Effects of repetition learning on upright, inverted and contrast-reversed face processing using ERPs

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The effects of short-term learning on memory for inverted, contrast-reversed and upright faces were investigated using event-related potentials (ERPs) in a target/nontarget discrimination task following a learning phase of the target. Subjects were equally accurate for all three face types although responding more slowly to inverted and negative faces compared to upright faces. Face type affected both early ERP components P1 and N170, and long-latency components at frontal and parietal sites, reflecting the difficulty of processing inverted faces. Different effects of face type were found for P1 and N170 latencies and amplitudes, suggesting face processing could start around 100–120 ms and is sensitive to facial configuration. Repetition effects were also found on both early and long-latency components. Reduced N170 latency and amplitude for repeated targets are likely due to perceptual priming. Repetition effects on the N250 were delayed for inverted and negative faces, suggesting delayed access to stored facial representations for these formats. Increased frontopolar positivity at 250–300 ms and parietal positivity from 300 to 500 ms reflected familiarity 'old–new' repetition effects that were of similar magnitude for all three face types, indexing the accurate recognition of all faces. Thus, while structural encoding was disrupted by inversion and contrast-reversal, the learning phase was sufficient to abolish the effects of these configural manipulations behaviourally; all three face types were equally well recognised and this was reflected as equally large parietal old–new effects.

Introduction

Face inversion is well known to impair face perception and recognition by disrupting configural information at the encoding stage of face processing (Bartlett and Searcy, 1993; Freire et al., 2000; Leder and Bruce, 2000; Rhodes et al., 1993; Searcy and Bartlett, 1996). Similar to this ''inversion effect'', the ''contrast-reversal effect'' derived from reversing the contrasts in face

pictures also impairs face recognition at the encoding level (Bruce and Langton, 1994; Hole et al., 1999; Kemp et al., 1990; Lewis and Johnston, 1997; White, 2001). Although contrast-reversed (negative) faces seem to be processed holistically like upright faces (Hole et al., 1999), contrast-reversal also disrupts configural information (Kemp et al., 1990; Lewis and Johnston, 1997; Liu and Chaudhuri, 1998), like inversion. Additive effects of inversion and contrast-reversal on performances have suggested that they impair different face processes (Bruce and Langton, 1994; Kemp et al., 1990; Lewis and Johnston, 1997).

Numerous electrophysiological studies recording event-related potentials (ERPs) from the scalp have also investigated inversion effects. P1, an early visual endogenous ERP component appearing around 100–120 ms, seems sensitive to faces (Halit et al., 2000; Itier and Taylor, 2002, 2004a; Linkenkaer-Hansen et al., 1998; Taylor, 2002; Taylor et al., 2001), being shorter and sometimes smaller for upright than inverted faces and larger to faces than to objects categories in some studies (e.g. Itier and Taylor, 2004a). Much more frequently measured, the negative component N170, occurring between 140 and 200 ms after stimulus onset, is systematically larger and often earlier to faces than to other object categories (e.g. Bentin et al., 1996; George et al., 1996; Itier and Taylor, 2004a) and is considered a neurophysiological correlate of face perception. N170 is usually delayed and larger for inverted than upright faces (Bentin et al., 1996; de Haan et al., 2002; Eimer, 2000a; Itier and Taylor, 2002, 2004a; Linkenkaer-Hansen et al., 1998; Rossion et al., 1999, 2000; Sagiv and Bentin, 2001; Séverac-Cauquil et al., 2000; Taylor et al., 2001), and these effects are thought to reflect the processing disruption of face configuration by inversion. Similarly delayed latencies and enlarged amplitudes of N170 were found for negative faces compared to upright faces (Itier and Taylor, 2002), also reflecting face configural disruption by contrast-reversal. N170 is often thought to reflect automatic face processing as some studies failed to find familiarity (e.g. Bentin and Deouell, 2000; Eimer, 2000b; Henson et al., 2003; Schweinberger et al., 2002a) or repetition effects (e.g. Eimer, 2000b; Pfütze et al., 2002; Schweinberger et al., 2002a,b) on N170. However, others have found familiarity effects under the form of smaller N170 amplitude for familiar faces compared to faces seen for the first time (George et al., 1997; Jemel et al., 2003) while others found the opposite effect, that is, larger amplitude for familiar faces (Caharel et al., 2002). Repetition effects on N170 with unfamiliar faces have been reported, restricted to the right hemisphere

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(Campanella et al., 2000), or bilateral (Guillaume and Tiberghien, 2001; Itier and Taylor, 2002); this suggests that this component could be influenced by priming and learning. This discrepancy in the literature could come from the stimuli (Mooney vs. greyscale pictures of faces, same or different pictures of the face between first and second presentation, neutral vs. emotional faces), and/or from the paradigm used (immediate or delayed repetitions, one vs. several repetitions of the same face, etc.). Using a study phase-test phase paradigm, we wished to investigate these repetition effects on the N170 and see whether they would differ according to face type and to the number of target presentations.

Early ERP components are the focus of the majority of face studies. However, in repetition paradigms, late ERP components are also a reliable neurophysiological index of cognitive events as they reflect memory-related processes associated with the repeated items. A negative component found between 200 and 300 ms at temporal parietal sites, the N250, has been shown to be sensitive to immediate (Begleiter et al., 1995; Schweiburger et al., 1995) and short lag face repetitions (Pfütze et al., 2002) but not to long lag repetitions of faces (Schweinberger et al., 2002a). N250 is more negative for repeated than new face stimuli and is a good index of repetition priming (Schweinberger et al., 2002b). However, it has not been investigated with inverted and negative faces. In the present study, it was used to compare the repetition effects of upright, inverted and negative faces. Longer-latency repetition effects are also commonly analysed in the ERP literature. Some experiments using study phase–test phase paradigms have found that during the study (or learning) phase, more positive amplitudes were found for items that would be successfully recognised later in the test phase compared to items that would not be recognised. This effect was called the Dm (difference in subsequent memory) by Paller et al. (1987). Measured during encoding (learning) trials, it is predictive of memory performances at test, and was found for words (Paller et al., 1987) and also for faces (Sommer et al., 1995, 1997). Other studies have measured ERPs during the test phase or recognition trials and have found an ERP correlate of repetition differentiating new and old items. Larger amplitudes are typically found for repeated or studied (old) items compared to new, unstudied items. These so-called "old–new" repetition effects have been found at frontal and parietal sites for words (for a review, see Rugg and Allan, 2000), objects (Curran and Cleary, 2003; Nielsen-Bohlman and Knight, 1994;) and faces (Paller et al., 1999, 2000; Schweinberger et al., 1995; Schweinberger et al., 2002a,b). Although the exact timing and localisation of the effects varies between studies, recent research suggests that an early old–new effect occurring from 300 to 500 ms and situated frontally could be a neural correlate of familiarity, while a later centro-parietal component, from 500 to 800 ms, indexed recollection. In these memory tasks, familiarity usually refers to a global similarity in memory between new and old items while recollection refers to the retrieval of specific information concerning studied items (e.g. context, source, associative information). In an n-back task where upright, inverted and contrast-reversed (negative) faces repeated only once with 0 or 1 intervening face, Itier and Taylor (2002) found frontal and parietal repetition effects that varied in amplitude depending on face type. They hypothesised that the larger old–new effects found for upright faces reflected a better recognition than the other two face types for which the old–new effects appeared weaker. In the present study, we wished to investigate whether sufficient learning of a target face would lead to similar repetition effects between upright, inverted and negative faces.

This would suggest that faces were encoded well enough to be recognised similarly between face types despite configural disruption by inversion and contrast-reversal. We investigated early (P1, N170) and late ERP components as neurophysiological correlates of face processes, while subjects were engaged in a learning phase–test phase paradigm involving upright, inverted and negative faces. As inversion and contrast-reversal impair the encoding stage of face processing, shown in the behavioural literature, we wished to determine if longer exposure to inverted or negative target faces would diminish these effects at the behavioural level, and if so, how this was indexed neurophysiologically. The structural encoding in the ERP face literature, which is different from the general term "encoding" in memory paradigms, refers to the early stages of perception where the facial features are integrated to generate a face representation. This process is believed to occur at the level of the P1–N170. However, note that regardless of whether the trial is a learning trial (in a study phase) or a recognition trial (in a test phase), these early processing stages are still necessary. Accordingly, if the hypothesis of configural disruption at the encoding step of face processing is correct, the disruption of P1 and N170 components by inversion and contrast-reversal should still be seen, even after many repetitions of a target face. However, what should vary with learning are the later repetition effects related to memory processes. In the case of diminished or no behavioural inversion and negative effects, which would suggest learning of these faces despite configural disruption, repetition effects should be similar across face types, or the difference in repetition effects between face types be small. Subjects were presented with blocks of upright, inverted and negative faces and had to recognise target faces intermixed with nontarget new faces, after having learned the targets in a prior learning (study) phase. We thus had several goals: (1) to compare the effects of inversion and contrast reversal on encoding and recognition processes in this paradigm, (2) to investigate whether a long exposure to the target before test would diminish the inversion and contrast-reversal effects at the behavioural level, and the neurophysiological correlates of these effects; (3) to determine the magnitude of the repetition effect with few vs. many repetitions of the target. This last point was investigated by analysing the ERPs recorded in the first half and in the last half of target presentations in the test phase separately.

