Research report

Effects of face inversion on the structural encoding and recognition of faces
Evidence from event-related brain potentials

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Abstract

It was investigated how face inversion affects face-specific components of event-related brain potentials (ERPs) which are assumed to reflect the structural encoding and the recognition of faces. ERPs were recorded to upright and inverted photographs of familiar faces, unfamiliar faces, and houses. In Part I, participants had to detect infrequently presented targets (hands), in Part II, attention was either directed towards or away from the pictorial stimuli. When compared with upright unfamiliar faces, upright familiar faces elicited an enhanced negativity between 300 ms and 450 ms ('N400f') and an enhanced positivity between 450 and 650 ms post-stimulus ('P600f'). It is suggested that these ERP modulations are generated by processes involved in the recognition of faces. Face inversion is known to disrupt face recognition processes. Accordingly, 'N400f' and 'P600f' were generally absent in response to inverted familiar and unfamiliar faces. The face-specific N170 component at lateral posterior electrodes was not affected by face familiarity, indicating that it reflects processing stages prior to face identification. N170 was delayed and enhanced for inverted relative to upright faces. While N170 enhancements were also observed for inverted relative to upright houses, the N170 latency shift caused by stimulus inversion was face-specific. Directing attention away from the faces towards a demanding primary visual task resulted in an N170 delay for inverted as well as for upright faces, suggesting that the time course of structural encoding of faces is affected by attentional factors. These results demonstrate that ERPs can be used as electrophysiological markers of specialised brain processes underlying the structural encoding and subsequent recognition of faces.   © 2000 Elsevier Science B.V. All rights reserved.

1. Introduction

It is widely acknowledged that face recognition is subserved by highly specialised processes that are qualitatively different from processes underlying the identification of other kind of objects. For example, face recognition is more impaired than object recognition when line drawings are presented instead of photographs [6], suggesting that surface features like pigmentation or shading are more critical for the identification of faces than for the recognition of other objects. On a more general level, it has been argued that face recognition is essentially based on 'holistic' representations of prototypical configurations of face components, while object recognition operates primarily on representations where objects are decomposed into constituent parts [9,13]. Parts of faces are recognised better when shown in the context of a whole face than in isolation, whereas no such advantage for wholes has been observed for parts of other kinds of objects [32]. Most importantly, face recognition is much more affected by stimulus inversion than object recognition ('face inversion effect') [34,33]. When faces are presented upside-down, configurational information relevant for the identification of faces is disrupted.

Electrophysiological and brain imaging studies have suggested the existence of anatomically distinct brain regions devoted to face processing. Face-specific cells that

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respond strongly to faces, but not to other types of objects have been identified in the macaque temporal cortex in the inferior temporal gyrus and on the banks and the floor of the superior temporal sulcus [26]. Importantly, many of these cells are sensitive to the configuration of face components. Their activity is reduced when facial features are rearranged, or only single face component are presented [8]. Recent fMRI studies (cf. [27,21,18,16,19]) have located an area in the fusiform gyrus that is strongly activated when faces are presented, but not in response to houses, scrambled faces, or hands (but see [14,15]). Additional neuropsychological evidence for the existence of separate face-specific processing modules comes from double dissociations between face and object recognition. In Prosopagnosia, face recognition is disproportionally impaired, and in the most extreme cases, object recognition capabilities seem entirely unaffected [7,31,24]. In contrast, other agnosic patients are unable to identify different types of non-face objects, while face recognition remains remarkably intact [23,25].

Face-specific modulations of event-related brain potentials (ERPs) provide yet another source of evidence for specialised brain processes subserving face perception and recognition. Faces elicit a negative potential with a latency of 170 ms (N170) at lateral posterior temporal sites as well as a frontocentral positivity in the same latency range [2–4,10–12,17,20]. In contrast, no N170 is triggered by cars, hands, furniture, or by scrambled faces [2]. Because face-specific N170 components have been found not only to intact upright faces, but also to inverted faces or isolated eyes (but see [10]), it has been argued that the N170 reflects the perceptual encoding of face components rather than processing stages involved in face identification [2]. If this interpretation was correct, the N170 should not be affected by the familiarity of a face. This has indeed been demonstrated in recent studies [12,3] that compared ERPs elicited by familiar and unfamiliar faces, and found that the face-specific N170 component at lateral temporal electrodes was entirely unaffected by the familiarity of a face. This strongly suggests that the N170 reflects the early pre-categorical structural encoding of faces rather than subsequent face recognition processes. However, ERP modulations sensitive to face familiarity have been observed at longer latencies. In a study where ERPs were recorded in response to familiar faces, unfamiliar faces, and houses, while participants had to respond to infrequently presented hand stimuli [12], familiar faces elicited an enhanced negativity between 300 ms and 500 ms ('N400f'), which was followed by an enhanced positivity beyond 500 ms post-stimulus ('P600f'). These effects were maximal for the first presentation of individual familiar faces, and were attenuated, but still reliable, for subsequent presentations of the same faces. Because of their sensitivity to face familiarity, the 'N400f' and 'P600f' are likely to indicate processes involved in the

recognition and identification of faces (see also [3] for similar results).

While all of these observations were based on ERPs recorded at the scalp surface, recent intracortical ERP recording studies have identified a series of face-specific components in ventral occipital and temporal areas [1,22,28]. A negative component with a latency of about 200 ms (N200) recorded from ventral occipitotemporal cortex was unaffected by the familiarity of faces and showed no habituation, suggesting that this potential reflects the pre-categorical perceptual analysis of faces. In contrast, a later positive potential (P350) originating from posterior lateral and anterior ventral temporal cortex showed habituation, indicating that this component is generated by face-specific processes which are subject to top–down influences.

If ERP components are to be used as markers for successive stages involved in face perception and recognition, face-specific ERP effects should be shown to be sensitive to experimental manipulations known to affect the efficiency of face processing. Because stimulus inversion is known to disrupt face recognition, ERP components that reflect the encoding and recognition of faces should be strongly influenced by the difference between upright and inverted face stimuli. Several studies have found effects of face inversion on the N170 component. When compared to upright faces, the N170 is delayed by about 8 ms in response to inverted faces. Although small, this latency shift is remarkably robust and has been reported in several studies [2,29,30]. The delay of the N170 may be due to inadequate configural information provided by upside-down faces [29]. In line with this idea, N170 latency shifts have also been observed for faces with eyes removed relative to intact faces [10], and when participants were engaged in the analytical processing of face components [20]. N170 amplitude can also be affected by the orientation of face stimuli. Larger N170 amplitudes for inverted relative to upright faces have been observed under conditions where discriminations between faces were required [29,30]. This effect may be due to the fact that inverted faces are more difficult to process than upright faces, resulting in a sustained attentional 'processing negativity' overlapping with the N170 component [17].

Because the N170 is unaffected by the familiarity of faces [12,3], and therefore assumed to reflect processing stages prior to face identification, it is unlikely that effects of face inversion on this component are directly linked to the disruption of face recognition caused be face inversion. In contrast to the N170, subsequent ERP modulations ('N400f', 'P600f') are sensitive to face familiarity [12,3]. If these components were generated by brain processes involved in face recognition, they should be attenuated or completely absent when familiar and unfamiliar faces are presented upside-down. In contrast, if the 'N400f' and 'P600f' were found to be unaffected by face inversion, this

would cast considerable doubt on their interpretation as electrophysiological markers of face recognition processes. Since these predictions have never been tested, the main objective of the present experiment was to investigate if and how face inversion affects ERP components sensitive to the familiarity of faces.

