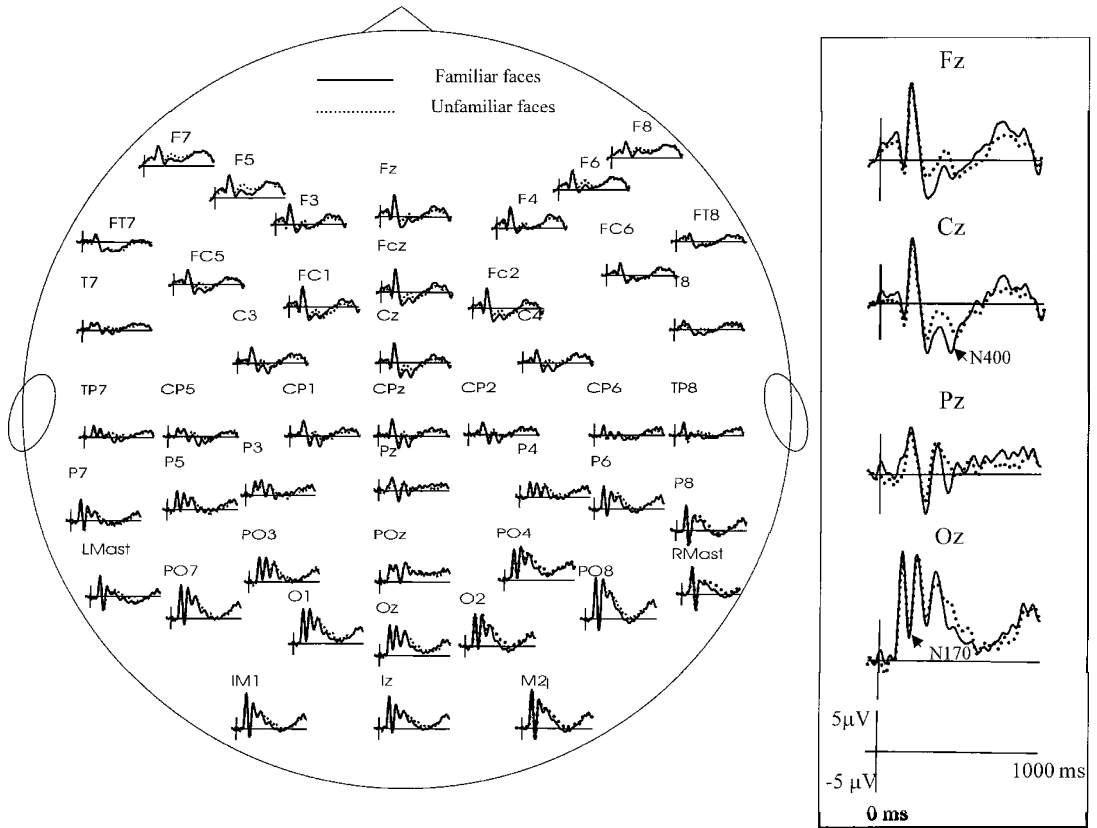


Fig. 4. ERPs elicited by familiar and unfamiliar faces at all scalp locations in Experiment 2. Note the frontocentral distribution of the face-N400.

effect significantly interacted with the anterior/posterior distribution [$F(1,23) = 4.57, P < .05$]. Post hoc univariate contrasts showed that the familiarity effect was larger over the anterior ($0.76\mu\text{V}$) than the posterior quadrants ($0.55\mu\text{V}$), but was statistically significant over both [$F(1,23) = 7.7, P < .05$ and $F(1,23) = 32.0, P < .001$].

Across familiar and unfamiliar faces, the ERPs were more negative over the anterior ($-1.0\mu\text{V}$) than the posterior ($1.35\mu\text{V}$) regions [$F(1,23) = 75.9, P < .001$], and slightly (but not significantly) less positive over the left ($0.0\mu\text{V}$) than the right ($0.3\mu\text{V}$) hemisphere [$F(1,23) = 1.63, P = .21$]. No other interactions were significant.

Scrutiny of the individual responses revealed that this pattern was clear in only 16 out of the 24 of participants (Group A). The relationship between

the ERPs elicited by familiar and unfamiliar faces in the other 8 participants (Group B) was less clear, and, at least at some scalp sites, even inverse (i.e. unfamiliar faces were less positive than familiar faces). The difference between the two groups at selected electrode sites is presented in Fig. 5.