Material and method

Subjects

Thirty-six subjects ranging from 20 to 33 years (mean age = 25.1 years) participated in the study (18 females) and had normal or corrected-to-normal vision. Nine were left-handed (three females). All subjects gave written informed consent. The procedure was approved by the French Comité Opérationnel pour l'Ethique dans les Sciences de la Vie du CNRS.

Stimuli and apparatus

Stimuli consisted of 378 different unfamiliar Caucasian grey-scale faces (half females). Faces were without paraphernalia, glasses or earrings that could help recognition or discrimination; males were clean-shaven. Eighteen blocks of stimuli were presented, six of upright faces, six of inverted and six of negative

faces. Block order was counterbalanced across subjects and upright, inverted and negative blocks were shuffled with the constraint that two successive blocks could not be of the same face type. Faces presented upright to Subject 1 were presented inverted to Subject 2 and in contrast-reversed format to Subject 3, etc. To prevent recognition from being based on gender discrimination, half of the blocks in each face types were only women's faces; the other half were only men's faces. Each block contained 21 different faces, 20 nontargets and one target face. Stimuli were presented for 500 ms on a computer monitor by the software Presentation that also recorded reaction times (RTs). The intertrial interval was randomised between 1200 and 1600 ms.

Procedure

Subjects were seated in a darkened room in front of the monitor situated 80 cm from them, on which the faces (11 × 11° visual angle) appeared centred on a black background. Subjects fixated a central white cross appearing during the ISI. Each block was composed of two phases. Each block started with

a learning phase in which the target face was presented 10 times; subjects had to press the target button (right control key of the keyboard) each time the face appeared. In the test phase immediately following the learning phase, the target was repeated 12 times pseudo-randomly amongst 20 nontarget faces (Fig. 1) and subjects had to press the target button each time they recognised the target and the nontarget button (left control key) for all other nontarget faces. The target face could be repeated several times successively or could be repeated after one to four intervening distractor faces maximum. Right and left control keys were counterbalanced for targets and nontargets across subjects. For this test phase, subjects were asked to respond as fast and accurately as possible.

Electrophysiology

While subjects were performing the task, EEG activity was recorded from 35 electrodes mounted in an EasyCap (10/10 system), including three ocular electrodes monitoring vertical and horizontal eye movements. Electrode impedances were kept below
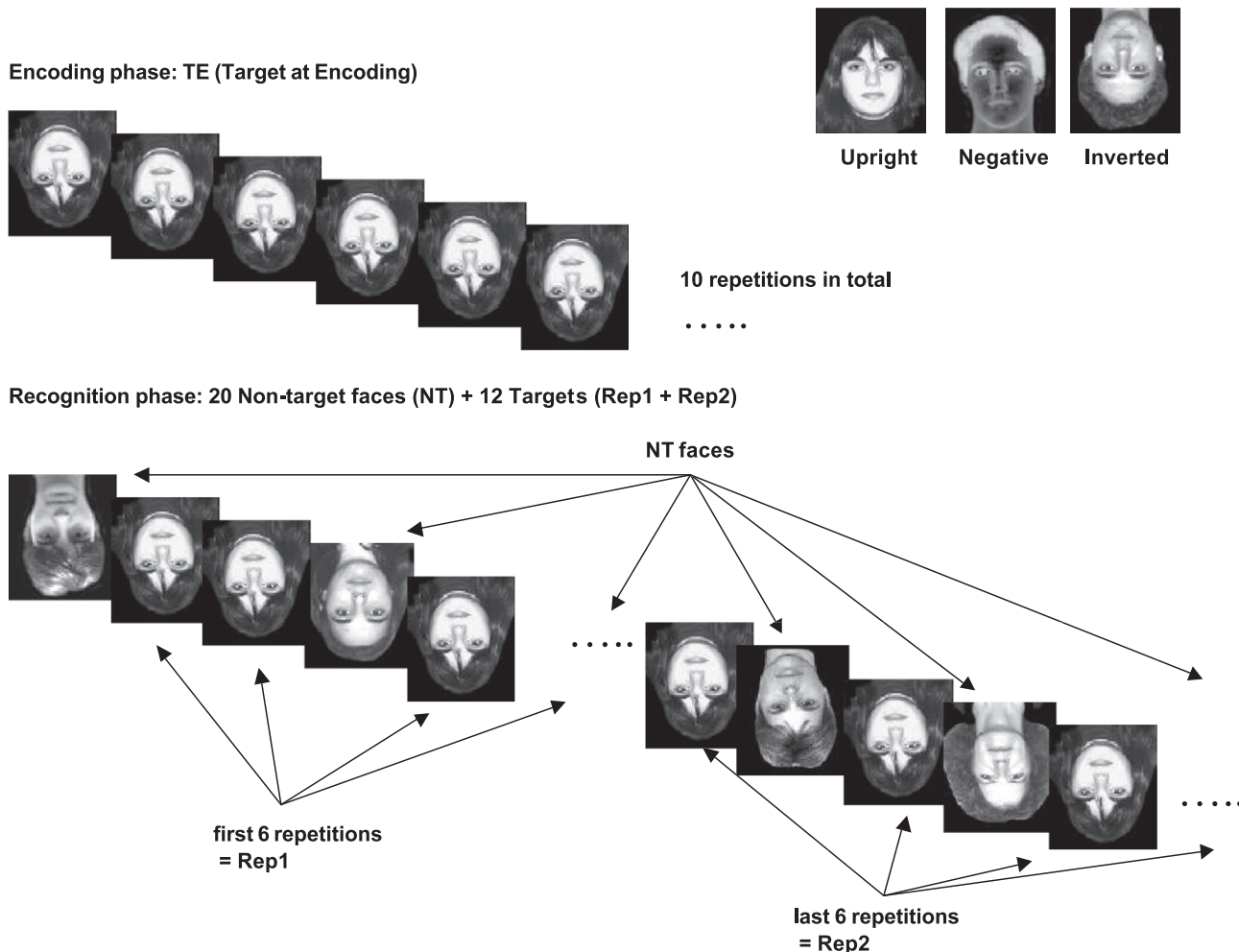

Fig. 1. Schematic view of the experiment. On the top right corner, examples of upright, negative and inverted faces used are displayed. The experiment consisted of a learning phase followed immediately by a test phase. In the learning phase, the target was presented 10 consecutive times. In the test phase, the target was repeated 12 times, intermixed with (new) nontarget (NT) faces. The first six (Rep1) and the last six (Rep2) repetitions of the target were analysed separately and compared to NT faces.

5 kΩ. During acquisition, Cz was the reference lead, and an average reference was calculated off-line. NeuroScan 4.1 recorded continuous EEG with a sampling rate of 500 Hz (bandpass 0.1–100 Hz) and the signal was amplified using SynAmps system. Only correct trials were analysed. After baseline correction, trials contaminated with ocular movements or artefacts >100 μV were rejected. For each face type (upright, inverted and negative), ERPs were averaged according to four conditions: encoding/learning of targets during the study phase (TE), nontargets (NT), the first six target presentations (Rep1) and the last six target presentations (Rep2) in the test phase. Averaged trials were digitally filtered (0.1–30 Hz).

Data analyses

Hits were defined as correct responses to targets. Correct responses to nontargets were defined as correct rejections. Percentages of hits/correct rejections and reaction times (RTs) were calculated for each subject in each condition. They were analysed using 3×3 ANOVAs, where face type (upright, inverted and negative) and conditions (NT, Rep1 and Rep2) were intra-subject factors.

Peak measures of P1 (maximal around 110 ms) and N170 (maximal around 160 ms) components were taken within a ± 30 ms window centred on the maximum of the grand-average means. P1 and N170 were measured at TP9, TP10, P7, P8, PO9, PO10, O1 and O2 sites. Latencies were measured at the electrode where components were maximal over each hemisphere and the amplitudes at each of the four electrodes were taken at this latency (Picton et al., 2000). Repeated-measures ANOVAs were run on peak latencies and amplitudes using Greenhouse–Geisser adjusted degrees of freedom and post hoc *t* statistics used Bonferroni corrections for multiple comparisons.

ERPs in study and test phases were analysed separately as task requirements, cognitive processes, probability of the target appearance and average time between successive repetitions were different in the two phases. Face type (upright, inverted, negative) and hemisphere were intra-subject factors. In the test phase, condition

(NT, Rep1 and Rep2) was a further intra-subject factor. Electrode (4) was a factor for amplitude. However, a first analysis revealed that all the effects found with P1 were seen at O1 and O2 only; thus, P1 amplitude measures were analysed using only these two electrodes.