The setup of the present study was similar to a previous experiment investigating ERP correlates of face familiarity [12]. The experiment consisted of two parts, where familiar faces (politicians, movie stars, musicians, and other celebrities), unfamiliar faces, and non-face stimuli (houses) were presented in random order and either upright or upside-down. To determine whether participants could identify most of the faces labelled 'familiar', a face recognition test was run at the end of the experiment. In the first half of the experiment, participants were instructed to respond to infrequently presented left-pointing or right-pointing hands ('Detect Hands' task), and to ignore all other stimuli. ERPs elicited by familiar and unfamiliar faces were compared separately for upright and for inverted face stimuli. Based on previous results [12], it was expected that upright familiar faces would elicit an enhanced negativity in the N400 time range ('N400f') as well as a subsequent positivity ('P600f') when compared to upright unfamiliar faces. The critical question was what would happen to these components when familiar and unfamiliar faces were presented upside-down. If the 'N400f' and 'P600f' were closely linked to ongoing face recognition processes, they should be strongly affected by the disruption of these processes caused by face inversion.

A second aim of the present study was to further investigate effects of face inversion on the N170 component by testing whether these effects are modulated by face familiarity and attentional task demands. If N170 latency shifts and amplitude enhancements produced by inverted faces were due to the increased difficulty of structural encoding and face recognition due to the lack of sufficient configural information, these effects may be more pronounced for familiar faces, which can be recognised, than for unfamiliar faces, which can not. To explore this possibility, effects of face inversion on the N170 were quantified separately for familiar and for unfamiliar faces. Moreover, if N170 face inversion effects reflected increased demands on face processing modules when confronted with upside-down faces, they should be affected by the attentional requirements of a given task. They should be elicited in tasks which require attention to be focused on individual faces [29,30], but presumably not when attention is actively directed away from face stimuli to a highly demanding primary visual task. To investigate this possibility, photographs of upright and inverted familiar faces, unfamiliar faces, and houses were presented simultaneously with superimposed alphanumerical character strings in the second half of this experiment. Participants had to direct their attention to faces and houses in order to

detect immediate repetitions of these stimuli ('Detect Repetitions'), or to attend to the character strings in order to detect the presence of a digit embedded within this string, while ignoring the photographs present in the background ('Detect Digits'). If face inversion effects on the N170 component were sensitive to the current focus of attention, these effects should be present in the 'Detect Repetitions' task where faces have to be attended, but not in the 'Detect Digits' condition where attention is engaged elsewhere.

2. Materials and methods

2.1. Participants

Nineteen paid volunteers participated in the experiment, which was undertaken with the understanding and written consent of each participant. Two participants were excluded because their error rate exceeded 20% in the face recognition test delivered at the end of the experiment, and two were excluded because of a large number of eye blinks during the experiment, resulting in the rejection of more than 40% of all trials. Thus fifteen participants (eight female), aged 18–30 years (mean age: 24.9 years) remained in the sample. Fourteen participants were right-handed, one was left-handed, and all had normal or corrected-to-normal vision. None of them had participated in previous experiments on face perception and recognition.

2.2. Stimuli and apparatus

Participants were seated in a dimly lit sound attenuated cabin, with response buttons under their left and right hands. A computer screen was placed 110 cm in front of the participant's eyes. Stimuli were photographs of familiar and unfamiliar faces, houses, and hands that were digitally scanned, processed by graphics software, and presented on a computer monitor in front of a white background. The stimulus set was identical to the stimulus set used in [12]. The familiar faces were photographs of well-known politicians, movie stars, musicians, and other celebrities. Fifty images of familiar faces, fifty images of unfamiliar faces and thirty-two images of houses were used. All face images showed a frontal view, with eyes positioned in the middle of the image. In half of the trials, faces and houses were presented upright, in the other half, they were inverted. In Part I ('Detect Hands'), four images of left-pointing hands and four images of right-pointing hands were presented in addition to faces and houses, and these served as target stimuli (see below). Face and house stimuli occupied a visual angle of approximately 4.5°×4°, and hand stimuli occupied a visual angle of about 5.5°×4°. All stimuli were presented for 300 ms at the centre of the

screen, and successive stimulus presentations were separated by intertrial intervals of 1200 ms. In Part II, upright and inverted face and house stimuli were presented together with an upright five-item string of red alphanumeric characters, centred at fixation, and occupying a visual angle of about 2.5°×0.5°.

2.3. Procedure

The experiment consisted of two successive parts. Participants were instructed to respond as quickly and accurately as possible to the respective target stimuli, to withhold responses to all other stimuli, and to maintain central eye fixation during the trials. Part I ('Detect Hands') consisted of 1152 trials, where upright and inverted familiar and unfamiliar faces, upright and inverted houses and hands were presented in random order. Each stimulus was randomly drawn from the respective stimulus set, with the exception that immediate stimulus repetitions were not allowed. After every 96 trials, a brief rest period was included, and participants could initiate the next run of trials by pressing the right button. Familiar and unfamiliar faces and houses were presented in 400 trials each (200 upright, 200 inverted), and houses were presented in 256 trials (128 upright, 128 inverted). Fifty different familiar faces, fifty unfamiliar faces and thirty-two houses were used, so that each individual face and house stimulus was presented on average four times in an upright position, and four times inverted. In 96 trials, left-pointing and right-pointing hands were presented with equal probability. Participants were instructed to respond with a left button press to hands pointing to the right side, and with a right button press to hands pointing to the left. Prior to the start of the 'Detect Hands' blocks, a brief training block was delivered, where different face and house photographs were presented.

Part II consisted of ten blocks with 120 trials each. Presentation conditions were similar to Part I, except that no hands were shown, and each photograph was presented simultaneously with an upright alphanumeric string superimposed on the centre of the image. In five blocks ('Detect Digits'), the participants' task was to respond with a left-hand button press whenever they detected a digit within this string. In 12 trials per block, one digit was presented together with four letters, and appeared equiprobably in one of the five serial positions within the string. These target strings were presented equally often in front of upright and inverted familiar faces, unfamiliar faces, and houses. In the remaining 108 non-target trials, the strings consisted exclusively of letters, and upright and inverted familiar faces, unfamiliar faces, and houses were presented with equal probability (18 trials per block for each combination of stimulus category and orientation). Immediate stimulus repetitions were not allowed. In the other five blocks ('Detect Repetitions'), all images were presented together with a five-item letter sequence, and

participants' task was to respond with a left-hand button press whenever the image presented in the previous trial was immediately repeated. Repetitions occurred in 12 trials per block, and were equiprobable for upright and inverted familiar faces, unfamiliar faces, and houses. In the remaining 108 non-target trials per block, non-repeated upright and inverted familiar faces, unfamiliar faces, and houses were presented with equal probability. 'Detect Digits' and 'Detect Repetitions' blocks were delivered in randomised order. Participants received a brief training block for each of the two task conditions prior to the start of Part II.

At the end of the experiment, a face recognition test block was delivered where all 100 familiar and unfamiliar face stimuli employed before were presented upright and in random order. Participants had to judge the familiarity of each face by classifying them into one of four categories: (1) Definitely familiar face (name and profession known); (2) Familiar face (name not known); (3) Unfamiliar face (although vague feeling of familiarity); (4) Definitely unfamiliar face. Categories 1 to 4 were mapped to button press responses with the left middle and index finger, and right index and middle finger, respectively. Each face stimulus remained on the screen until a response was made. Responses were classified as correct when categories 1 or 2 were chosen for familiar faces, and categories 3 or 4 for unfamiliar faces.

2.4. Recording and data analysis

EEG was recorded with Ag–AgCl electrodes from Fpz, Fz, Cz, Pz, T5, O1, T6, and O2 (according to the 10–20 system). EEG was measured relative to a reference electrode positioned on the tip of the nose. Electrode impedance was kept below 5 kΩ. The amplifier bandpass was 0.10–40 Hz. EEG and EOG were sampled with a digitisation rate of 200 Hz, and stored on disk. The latency of manual responses (if present) was measured on each trial. EEG was epoched off-line into periods of 900 ms, starting 100 ms prior to the onset of a stimulus, and ending 800 ms after stimulus onset. Trials with eyeblinks (electrode Fpz exceeding 60 μV in the 800 ms interval following imperative stimulus onset), movement artefact (voltage on any recording electrode exceeding ±80 μV in the 800 ms interval following stimulus onset), or overt responses on non-target trials were excluded from further EEG analysis. ERPs were computed exclusively on the basis of non-target trials. For Part I, EEG was averaged separately for all combinations of stimulus type (familiar face, unfamiliar face, house) and orientation (upright, inverted). For Part II, these averages were computed separately for the 'Detect Digits' and the 'Detect Repetitions' task.

