Early electrophysiological responses to multiple face orientations correlate with individual discrimination performance in humans

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Picture-plane inversion dramatically impairs face recognition. Behavioral and event-related potential (ERP) studies suggest that this effect takes place during perceptual encoding of the face stimulus. However, the relationship between early electrophysiological responses to upright and inverted faces and the behavioral face inversion effect remains unclear. To address this question, we recorded ERPs while presenting 10 subjects with face photographs at 12 different orientations around the clock (30° steps) during an individual face matching task. Using the variability in the electrophysiological responses introduced by the multiple orientations of the target face, we found a correlation between the ERP signal at 130–170 ms on occipito-temporal channels, and the behavioral performance measured on the probe stimulus. Correlations between ERP signal and behavioral performance started about 10 ms earlier in the right hemisphere. Significant effects of orientation were observed already at the level of the visual P1 (peaking at 100 ms), but the ERP signal was not correlated with behavior until the face-sensitive N170 time window. Overall, these observations indicate that plane-inversion affects the perceptual encoding of faces as early as 130 ms in occipito-temporal regions, leading directly to an increase in error rates and RTs during individual face recognition.
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Keywords: Event-related potentials; P1; N170; Face processing; Inversion effect

Introduction

Presenting face stimuli upside-down (either flipped vertically or rotated by 180°) dramatically affects their recognition (e.g. Hochberg and Galper, 1967). This observation has become particularly important in the face processing literature, for several reasons. First, the effect of inversion for faces is much larger than for other object categories, a phenomenon known as the 'face inversion effect' (Yin, 1969). This effect is one of the first cited evidence in favor of specific brain mechanisms for faces (i.e. those that are particularly affected by inversion, Yin, 1969), together with the observation of recognition impairments specific for faces following brain damage ('prosopagnosia', Bodamer, 1947) and of inferior–temporal cortex neurons responding selectively to faces in the monkey brain (Gross et al., 1972). Second, the effect is extremely robust, and has been observed in a variety of conditions: for familiar and unfamiliar faces, in old/new recognition tasks or matching tasks, with or without delay between stimuli to match (for a recent review, see Rossion and Gauthier, 2002). Finally, a large number of behavioral studies support the view that inversion of a face affects mainly, but not exclusively, the processing of facial configuration. For instance, when faces are inverted the recognition of facial features is no longer (or less) affected by the presence of other features, or by the whole face stimulus (e.g. Sergent, 1984; Tanaka and Farah, 1993; Young et al., 1987). Moreover, most studies show that the perception of metric distances between features (i.e. mouth–nose distance, eyes height within the face stimulus…) is more affected by inversion than the perception of local cues (shape of the mouth, color of the eyes…) (e.g. Barton et al., 2001; Collishaw and Hole, 2000; Freire et al., 2000; Goffaux and Rossion, in press; Le Grand et al., 2001; Leder and Bruce, 2000; Rhodes et al., 1993). These observations are particularly important for experimental studies of face perception because a simple stimulus transformation such as inversion can be used to disrupt configural processes (e.g. Collishaw and Hole, 2000; Goffaux and Rossion, 2006; Young et al., 1987).

Inversion appears to affect *perceptual encoding* of faces, since large decreases of performance with inversion are observed during simultaneous presentation of unfamiliar faces, i.e. without any memory component involved (e.g. Farah et al., 1998; Moscovitch et al., 1997; Searcy and Bartlett, 1996). Moreover, the inversion effect is equally large whether the faces are presented simultaneously or with various delays (1, 5 or 10 s) during individual discrimination tasks (Freire et al., 2000). Recent neuroimaging

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studies support a perceptual encoding account of the face inversion effect since the processing of upright and inverted face stimuli differ mainly in visual areas responding preferentially to faces, such as the middle fusiform gyrus or 'fusiform face area' ('FFA', e.g. Haxby et al., 1999; Mazard et al., 2006; Yovel and Kanwisher, 2005). However, establishing the perceptual nature of the face inversion effect requires high temporal resolution methods such as event-related potentials (ERPs) recorded on the human scalp, which are able to track the time course of upright and inverted face processing at the millisecond (ms) range. Early ERP work by Jeffreys (1993), who focused on the so-called vertex-positive potential (VPP) peaking between 140 and 180 ms following face stimulation, showed that face inversion delays this electrophysiological component by about 10 ms. More recent ERP studies have reported the same delay on the N170, the negative counterpart of the VPP (Joyce and Rossion, 2005) at occipito-temporal sites (e.g. Bentin et al., 1996; de Haan et al., 2002; Eimer, 2000; Itier et al., 2006b; Itier and Taylor, 2004; Linkenkaer-Hansen et al., 1998; Milivojevic et al., 2003; Rebai et al., 2001; Rossion et al., 1999, 2000, 2003; Rousselet et al., 2004; Sagiv and Bentin, 2001; for magnetoencephalography (MEG) evidence, see e.g. Itier et al., 2006a; Linkenkaer-Hansen et al., 1998). Paradoxically, most but not all of these studies have also found a significant *increase* of voltage amplitude of the N170 to inverted relative to upright faces (e.g. Itier et al., 2006b; Itier and Taylor, 2004; Linkenkaer-Hansen et al., 1998; Rossion et al., 1999, 2000; Rousselet et al., 2004; Sagiv and Bentin, 2001). A few studies have also disclosed latency and amplitude increases as starting earlier, at the level of the P1, a visual ERP component peaking at about 100 ms following stimulus onset and originating from striate and extrastriate visual areas (Itier et al., 2006a; Itier and Taylor, 2002; 2004; Linkenkaer-Hansen et al., 1998).

Despite the numerous studies that have described the effects of face inversion on early visual ERPs, the relationship between these early electrophysiological modulations and the behavioral effect of inversion is unclear. In particular, how does the P1/N170 latency and amplitude increases relate to the difficulty of encoding faces presented upside-down? The main goal of the present ERP study was to address this question. That is, to determine the exact time-course of the behavioral face inversion effect: when does the processing of upright and inverted faces start to differ reliably in the human brain, leading ultimately to an increase in error rates and response times during individual discrimination/recognition tasks? Clarifying the relationships between these early electrophysiological effects and behavior may be a critical step towards our understanding of the nature of the face inversion effect. If there were no relationship between early electrophysiological parameters and behavioral effects of inversion, this would seriously cast doubt on the perceptual encoding hypothesis. However, if there were systematic relationships between the electrophysiological parameters of early visual components and behavior, this would clearly demonstrate the perceptual encoding basis of the face inversion effect, and would strengthen the interest of these measures to understand the nature of this effect (i.e. which perceptual processes are affected by inversion).