Longer-latency ERPs were also analysed by calculating mean amplitudes for each face type and condition within eight 50-ms windows starting from 200 to 600 ms at frontal sites Fp1, Fp2, F3, F4 and Fz. The same was done at parietal electrodes Pz and POz. The choice of these electrodes derives from the literature on old–new repetition effects (e.g. Paller et al., 1999; Rugg and Allan, 2000) and from a previous n-back study using the same face types (Itier and Taylor, 2002). Finally, we measured the N250 (e.g. Schweinberger et al., 1995; Schweinberger et al., 2002a,b) at P7, P8, PO9, PO10 and TP9, TP10 sites as mean amplitudes calculated within three 50-ms windows from 250 to 400 ms. All time windows were defined after inspection of the grand averages. These longer-latency ERPs were analysed only for the test phase.

Results

Behavioural results

Hits and correct rejections

No face type effects were found for hits. A main effect of condition [$F(1.9,68.9) = 14.93$, $P < 0.0001$] was due to correct responses to nontarget (NT) faces being higher than hits to repeated targets Rep1 and Rep2 ($P < 0.0001$ and $P < 0.004$, respectively) (Fig. 2). There was a trend for Rep2 faces to be better recognised than Rep1 ($P < 0.96$) as seen in Fig. 2. When we reanalysed the data with only Rep1 and Rep2, the main effect of condition was still significant [$F(1,36) = 4.98$, $P < 0.032$], Rep2 faces being slightly better recognised than Rep1 faces (95.5% vs. 94.3%).

Reaction times

A main effect of face type [$F(1.7,61.8) = 38.71$, $P < 0.0001$] was due to upright faces having faster RTs than inverted and
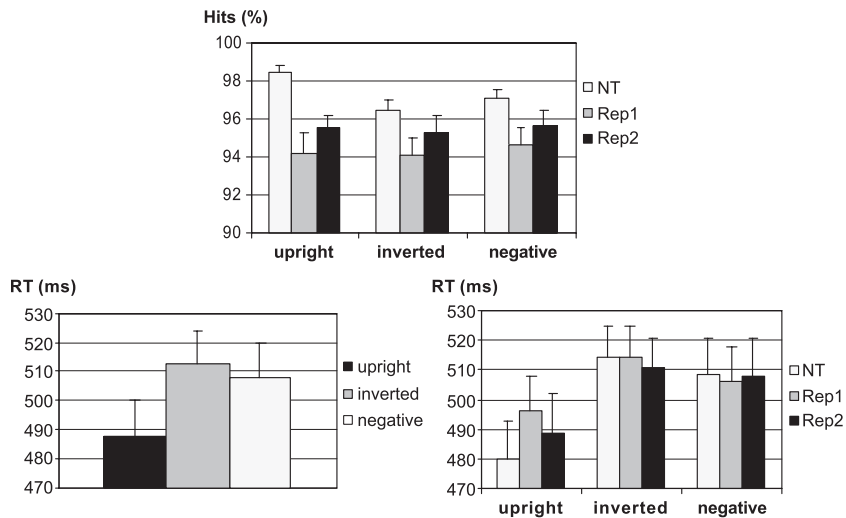

Fig. 2. Mean hits for targets and correct rejections for nontargets (%) and reaction times (RT) for face types (upright, inverted, negative) and memory conditions (NT, Rep1, Rep2). Note the slightly larger hit rate for Rep2 condition for all face types.

negative faces ($P < 0.0001$ for each comparison) that did not differ (Fig. 2). No condition effect was found. However, a face type × condition interaction [$F(3,110.2) = 5.28$, $P < 0.002$] revealed that NT elicited faster responses than repeated targets for upright faces only; there was a trend for faster RT for Rep2 compared to Rep1 for upright faces (Fig. 2) but it did not reach significance. No condition differences were found for inverted and negative faces.

Early ERP components

P1 component

Study phase.

Latency. A main effect of face type [$F(1.6,57.4) = 16.91$, $P < 0.0001$] was due to delayed P1 for inverted compared to upright and negative faces ($P < 0.0001$ for each comparison) (Fig. 3).

Amplitude. P1 was larger for inverted than negative and upright faces [$F(1.8,62.5) = 44.37$, $P < 0.0001$]; as seen in Fig. 3, P1 to upright faces was also larger than negative faces ($P < 0.0001$).

Test phase.

Latency. P1 was delayed [$F(1.8,64.2) = 25.33$, $P < 0.0001$] for inverted compared to upright and negative faces ($P < 0.0001$ for each comparison) that did not differ, similar to the study phase. No memory condition effect was found.

Amplitude. P1 was also larger [$F(1.8,61.6) = 52.65$, $P < 0.0001$] for inverted compared to upright and negative faces ($P < 0.0001$ for each comparison), and also larger for upright than negative faces ($P < 0.0001$), with no effect of condition.

N170 component

Study phase.

Latency. A main effect of face type [$F(1.9,65.1) = 45.56$, $P < 0.0001$] was due to N170 being delayed for both inverted and
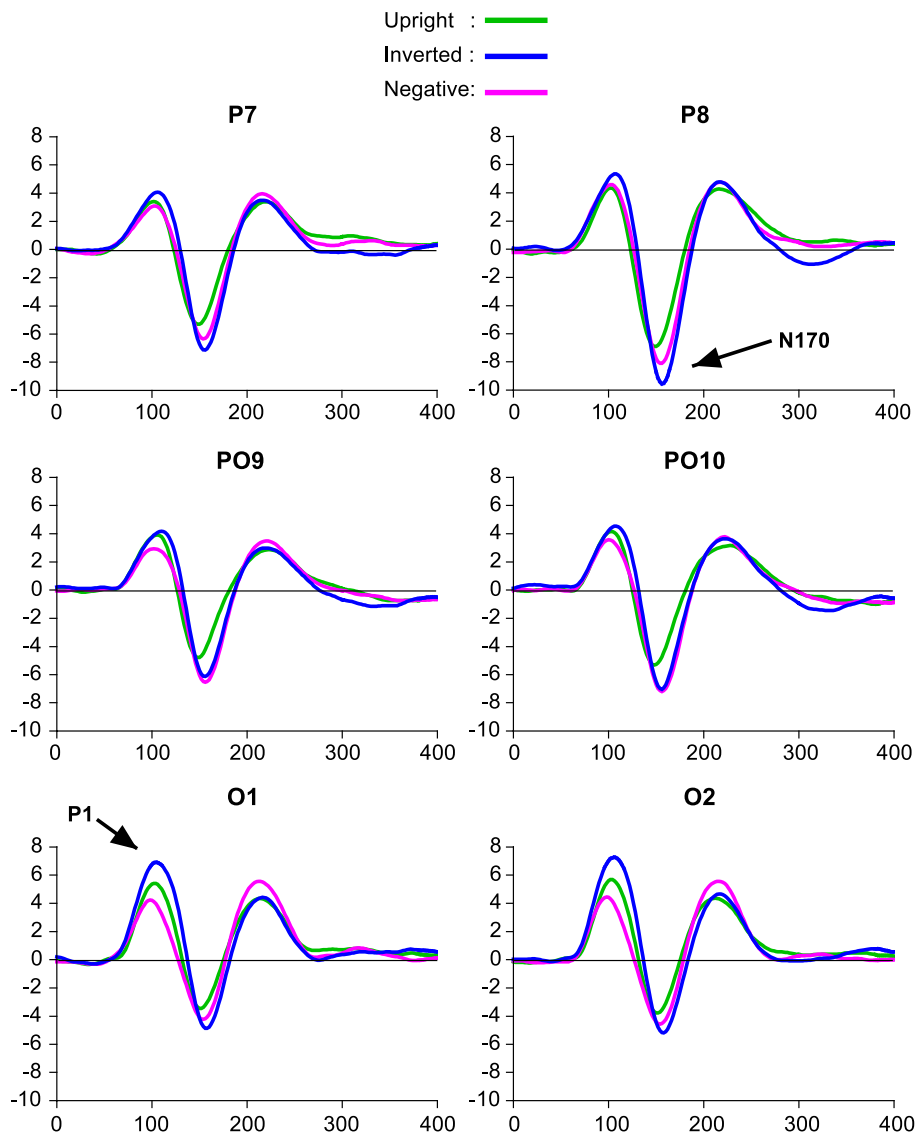

Fig. 3. Grand-averaged ERPs, showing the P1 and N170 components at posterior parietal (P7/P8), parietooccipital (PO9/PO10) and occipital (O1/O2) electrodes for upright, inverted and negative faces.

negative compared to upright faces ($P < 0.0001$ for each comparison). N170 for inverted and negative faces did not differ significantly.

Amplitude. N170 was larger for inverted and negative compared to upright faces [main effect of type, $F(1.9,68.1) = 12.88$, $P < 0.0001$; $P < 0.0001$ for each pairwise comparison] and larger over the right than the left hemisphere [$F(119.7,19.2) = 6.22$, $P < 0.017$]. A main effect of electrode [$F(1.9,69.2) = 21.41$, $P < 0.0001$] reflected that N170 was largest at posterior parietal (P7, P8) and parietal–occipital (PO9, PO10) sites. Inverted and negative faces did not differ except at P7 and P8 electrodes [face type × electrode interaction, $F(3.3,114.8) = 7.41$, $P < 0.0001$] where inverted faces were larger than negative faces (Fig. 3). A hemisphere × electrode interaction [$F(1,4,49.78) = 4.17$, $P < 0.033$] was due to the larger amplitudes on the right hemisphere being restricted to P8 and PO10 sites, that is, to the electrodes where N170 was maximal.