Since we assumed that the difference between the two groups might reflect strategic differences in task performance (see following), the familiarity effect was analysed separately for each group. ANOVAs were calculated using only the anterior two quadrants, but the distribution was analysed in detail, using each electrode site as a separate level. Hence the factors were Familiarity (familiar, unfamiliar), site (F7/8, F5/6, F3/4, FT7/8, FC5/6 FC1/2, T7/8, C3/4, TP7/8, CP5/6, CP1/2), and Hemisphere (left, right). These analyses showed that the

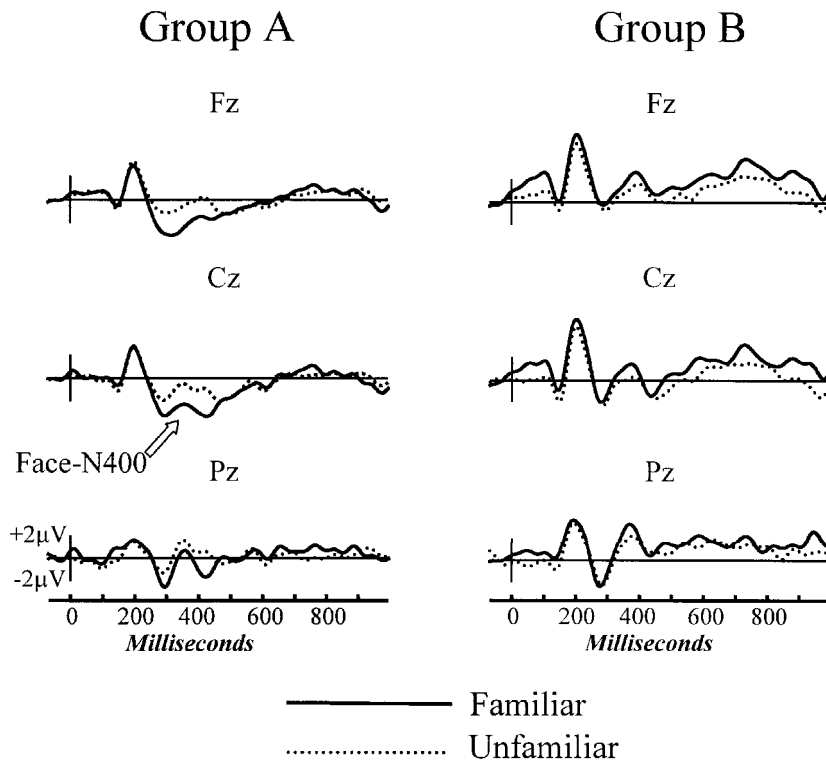


Fig. 5. *N400 modulation in the post hoc determined groups of participants in Experiment 2. Group A included 16 subjects in which the face-N400 was larger for familiar than for unfamiliar faces and Group B included 8 subjects in which this relation was reversed.*

familiarity effect was significant for Group A [$F(1,15) = 29.1, P < .001$] but not for Group B [$F(1,7) < 1.00$]. For both groups the site effect was significant [$F(10,150) = 15.21, P < .001, G-G$ Epsilon = 0.28, and $F(10,70) = 2.95, P < .001, G-G$ Epsilon = 0.20 for Group A and Group B, respectively]. The interaction between the familiarity and the site effect was significant for Group A [$F(10,150) = 3.06, P < .001, G-G$ Epsilon = 0.41], but not for Group B [$F(10,70) = 1.58, P = .22, G-G$ Epsilon = 0.34]. There was no effect of hemisphere for either group, and no interactions with the hemisphere effect ($F < 1.00$). Finally, the three-way interaction was also not significant [$F(10,150) = 1.15, P = .34$, and $F(10,70) = 1.79, P = .18$, for

Group A and Group B, respectively]. The distribution of the familiarity effect was further analysed in a series of ANOVAs. The overall pattern emerging from these analyses was that the effect was larger at more central than more lateral sites without any effect of the anterior posterior distribution⁶.

Discussion

The results of the present experiment supported the hypothesis that the N170 is not susceptible to top-down influences of familiarity, and is probably not associated with a neural mechanism that is directly involved in the process of face recognition or face

⁶To recall, only the anterior scalp site was examined in these analyses, which explains the absence of the familiarity \times site interaction that was observed in the previous analysis. Details regarding the results of different ANOVAs are available from the first author.

EXPERIMENT 3

identification. Although face identification must have been attempted in every trial, the N170 elicited by familiar faces was almost identical to that elicited by unfamiliar faces.

Interesting differences were found, however, between the ERPs elicited by familiar and unfamiliar faces starting at about 250msec. From this latency on, all faces elicited a negative potential lasting for about 250msec. This potential was significantly larger (more negative) for familiar than for unfamiliar faces. The centro-frontal scalp distribution of this potential, its time course, and its susceptibility to stimulus familiarity indicate that it might be associated with similar cognitive mechanisms as the N400. Therefore, we will call this potential "face-N400" to distinguish it from the "classical" N400, which has been associated primarily with the semantic processing of words.

Although the familiarity effect was statistically significant across the whole sample, familiar faces elicited a more negative (or less positive) face-N400 in only 16 of the 24 subjects. Among the remainder, seven showed a slightly inverse pattern and for one the mean amplitude across channels was equal for familiar and unfamiliar faces. This pattern might have reflected only random variability among participants but it also could have reflected strategic differences in task performance. A deeper analysis of the latter option was not possible, however, in the present experiment, because using the oddball paradigm we could not monitor the participants' performance sufficiently well. Therefore, a better monitoring of the trial-by-trial performance was attempted in Experiment 3, where subjects were instructed to respond as fast as possible by button-press to each face, categorising it as a politician or a non-politician. This procedure should allow better control of performance. Indeed, such a procedure should usually elicit a P300 for non-politicians as well as for politicians, hence hindering the N400 effects to some extent. On the other hand, on the basis of the knowledge about the latency and scalp distribution of the effect obtained in Experiment 2, we hoped to detect the modulation of the face-N400 on the generally positive-going P300 potential (for such a procedure, see, for example, Bentin, McCarthy, & Wood, 1985).