To clarify the time course of the relationships between behavioral effects of face inversion and early face processes identified in human ERP studies, the present study differs from previous work in several ways. First, while most ERP studies on this topic have examined the effect of face inversion on the P1 and N170 components during tasks that are not associated with a behavioral inversion effect (i.e. orientation judgments, unrelated target detection or passive viewing) (e.g. Bentin et al., 1996; de Haan et al., 2002; Eimer, 2000; Linkenkaer-Hansen et al., 1998; Milivojevic et al., 2003; Rebai et al., 2001; Rossion et al., 2000, 2003; Sagiv and Bentin, 2001), we measured ERP responses to faces during a delayed individual face matching (same/different) task. Second, and most importantly, we recorded ERPs in response to photographs of faces presented at 12 different orientations from 0° to 360° in 30° steps, rather than contrasting only upright and inverted faces as in previous studies. Presenting face stimuli at multiple orientations allowed us to characterize and correlate both the patterns of modulation of the P1 and N170 parameters and the pattern of behavioral responses, as a function of angles of face rotation. Two previous ERP studies have used multiple face orientations to characterize the time-course of face processes, but did not address the questions raised here. Jeffreys (1993) observed a linear increase of the latency of the VPP as a function of face orientation from 0° to 120°, and then slightly decreased again between 120° and 180°. There was no amplitude modulation of the VPP with the angle of face rotation due to face orientation reported in that study. Most importantly, there were no quantitative data analysis, and no behavioral data to compare with the ERP latency modulations. More recently, Milivojevic et al. (2003) recorded ERPs during a sex classification task of 'Thatcherized faces'[1] presented at six angular departures from the upright but only analyzed their data in terms of an interaction between "thatcherization" and orientation, and did not report main effects of face orientation. Third, and finally, besides the analysis of specific ERP components (P1, N170), we took advantage of the variability in the ERP and behavioral responses introduced by our parametric manipulation of face orientation to relate the two measures, and search for spatio-temporal regions where the pattern of ERP modulations paralleled behavioral performance. More precisely, to determine the time-course of the face inversion effect at a global level, we correlated behavioral data with ERP signal at each time point and at each scalp electrode. Similar approaches of correlating behavioral and neurophysiological responses to characterize the relationships between face perceptual processes and decision making have been recently applied to single neuron recordings in the monkey inferior–temporal cortex (Keysers et al., 2001) or single-trial EEG analysis in humans (Philiastides and Sajda, 2006).

According to the perceptual encoding view, the effect of face orientation measured behaviorally should be directly related to early ERP differences between face orientations. We hypothesized that systematic relationships between behavior and ERPs would emerge during the N170 time window, following the P1 component. This is because the N170 is the first component that shows a reliable larger response to faces than objects (e.g. Bentin et al., 1996; Rossion et al., 2000; Rousselet et al., 2004) and is thought to reflect a structural encoding stage (Bentin et al., 1996; Eimer, 2000). That is, a stage at which faces are not only discriminated from other object categories, but also at which individual representations of faces are activated (Jacques and Rossion, 2006), and which should thus be particularly sensitive to inversion (Rossion and Gauthier, 2002).

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[1] If the eyes and mouth of a picture of a face are inverted, the face appears grotesque, unless it is presented upside-down. The normal appearance of the distorted face is known as the 'Thatcher illusion' because it was first demonstrated with the face of the former British prime minister, Margaret Thatcher (Thompson, 1980).

Material and methods

Subjects

Ten paid volunteers (10 males, 2 left-handed, mean age 21.8± 1.8 years) participated in this study. All subjects had normal or corrected-to-normal vision.

Stimuli

Thirty front view face pictures (15 males) without glasses, facial hair and make-up, and with neutral expression were used in this study. All face photographs were edited to remove backgrounds, hair, and everything below the chin, and were equated for mean luminance within the same face–gender. All stimuli subtended approximately 2.8°×3.7° of visual angle.

Procedure

After electrode-cap placement, subjects were seated in a light- and sound-attenuated room, at a viewing distance of 100 cm from a computer monitor. Stimuli were displayed using E-prime 1.1 (Psychology Software Tools, Inc.), on a light grey background. In each trial, two faces (target and probe) were presented sequentially, both in one of twelve picture-plane orientation (0°, 30°, 60°, 90°, 120°, 150°, 180°, 210°, 240°, 270°, 300°, or 330°) (Fig. 1A). The probe face was always presented at the same orientation as the target face. A trial started with a fixation point displayed at the center of the screen for 100 ms (Fig. 1B). Approximately 250 ms (randomized between 200 and 300 ms) after the offset of the fixation point, a first face (target) appeared for 400 ms, immediately followed by a square textured mask (with the same spatial frequency power spectrum as a face) for 200 ms. After an interval of about 800 ms (700 to 900 ms), a second face (probe) appeared for 200 ms. The offset of the second face was followed by an inter-trial interval of ~1550 ms (1400 to 1700 ms). In half of the trials, the second face stimulus was of the same identity (same

picture) as the first face. To avoid subjects to rely on purely image-based cues to perform the task, the second face of each trial was 10% larger (~3.1×4.1° in size) than the first face and the two stimuli were separated by a mask. The same pairs of faces were presented at each orientation. Whenever the faces were different, two faces of the same gender were presented. Subjects performed an identity matching task between the target and probe faces of each trial, and gave their response by pressing on one of two keys with their right hand (keys counterbalanced across subjects). They were instructed to maintain eye gaze fixation to the center of the screen during the whole trial and to respond as accurately and as fast as possible. Four subjects performed 120 trials per orientation condition (total: 1440 trials) and 6 subjects performed 108 trials per orientation (total: 1296 trials). The order of all the conditions was randomized within each block.

EEG recordings and ERP analyses

EEG was recorded from 58 tin electrodes, mounted in an electrode cap (Quikcap, Neuromedical supplies, Inc.) adapted from the 10–20 standard montage. Vertical and horizontal eye movements were monitored using 4 additional electrodes placed above and below the left eye orbit and on the outer canthus of each eye. During EEG recording, all electrodes were referenced to the left earlobe and electrode impedances were kept below 10 kΩ. EEG was digitized at a 1000 Hz sampling rate and a digital anti-aliasing filter of 0.27 * sampling rate was applied at recording (at 1000 Hz sampling rate, the usable bandwidth is 0 to ~270 Hz).

EEG signal was filtered with a 0.3–30 Hz band-pass filter. Time windows in which the standard deviation of the EEG on any electrode within a sliding 200-ms time window exceeded 35 μV were marked as either EEG artefacts or blink artefacts. Blink artefacts were corrected by subtraction of vertical electrooculogram (EOG) propagation factors based on EOG components derived from principal component analyses. For each subject, averaged epochs ranging from −200 to 600 ms relative to the onset of the target face and containing no EEG artefacts were computed for each
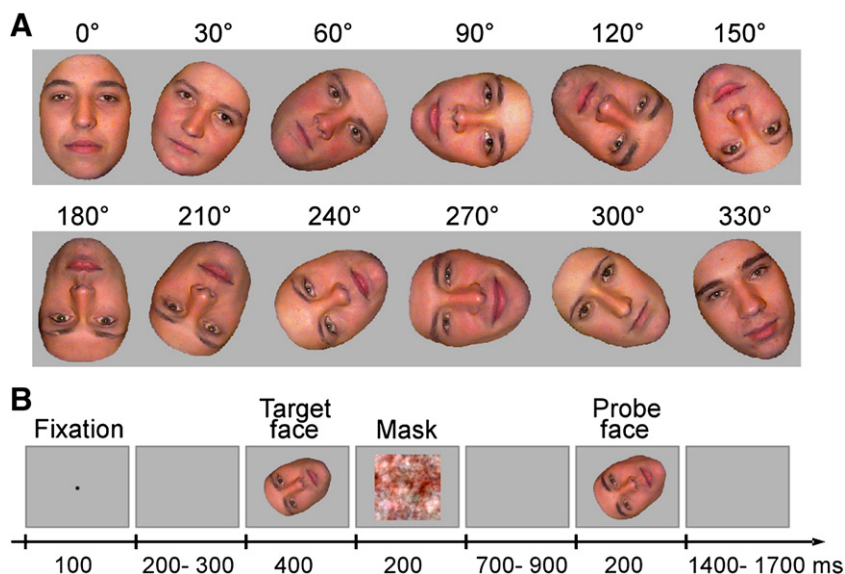

Fig. 1. Examples of face stimuli at 12 orientations (A) and time-line of a trial sequence (B).

condition separately and baseline corrected using the 200-ms prestimulus time window. Subjects' averages were then re-referenced to a common average reference (Joyce and Rossion, 2005).