All measures were taken relative to the mean voltage of the 100 ms interval preceding stimulus onset. ERP effects of experimental variables were determined by conducting repeated measures analyses of variance on ERP mean

amplitude and peak latency measures. Effects of experimental variables on N170 amplitude and latency values were investigated by repeated measures ANOVAs conducted separately for Part I and Part II. ERP components sensitive to face familiarity were analysed only for Part I.[1] Greenhouse–Geisser adjustments to the degrees of freedom were performed when appropriate. To test specific effects or interactions, additional ANOVAs or paired *t*-tests were employed.

3. Results

3.1. Performance in the face recognition test

Participants showed a good ability to identify familiar faces and to discriminate between the familiar and unfamiliar faces used in this experiment. Overall, less than 10% of all faces were classified incorrectly. Only 5.7% of all familiar faces were incorrectly categorised as unfamiliar or definitely unfamiliar, while 87.7% of these faces were classified as definitely familiar (category 1). To determine whether specific familiar faces were systematically unrecognised, identification performance was analysed separately for each of the 50 familiar faces. Forty nine of these faces were correctly identified by at least twelve participants, while the one remaining familiar face was correctly classified by eight participants. 12.1% of all unfamiliar faces were incorrectly classified as familiar, but only 1.9% of them were judged to be definitely familiar.

3.2. Behavioural performance

In Part I ('Detect Hands'), mean reaction time (RT) to target stimuli was 565 ms and 553 ms, for left and right responses, respectively, and this difference was not significant. Participants missed 1% of all target stimuli, and responded on the wrong side on 3.8% of all target trials. In Part II, RT was faster in the 'Detect Repetitions' task than in the 'Detect Digits' task of (542 ms versus 568 ms), although this difference was not reliable. Participants missed 10.7% of all targets in the 'Detect Digits' task, and 5.1% in the 'Detect Repetitions' task, and this difference was significant (t (14)=2.33; $P<0.036$). The rate of False Alarms to non-target stimuli was 0.4% and 0.3% in these two tasks, respectively.

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[1]As a result of the limited number of trials contributing to the averages for each combination of experimental conditions in Part II, and the due to the fact that ERP modulations sensitive to face familiarity decrease in amplitude as a function of number of repetitions of individual familiar faces [12], ERP effects of face familiarity observed in Part II were generally too small to yield overall reliable effects.

3.3. Effects of stimulus category and face inversion on N170 amplitude and latency

Fig. 1 shows grand-averaged ERPs in response to upright and inverted faces (collapsed across familiar and unfamiliar faces) and to upright and inverted houses in Part I ('Detect Hands'). N170 amplitude was quantified as mean amplitude within the 150–200 ms post-stimulus latency window, and was analysed at lateral temporal and occipital electrodes for the factors stimulus category (house versus face, collapsed across familiar and unfamiliar faces), orientation (upright versus inverted), and electrode side (left versus right). When compared to houses, faces elicited a distinct N170 component, as reflected by a highly significant main effect of stimulus category at temporal electrodes (F (1,14)=28.59, $P<0.001$). This effect failed to reach significance at occipital sites (F (1,14)=3.23; $P<0.094$). Although this effect tended to be larger over the right hemisphere (mean amplitude values for faces versus houses: +0.19 μV versus +1.51 μV; −1.12 μV versus +2.24 μV, for T5 and T6, respectively), stimulus category×recording side interactions failed to reach significance. At midline electrodes, an enhanced positivity was elicited by faces relative to houses in the N170 latency range (see Fig. 1), and this was reflected in a main effect of stimulus category (F (1,14)=51.77; $P<0.001$).

As can be seen in Fig. 1, a larger N170 component was elicited by inverted as compared to upright faces. However, a similar effect of stimulus inversion was also obtained for houses. This was reflected in a main effect of orientation at lateral temporal electrodes (F (1,14)=37.85; $P<0.001$), which was accompanied by a orientation× recording side interaction (F (1,14)=6.71; $P<0.021$). Importantly, there was no indication of any stimulus category×orientation interaction ($F<1$). Subsequent *t*-test revealed significantly enlarged N170 amplitudes for inverted relative to upright faces as well as for inverted relative to upright houses at T6 (both t (14)>3.4; both $P<0.004$), but not at T5. Mean amplitude values at T6 were −0.43 μV and −1.8 μV for upright and inverted faces, and +2.93 μV and +1.56 μV for upright and inverted houses. At lateral occipital electrodes, larger N170 amplitudes were elicited by inverted relative to upright houses (F (1,14)=9.82; $P<0.007$), whereas no such effect was present for faces ($F<1$).

Fig. 1 also shows a shift in latency for the N170 elicited by inverted as compared to upright faces at lateral temporal electrodes. N170 latency was quantified as the negative peak latency at lateral posterior electrodes between 150 and 200 ms post-stimulus. Main effects of orientation were present at lateral temporal and occipital electrodes (F (1,14)=32.26 and 5.26; $P<0.001$ and 0.038, respectively), and these were accompanied by stimulus category× orientation interactions (F (1,14)=6.46 and 7.01; $P<0.023$ and 0.019, for lateral temporal and occipital sites, respec-

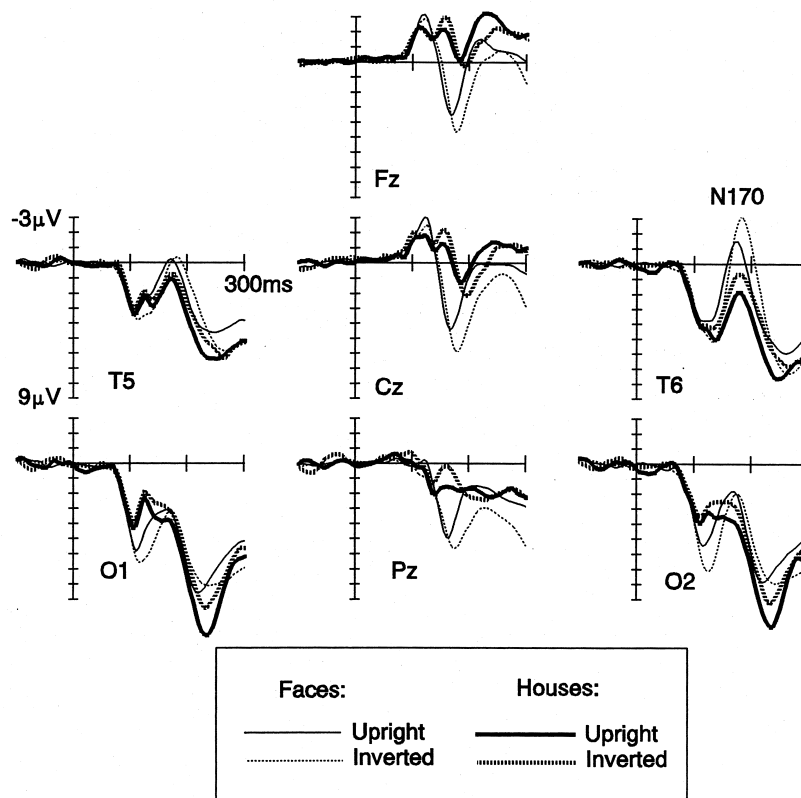## ERPs to faces and houses - Part I

Fig. 1. Grand-averaged ERPs recorded in the first 300 ms following stimulus onset at midline and lateral posterior electrodes in response to faces (thin lines) and houses (thick lines) in Part I ('Detect Hands'). Solid lines indicate ERPs elicited by upright stimuli, dashed lines indicate ERPs elicited by inverted stimuli. ERPs to faces are collapsed across familiar and unfamiliar faces.

tively). Subsequent *t*-tests revealed small, but highly consistent delays of the N170 elicited by inverted relative to upright faces at lateral temporal and occipital sites (all *t* (14)>2.79; all *P*<0.014). Table 1 (top rows) shows N170 latencies for upright and inverted familiar and unfamiliar faces at lateral temporal electrodes. No effect of stimulus orientation on N170 latency was found for houses (Fig. 1).