The present experiment was identical with Experiment 2 except that, rather than counting politicians, the participants were instructed to press, on each trial, one button if the presented face was that of a politician and another button if it was not. Unlike a regular face recognition task, this task allows comparison of the ERPs and RTs elicited by familiar and unfamiliar faces within the same response category, that of non-politicians. Hence, differences between the responses to familiar and unfamiliar faces, in performance as well as in ERPs, should reflect primarily stimulus encoding and decision-making factors rather than response selection and execution.

Despite possible interference with ERPs due to speeded motor movements, the availability of overt responses in each trial had several advantages. First, we were able to include in the averaged ERPs only trials in which the face identification was correct. Although, in principle, we were interested in the process rather than in its outcome, each response category might involve different processes, and therefore the inclusion of ERPs elicited by faces that were incorrectly identified might add noise to the averaged response. Second, and more important, we had specific predictions regarding the implication of different performance strategies on the response time.

Within the framework of the Bruce and Young (1986) model the task of detecting politicians could have been accomplished by adopting different strategies. One strategy could be to make a "non-politician" decision for unfamiliar faces on the basis of the negative outcome of the familiarity check, whereas familiar faces should require an additional process of person identification before classifying them to either of the response categories. Such a strategy should have required longer and more extensive processing for familiar than for unfamiliar faces and, therefore, the RTs will be faster for the former stimuli. An alternative strategy, however, might have been to categorise all faces on the basis of fully identifying them (or attempting to do so). This exhaustive identification procedure will, by necessity, end sooner for

familiar than for unfamiliar faces and, therefore, a decision will always be reached faster for familiar non-politicians than for unfamiliar faces. If the amplitude of the face-N400 positively correlates with the stimulus processing time, the former performance strategy should lead to larger face-N400 potentials for familiar than for unfamiliar faces, whereas the latter strategy should result in a reversed relation. In the present experiment we examined these hypotheses in two steps. First we examined for each participant whether larger face-N400 potentials are associated with slower responses. Second, if this hypothesis was supported by the data, we examined whether participants who respond more slowly to familiar than to unfamiliar faces are also those who elicit larger face-N400 in response to familiar than to unfamiliar faces and vice versa.

Method

Participants

The participants were 24 right-handed undergraduates (8 men) who had not participated in the former experiments.

Task and Procedure

The stimulus presentation procedure and ERP data collection were identical with those used in Experiment 2. Subjects were instructed to respond on each trial pressing a right-hand button whenever the face of a politician was presented and a left-hand button whenever the presented face was not that of a politician. Speed and accuracy were equally emphasised.

Results

Overt Performance

The RTs and percentage of errors for the different categories of faces are presented in Table 1. The RTs were trimmed for each participant, excluding those that were longer or shorter than 2 SDs from the mean of each condition. The percentage of outliers never exceeded 5% of the trials.

Across all subjects, the RTs were almost identical for all three face categories [$F(2,46) < .001$]. In

Table 1. RTs (in msec) and Percentage Errors (SEm) in Response to Faces of Politicians, Unfamiliar Faces, and Familiar Non-politicians

	Unfamiliar	Familiar	Politicians
Mean RT	666 (10.6)	665 (8.2)	661 (7.0)
% errors	2.32(1.2)	3.84 (0.55)	5.65 (0.9)

contrast, the percentage of errors differed across the categories [$F(2,46) = 3.81, P < .05$, G-G Epsilon = 0.671]. Post hoc univariate contrasts showed that more errors were made in response to politicians than to non-politicians [$F(1,23) = 5.5, P < .05$], whereas the difference between familiar non-politicians and unfamiliar faces was not statistically significant [$F(1,23) = 1.76, P = .20$].

This analysis should be interpreted as a demonstration that deciding that a particular face is not the face of a politician is equally fast and accurate for familiar and unfamiliar faces. Nonetheless, considering the two alternative strategies described earlier, two subgroups of participants could be formed on the basis of individual patterns of RTs to non-politicians. Fourteen participants (Group 1) responded faster to unfamiliar (640msec) than to familiar faces (659msec) i.e. they putatively used the familiarity criterion strategy, whereas the other 10 participants (Group 2) responded faster to familiar (674msec) than to unfamiliar faces (701msec) i.e. they putatively used the full identification strategy. The responses of the two groups to politicians was almost the same [657msec for Group 1 and 666msec for Group 2, $t(21) = 0.63, P = .55$]. In contrast, the responses to non-politicians were overall significantly slower in Group 2, i.e., those participants who responded faster to familiar than to unfamiliar faces, than in Group 1 [687msec vs. 650msec $F(1,22) = 5.13, P < .05$].