Statistical analyses

Behavior

Correct response times, error rates, and inverse efficiency scores (Akhtar and Enns, 1989; Kennett et al., 2001) were submitted to a repeated-measures analysis of variance (ANOVA) with orientation as a within-subject factor. The inverse efficiency score (expressed in ms) is equal to the mean response time divided by the proportion of correct responses, calculated separately for each condition and each subject. A low value on this measure indicates a good recognition performance. This measure is used to combine response time and accuracy data in a single parameter, in order to dismiss possible criterion shifts or speed–accuracy tradeoffs.

Electrophysiology

We analyzed the ERP response to the first face (target face) of each trial only, for two reasons. First, its orientation was not predictable, contrary to the second face (probe). Second, while the processing of the first stimulus is critical for the performance during the individual discrimination task, the EEG related to the target stimulus could not be contaminated by any decisional or motor components. Thus, this kind of analysis reinforces the interest of correlation measures because they were made between an electrophysiological signal and a behavioral response measured on different stimuli, at a different time.

Peak analyses. Two clear visual ERP components time-locked to the onset of the target face were analysed: the P1 and the N170. Peak amplitude and latency of the P1 and N170 were extracted automatically at the maximum amplitude value between 80 and 140 ms for the P1 and at the minimum amplitude value between 120 and 190 ms for the N170 at two occipito-temporal electrode site in the left and right hemisphere (PO7 and PO8) where both components peaked maximally in all conditions (see Fig. 3). In the peak analyses, we only included face orientations for which the eyes region – the area of the face with the highest contrast – have a contralateral visual field position relative to the electrode position. Thus analyses on electrode PO8 (right hemisphere) were performed on orientations going counterclockwise from 0° to 180° (eyes in left visual field), whereas analyses on PO7 (left hemisphere) included clockwise orientations from 0° to 180° (eyes in right visual field). Amplitude and latency values of the P1 and N170 were submitted to repeated-measure ANOVAs with *orientation* (7 levels) and *hemisphere* (right vs. left) as factors. Greenhouse–Geisser adjustments to the degrees of freedom were used when appropriate.

Correlation analyses. In order to find brain responses related to our face discrimination task, we searched for ERP signals across time and space that would parallel behavioral performance pattern as a function of face orientation. To achieve this, we computed Pearson's correlations between behavioral data and the amplitude of the electrophysiological signal at each time point and each of the 58 electrodes from −100 to 400 ms relative to the onset of the target stimulus. This was done separately for response time, error rate and inverse efficiency data. To compute the correlation

coefficient and the corresponding *p*-value at each time point and each electrode, we used *z*-score transformed behavioral and electrophysiological data from each subject over all orientations (10 subjects * 12 orientations = 120 points). Data were *z*-scored in order to remove between-subject differences that were not related to our face orientation manipulation (e.g. general ERP amplitude or behavioral differences between subjects). In calculating statistically significant correlations, given the large number of correlations computed (58 * 500 = 29 000 correlations per behavioral measure), we adjusted the significance threshold by using the false discovery
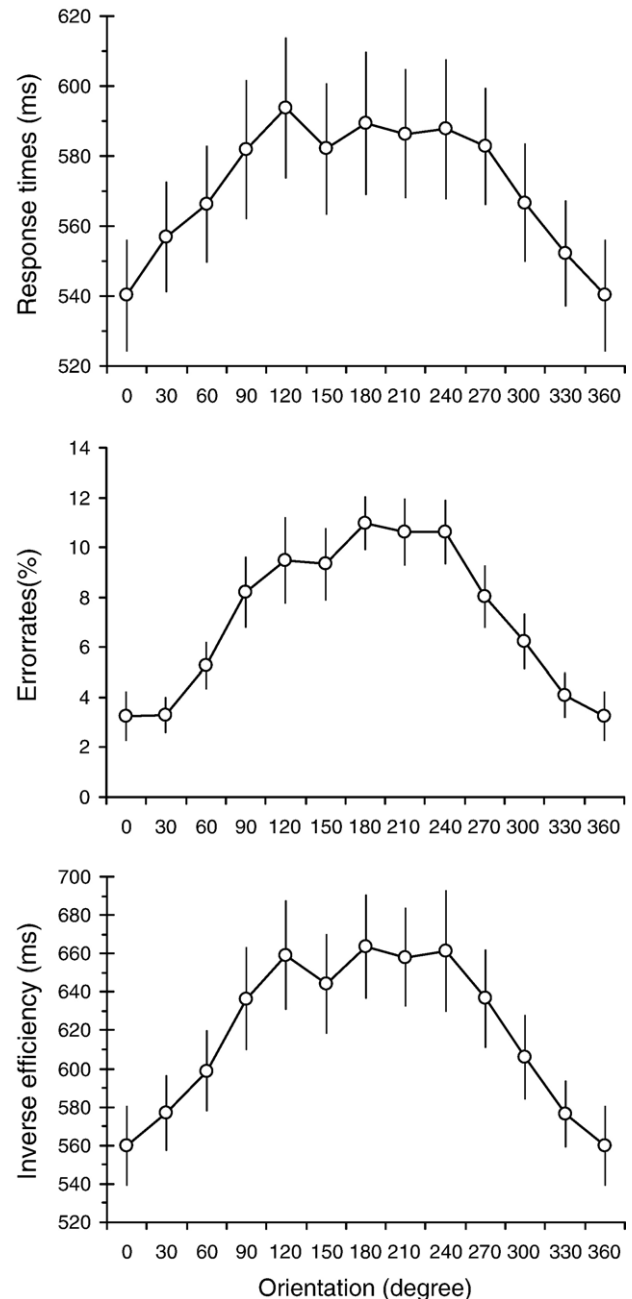

Fig. 2. Behavioral results: response times (top), error rates (middle) and inverse efficiency (bottom) as a function of face orientation. The 360° point in each graph is a duplicate of the 0° point. Error bars are standard error of the mean.

rate (FDR) procedure (Benjamini and Hochberg, 1995; see Genovese et al., 2002 for an application to neuroimaging). This procedure examines the distribution of *p*-values in the data and allows computing a threshold that ensures that the rate of falsely rejected null hypothesis (false positive) does not exceed a given percentage. In this case, the acceptable rate of false positive was set to 1% and a corresponding significance threshold was then determined with the FDR procedure. This procedure was performed independently for each behavioral measure.

Results

Behavioral results

The relationship between face orientation and behavioral responses is plotted in Fig. 2. The points plotted at 360° are duplicates of the 0° point and are included for clarity. Analyses revealed a significant effect of *orientation* for response times ($F(3.8,34)=13.8$, $p<0.001$), error rates ($F(3.9,34.9)=15.57$, $p<0.001$) and inverse efficiency ($F(3.5,31.4)=24.14$, $p<0.001$). The pattern of modulation with orientation was an increase in response times, error rates and inverse efficiency as the face was rotated from 0° (360°) to 120° (240°) and then no further increase for orientations going from 120° to 240°. Thus, in this matching task varying the face orientation in the 120°–240° range had little effect on individual discrimination performances. The trend of the

relationship between face orientation and behavioral measures was assessed by applying polynomial contrasts on the data averaged across clockwise and counterclockwise orientations (e.g., 30° and 330° were averaged). These analyses revealed that response time and inverse efficiency functions included both a significant linear ($p<0.001$) and quadratic ($p<0.001$) component. Error rates showed a significant linear ($p<0.001$) and a non-significant trend for a cubic ($p=0.084$) component. Behavioral data thus showed a strong linear relationship between the increasing orientation and subject's performance.