3.4. Effects of face familiarity and attentional demands on N170 components elicited by face stimuli

Fig. 2 (top) shows ERPs elicited at T5 and T6 in response to upright and inverted faces in Part I, displayed separately for familiar and unfamiliar faces. Effects of face inversion on N170 amplitude (at T6) and N170 latencies (both at T5 and T6) were virtually identical for both types of face stimuli, and this was confirmed by the lack of any familiarity×orientation interactions for either N170 amplitudes or latencies (both *F*<1), demonstrating that the increase in N170 amplitudes as well as the delay in N170 latencies for inverted faces were entirely unaffected by face familiarity. This can also be seen in Table 1 (top rows), where N170 peak latencies at T5 and T6 in response to upright and inverted faces are shown separately for familiar and unfamiliar faces. Importantly, there was also no main effect of familiarity on lateral temporal N170

Table 1

Peak latencies (in ms post-stimulus) of the N170 at lateral temporal electrodes in response to upright and inverted familiar and unfamiliar faces in the 'Detect Hands' task (Part I) and the 'Detect Repetitions' and 'Detect Digits' tasks (Part II)

	T5 (left hemisphere)		T6 (right hemisphere)	
	Upright	Inverted	Upright	Inverted
Detect Hands–Familiar Faces	167	175	170	177
Detect Hands–Unfamiliar Faces	163	175	169	175
Detect Repetitions–Familiar Faces	173	178	172	178
Detect Repetitions–Unfamiliar Faces	170	182	170	177
Detect Digits–Familiar Faces	180	179	177	179
Detect Digits–Unfamiliar Faces	177	179	175	175

ERPs to faces - Part I

Familiar Faces
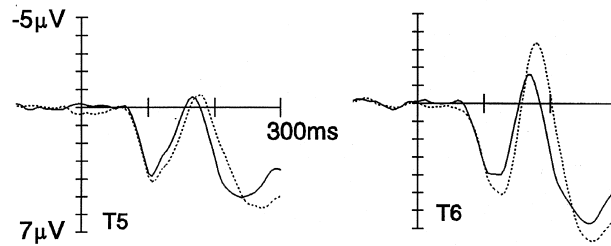
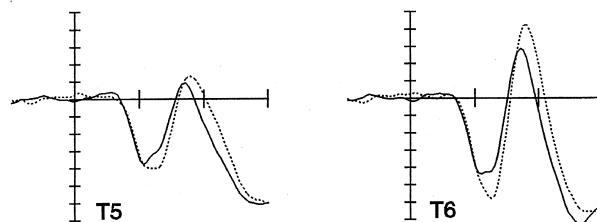## Unfamiliar Faces
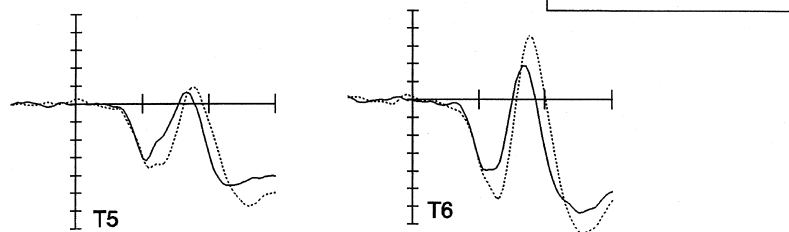
ERPs to faces - Part II

Detect Repetitions
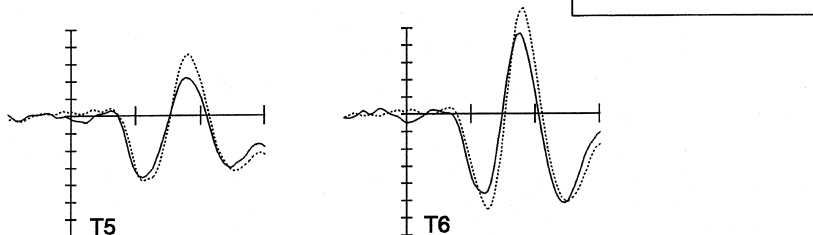

Detect Digits

Fig. 2. Top panels: Grand-averaged ERPs recorded in the first 300 ms following stimulus onset in Part I ('Detect Hands') at lateral temporal electrodes in response to familiar faces (top) and unfamiliar faces (bottom) when faces were upright (solid lines) or inverted (dashed lines). Bottom panels: Grand-averaged ERPs recorded in Part II at lateral temporal electrodes in the 'Detect Repetitions' condition (top) and the 'Detect Digits' condition (bottom) when faces were upright (solid lines) or inverted (dashed lines).

amplitudes ($F < 1$) or latencies ($F < 2.3$), indicating that the N170 is unaffected by familiarity (see also Figs. 3 and 4).

Fig. 2 (bottom) shows ERPs elicited at T5 and T6 in response to upright and inverted faces (collapsed across familiar and unfamiliar faces) in Part II, displayed separately for both task conditions. Larger N170 components were elicited in the 'Detect Digits' task relative to the 'Detect Repetitions' task, presumably reflecting differences
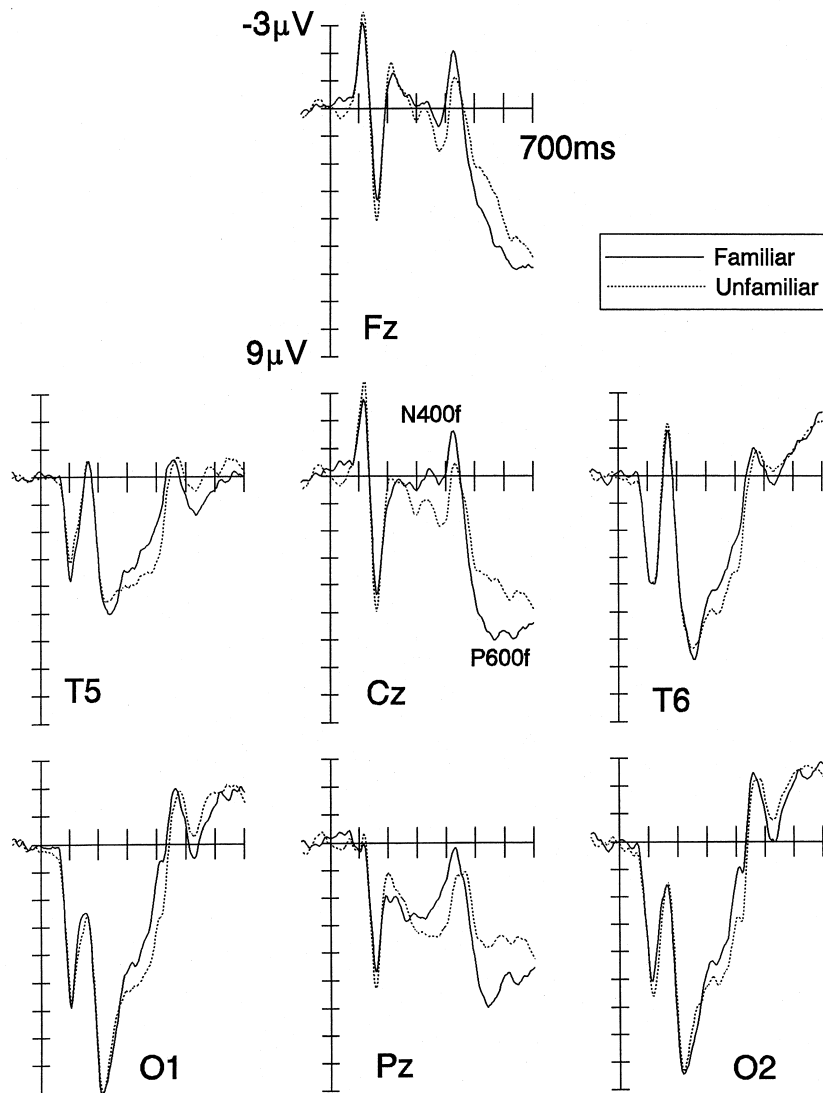
ERPs to familiar and unfamiliar upright faces