ERPs

In an attempt to understand better the pattern of ERP differences between familiar and unfamiliar faces, our major purpose in the present experiment was to examine the extent to which differences in the pattern of reaction times might account for the face-N400 modulation by face-familiarity. We have assumed that the size of the N400 is influ-

enced by the time required to process a stimulus, so that longer processing time is reflected by larger N400s. On the basis of this assumption we predicted that participants for which the face-N400 elicited by familiar faces was larger (more negative) than that elicited by unfamiliar faces would respond more slowly to familiar than to unfamiliar faces, and vice versa.

As a first step we had to demonstrate that, regardless of face familiarity, longer RTs were indeed associated with larger face-N400s. With this purpose in mind, we separately averaged (within subjects) the EEG for trials in which the RTs were faster than the mean (in each condition), and those in which the RTs were slower than the mean. As illustrated in Fig. 6, for both familiar and unfamiliar faces, the ERPs elicited on trials in which the RTs were slower than the mean included a conspicuous negative potential that was absent from the ERPs elicited in trials in which the RTs were faster than the mean. However, the diver-

gence between the two ERPs and the peak of the negative potential elicited by "slow" trials were later than the face-N400 that was described and analysed in Experiment 2. In fact, the current ERP manifestations seemed to be related to a shift in the latency of a late positive ERP component. Therefore, the present RT-influenced negativity and the face-N400 might have been associated with different cognitive mechanisms. With this caveat in mind, we continued our analysis.

Having established an association between the response time and the ERP elicited by faces, and assuming that the RTs reflect to some extent the time required for processing the face, we proceeded with the examination of a possible correlation between the influence of face familiarity on RTs and on ERPs. This was done by examining the ERPs elicited by familiar and unfamiliar faces separately for participants in Group 1 and in Group 2. If the magnitude of the face-N400 was influenced by the time required to identify the faces, it should

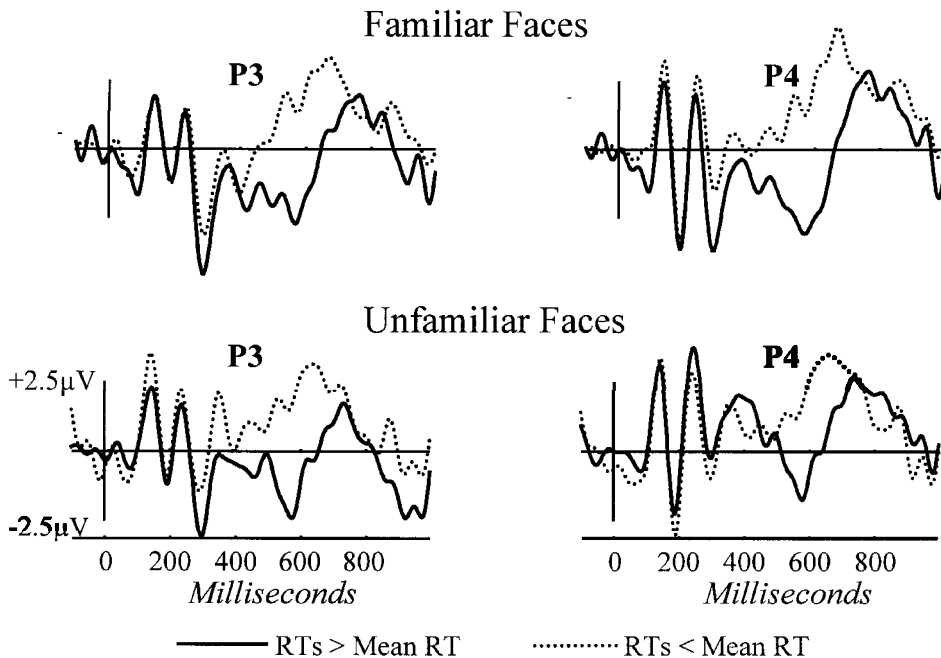


Fig. 6. ERPs elicited in trials in which the response to the non-politicians was faster than the mean RT, and ERPs in trials in which the response was slower than the mean RT, and the ERPs in trials in which the response was slower than the mean RT in each stimulus category. Note that the latency of the negative potential elicited in slow-RT but not in fast-RT trials was later than that of the face-N400. The effect of the response speed on the ERPs did not interact with face familiarity.

have been larger for familiar than unfamiliar faces in Group 1 (in which the RTs to familiar faces was longer than to unfamiliar faces) and larger for unfamiliar than for familiar faces in Group 2 (in which the RTs to unfamiliar faces was longer than to familiar faces). This comparison is presented in Fig. 7.

Contrary to our expectations, the ERPs elicited by the two groups during the time range of the face-N400 were similar. ANOVA showed that the mean amplitude elicited by familiar faces across all electrodes ($-1.2\mu\text{V}$) was more negative than that elicited by unfamiliar faces ($-0.6\mu\text{V}$) [$F(1,22) = 4.48, P < .05$], and that there was no interaction

between the effect of familiarity and the effect of group [$F(1,22) < 1.0$]⁷. As can be seen in Fig. 7, however, an interaction in the expected direction seemed to emerge during a later epoch of the waveforms. During this epoch, a negative-going deflection was evident in the ERPs elicited by familiar faces in Group 1, and by unfamiliar faces in Group 2. Although this was not predicted a priori, we analysed the difference between the mean amplitude elicited by familiar and unfamiliar faces from 500 to 700msec. This analysis revealed that the observed interaction between the familiarity and group effects was statistically significant [$F(1,22) = 5.5, P < .05$].