Electrophysiological results

Grand average ERP waveforms elicited by faces in 7 different orientations on each electrode (PO7/8) are depicted in Fig. 3. Peak amplitude and latency of the P1 and N170 across the different orientations are shown in Fig. 4.

P1 latency and amplitude

At the level of the P1 component there was an non-significant trend for an effect of orientation ($F(2.7,24.7)=3.03$, $p=0.052$) on P1 latency, which was due to small differences in the range of orientations from 360° to 300° and between 240° and 270° on electrode PO8 (Fig. 4A).

P1 amplitude was also affected by face orientation as revealed by a significant orientation effect ($F(2.8,25.4)=6.09$, $p<0.005$).
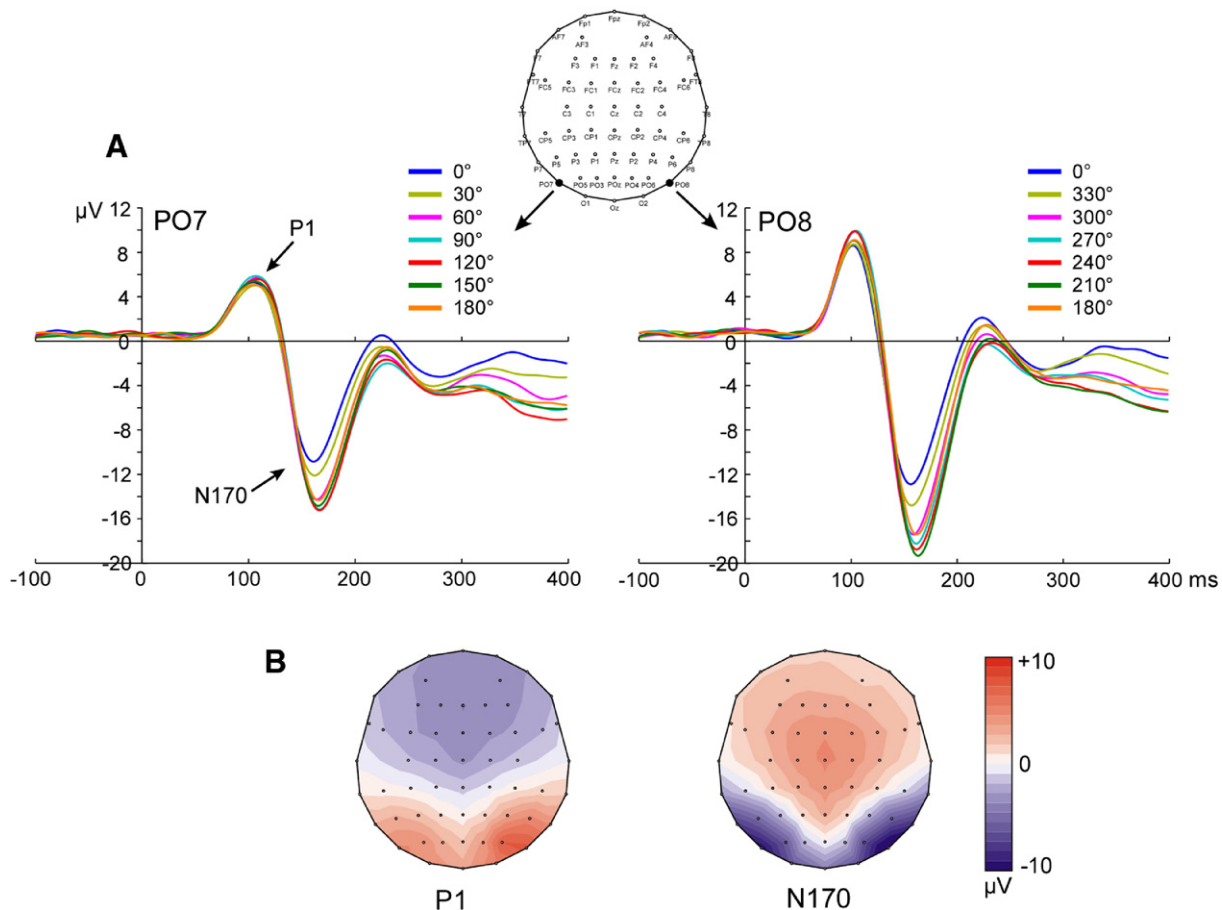

Fig. 3. (A) Grand average ERP waveforms at two occipito-temporal electrodes (PO7=left hemisphere; PO8=right hemisphere). (B) Scalp distribution (top view) of the P1 (around 100 ms) and N170 components (around 160 ms) for an upright face.
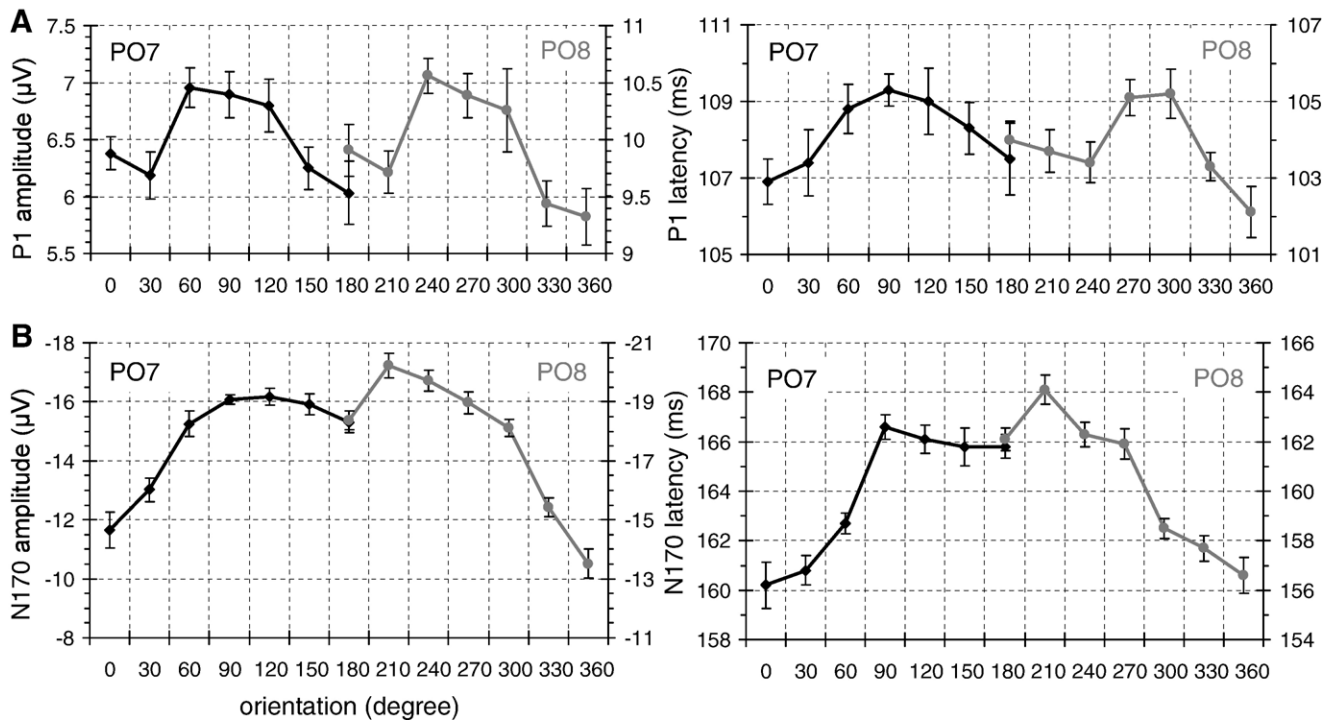
Fig. 4. Peak amplitudes and latencies of the P1 (A) and N170 (B) components as a function of face orientation. Data are shown for orientations in which the eyes are in the contralateral visual field relative to the electrode position. Amplitude and latency values at PO7/8 are thus reported for orientations going clockwise/counter-clockwise from 0° to 180°. For the N170 amplitude (B–left), the y-axis has been reverted. Error bars represent standard errors of the mean computed after subtracting the mean amplitude/latency over all orientations to the amplitude/latency in each orientation in each subject independently.