Fig. 3. Grand-averaged ERPs recorded in the first 700 ms following stimulus onset in Part I ('Detect Hands') at midline and lateral posterior electrodes in response to upright familiar faces (solid lines) and upright unfamiliar faces (dashed lines).

in the attentional demands of these two tasks. This was reflected in effects of task condition on N170 mean amplitudes at lateral temporal and occipital electrodes (F (1,14)=19.92 and 21.87; P<0.002 and 0.001, respectively). Similar to Part I, N170 amplitudes were larger for inverted as compared to upright faces at lateral temporal electrodes (F (1,14)=21.70; P<0.001). Enhanced N170 amplitudes for inverted as compared to upright faces were present at T5 as well as at T6 (both F (1,14)>8.8; both P<0.01). No indication of any task condition×orientation interaction was obtained (F<1), suggesting that the effect of face inversion on N170 amplitudes was independent of attention being directed towards or away from the face stimuli. Effects of stimulus inversion were also present for

ERPs elicited in Part II in response to houses (not shown in Fig. 2), with larger temporal and occipital N170 components for inverted relative to upright houses (both F (1,14)>25.7; both P<0.001).

As in Part I, a main effect of orientation on N170 latency was found (F (1,14)=21.39; P<0.001), as N170 peak amplitudes were again delayed for inverted as compared to upright faces. However, this effect was accompanied by a highly significant task condition× orientation interaction (F (1,14)=13.60; P<0.002). While N170 latency was reliably delayed for inverted faces at T5 and at T6 in the 'Detect Repetitions' task (both t (14)>4.0; both P<0.001), no reliable latency differences were measured in the 'Detect Digits' task (both t<1). As can be

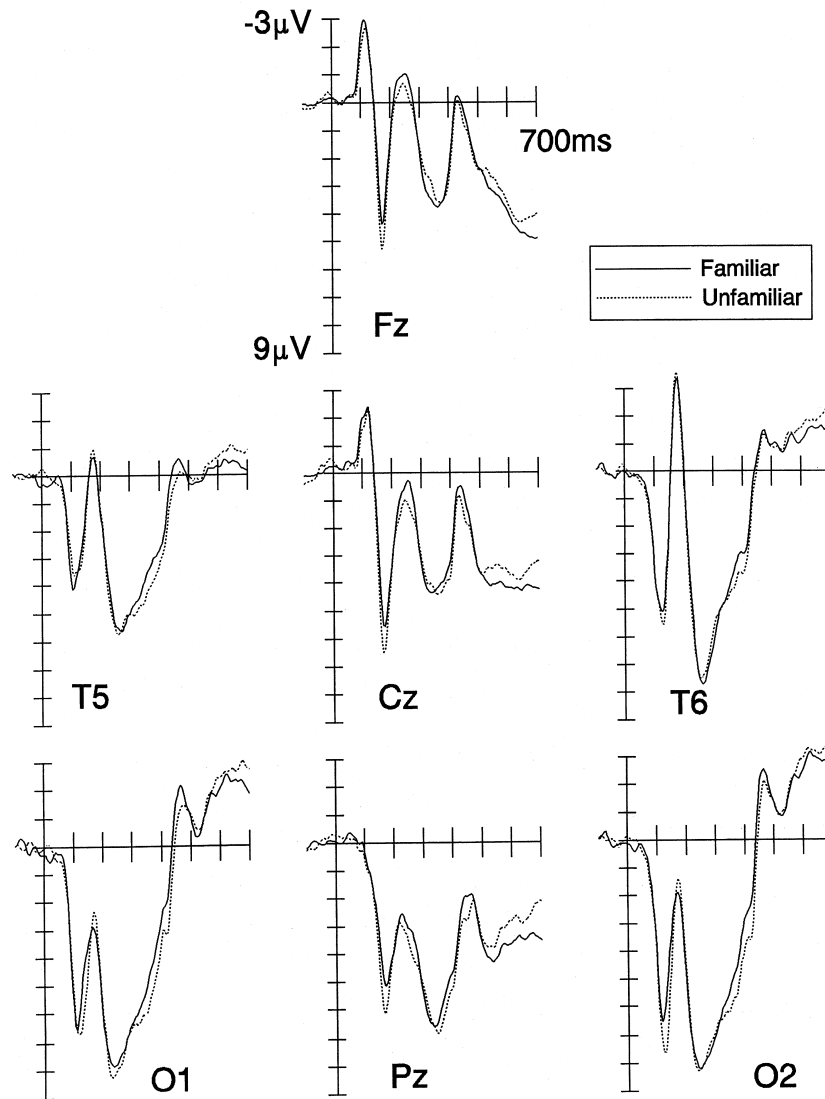# ERPs to familiar and unfamiliar inverted faces

Fig. 4. Grand-averaged ERPs recorded in the first 700 ms following stimulus onset in Part I ('Detect Hands') at midline and lateral posterior electrodes in response to inverted familiar faces (solid lines) and inverted unfamiliar faces (dashed lines).

seen from Table 1 (bottom rows), N170 was delayed for both upright and inverted faces in the 'Detect Digits' task relative to upright faces presented in the 'Detect Repetitions' task. This was further investigated by ANOVAs conducted separately for N170 latency values obtained for upright and inverted faces. A main effect of task condition was present for upright faces (F (1,14)=11.02; $P<0.005$), reflecting an N170 delay in the 'Detect Digits' relative to the 'Detect Repetitions' task, while no differences between task conditions were found for inverted faces ($F<1$). As before, face familiarity failed to affect N170 amplitudes ($F<1$) and latencies ($F<2.8$) in Part II, thus confirming previous findings that the N170 is not affected by the familiarity of faces.

3.5. Effects of face inversion on ERP components sensitive to face familiarity ('N400f' and 'P600f')

Fig. 3 shows grand-averaged ERPs elicited in Part I ('Detect Hands') in response to familiar and unfamiliar upright faces, and Fig. 4 shows ERPs to inverted familiar and unfamiliar faces in the 'Detect Hands' task. Difference waveforms obtained by subtracting ERPs to unfamiliar faces from ERPs to familiar faces, separately for upright and inverted face stimuli, are shown in Fig. 5. For upright faces, familiarity was reflected in an enhanced negativity between 300 and 450 ms post-stimulus elicited by familiar as compared to unfamiliar faces ('N400f'). Beyond 450 ms post-stimulus, familiar faces elicited an enlarged positivity