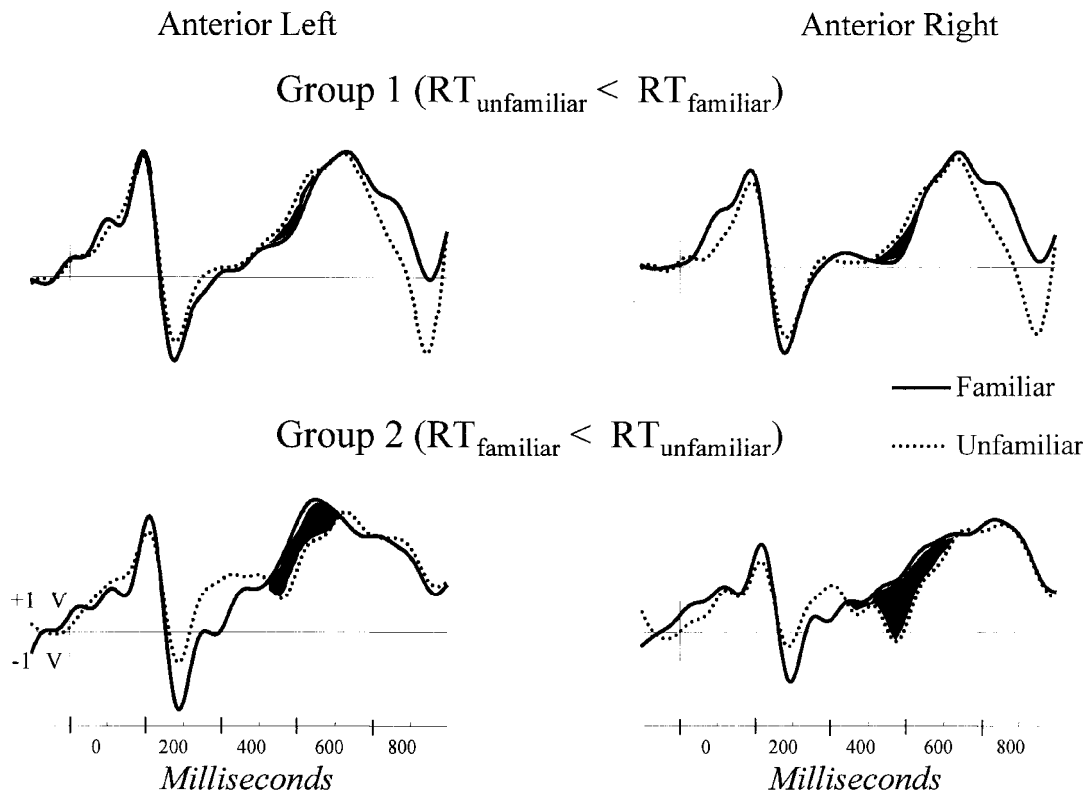


Fig. 7. Spatial averaging of the ERPs elicited by familiar and unfamiliar faces at the anterior right and anterior left scalp sites in participants who responded faster to unfamiliar than to familiar faces (Group 1) and participants who responded faster to familiar than to unfamiliar faces (Group 2).

⁷ A more detailed analysis, with the scalp site as an independent variable, did not reveal any interesting interactions with the factor of group. Therefore, to simplify the presentation these analyses are not presented. They are available upon request from the first author.

Finally, as in the previous experiments, a clear N170 was elicited by all faces. As is evident in Fig. 8, despite the requirement to respond quickly to each stimulus, face familiarity had no effect on either the amplitude or the latency of this potential.

Statistical analysis showed that the amplitudes of the N170 elicited by familiar and unfamiliar faces were similar [$F(1,23) < 1.00$], significantly higher over right ($-8.43\mu\text{V}$, averaged over P8, RMast, PO8, PO4, and IM2) than over left ($-5.45\mu\text{V}$, averaged over P7, LMast, PO7, PO3, and IM1) hemisphere sites [$F(1,23) = 27.6$, $P < .001$], and different at different sites [$F(4,92) = 2.67$, $P < .05$, G-G Epsilon = 0.55]. The only significant interaction was between the effects of site and hemisphere [$F(4,92) = 3.51$, $P < .05$, G-G Epsilon = 0.58]. Post hoc univariate contrasts showed that the amplitude at PO3 was smaller than at the other left hemisphere sites [$F(4,92) = 5.6$, $P < .001$, G-G Epsilon = 0.6], whereas over the right hemisphere sites the effect was not significant [$F(4,92) = 1.49$, $P = .21$, G-G Epsilon = 0.52].

Because the need to produce speeded responses might have influenced the time course of the brain activity, we analysed the latencies of the N170, using the same design as for the analysis of the amplitudes. This analysis showed that the latency

of the N170 was the same in response to familiar and unfamiliar faces (166msec).