This was due to P1 amplitude being larger in the 60°–120° range on PO7 and in the 240°–300° ranges on PO8. There was also a significant effect of hemisphere ($F(1,9)=16.32$, $p<0.005$), the P1 being larger in the right (mean: 9.9 μV) than in the left hemisphere (mean: 6.5 μV). Thus, the P1 was larger and delayed around the 90° and 270° orientations (i.e. horizontal orientations). In contrast, amplitudes and latencies were smaller near vertical orientations (0° and 180°). This was reflected by polynomial contrasts showing that variations in P1 latency include a significant quadratic component only ($p<0.001$) and no linear component ($p=0.39$). Variations in P1 amplitude included both a quadratic ($p<0.005$) and a fourth order ($p<0.01$) component, and again no linear component ($p=0.43$).

In summary, while there were P1 effects of orientation, there was no linear relationship between the increasing face orientation and ERP amplitude or latency variations at the P1 level, unlike what was observed for behavioral measures.

N170 latency and amplitude

During the N170 time window, face orientation had a highly significant effect on both latency ($F(2.5,22.7)=23.75$, $p<0.001$) and amplitude ($F(2.7,23.9)=52.53$, $p<0.001$) (Fig. 4B). There was also a non-significant trend for an effect of hemisphere on N170 latency ($F(1,9)=4.7$, $p=0.059$), due to slightly longer peak latencies in the left hemisphere (PO7).

On both occipito-temporal electrodes (PO7/8), the maximum amplitude and latency increase of the N170 was in the 0° to 90° range (or 360° to 270°; Fig. 4B). On electrode PO7, the amplitudes and latencies remained roughly stable from 90° to 150° and then a slight amplitude decrease at 180°. On PO8, the rate of amplitude and latency increase from 270° to 210° was small, and there was a dip at 180° (Fig. 4B).

Polynomial contrasts revealed that the relationship between face orientation and N170 latency was a combination of linear ($p<0.001$), quadratic ($p<0.02$), cubic ($p<0.002$) and 6th order

Fig. 5. Correlation analyses between electrophysiological signal and behavioral face discrimination. (A) Significant correlations at each electrode as a function of time (−100 to 400 ms relative to stimulus onset) for response times, error rates and inverse efficiency. The p threshold computed with the FDR procedure (see methods) is shown above each plot. Each colored point on the plot is thus associated with a p-value inferior to the mentioned p threshold, which sets the false positive rate to 1%. The sign of the correlation (positive: red color; negative: blue color) mostly depends on the polarity of the ERP component. For instance, in the N170 time range (~150–220 ms), correlations are negative on posterior electrodes, but given the polarity reversal of the N170 at central and frontal electrodes (i.e. the Vertex Positive Potential), the correlation has a positive sign at these locations. Arrows on the inverse efficiency plot indicate spatio-temporal locations of maximum correlation strength in the 110–145 ms range (depicted in B) and in the N170 time range (depicted in C). (B) Left: ERP amplitude averaged over all subjects at 130 ms (maximum correlation in this time range) at electrode PO8 and inverse efficiency data are shown on the same plot for comparison. Right: scatter plot between z-scored ERP amplitudes at 130 ms and inverse efficiency data for all subjects x orientations (120 points). (C) Left: ERP amplitude averaged over all subjects at 180 ms (maximum correlation in the N170 time range) at electrode PO8 and inverse efficiency data. For purpose of clarity given the sign of the correlation, the ERP amplitude axis has been reverted so that positive values are positioned lower on the axis. Right: scatter plot between ERP amplitude and inverse efficiency. Note here that the sign of the correlation is negative because the N170 is a negative component (higher negative values mean higher component amplitudes).
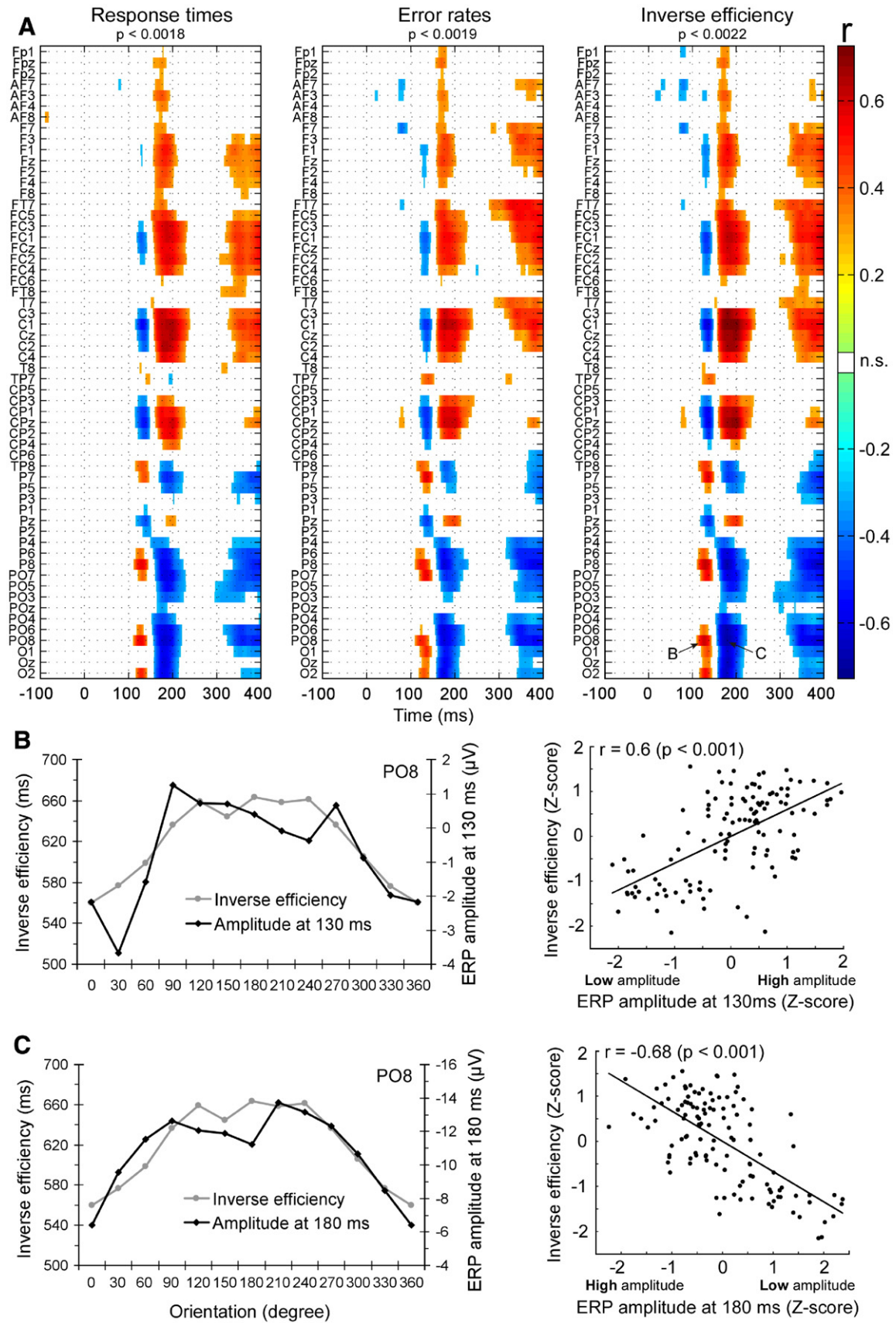
($p<0.003$) components. Similarly, N170 amplitude modulations with orientation included a linear ($p<0.001$), a quadratic ($p<0.001$) and a 5th order ($p<0.005$) component. Thus, unlike the P1, these analyses revealed a linear relationship between the increasing face orientation and ERP amplitude or latency variations at the N170 level, in line with behavioral measures. Moreover, the departure from linearity of the overall pattern was due to a shift between 60° and 90° (270°) which is also highly similar to behavioral observations (compare Figs. 2 and 4).