Test phase.

Latency. N170 was again delayed for both inverted and negative faces compared to upright faces [$F(1.9,68.2) = 80.93$, $P < 0.0001$; pairwise comparisons $P < 0.0001$], with no difference between inverted and negative faces. A main effect of condition [$F(1.7,60.2) = 14.5$, $P < 0.0001$] reflected shorter N170s for repeated compared to nontarget faces (Fig. 4), with no significant difference between Rep1 and Rep2 faces.

Amplitude. A main effect of face type [$F(1.8,62.5) = 44.98$, $P < 0.0001$] was due to larger N170s for inverted and negative compared to upright faces ($P < 0.0001$ for each comparison). A condition effect was also found [$F(1.8,62.4) = 7.54$, $P < 0.002$] due to smaller amplitudes for Rep2 than NT and Rep1 faces ($P < 0.044$ and $P < 0.006$, respectively) that did not differ (Fig. 4). A main effect of electrode [$F(2.1,72.1) = 25.87$, $P < 0.0001$]

reflected the largest N170 amplitudes at P7/8 and PO9/10 sites; a face type × electrode interaction [$F(3,103.3) = 9.04$, $P < 0.0001$] was due to larger amplitudes for inverted than negative faces at these sites only.

Summary

Face type effects were found as early as P1, on both latency and amplitude, and varied with inversion and contrast-reversal. Face type also affected N170 latency and amplitude, similarly for inverted and negative faces, being larger and later than for upright faces. For both components, the same face type effects were seen for study and test phase analyses. A repetition effect was found on N170 latency for both sets of repeated faces, but on N170 amplitude only for Rep2 faces.

Late components

Main effects of face type, memory conditions, electrode and their interactions on mean amplitudes between 200 and 600 ms at frontal and parietal electrodes are seen in Table 1 with F and P values. The analysis of the posterior temporal N250 component is displayed in Table 2.

Face type effects

Mean amplitude analyses at frontal sites (Fp1, Fp2, F3, F4, Fz) revealed that a main effect of face type was present from 200 to 400 ms. Between 200 and 250 ms, greater negativity was seen for contrast-reversed compared to inverted and upright faces, that did not differ, and this corresponded to the amplitude of the frontal N2 (Fig. 5A). Between 250 and 350 ms, mean amplitudes were largest for inverted faces at frontal electrodes, amplitudes for negative and upright faces not differing (Fig. 5A).
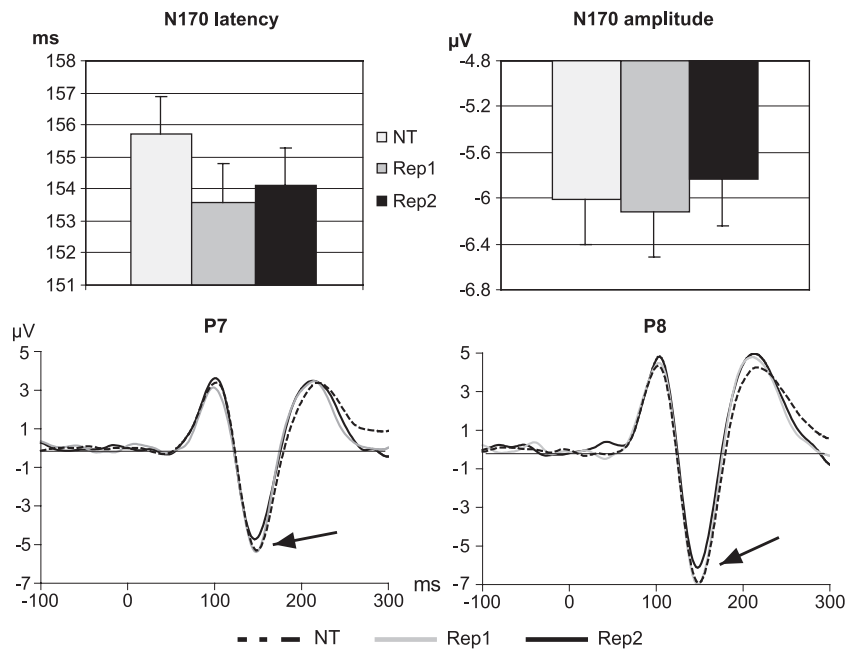
Fig. 4. Condition effects on N170 latency and amplitude. Bar graphs display the mean latency and amplitudes across electrodes, while ERPs are displayed only for P7 and P8 electrodes. NT = nontargets; Rep1 = first six target repetitions; Rep2 = last six target repetitions.

Table 1
F and P values of the main effects of face type, condition, electrode, and their interactions, for mean amplitudes calculated at (A) frontal and (B) parietal electrodes, between 200 and 600 ms (eight 50-ms time windows)

	Main effects	Statistics	200–250 ms	250–300 ms	300–350 ms	350–400 ms	400–450 ms	450–500 ms	500–550 ms	550–600 ms
Frontal electrodes Fp1/Fp2 F3/F4 Fz	Face type	F value	9	4.81	21.14	5.26	–	–	–	–
		P value	0.0001	0.011	0.0001	0.012				
	Condition	F value	4.2	35.48	22.56	–	24.05	8.73	–	–
		P value	0.02	0.0001	0.0001		0.0001	0.0001		
	Type × condition	F value	–	–	–	8.62	–	3.46	–	–
		P value				0.0001		0.019		
	Electrode	F value	71.02	38.95	9.64	86.53	72.04	27.89	–	–
		P value	0.0001	0.0001	0.002	0.0001	0.0001	0.0001		
	Type × electrode	F value	–	6.76	10.07	8.11	–	–	4.69	–
		P value		0.001	0.0001	0.0001			0.023	
	Condition × electrode	F value	–	3.53	–	7.69	8.34	–	–	–
		P value		0.008		0.0001	0.0001			
Parietal electrodes Pz–POz	Face type	F value	32.97	10.04	–	4.88	8.34	12.5	13.15	8.03
		P value	0.0001	0.0001		0.012	0.002	0.0001	0.0001	0.001
	Condition	F value	6.93	3.97	9.24	40.51	18.93	–	–	7.77
		P value	0.002	0.025	0.0001	0.0001	0.0001			0.002
	Electrode	F value	112.39	–	23.12	22.09	12.81	7.36	–	7.93
		P value	0.0001		0.0001	0.0001	0.001	0.01		0.008
	Type × condition	F value	–	–	–	–	–	4.26	5.87	–
		P value						0.008	0.007	
	Type × electrode	F value	19.63	–	–	7.41	–	–	–	8.11
		P value	0.0001			0.001				0.001
	Condition × electrode	F value	7.11	–	8.85	6.79	4.09	4.65	4.1	–
		P value	0.002		0.001	0.002	0.024	0.017	0.029	

From 350 to 400 ms, both negative and inverted faces elicited larger amplitudes than upright faces. An effect of electrode was found from 200 to 500 ms. Between 200 and 300 ms, mean amplitudes were maximal at Fp1/Fp2 sites while between 300 and 500 ms they were minimal at these sites and maximal at F3, F4 and Fz sites with no significant differences amongst these three electrodes. The type × electrode interaction found from 250 to 400 ms revealed that the amplitude difference between inverted and the other two face types was maximal at Fp1 and Fp2 electrodes.

At parietal sites Pz and POz, face type effects were seen from 200 to 300 ms and from 350 to 600 ms. The first period reflected larger amplitudes for upright than inverted faces (and larger amplitudes for upright than negative face from 250 to 300 ms). In contrast, in the second period, inverted and negative faces elicited larger amplitudes than upright faces (Fig. 5A). In the 200–250 ms window, amplitudes were larger at POz than at Pz electrode, while the opposite was found between 300 and 500 ms before going back to larger amplitudes at POz site in the 550–600 ms window (see electrode effect in Table 1). The type × electrode interactions found in three time windows were due simply to type differences being always maximal at POz, regardless of whether mean amplitudes were larger at POz or at Pz.

Repetition effects

Memory conditions (including target in the study phase as a baseline comparison) are shown at all electrodes in Fig. 6.