Difference Waveforms
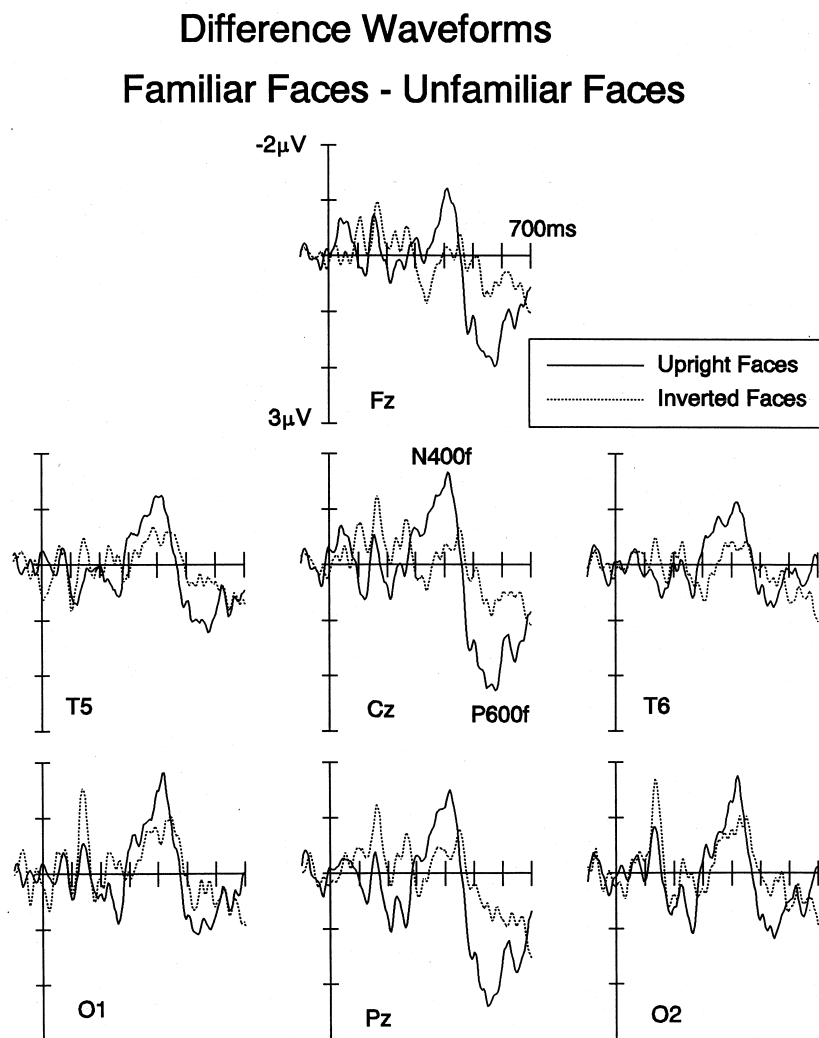## Familiar Faces - Unfamiliar Faces

Fig. 5. Difference waveforms obtained in the first 700 ms following stimulus onset in Part I ('Detect Hands') at midline and lateral posterior electrodes by subtracting ERPs to unfamiliar faces from ERPs to familiar faces for upright faces (solid lines) and inverted faces (dashed lines).

('P600f'). Both effects were larger at midline electrodes than at lateral sites, and most pronounced at Cz and Pz. For inverted faces, 'N400f' and 'P600f' effects were considerably attenuated. These effects were statistically analysed on the basis of mean amplitudes obtained in response to face stimuli within two time windows centred on the average latencies of these components ('N400f': 320–440 ms post-stimulus; 'P600f': 450–650 ms post-stimulus). ANOVAs were conducted separately for midline, temporal, and occipital electrodes, for the factors face familiarity, orientation, and electrode location (frontal versus central versus parietal for midline electrodes; left versus right for lateral temporal and occipital sites).

Main effects of familiarity were present in the 'N400f' latency range at midline electrodes as well as lateral temporal and occipital sites (all $F (1,14) > 8.10$; all $P < 0.013$), reflecting enhanced negativities for familiar as compared to unfamiliar faces. At midline electrodes, a marginally significant familiarity×electrode location interaction ($F (2,28) = 3.65$; $P < 0.068$; $\epsilon = .593$) suggested that

this effect tended to be larger at Cz and Pz than at Fz. Most importantly, significant familiarity×orientation interactions were obtained at midline sites ($F (1,14) = 7.30$; $P < 0.017$) and lateral temporal electrodes ($F (1,14) = 4.84$; $P < 0.045$), indicating that these effects were affected by the difference between upright and inverted faces (see Fig. 5). At lateral occipital sites, this familiarity×orientation interaction almost reached significance ($F (1,14) = 4.34$; $P < 0.056$). Enhanced negativities for familiar as compared to unfamiliar upright faces were present at all midline electrodes (all $t (14) > 3.82$; all $P < 0.002$), whereas no reliable effects of familiarity were obtained for inverted faces (all $t < 1.2$).[2] Enhanced negativities for upright famil-

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[2] As the difference waveforms shown in Fig. 5 suggested that the 'N400f' at midline electrodes might be delayed for inverted relative to upright faces, an additional analysis was conducted on the basis of mean amplitudes obtained between 400 and 450 ms post-stimulus. While significantly enhanced negativities for familiar faces were obtained with upright stimuli (all $t (14) > 3.98$; all $P < 0.001$), no reliable 'N400f' effects were found for inverted faces.

iar as compared to upright unfamiliar faces were present at all lateral temporal and occipital sites (all t (14)$>$2.60; all $P<$0.02). Similar, although considerably smaller effects were also present in response to inverted faces at lateral posterior sites (all t (14)$>$2.25; all $P<$0.041), except for T6. Fig. 6 (top) shows the mean familiar face-unfamiliar face difference amplitudes obtained in the 'N400f' time range for upright and inverted faces. It demonstrates that 'N400f' effects were consistently larger in response to upright faces, and that these differences were most pronounced at midline electrodes.

In the 'P600f' latency range, a main effect of familiarity was present at midline electrodes (F (1,14)$=$10.07; $P<$0.007), reflecting enlarged positivities for familiar as compared to unfamiliar faces. Importantly, this effect was accompanied by a highly significant familiarity$\times$orientation interaction (F (1,14)$=$15.20; $P<$0.002). As can be seen from Figs. 3 and 4, a 'P600f' was clearly present in response to upright face stimuli, but not when inverted familiar and unfamiliar faces were presented. This was confirmed by subsequent t-tests, which revealed highly significant differences between upright familiar faces and upright unfamiliar faces at all midline electrodes (all t (14)$>$3.18; all $P<$0.007). In contrast, no reliable am-
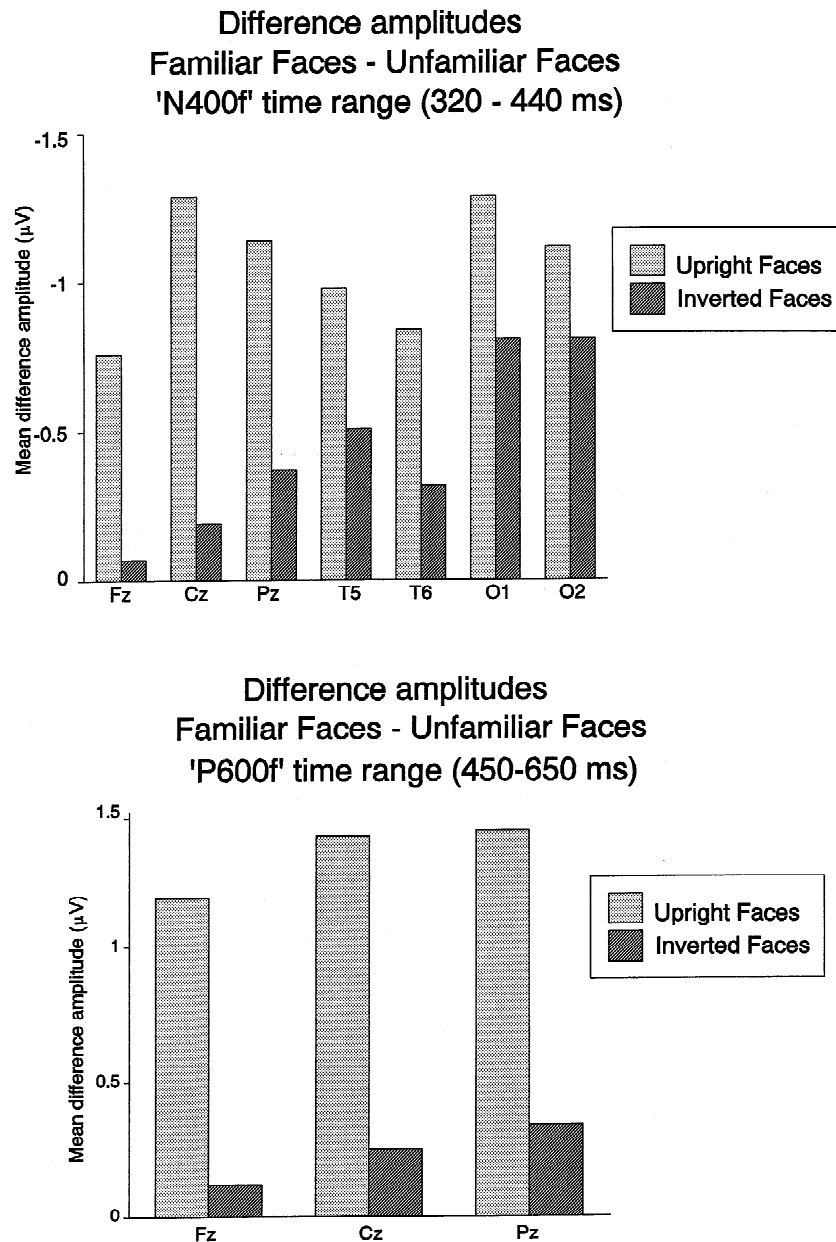