ERP signal amplitude correlated with behavioral face discrimination

We identified the time points at which the pattern of ERP responses to face stimuli at multiple orientations is related to behavioral performance at the individual face discrimination task by correlating the ERP signal amplitude with behavioral data at each time point and each electrode. Results from these analyses are reported in Figs. 5 and 6. Fig. 5 also shows the pattern of ERP amplitude and inverse efficiency modulations as a function of orientation at two different time points: 130 ms and 180 ms, respectively.

In this section, we describe the correlation patterns that were robust across electrodes and time samples: that is, three main spatio-temporal patterns of correlations at different latencies that were broadly distributed on the scalp. As shown in Fig. 5A, the patterns of correlations were remarkably similar across beha-

Fig. 6. Scalp distribution (top view) of the significant correlations between ERP signal and inverse efficiency at three different maximal correlation time windows: around 130 ms, 180 ms and 380 ms (see Figs. 5 and 7). The left column shows that for the first two windows, correlations first started in the right hemisphere (110 and 155 ms, respectively).

vioral measures. We thus focused on the correlations with inverse efficiency measures (response time/accuracy), since it is a combined description of both response time and accuracy data.

The earliest consistent correlation started at ~110 ms in the right hemisphere and ~120 ms in the left hemisphere (Fig. 6) and lasted until ~145 ms. In this time window, the correlation had a maximum at ~130 ms ($r=0.6$) over lower occipito-temporal electrodes (P7/8, PO7/8) with a reversed sign over central and centro-parietal electrodes (Fig. 6). When looking at the maximum correlation in each subject in this time window (100–160 ms) the coefficients ranged from 0.33 to 0.95 (mean=0.67±0.22) on PO8 and from 0.31 to 0.95 (mean=0.64±0.19) on PO7. As can be seen in Fig. 5B, the pattern of amplitude modulation at 130 ms closely resembles the pattern of inverse efficiency modulations with orientation. Notably, this early correlation peak occurred about 30 ms later than the P1 component peak, thus in the descending slope between the P1 and N170 component (Fig. 7).

This observation suggests that as early as 130 ms after the onset of the target face, the ERP signal predicts the behavioral performance at the face discrimination task that are measured relative to the probe face. In contrast, in the time range of the P1 component (~105 ms), the correlation with behavior was not significant on any electrode (max correlation: $r=-0.23$ at 102 ms, on FT7).

The next consistent correlation pattern was observed in the time window of the N170 between ~155 and 220 ms. The correlation started about 10 ms earlier in the right hemisphere (~155 ms) than in the left hemisphere (~165 ms) (Fig. 6) and had a maximal at ~180 ms ($r=-0.68$ on PO8; Fig. 5C), slightly after the N170 maximum peak. The correlation measured around the N170 maximum peak (at 164 ms) was highly significant ($r=-0.56$; $p<0.001$). The scalp topography of the correlation in the N170 time window (Fig. 6) was similar to the topography of the N170 (Fig. 3), with a broad posterior distribution (P7/8, PO7/8, PO5/6, P5/6, O1/2) and polarity reversal over central and frontal electrodes. For individual subject data in this time window (150–240 ms), the coefficients ranged from −0.57 to −0.87 (mean=−0.76±0.1) on PO8 and from −0.31 to −0.95 (mean= 0.7±0.2) on PO7.

The third pattern of correlations occurred at a later time window, starting at ~320 ms on PO8 (with a large inter-subject variability in the onset latency) and lasting until more than 600 ms after stimulus onset. The correlation was broadly distributed on posterior electrodes (but slightly more temporal than the N170) and again reversed polarity at central and fronto-central electrodes (Fig. 6). The maximum correlation coefficients in individual subjects during this time window (290–450 ms) ranged from −0.49 to −0.92 (mean=−0.72±0.13) on PO8 and from −0.3 to −0.88 (mean=0.71±0.17) on PO7.

Peaks in the correlation between ERP amplitude and behavioral data were temporally aligned with peaks in the standard deviation of the ERP amplitude measured in all orientations and with peaks in the difference between ERP waveforms recorded for a face at 0° and other orientations (at around 130 ms, 180 ms and 320–600 ms; Fig. 7). Given that correlations were computed with z-scored amplitude values that sets the standard deviation to 1, this result cannot be explained by larger within-subject variance between conditions at these time points. Rather, it suggests that spatio-temporal regions that discriminate the most between conditions contain information that can predict the behavioral output at the discrimination task. Notably, the early peak in the standard deviation between conditions (~130 ms and ~180 ms) did not match with the maxima of the ERP components P1 (~105 ms) and N170 (~160 ms).