The N250 component

As shown in Table 2, repetition (condition) effects were found from 250 to 400 ms. From 250 to 350 ms, repeated faces elicited more negative amplitudes than nontarget (new) faces (Fig. 6). Rep2 elicited more negative amplitudes than Rep1 faces at P7/P8 sites from 250 to 300 ms (condition × electrode interaction), but no significant differences between Rep1 and Rep2 faces were seen in the 300–350 ms interval. Between 350 and 400 ms, amplitude for Rep2 was more negative than for Rep1 and NT faces that did not differ. The repetition effect was not found for inverted faces between 250 and 300 ms and for upright faces between 350 and 400 ms (type × condition interactions). Thus, the repetition effect on the N250 amplitude was seen from 250 to 350 ms for upright faces, from 300 to 400 ms for inverted faces and from 250 to 400

Table 2
Analysis of the N250 ERP component measured as mean amplitudes over posterior temporal sites, between 250 and 400 ms (three 50-ms time windows)

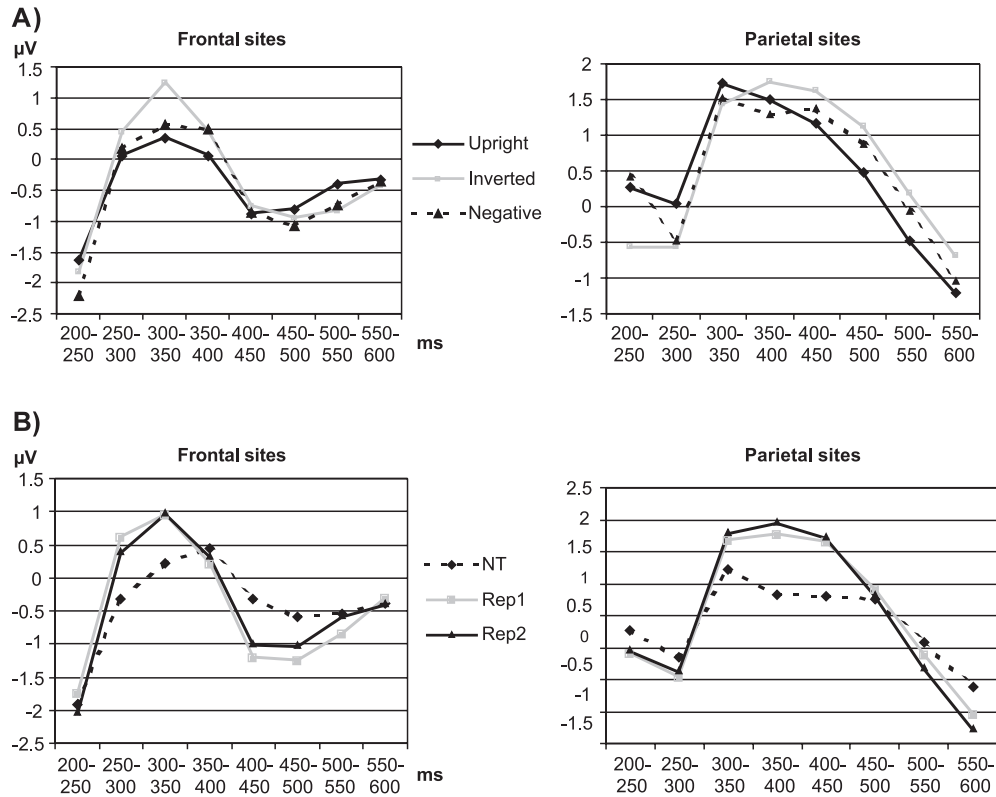|	Main effects	Statistics	250–300 ms	300–350 ms	350–400 ms
N250 mean amplitude P7, P8, PO9, PO10, TP9, TP10	Condition	F value	23.56	46.13	12.28
		P value	0.0001	0.0001	0.0001
	Type × condition	F value	5.57	–	15.38
		P value	0.001		0.0001
	Electrode	F value	–	16.45	28.83
		P value		0.0001	0.0001
	condition × Electrode	F value	6.16	–	10.42
		P value	0.001		0.0001

A)

B)

Fig. 5. Mean amplitudes for eight 50-ms time windows at frontal (Fp1, Fp2, F3, F4, Fz) and parietal (Pz, POz) sites for (A) upright, inverted and negative faces and (B) nontargets (NT) and repeated faces (Rep1 and Rep2).

ms for contrast-reversed faces. In other words, the repetition effect was delayed by approximately 50 ms for inverted faces and lasted 50 ms more for both inverted and negative faces compared to upright faces.

Frontal and parietal repetition effects

At frontal sites, two condition effects were seen that distinguished NT and repeated target faces at two different time periods. A large increase in amplitude for Rep1 and Rep2 compared to NT faces was seen from 250 to 350 ms, while from 400 to 500 ms, amplitudes decreased more for repeated than for NT faces (Fig. 5B). While the first effect reflects a repetition effect at frontal sites, maximal at Fp1/2 sites (see Fig. 7 at 276 and 304 ms), the second reflects a repetition effect occurring at parietal sites between 300 and 450 ms that was seen in opposite polarity at frontotemporal sites, and from 400 ms at frontal sites (Fp1/2, F3/4, Fz) (see 412 ms in Fig. 7). This reflected an evolution of this parietal repetition effect with time. There were thus two different repetition effects occurring at different times and showing different topographies (Figs. 5B and 7).

At frontal sites, a condition × electrode interaction was found in three different time windows (Table 1). From 250 to 300 ms, the difference simply reflected smaller amplitudes at Fz electrode for NT faces. From 350 to 400 ms, there was no condition effect yet a condition × electrode as well as a face type × condition interactions were seen. The face type × condition effect was due to larger amplitudes for NT than for repeated faces only for upright faces. As the condition effect

was seen only from 400 ms on, this interaction with face type reflected the faster onset of the second frontal repetition effect (and thus the faster onset of parietal/frontotemporal repetition effect) for upright faces compared to inverted and negative faces. The condition × electrode interaction found from 350 to 400 ms reflected larger amplitudes for upright NT faces compared to upright repeated faces that were seen only at Fp1/Fp2 electrodes. This effect of larger amplitudes for NT than repeated faces at frontal pole sites was then seen for all faces from 400 to 450 ms (only a condition × electrode interaction in that window). Again, this reflected the earlier onset of the parietal repetition effect for upright faces (seen polarity reversed at frontal sites), followed approximately 50 ms later by that of inverted and negative faces.

At parietal sites, a condition × electrode interaction was found from 200 to 250 ms and from 300 to 550 ms (Table 1). In the 200–250 ms period, this interaction reflected condition differences being maximal at POz. More interestingly, from 300 to 450 ms, the interaction reflected larger amplitudes for Rep2 than Rep1 (Fig. 8) which was maximal at Pz electrode, followed by smaller amplitudes for Rep2 compared to Rep1 at POz between 450 and 500 ms. This larger amplitude for Rep2 than Rep1 faces was found only for upright faces (face type × condition × electrode interaction, significant between 350 and 400 ms). Finally, the interaction from 500 to 550 ms reflected larger amplitudes at Pz than POz only for NT faces.