Discussion

The purpose of Experiment 3 was to explore the possibility that the difference in the direction of the familiarity effect on the face-N400 potential, which was found in one third of the participants in Experiment 2, revealed an interesting strategic difference in task performance rather than mere noise. This hypothesis was not supported by the results of the present experiment. Although the pattern of the ERPs within subjects was related to the pattern of their RTs (the two variables may have been influenced by the same cognitive process), this correlation was not evident during the face-N400 time range. Hence, the RT data could not provide an objective criterion for predicting the individual differences in the direction of the face-N400 effect. We are therefore left with an ad hoc conclusion that, across participants and accepting some variability, the main effect of familiarity on the ERPs was that familiar faces elicited a more negative face-N400 than unfamiliar faces. This effect will be discussed further in the General Discussion.

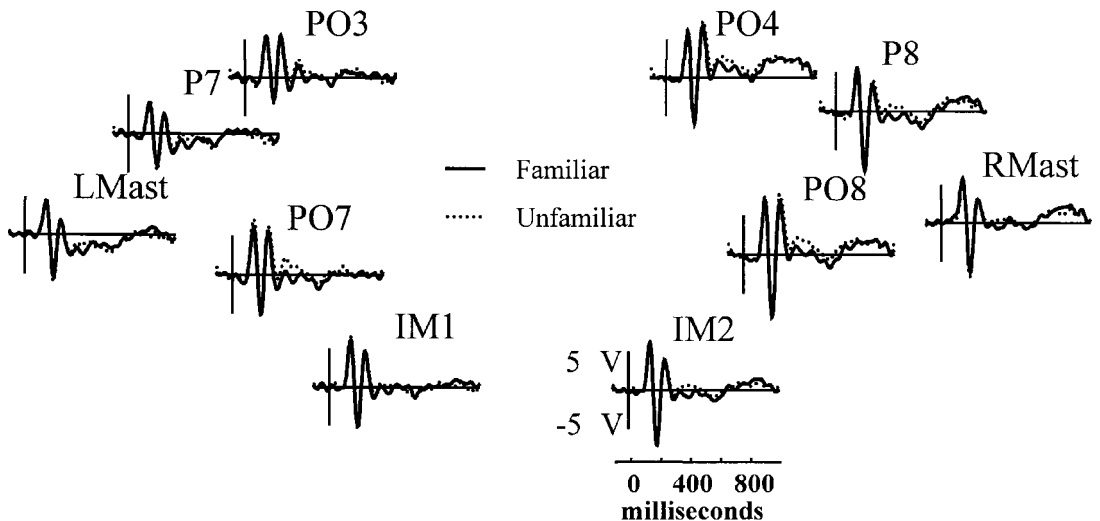


Fig. 8. The N170 elicited by familiar and unfamiliar faces in Experiment 3. Although face identification was required in each trial and only correct responses were included in the average, there was no effect of face familiarity.

Although the face-N400 effect could not be predicted by the pattern of the RTs, some evidence for the possible use of different strategies for categorising familiar and unfamiliar faces as non-politicians emerged in the analysis of the RTs. Indeed, across all subjects, familiar and unfamiliar faces were rejected equally quickly and accurately. Yet, comparing subjects who responded more quickly to familiar than to unfamiliar non-politicians with subjects who showed the opposite pattern, we found that the former group responded more slowly overall than the latter. This difference was not an obvious result of the group selection. It is consistent with the hypothesis that the faster rejection of unfamiliar than familiar faces is based on a familiarity check at the level of the face recognition units in Bruce and Young's model, whereas faster rejection of familiar than unfamiliar faces is a result of using the identification process at the level of the identity nodes. Although it is speculative, this interpretation is not contradicted by the present data.

Whereas the face-N400 familiarity effect did not correspond with the familiarity effect on RTs, across familiarity, RTs had a robust influence on ERP components elicited later than the N400. A within-subject comparison of the ERPs associated with long and short RTs revealed a distinctive negative component associated with slow but not fast RTs and with a delay in a subsequent positive deflection. This effect is congruent with older findings suggesting that ERPs in general and the latency of the P300 component in particular may reflect the stimulus processing time (e.g. McCarthy & Donchin, 1981), and that it is sensitive to categorical decision strategies as well as the difficulty of discriminating targets from nontargets (e.g. Kutas, McCarthy, & Donchin, 1977). Indeed, as is evident in Fig. 6, the late positive component in trials with long RTs peaked later and had a smaller amplitude than that elicited in trials with short RTs. It is conceivable that this late positive component is the P300, which is usually elicited within this latency range by nontrivial categorical decisions. If so, its latency, as well as the RTs, should be affected by the duration of stimulus processing until it is categorised.

Moreover, the pattern of the late positivity and its variation with the length of the RT were similar for familiar and unfamiliar faces. This similarity suggests that, within each category, there were faces that were more or less easy to categorise and that, in fact, the proportion of "easy" and "difficult" trials was not very different for familiar and unfamiliar faces. It is possible that different strategies are employed by each subject in categorising different faces, and that the choice of strategy in each trial is determined by factors that do not necessarily cut across the a priori determined face familiarity. Of course, given the post hoc nature of this hypothesis, it should remain tentative until directly tested in future research.