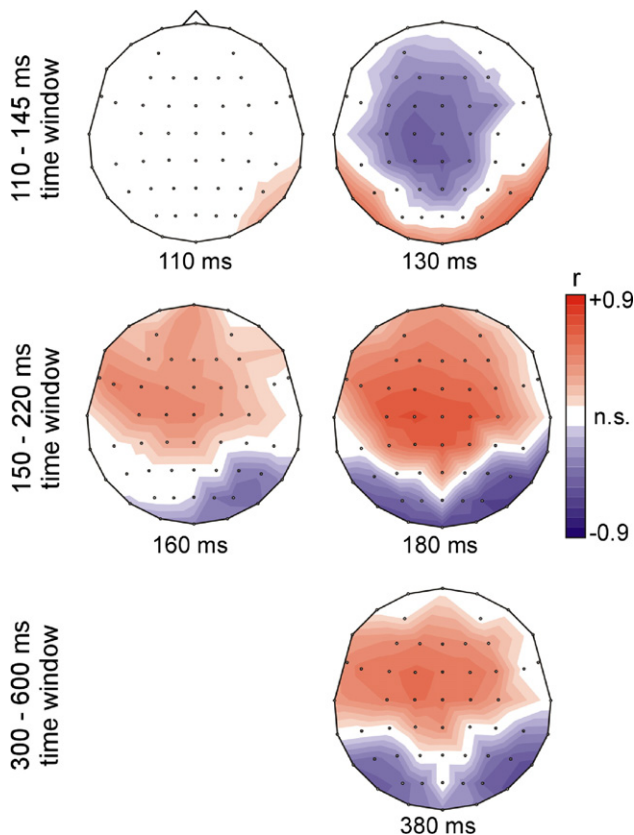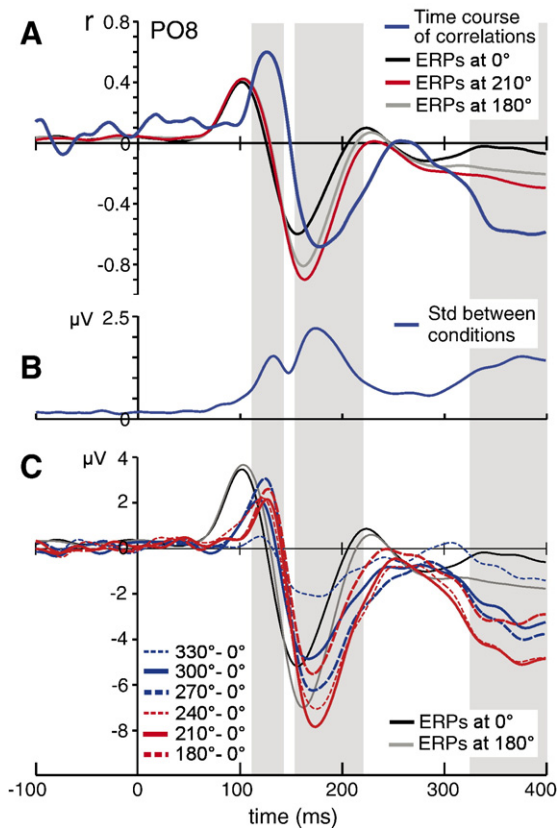Fig. 7. (A) Time course of the correlations performed at each time point −100 to 400 ms at electrode PO8, along with ERP waveforms shown for comparison. ERP waveforms to upright and inverted faces were scaled to fit on the same plot as correlation measures. (B) Standard deviation between ERP amplitudes measured in all orientations computed at each time point on the ERP waveforms averaged across subjects. Note the temporal alignment of peaks in the standard deviation with peaks in the time course of the correlation between ERP signal and behavior (shown in A). This suggests that temporal locations during which differences between conditions is maximal contains the largest amount of information useful to perform the discrimination task. (C) Difference waves between ERP elicited by a face at 0° and other face orientations. Note the increasing amplitude difference at around 130 ms after stimulus onset. ERP waves to upright and inverted faces are shown for comparison. ERP waveforms to upright and inverted faces were scaled to fit on the same plot as difference waves.

Finally, we computed correlations between behavioral face discrimination (inverse efficiency) and N170 latency measured at the component's peak. This analysis revealed that the latency of the N170 was strongly correlated with inverse efficiency ($r = 0.75$ on PO7 and 0.74 on PO8, $p < 0.001$).

ERP signal amplitude and N170 latency relationship

To complement these results and determine the onset time of the latency effect with orientation, we computed the correlations between the N170 peak latency (averaged across values measured at electrodes PO7 and PO8) and the amplitude of the signal at each time point, for each electrode. Similarly to correlations performed with behavioral data, both amplitude and latency values of individual subjects were z-scored before computing each correlation.

The spatio-temporal patterns of correlations between ERP signal amplitude modulated by face orientation and the N170

latency closely resembles the patterns observed when measuring correlations with behavior. This is not surprising given the strong correlation between N170 latency and behavior (see above). Thus there were again three main clusters of correlation between ERP signal amplitude and N170 peak latency (Fig. 8): around 130 ms, around 180 ms and around 350–600 ms. The most interesting observation was the finding that the ERP amplitude at 130 ms (increased relative positivity from 0° to 180°) (Fig. 8) predicts to a large extent the N170 latency modulation pattern with orientation ($r = 0.77$ at PO8). The maximum correlation coefficient for individual subjects in this time window (100–160 ms) ranged from 0.48 to 0.91 (mean = 0.82 ± 0.12) on PO8 and from 0.25 to 0.93 (mean = 0.69 ± 0.21) on PO7.

At the N170 peak (165 ms), the correlation between N170 latency and ERP amplitude was 0.55 ($p < 0.001$). We also looked at the correlation between N170 latency and amplitude measured at the peak, thus including amplitude values measured at different latencies. For orientations with eyes in the contralateral visual field, the correlation was −0.70 and −0.71 for PO7 and PO8, respectively.

Discussion

To summarize our findings, we observed significant effects of face orientation on both the P1 and N170, in line with previous observations. However, the patterns of modulation of behavioral responses with orientation were clearly different from the patterns observed for the P1 parameters (amplitude and latency), while they were remarkably similar to the patterns observed for the N170 parameters. Point-by-point correlation analyses performed over the entire scalp showed that the effect of face inversion as measured behaviorally originates at about 110–130 ms following stimulus onset, slightly earlier in the right hemisphere, and may involve multiple time-scales. Overall, these observations support the view that the behavioral inversion effect takes place during the perceptual encoding of faces, and precisely characterize its time-course.