Type × condition interactions at parietal sites were seen from 450 to 550 ms and reflected the end of the repetition effect for upright and negative faces, while it was still occurring for inverted
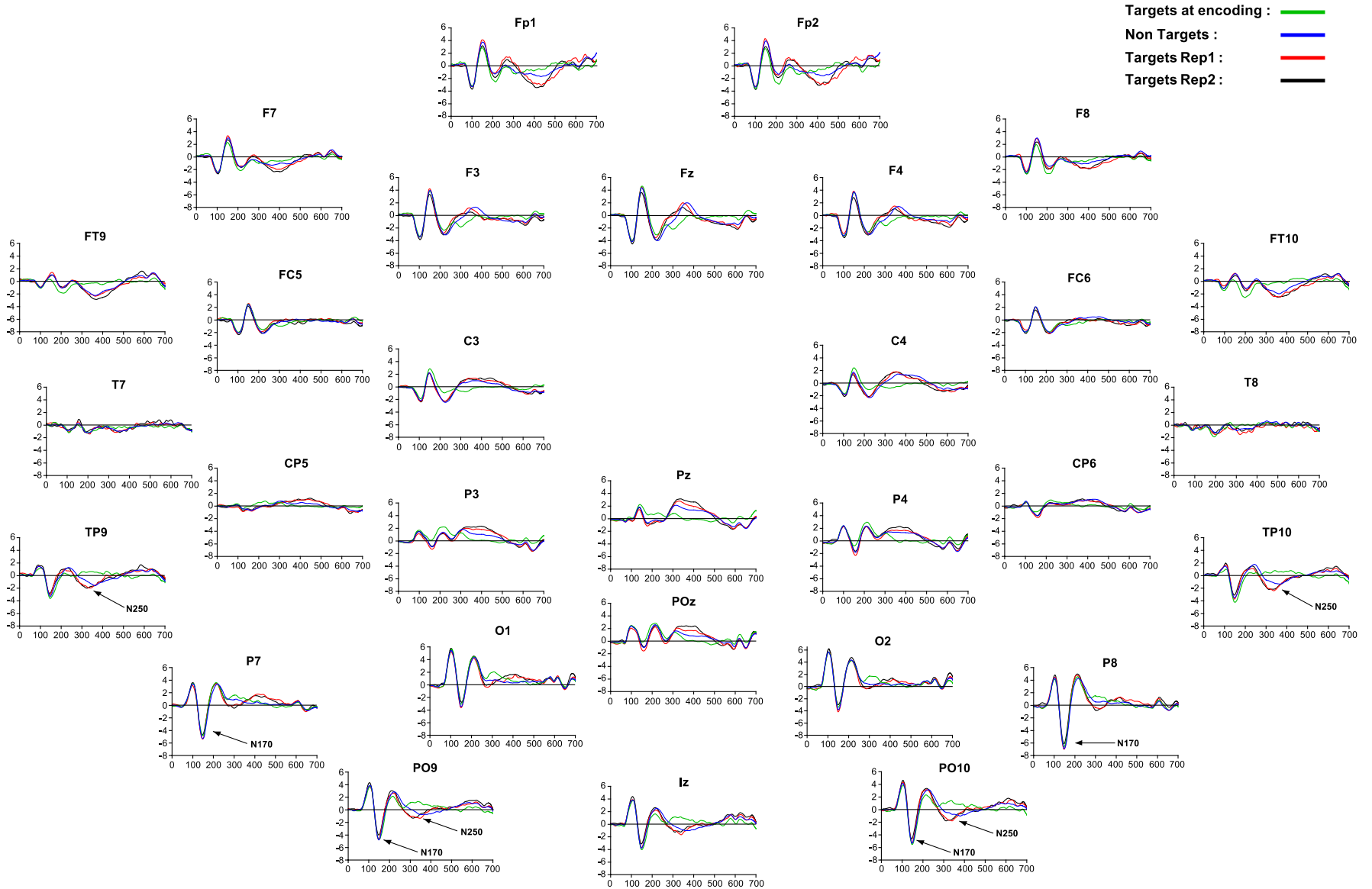
Fig. 6. Grand-averaged ERPs for the four conditions for upright faces at all electrode sites. Note the N170 and N250 at posterior temporal sites.
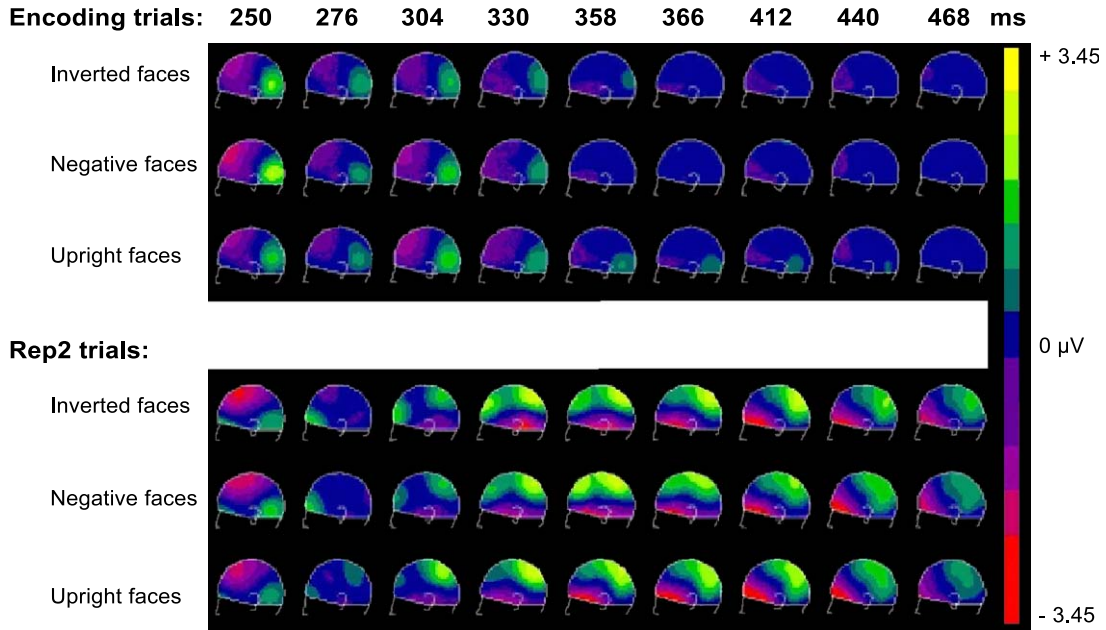
Fig. 7. Scalp voltage topographies displayed for inverted, negative and upright faces for the encoding/learning trials (TE) and for Rep2 trials at nine different latencies, showing the temporal evolution of these longer-latency distributional effects.

faces (Fig. 8). From 500 to 550 ms, the effect was ending for inverted faces while it reversed in favour of larger amplitudes for NT than Rep faces for upright and negative faces. Thus, between 450 and 500 ms, the face type × condition interaction simply reflected a delayed repetition effect for inverted faces compared to the other two face types.
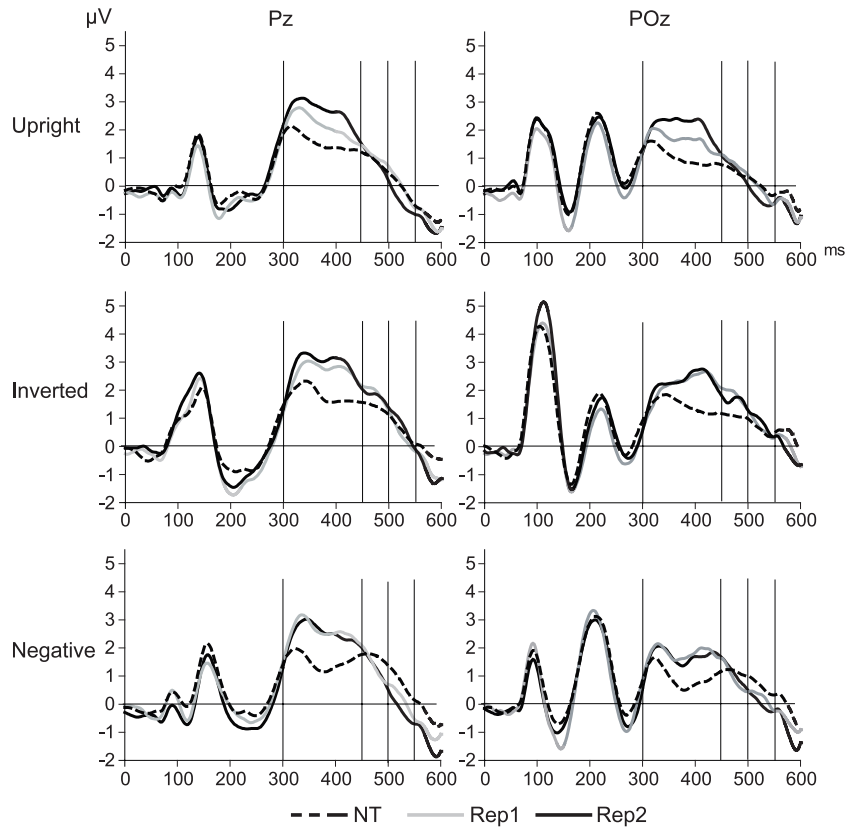

Fig. 8. The parietal repetition effect displayed at Pz and POz electrodes for upright, inverted and negative faces. The vertical bars at 450, 500, 550 ms represent the windows in which face type × condition interactions were found. The vertical bar at 300 ms shows the start of the parietal repetition effect.

Discussion

In this face recognition study, we investigated whether sufficient learning could abolish inversion and contrast-reversal effects, and if that was reflected in the ERP components.

Behavioural results showed that in the test phase, accuracy for upright, inverted and negative faces was not significantly different, either at condition Rep1 or Rep2. Thus, presenting a face 10 times was sufficient for subjects to perform equally well for all three face types. This result is due to the learning phase, as in a prior study using the same faces in a repetition task with no learning phase (n-back task with 0- and 1-lag), performances were reduced for inverted and negative faces compared to upright faces, even for immediately repeated faces (Itier and Taylor, 2002). However, inverted and negative faces were processed more slowly here than upright faces as revealed by increased reaction times for these two face types, reflecting the difficulty of processing such stimuli even after a learning phase including only one target face. Generally speaking, this study was much easier than the previous n-back task (Itier and Taylor, 2002). The percentage of hits on repeated faces were very high for all face types and similar to the hit rates obtained for immediate repetitions in the previous study, although there could be zero to four intervening faces between target repetitions. Similarly, RTs were generally faster here, about 50 to 60 ms faster than in the n-back task at condition 0-lag, and about 130 to 150 ms faster compared to the previous 1-lag condition. The task ease probably contributed to the absence of face type effects. We may not have found similar results if the task had involved several targets at a time rather than only one. However, the present data show that with sufficient learning and reduced memory load, inverted and contrast-reversal effects can be abolished at the accuracy level, although it seems that the processing of those stimuli, as reflected by reaction times, remains longer than that for upright faces.