Fig. 6. Top: Mean amplitude differences between ERPs elicited by familiar faces and ERPs elicited by unfamiliar faces in the 'N400f' time range at midline and lateral posterior electrodes, displayed separately for upright faces and inverted faces. Bottom: Mean amplitude differences between ERPs elicited by familiar faces and ERPs elicited by unfamiliar faces in the 'P600f' time range at midline electrodes, displayed separately for upright faces and inverted faces.

plitude differences were obtained for familiar and unfamiliar inverted faces (all t (14)<1.34).[3] This pattern of effects can also be seen in Fig. 6 (bottom), where the mean familiar face–unfamiliar face difference amplitudes obtained at midline sites in the 'P600f' time range are displayed for upright and inverted faces. No main effects of familiarity or familiarity×orientation interactions were obtained at lateral posterior electrodes.

4. Discussion

Event-related brain potentials have become an important tool in studying processes underlying face perception and recognition. Different face-specific ERP components are likely to reflect successive stages in the processing of faces from the perceptual analysis and structural encoding of face components up to the classification and identification of individual face stimuli. To understand if and how such ERP components are related to face-specific processing stages, it is essential to study how they are influenced by experimental manipulations that are known to have an impact on the quality of face perception and recognition. The present study investigated effects of face inversion on the face-specific N170 component and on subsequent ERP modulations which are sensitive to the familiarity of faces. Photographs of familiar faces, unfamiliar faces, and houses were presented either upright or upside-down, and participants responded to another stimulus category ('Detect Hands'), to repeated photographs ('Detect Repetitions'), or to digits embedded in character strings superimposed on the photographs ('Detect Digits').

In line with previous studies [2–4,10–12,17,20,29,30], the results from Part I ('Detect Hands') again confirmed that faces elicit a N170 component at lateral temporal electrodes as well as an increased positivity at midline sites within the same time range. The N170 was not affected by face familiarity, confirming previous results [12,3], and indicating that this component reflects processes prior to the recognition and identification of individual faces. When compared to upright faces, the N170 was enhanced and delayed in response to inverted faces, again confirming previous findings [2,29,30]. These effects were virtually identical for familiar and unfamiliar faces, suggesting that they are not related to differences in face recognition processes elicited by upright and inverted faces, but originate from processing stages prior to face identifica-

tion. Unexpectedly, an enhanced N170 was not only obtained in response to inverted faces, but also for inverted house stimuli (see Fig. 1). This effect was also found in Part II, and is inconsistent with a previous study [30] which reported N170 amplitude enhancements in response to inverted faces, but not for other types of inverted objects, including houses. Although it is unclear which factors are responsible for this discrepancy, the present results indicate that N170 amplitude enhancements resulting from stimulus inversion may not be entirely face-specific. In contrast, N170 latency shifts were found for inverted faces, but not in response to inverted houses, thus confirming previous results [30].

Effects of attentional task demands on N170 amplitude modulations and latency shifts induced by inverted faces were studied in Part II where attention was either directed towards faces and houses ('Detect Repetitions') or was directed away from these stimuli to the primary task of detecting a single digit embedded within a letter string ('Detect Digits'). The digit detection task was highly demanding, and this was reflected in significantly increased error rates relative to the 'Detect Repetitions' task. The fact that posterior N170 amplitudes were larger in the 'Detect Digits' task than in the 'Detect Repetitions' task also suggests that detecting digits among letters required focal attention. In spite of these differences in attentional demands, effects of face inversion on N170 amplitudes were very similar in both task conditions. This not in line with the idea that N170 amplitude modulations caused by face inversion reflect increased demands on face processing modules when confronted with inverted faces, resulting in an attentional 'processing negativity' [29,17]. If this was correct, this effect should be more pronounced when attention is directed towards face stimuli than under condition when attention is directed away from these stimuli. In contrast to effects of face inversion on N170 amplitudes, N170 latency shifts were affected by attentional task demands. While the N170 component was delayed for inverted relative to upright faces in the 'Detect Repetitions' tasks, it was delayed for inverted as well as for upright face stimuli in the 'Detect Digits' task where attention was directed away from the faces. Previous studies have found delayed N170 components with upright faces when the eyes were removed [10], or when attention was directed to single face components [20]. As N170 latency shifts may be linked to a delayed onset of processes involved in the structural analysis of face components, these findings suggest that the timing of structural encoding processes can be affected both by stimulus properties as well as by attentional factors. The configurational analysis of face features will be delayed when structural information is inadequate as a result of face inversion or the absence of face components [10]. It can also be delayed in response to intact, upright faces under conditions where attention is directed away from the configurational analysis of faces towards the analysis of

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[3]To test whether the 'P600f' was delayed for inverted face stimuli, two additional analyses were conducted on ERP mean amplitudes obtained at midline sites between 600 and 700 ms, and 700 and 800 ms post-stimulus, respectively. Between 600 and 700 ms, reliably enhanced positivities for familiar faces were found with upright stimuli at all midline sites (all t (14)>2.43; all P>0.029), but not in response to inverted faces. Beyond 700 ms post-stimulus, no significant familiarity effects were present for either upright or inverted faces.

individual face parts [20] or towards another demanding task (the present study).

The main objective of the present experiment was to study the impact of face inversion on ERP components sensitive to face familiarity ('N400f', 'P600f'). As face recognition is impaired when faces are presented upside-down [34,33], the idea that these components are electrophysiological markers of processes involved in face recognition entails that they should be strongly affected by face inversion. The results obtained in this experiment provide clear evidence in favour of this hypothesis. Relative to upright unfamiliar faces, upright familiar faces elicited an enhanced negativity between 300 and 450 ms post-stimulus ('N400f') which was followed by enlarged positivity between 450 and 650 ms ('P600f'). Both effects were largest at midline electrodes, and showed a centroparietal maximum (see [12] and [3] for similar results). In contrast, no reliable 'N400f' and 'P600f' components were elicited at midline electrodes when faces were inverted, and this difference was reflected in significant familiarity×orientation interactions. While no effects of face familiarity were obtained at all for inverted faces in the 'P600f' time range, small but significant differences between familiar and unfamiliar inverted faces emerged at lateral posterior electrodes in the 'N400f' latency window (see Fig. 4). The presence of an attenuated 'N400f' for inverted familiar faces may reflect the fact that while face inversion impairs face identification processes, it does not make face recognition entirely impossible. Inverted faces may have been successfully identified on some trials, and this may have resulted in a small but reliable 'N400f'.

The sensitivity of the 'N400f' and 'P600f' to face inversion confirms and extends earlier findings [12,3]. In these studies, ERPs to familiar and unfamiliar faces were necessarily obtained in response to different face stimuli. It is therefore hard to completely rule out the possibility that ERP differences between these two stimulus categories are at least partially caused by low-level visual feature differences between stimulus sets. Because stimulus inversion preserves basic visual stimulus attributes, the presence of face familiarity effects for upright faces, and the attenuation or absence of such effects for inverted faces observed in the present study cannot be due to systematic differences in visual-perceptual properties. The fact that face inversion not only has strong effects on behavioural measures of face recognition [34], but also affects ERP components sensitive to face familiarity demonstrates a strong link between these components and cognitive processes involved in the recognition and identification of familiar faces. This pattern of results provides support for the idea that the 'N400f' and 'P600f' are generated by brain processes underlying the recognition and semantic analysis of faces.