GENERAL DISCUSSION

The present study was designed to explore the process of face identification as reflected by ERPs. More specifically, our questions were: (1) Is the face-specific mechanism associated with N170 sensitive to the familiarity of the face? (2) Is the process of face identification reflected by identifiable scalp-recorded ERP components? The results provided clear answers to both questions. Regardless of whether face identity was relevant to the successful completion of the task, neither the amplitude nor the latency of the N170 were modulated by the familiarity of the face, and were similar when attention was directed toward face identification (Experiments 2 and 3) or not (Experiment 1). In contrast to the N170, a later negative component, ranging roughly from 250 to 500msec, was larger in response to familiar than to unfamiliar faces. Unlike the circumscribed posterior temporo-occipital distribution of the N170, the later negative component was recorded at all scalp sites, but it was most conspicuous over the frontal and central regions—a distribution that approximates the distribution of the N400. This distribution as well as theoretical considerations that will be elaborated below lead us to suggest that this negative component is a face-related analogue of the N400, which has been traditionally associated primarily (although not exclusively) with the processing of words.

The insensitivity of the N170 to the familiarity of the face provides additional support for Bentin et al.'s (1996) conclusion that the N170 is associated with an early visual mechanism dedicated to analysing physiognomic information and providing a sensory representation of the face to a higher-level perceptual system. As reviewed in the Introduction, this hypothesis was mainly based on the finding that the N170 is not affected by manipulations known to significantly impair face recognition (such as face inversion and the spatial redistribution of inner components within the face contour (Bentin et al., 1996). Finding that identical N170 potentials are elicited by familiar and unfamiliar faces, regardless of whether viewers intend to identify the faces or not, strongly supports the hypothesis that the brain mechanism with which the N170 is associated is triggered by the presence of a human face in the visual field but is not directly involved in face recognition.

Absence of familiarity effects of the N170 does not imply, however, that structural encoding does not affect the face recognition and face identification processes. This question was not addressed in the present study. Other studies of the N170, however, suggest that efficient identification of faces requires the normal functioning of the structural encoding mechanism (Bentin, et al., 1999). Abnormal N170 patterns were recorded in that study from two patients with considerably impaired ability to identify familiar faces. Specifically, although conspicuous N170s were elicited by faces in both patients, similar negative potentials were elicited by other semantic categories such as hands, animal faces, and items of furniture, as well as nonsense patterns of stimuli. Hence, although a visual structural encoding mechanism was active in these prosopagnostic patients, it was not efficient in selectively streaming this information to the face recognition units.

Integrating the absence of a face familiarity effect on the N170 with previous findings, we suggest that the N170 scalp-recorded potential is associated with a mechanism involved in the formation of sensory representations of faces and streaming these representations to further analysis

(by other brain structures) in order to be identified. This mechanism acts on the basic constituents of the face and is not influenced by top-down activity of the face recognition units. Moreover, since the N170 is larger when the inner components are presented without the face contour than when the whole face is presented (Bentin & McCarthy, 1999), there are good reasons to believe that the final integration of the components into a gestalt requires an additional mechanism, possibly reflected by the face-specific activity in the medial parts of the fusiform gyrus, revealed by the fMRI (Kanwisher, et al., 1997; McCarthy et al., 1997; Puce et al., 1995) as well as by intracranial recordings (Allison et al., 1994a, b). Given the orientation of the dipole generating the electrophysiological activity in the fusiform gyrus, its influence on the ERPs recorded over posterior-temporal areas at the scalp is probably small.

The negativity from 250 to 500msec that was modulated by face familiarity in the present study might be associated with the activity of face recognition and face identification mechanisms (Bruce & Young, 1986). According to Bruce and Young's model, the internal representation generated by the structural encoder is tested by a series of face-recognition units, analogous to the logogens in Morton's (1969) model of word recognition. Only if a positive match is achieved at this level, are face identity nodes activated to provide the semantic information relevant to the recognised face. Hence, as is true for lexical access, both familiar and unfamiliar faces should activate the face recognition units, but only familiar faces can fully activate a particular entry in this system. Furthermore, only familiar faces can activate particular nodes in semantic memory. Consequently, any ERP component that is associated with semantic activity should be greater for familiar than for unfamiliar faces. Previous studies have convincingly associated the N400 with the activation of semantic memory.

Initially, the N400 was linked with the processing of semantically anomalous words placed in final sentence position either in reading (Kutas & Hillyard, 1980) or in speech perception (McCallum, Farmer, & Pocock, 1984). It was

found that its amplitude can be modulated by the degree of expectancy (cloze probability) as well as the amount of overlap between the semantic characteristics of the expected and the actually presented words (Kutas, Lindamood, & Hillyard, 1984; see also Kutas & Hillyard, 1989). Therefore, it was assumed to reflect a post-lexical process of semantic integration, and to be modulated by the difficulty of integrating the word into its sentential context (e.g. Rugg, 1990). It is unlikely, however, that simple lexical activation is a major factor eliciting or modulating the N400, because closed-class words, although represented in the lexicon, neither elicit nor modulate this component (Nobre & McCarthy, 1994).