There was no priming effect on the behavioural data when NT were compared to repeated faces (no decreased RTs or better performances for repeated faces compared to new faces). It seemed easier for subjects to discriminate nontargets as new faces than to recognise the targets regardless of face type. For upright faces, subjects were also faster to respond to NT than to repeated faces, suggesting a different strategy for upright than the other two face types, although task ease could again explain this result. However, when only repeated faces were compared, hit rates were better for Rep2 than Rep1 faces for all face types (Fig. 2), suggesting a learning effect due to the number of target presentations. It is possible that a larger number of repetitions were necessary to obtain reduced RTs. Only for upright faces was there a trend for RTs to Rep2 to be slightly faster than for Rep1. With a larger number of target presentations, this may have reached significance not only for upright but also for inverted and negative faces. Even if the effect was small and limited to accuracy, it nevertheless shows that learning an inverted or a contrast-reversed face is possible, provided a sufficient number of repetitions.

Effects of face type on ERPs

Although no differences in accuracy were found between types of faces, RTs were slowed for inverted and negative faces as were latencies of both P1 and N170, along with amplitude modulations. P1 was delayed and larger for inverted faces compared to upright faces, but was only smaller for negative faces. These results for inverted faces agree with other studies in adults (Itier and Taylor, 2002; Linkenkaer-Hansen et al., 1998; Taylor et al., 2001) and children (Itier and Taylor, 2004b,c; Taylor et al., 2001) showing face inversion effects as early as the P1 component and suggest an early face processing stage around 110 ms (Debruille et al., 1998; Itier and Taylor, 2004a; Taylor, 2002) sensitive to face configuration (Halit et al., 2000; Itier and Taylor, 2002, 2004a,b,c). These early effects of face processing have also been found in magnetoencephalography (MEG) studies (Halgren et al., 2000; Linkenkaer-Hansen et al., 1998) and the recent finding by Liu et al. (2002) of larger amplitudes of the M100, likely the MEG equivalent of P1, for faces than for objects supported the earlier studies that M100 is face-sensitive. The ERP P1 was also found to be significantly larger to upright and inverted faces than to six categories of objects (Itier and Taylor, 2004a). Thus, the present ERP data contribute as further evidence that facial configuration processing starts around the time of P1. Configural disruption by inversion is likely the reason for the increased latency and amplitude of P1 for inverted compared to upright faces. The amplitude difference between negative and upright faces could reflect, in addition to the effects of configural disruption, an influence of luminance and contrast known to act upon neurons of early visual areas (V1, V2) that are part of the numerous extrastriate regions from which P1 originates (Di Russo et al., 2001; Foxe and Simpson, 2002). The background of our stimuli was always black, resulting in the negative faces being darker than the positive ones. In contrast, upright and inverted faces were globally equiluminant, and luminance and mean contrast of the pictures could thus not account for the inversion effects on P1. Local contrasts, however, are changed between inverted and upright faces, resulting in an asymmetry between the upper and lower parts of the face picture, which could account for the effects. However, local contrasts and their repartition in the image define a configuration and the effects on P1 are thus not low-level (see discussion in Itier and Taylor, 2004a). Alternatively, attention could be a factor influencing these early effects on P1, as also hypothesised by others (Halit et al., 2000; Taylor, 2002; Taylor et al., 2001). However, it would seem reasonable to expect similar attentional effects for inverted and negative faces as they are more difficult to process usually. Yet, effects on P1 were different between inverted and contrast-reversed faces. Although not always found (e.g. Rossion et al., 1999), P1 is more often not analysed and it is thus difficult to draw firm conclusions. Furthermore, effects seen on P1 may be task-dependent and modulated by other additional factors that vary from study to study, rendering the interpretations subject to debate. Nevertheless, the present data and the others reviewed above strongly suggest that there is more face processing happening around 100–120 ms than previously thought. More carefully controlled stimuli should be used in future studies to investigate systematically the sensitivity of P1 to faces.

The N170 component showed the classic inversion effects of delayed latency and enhanced amplitude (Bentin et al., 1996; de Haan et al., 2002; Eimer, 2000a; Itier and Taylor, 2002; Linkenkaer-Hansen et al., 1998; Rossion et al., 1999, 2000; Sagiv and Bentin, 2001; Séverac-Cauquil et al., 2000; Taylor et al., 2001) and the effects of contrast-reversal on this component replicated those of Itier and Taylor (2002). No differences between inverted and negative faces were found on N170 except at posterior parietal sites where N170 was slightly larger for inverted compared to negative faces. N170 to contrast-reversed faces was also larger than to inverted faces at occipital sites in our previous study, suggesting

different underlying generators for inverted and negative faces (Itier et al., in press). Thus, inversion and contrast-reversal have a different impact on P1 and N170, reflecting different disruptions of face structural encoding can lead to similar behavioural impairments. Itier and Taylor (2002) hypothesised that P1 reflected a holistic processing stage (the perception/detection of a face as a face) while N170 reflected the configural/relational processing enabling later identity recognition. The present data agree with this hypothesis of face detection at approximately 100–120 ms and face identity processing around 170 ms (see repetition effects on N170 in the following section), supported recently by Liu et al. (2002) in MEG. P1 and N170 thus seem to reflect two early stages of face processing, which are differentially sensitive to inversion and contrast-reversal. The data also show that learning inverted and contrast-reversed faces does not overcome these configural disruptions on early face processing steps. This agrees with a recent study showing that even after 1100 exposures to the same inverted faces, subjects were still incapable of processing them holistically (Robbins and McKone, 2003). It seems that the perception of these configurally changed faces remains disrupted but that, with enough repetitions, other mechanisms enable the facial representations to be stable enough to lead to accurate recognition.

Face type also affected long-latency ERPs at frontal and parietal sites during the test phase. From 250 to 400 ms, amplitudes were more positive for inverted compared to upright and negative faces at all frontal sites analysed, but the effect was most pronounced at frontal pole electrodes Fp1–Fp2. Inverted faces also yielded larger amplitudes at parietal sites from 350 to 600 ms, the effect being larger at the POz than Pz electrode. These effects are similar to those reported by Itier and Taylor (2002) and likely reflect the difficulty associated with processing inverted and negative faces due to configural disruption.

Effects of repetition on ERPs

Repetition effects were seen on both early and late ERP components. N170 was affected by target repetitions on both latency and amplitude, regardless of face type. Shorter latencies were found for both Rep1 and Rep2 faces while the reduced amplitude was only found for Rep2 faces (Fig. 4). These effects are similar to the phenomenon found in monkey single cell recordings called "repetition suppression" (for a review, see Desimone, 1996; Wiggs and Martin, 1998). Repetition suppression refers to a reduced response of neurons for a repetition of a stimulus but not for the presentation of novel stimuli. Interestingly, up to 1/3 of the inferior temporal neurons of monkeys show repetition suppression and the N170 likely originates in part from the inferior temporal regions. Repetition suppression can also be seen as early as 100 ms in the monkey and would thus not be surprising at approximately 150 ms in humans. According to Wiggs and Martin (1998), this neuronal mechanism could be the basis of perceptual priming, as in PET and fMRI studies, perceptual priming reduces activity in occipital and/or inferior temporal brain regions (Buckner et al., 1998; Cabeza and Nyberg, 1997, 2000). Repetition priming usually refers to the improvement of task performance for repeated stimuli and can be seen as a decrease in activation of specific areas (for a review, see Schacter and Buckner, 1998) that facilitates the perception of the repeated items. Although small, we did find a priming effect on behavioural measures as Rep2 faces led to better performances than Rep1 faces, regardless of face type. However, no reduction of N170 amplitude for Rep1 faces was seen, suggest-

ing the number of presentations was important. This contrasts with the fact that priming can usually be seen after a single short exposure to a stimulus. Alternatively, although the amplitude was not modified for Rep1 faces, the latency was already shorter for Rep1 compared to nontargets, suggesting a facilitatory process occurring after the first few repetitions of the target face, which can be seen as a priming effect. Furthermore, repetition suppression is graded, neurons firing less with increasing repetitions before reaching a plateau (Wiggs and Martin, 1998). This could explain the difference seen between Rep1 and Rep2: the plateau would be reached after the first six repetitions (i.e. after Rep1) and the signal would be sufficiently reduced by Rep2 to be seen on the N170 amplitude. In contrast, during the first repetitions (Rep1), the reduction would not be sufficient to be recorded, yet the latency shortening could be seen thanks to the timing accuracy of the ERP technique. An alternative explanation of N170 amplitude effects could be a difference in attention. If that was the case, we would expect larger N170 amplitudes for the most attended faces, that is, for the targets, whereas the opposite was found. These effects of decreased N170 latency and amplitude with repetition likely reflect repetition suppression and, along with improved performances with repetition, could reflect perceptual priming. As repetition priming is thought to probe the operation of the face recognition system (Ellis et al., 1990), finding repetition effects on the N170 would suggest this component is sensitive to an early identity processing and not only to the structural encoding of faces. This hypothesis is in agreement with other studies showing repetition or familiarity effects on the N170 (Campanella et al., 2000; George et al., 1997; Guillaume and Tiberghien, 2001, Itier and Taylor, 2002; Jemel et al., 2003), although others have not found familiarity or repetition effects on N170 (Bentin and Deouell, 2000; Eimer, 2000b; Pfütze et al., 2002; Schweinberger et al., 2002a,b). This could be due to the stimuli used (same or different photos between first and second presentation, greyscale vs. Mooney faces, neutral vs. emotional faces), the task design (n-back task, study phase-test phase designs, delayed same–different matching task) or to the measurement. For instance, several studies only measured the N170 amplitude and not its latency (e.g. Eimer, 2000b; Schweinberger et al., 2002a) over large time windows, which could obscure a small effect limited to the peak of the N170 as it is the case in the present study. So far, no systematic analysis of the differences in task design has been done to understand the origins of these inconsistencies in the literature. Concerning repetition effects however, one possible factor could be the number of intervening items between first and subsequent presentations. In several studies that did not find repetition effects, intervening items could number a hundred or more (e.g. Eimer, 2000b; Schweinberger et al., 2002a) while the studies including the present, which found repetition effects on the N170, had only a few intervening items or immediate repetitions (Campanella et al., 2000; Guillaume and Tiberghien, 2001; Itier and Taylor, 2002). These effects on the N170 are likely task-dependent and thus not completely automatic, in agreement with other modulations such as top-down effects seen on this component (Bentin and Golland, 2002; Bentin et al., 2002; Jemel et al., 2003).