According to an influential model of face processing [5], recognising individual faces is achieved by comparing structural descriptions provided by the perceptual analysis of a face with stored representations of individual faces (face recognition units). When such units are activated due to their match with a structural description, person identity nodes in semantic memory can be accessed, resulting in face identification. The present results suggest that the 'N400f' and 'P600f' reflect brain mechanisms involved in the activation of stored representations of familiar faces and subsequent activations of semantic memory, while the N170 is linked to the pre-categorical perceptual analysis of faces. The N170 may thus reflect similar processes as the face-specific N200 component recorded intracortically from ventral occipitotemporal cortex [1,22,28], although the latency difference between these two components makes it unlikely that they are produced by a common neural generator process. The 'N400f' and 'P600f' may be related to the late face-specific positive potential (P350) recorded from posterior lateral temporal and anterior ventral temporal cortex which was found to be sensitive to top–down influences [27]. Further studies employing high-density EEG recordings are necessary to determine the scalp distribution of ERP components sensitive to face familiarity in order to relate them more directly to results obtained with fMRI and intracortical ERP recording, and to determine underlying neural generator processes.

References

[1] T. Allison, A. Puce, D.D. Spencer, G. McCarthy, Electrophysiological studies of human face perception. I. Potentials generated in occipitotemporal cortex by face and non-face stimuli, Cerebral Cortex 9 (1999) 415–430.

[2] S. Bentin, T. Allison, A. Puce, E. Perez, G. McCarthy, Electrophysiological studies of face perception in humans, J. Cogn. Neurosci. 8 (1996) 551–565.

[3] S. Bentin, L.Y. Deouell, Structural encoding and identification in face processing: ERP evidence for separate processes, Cogn. Neuropsychol. 17 (2000) 35–54.

[4] K. Bötzel, S. Schulze, S.R.G. Stodiek, Scalp topography and analysis of intracranial sources of face-evoked potentials, Exp. Brain. Res. 104 (1995) 135–143.

[5] V. Bruce, A. Young, Understanding face recognition, Brit. J. Psychol. 77 (1986) 305–327.

[6] G.M. Davies, H.D. Ellis, J.W. Shepherd, Face recognition accuracy as a function of mode of representation, J. Appl. Psychol. 63 (1978) 180–187.

[7] E. De Renzi, Current issues in prosopagnosia, in: H.D. Ellis et al. (Ed.), Aspects of Face Processing, Nijhoff, Dordrecht, 1986, pp. 243–252.

[8] R. Desimone, T.D. Albright, C.G. Gross, C. Bruce, Stimulus

selective properties of inferior temporal neurons in the macaque, J. Neurosci. 4 (1984) 2051–2062.

[9] R. Diamond, S. Carey, Why faces are and are not special: An effect of expertise, J. Exp. Psychol. Gen. 115 (1986) 107–117.

[10] M. Eimer, Does the face-specific N170 component reflect the activity of a specialized eye detector?, NeuroReport 9 (1998) 2945–2948.

[11] M. Eimer, R.A. McCarthy, Prosopagnosia and structural encoding of faces: Evidence from event-related potentials, NeuroReport 10 (1999) 255–259.

[12] M. Eimer, Event-related brain potentials distinguish processing stages involved in face perception and recognition, Clin. Neurophysiol. 111 (2000) 694–705.

[13] M.J. Farah, Patterns of co-occurrence among the associative agnosias: Implications for visual object recognition, Cogn. Neuropsychol. 8 (1991) 1–19.

[14] I. Gauthier, M.J. Tarr, A.W. Anderson, P. Skudlarski, J.C. Gore, Activation of the middle fusiform 'face area' increases with expertise in recognizing novel objects, Nat. Neurosci. 2 (1999) 568–573.

[15] I. Gauthier, P. Skudlarski, J.C. Gore, A.W. Anderson, Expertise for cars and birds recruits brain areas involved in face recognition, Nat. Neurosci. 3 (2000) 191–197.

[16] N. George, R.J. Dolan, G.R. Fink, G.C. Baylis, C. Russell, J. Driver, Contrast polarity and face recognition in the human fusiform gyrus, Nat. Neurosci. 2 (1999) 574–580.

[17] N. George, J. Evans, N. Fiori, J. Davidoff, B. Renault, Brain events related to normal and moderately scrambled faces, Cogn. Brain Res. 4 (1996) 65–76.

[18] E. Halgren, A.M. Dale, M.I. Sereno, R.H.B. Tootell, K. Marinkovic, B.R. Rosen, Location of human face-selective cortex with respect to retinotopic areas, Hum. Brain Mapp. 7 (1999) 29–37.

[19] J.V. Haxby, L.G. Ungerleider, V.P. Clark, J.L. Schouten, E.A. Hoffman, A. Martin, The effect of face inversion on activity in human neural systems for face and object perception, Neuron 22 (1999) 189–199.

[20] B. Jemel, N. George, L. Chaby, N. Fiori, B. Renault, Differential processing of part-to-whole and part-to-part face priming: An ERP study, NeuroReport 10 (1999) 1069–1075.

[21] N. Kanwisher, J. McDermott, M. M Chun, The Fusiform Face Area: A module in human extrastriate cortex specialized for face perception, J. Neurosci. 17 (1997) 4302–4311.

[22] G. McCarthy, A. Puce, A. Belger, T. Allison, Electrophysiological studies of human face perception II. Response properties of face-specific potentials generated in occipitotemporal cortex, Cerebral Cortex 9 (1999) 431–444.

[23] R.A. McCarthy, E.K. Warrington, Visual associative agnosia: A clinico–anatomical study of a single case, J. Neurol. Neurosurg. Psychiat. 49 (1986) 1233–1240.

[24] J. McNeil, E.K. Warrington, Prosopagnosia: A face-specific disorder, Q. J. Exp. Psychol. 46A (1993) 1–10.

[25] M. Moscovitch, D. Winocur, M. Behrmann, What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition, J. Cogn. Neurosci. 9 (1997) 555–604.

[26] D.I. Perrett, E.T. Rolls, W. Caan, Visual neurons responsive to faces in the monkey temporal cortex, Exp. Brain Res. 47 (1982) 329–342.

[27] A. Puce, T. Allison, M. Asgari, J.C. Gore, G. McCarthy, Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study, J. Neurosci. 16 (1996) 5205–5215.

[28] A. Puce, T. Allison, G. McCarthy, Electrophysiological studies of human face perception III. Effects of top–down processing on face-specific potentials, Cerebral Cortex 9 (1999) 445–458.

[29] B. Rossion, J.F. Delvenne, D. Debatisse, V. Goffaux, R. Bruyer, M. Crommelinck, J. M Guerit, Spatio–temporal localization of the face inversion effect: An event-related potentials study, Biol. Psychol. 50 (1999) 173–189.

[30] B. Rossion, I. Gauthier, M.J. Tarr, P. Despland, R. Bruyer, S. Linotte, M. Crommelinck, The N170 occipito–temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain, NeuroReport 11 (2000) 69–74.

[31] J. Sergent, J.L. Signoret, Varieties of functional deficits in prosopagnosia, Cerebral Cortex 2 (1992) 375–388.

[32] J. Tanaka, M.J. Farah, Parts and wholes in face recognition, Q. J. Exp. Psychol. 46A (1993) 225–246.

[33] T. Valentine, Upside-down faces: A review of the effect of inversion upon face recognition, Brit. J. Psychol. 79 (1988) 471–491.

[34] R.K. Yin, Looking at upside-down faces, J. Exp. Psychol. 81 (1969) 141–145.