This pattern of results suggests that the N400 is not associated with a visual mechanism dedicated to processing of letters, but rather with a higher-level processing system. Moreover, it is probably not elicited exclusively by words because negative waveforms peaking at about 400msec were modulated by the immediate repetition of unfamiliar faces (Bentin & McCarthy, 1994) and other pictorial stimuli (Barrett & Rugg, 1989). Hence, the currently existing evidence indicates that the N400 is elicited only by stimuli that allow deep (semantic) processing. This pattern is consistent with the assumption that the N400 reflects the process of searching for a link between a stimulus and its semantic representation.

The present data suggest that the face-N400 modulated by familiarity was elicited by a similar mechanism of activating the "person identity nodes" by the recognised, familiar structural representation of a face. The fact that it was larger for familiar than for unfamiliar faces is congruent with this hypothesis. As suggested in Bruce and Young's model, described earlier, only familiar faces should activate the semantic person identity nodes, and therefore the semantic processes with which the N400 is associated should be more conspicuous in the ERPs elicited by familiar than by unfamiliar faces. Whether this face-N400 is associated with the same semantic mechanism as the N400 elicited by words (hence nonspecific), or whether it is specific to face processing, should be investigated in future studies.

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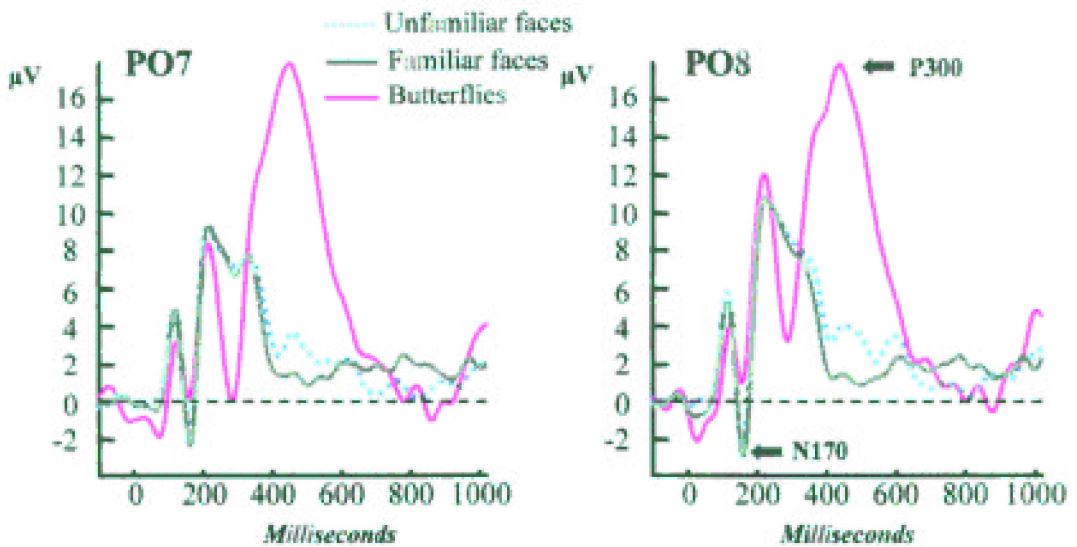
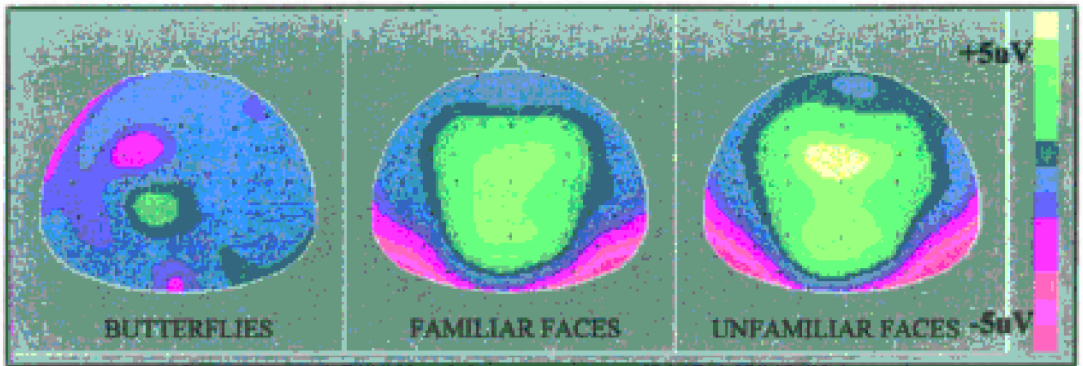


Plate 1 (Bentin and Deouell). *Upper panel: Scalp spline interpolations of the potentials elicited by familiar faces, unfamiliar faces, and butterflies at 164msec—the peak latency of the N170. Lower panel: The ERPs elicited by butterflies (targets) and by familiar and unfamiliar faces (distractors) in Experiment 1, at PO8 (right hemisphere) and PO7 (left hemisphere).*