In contrast, a more consistent repetition effect on ERPs is found on the N250 component. In the present study, we found that the N250 was more negative for the repeated than the new faces. This effect had been assessed only visually by Itier and Taylor (2002) who called it a "reactivation of face processing areas". Its larger amplitude for familiar than unfamiliar faces has led to the

hypothesis that it could reflect the perceptual recognition of the individual stimuli and not simply index face repetition (Pfütze et al., 2002; Schweinberger et al., 1995). Interestingly, in the present data, N250 was also largest to Rep2 faces from 250 to 300 and 350 to 400 ms, suggesting that the increasing number of repetitions increased the familiarity of the target faces. Another important finding was the delayed repetition effect for inverted faces and its longer latency for inverted and negative compared to upright faces. As two to four intervening faces between repetitions reduce the N250 amplitude compared to when immediate repetitions were used, the N250 was thought to index the access to stored facial representations (Pfütze et al., 2002; Schweinberger et al., 1995). The present data would argue that it takes longer to access facial representations when the face is inverted or in contrast-reversed format, than when it is upright. Thus, although an identity priming seems to begin as early as the N170 for all three face types, the access to the representations of faces whose configuration has been altered is more difficult. Schweinberger et al. (2002b) modelled the source of the N250 and found it more anterior and medial than that of N170 in temporal ventral areas that could be the fusiform gyrus (FG). Interestingly, fMRI studies found that the difference between familiar and unfamiliar faces was found in the FG as well (e.g. Henson et al., 2000, 2003). Given that face processing involves a network of different brain areas (Haxby et al., 2000), it is possible that early priming effects on the N170 that seem to originate from lateral parts of the temporal region (like the STS region, e.g., Henson et al., 2003; Itier and Taylor, 2004a; Watanabe et al., 2003) could influence later identity processes in the fusiform gyrus.

Condition effects were also seen on longer-latency ERP components measured at frontal and parietal sites. At frontal sites, there were two time periods reflecting different effects (Fig. 5B, Table 1). From 200 to 350 ms, a larger positivity was found frontally for repeated faces compared to NT faces. This effect was restricted to frontal pole electrodes during the 250–300 ms period (Fig. 7). From 400 to 500 ms, amplitudes for repeated faces decreased more dramatically than amplitudes for new faces. At parietal sites, the larger positive amplitudes for repeated faces started from 300 ms and lasted until 450 ms, with its polarity reversal seen at the same period over frontotemporal and frontal electrodes.

Both the orbitofrontal and the parietal increased positivities for repeated faces reflect the old–new repetition effects obtained in the ERP literature. Most previous work on repetition effects in ERPs has used words, and the early frontal effect is attributed to the "familiarity" component of recognition while the later parietal effect is thought to reflect recollection (for a review, see Rugg and Allan, 2000), although the timing of these effects are somehow longer for words. The familiarity effect is often frontally distributed and occurs between approximately 300 and 500 ms while the parietal recollection effect is centro-parietal and occurs from approximately 500 to 800 ms. According to this, our effects seem earlier than what is usually reported. Most of the studies describing familiarity processes used famous faces and compared them to the processing of unfamiliar faces, which differs from the repetition effects measured for both unfamiliar and familiar faces. Henson et al. (2003) found a familiarity effect between 600 and 800 ms at frontal sites and a repetition priming effect between 400 and 600 ms at centro-parietal sites for both unfamiliar and familiar faces. Schweinberger et al. (2002a) reported a repetition effect between 500 and 600 ms for familiar faces while it was between 600 and 700 ms for unfamiliar faces. In contrast, Schweinberger et al. (1995) reported repetition effects under the form of central positivities and prefrontal negativities, reaching a maximum around 410 ms for unfamiliar faces.

The familiar effect has also been compared to the N400 reported in some face studies. For instance, Eimer (2000b) found a N400 at centro-parietal medial electrodes more negative between 300 and 500 ms for famous than for unfamiliar faces (familiarity effect). In the same study, he also reported a repetition effect at midline and posterior sites in the N400 range for famous faces while no repetition effect was found for unfamiliar faces. These inconsistencies in the literature are partly due to the use of different reference electrodes (see Curran and Cleary, 2003, for an attempt to link the N400 with the frontal repetition effect indexing familiarity and discussion on the reference issue). Using original study phase–test phase paradigms, Paller et al. (1999, 2000) found that face recollection was expressed at frontal and centro-parietal sites between 300 and 600 ms, a timing and topography similar to the present effects. Therefore, the present repetition effects could be either familiarity or recollection effects. The differences from 300 to 500 ms at parietal sites could reflect the familiarity effect (the negative counterpart seen at frontal sites could be the equivalent of the N400). However, if that is the case, what does the earlier frontal repetition effect index? The latter starts a little before the N250 that peaks around 300 ms, and thus is unlikely the polarity reversal of the N250 (this is clear in Fig. 7 at 276 ms). Alternatively, if one assumes that repetition leads to increasing familiarity until familiarity becomes recognition or recollection, then the frontopolar effect could reflect familiarity while the parietal effect seen polarity reversed at frontal sites could be recollection processes. A third possibility is that both frontopolar and parietal repetition effects reflect familiarity. Whatever the exact processes these repetition effects index, they were similar across face types. The fact that larger amplitudes for inverted faces were found at the same frontal sites during the same period of time as the repetition effect could suggest an effect of difficulty associated with the familiarity processes; because inverted faces are hard to learn and process, it is possible that more activity is required in frontal areas in order for the familiarity judgement to succeed.

An interesting result in the present study is that the parietal activity was found for all face types, whereas in a previous study on face repetition using the same faces, the parietal positivity was almost nonexistent for inverted and negative faces (Itier and Taylor, 2002). It has been suggested that the magnitude of the parietal 'old–new' effect indexes recognition in a graded manner (Wilding, 2000; Wilding and Rugg, 1996). In this view, the parietal activity that was found for all face types suggests that all were accurately recognised, which is in agreement with the absence of face type effects on accuracy rates. The only difference between face types lay in a delayed repetition effect at parietal sites for inverted faces (Fig. 8). Interestingly, between 350 and 400 ms, Rep2 faces elicited larger amplitudes than Rep1 faces, only for upright faces. This suggests a differential effect of long-lasting repetitions depending on face type, that is, better stabilisation of facial representations when in the upright orientation. This difference could be related to the improvement of performances at the accuracy level for upright Rep2 faces. However, improvements were seen for all face types and Rep2 faces may elicit larger amplitudes than Rep1 for inverted and negative faces as well if the number of repetitions was further increased. We believe the repetition effects we see at both frontal and parietal sites index

familiarity processes and the data show that familiarity continues to increase with the number of repetitions, albeit more slowly for inverted and negative faces.

In conclusion, learning a target face can abolish face inversion and contrast-reversal effects at the accuracy level in a subsequent target detection task, although inverted and negative faces were still processed more slowly than upright faces. Early ERP components such as P1 and N170 were affected by both face manipulations reflecting their sensitivity to facial configural changes. P1 likely reflects early stages of face detection while N170 could reflect the earliest facial identity processes. Identity priming affecting the N170 reinforces this last hypothesis. Reliable repetition effects were seen at the temporal N250, but delays for inverted and longer latencies for both inverted and negative compared to upright faces in these repetition effects, argue for more difficult access to facial representations for these configurally changed faces. Inversion and contrast-reversal also affected longer-latency ERP components at frontal sites, reflecting the difficulty of processing such faces. Memory conditions were seen as two 'old–new' effects, one orbitofrontal positivity for repeated faces from 250 to 300 ms and the second one at parietal sites between 300 and 500 ms, both likely reflecting familiarity processes linked to target recognition. These frontal and parietal repetition effects were equally pronounced for all three face types reflecting accurate recognition for upright but also for inverted and negative faces. The amplitude difference between Rep2 and Rep1 upright faces suggests familiarity continues to increase with the number of repetitions.

Acknowledgments

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