Functional dissociation between P1 and N170 for face inversion

As indicated in the introduction, most electrophysiological studies report the earliest difference between upright and inverted faces at the level of the first component that is consistently larger in amplitude to face stimuli than objects, the N170 (Bentin et al., 1996; de Haan et al., 2002; Eimer, 2000; Linkenkaer-Hansen et al., 1998; Milivojevic et al., 2003; Rossion et al., 1999, 2000, 2003; Rousselet et al., 2004; Sagiv and Bentin, 2001; and its counterpart the VPP, see Jeffreys, 1996; Joyce and Rossion, 2005). However, a few studies have found that the earlier P1 component was also sensitive to face orientation (Itier et al., 2006a; Itier and Taylor, 2002, 2004; Linkenkaer-Hansen et al., 1998). In both cases, the latency of the components is delayed when faces are presented upside-down, and their amplitude is – somewhat paradoxically – increased. The effect of face inversion on the P1 has been taken by some authors as evidence that the earliest face-sensitive cortical processes take place during the time window of this component (Itier and Taylor, 2002). Here, one of the most interesting finding was that while there were small but significant orientation effects at the level of the P1, these effects were not correlated with the pattern of responses observed behaviorally. For instance, the P1 was most delayed and enhanced at around 90° rotation of the face
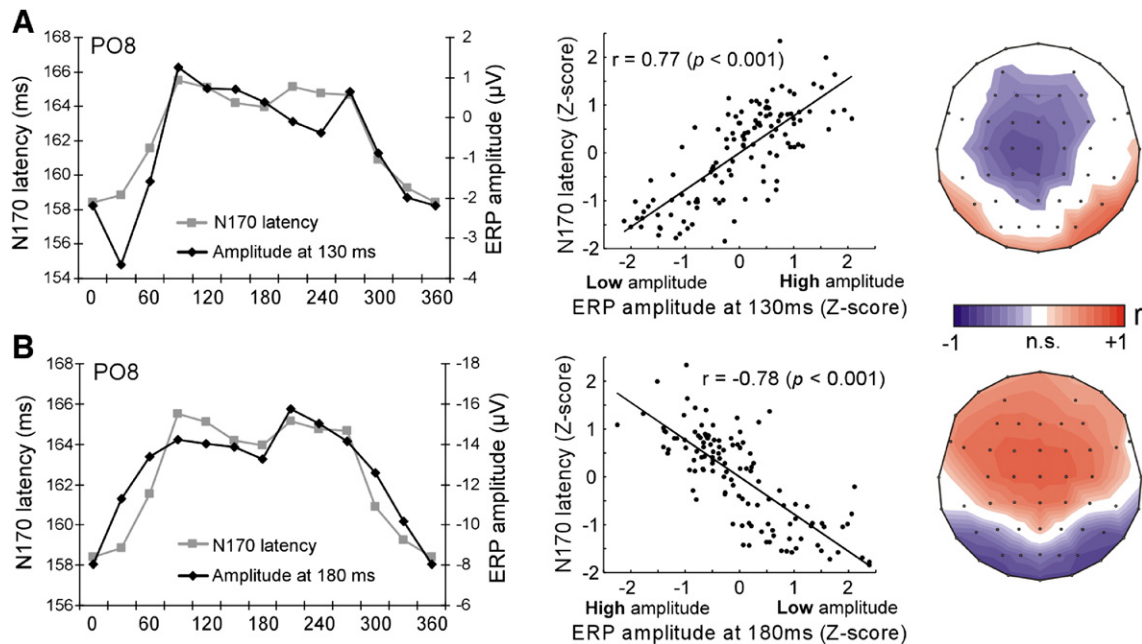
Fig. 8. Correlation analyses between ERP amplitude at each time point and N170 peak latency. The figure shows results of this analysis at two time points where the correlations were maximal. (A) Left: ERP amplitude at 130 ms and N170 latency averaged over all subjects at electrode PO8 are shown on the same plot for comparison. Middle: Scatter plot between z-scored ERP amplitudes at 130 ms and N170 latency for all subjects×orientations (120 points). Right: Scalp distribution of the significant correlation between ERP amplitude at 130 ms and N170 latency. (C) Correlation between ERP amplitude at 180 ms and N170 latency, see (B) for details.

and then decreased again toward 180°. In contrast, behavioral performances continued to be modulated up to 120° with no further modulation from 120° to 180°, as was observed for the N170 component. This was confirmed by the finding that P1 modulations with face rotation only included a significant non-linear trend, while N170 and behavioral patterns included significant linear *and* non-linear trends. Moreover, significant correlations between behavior and electrophysiological signal emerged only *after* the P1 peak, earlier in the right hemisphere (∼110 ms), and were maximal at 130 and 180 ms in the two hemispheres. The absence of any consistent relationship between behavior and the EEG signal at the P1 is in line with the less consistent inversion effects found for this component. It suggests that P1's effects in previous studies as well as in the present work may be due to low-level differences between upright and upside-down faces, such as the location of high-contrast regions of the face (i.e. the eyes or eyebrows) in the upper or lower visual field for instance, which are not directly related to behavioral impairment at recognizing inverted faces. Along these lines, it is interesting to observe that in the present study, the P1 was most enhanced in amplitude when faces were tilted horizontally (60°–120° or 300°–240°), especially when the high-contrast face regions (i.e. eyes and eyebrows) was presented in the visual field contralateral to the recording sites. Also in agreement with this suggestion, we note that most studies reporting clear P1 effects used large face stimuli presented with the hairline, leading to strong differences in contrast stimulation between upper and lower visual field when comparing upright an inverted faces (e.g. Itier and Taylor, 2002, 2004).

A functional dissociation between the P1 (or M100 in MEG) and the N170 (or M170 in MEG) is also supported by the finding that the P1/M1, a component that is known to reflect activation from striate and early extrastriate visual areas (Clark et al., 1995;

Di Russo et al., 2002; Gomez Gonzalez et al., 1994), is strongly correlated with the amount of noise in an image (Tarkiainen et al., 2002) or the noise's spatial frequency (Tanskanen et al., 2005), but is not correlated with the amount of face information in the image (Jemel et al., 2003; Tanskanen et al., 2005; Tarkiainen et al., 2002). By contrast, in the same studies, the amplitude and latency of the N170/M170 is strongly correlated with the perception of a face stimulus. To our knowledge, the present study reports the first evidence that the effects of picture-plane rotation on the P1 and N170, albeit sometimes similar when 2 orientations are considered only, are functionally dissociated.

Face inversion effects take place at multiple time-scales

The analysis reported here go beyond a mere debate between ERP components (P1 vs. N170) as stages of face processing: by performing point-by-point correlations between electrophysiological and behavioral responses, we were able to clarify the exact time point at which the face inversion effect originates, i.e. in the slope between the P1 and N170 peaks. We also found that ERP amplitude was tightly related to behavioral performances around the N170 peak. Even though these early electrophysiological signals do not reflect perceptual decision making processes *per se*, as in recent studies of correlation between behavioral performance at face processing tasks and EEG activity (Philiastides and Sajda, 2006), the information present in the neural response during these early encoding time windows at occipito-temporal sites largely determines the behavioral discrimination decision on the probe face (Keysers et al., 2001; VanRullen and Thorpe, 2001). Importantly, this analysis was performed without making any assumption about the electrodes of interest, searching for the spatio-temporal windows that are critical for the face inversion effect over the entire scalp. These correlations were observed on

the first (target) face stimulus – on which no behavioral response was performed – reinforcing the view that face inversion affects the extraction of critical information during perceptual encoding.

An interesting outcome of our point-by-point analyses is the finding of 3 distinct spatio-temporal ERP time windows that strongly paralleled behavioral responses, specifically: 110–145 ms (maximal correlation at 130 ms), 155–220 ms (maximal correlation at 180 ms), and 320–600 ms. The first two time windows may actually correspond to a single window, for several reasons. First, the absence of correlation between 145 and 155 ms may be due to the peculiarities of the ERP methods, which detect changes of neural activation rather than sustained states (Jacques and Rossion, 2006; Naatanen and Picton, 1987). More precisely, it is during this time-period that most ERP waveforms in the different conditions crossed one another (Fig. 3), resulting in an absence of difference between conditions, hence an absence of correlation during that particular time-period and correlations of opposite signs in the ~130 ms and ~180 ms time windows. Second, multiple evidence from EEG and MEG source localization (Herrmann et al., 2005; Itier et al., 2006a; Rossion et al., 2003; Watanabe et al., 2003), intracranial recordings (Allison et al., 1999) and the combination of EEG and fMRI data (Henson et al., 2003) suggest that the N170 originates from a network of regions including the middle fusiform gyrus, the inferior occipital cortex, and the inferior, middle and superior temporal gyri. The topographical difference between the correlations at 130 ms and 180 ms may be due to face orientation modulating different neural sources of the N170 at different time courses, rather than to different brain regions being active at these different time windows. This is most plausible given the largely overlapping topographies and the close temporal vicinity of the two patterns.

An alternative account would be that these two early time windows during which behavior correlates best with ERP signal correspond respectively to impairments in the categorization of the stimulus as a face (or face detection) and to the encoding of its unique identity. Insofar as face inversion affects both face detection (Lewis and Edmonds, 2003; Purcell and Stewart, 1988; Rousselet et al., 2003; Tomonaga, 2007) and the encoding of an individual face representation (e.g. Freire et al., 2000; Sergent, 1984; Yin, 1969; albeit with a more detrimental effect on face individualization for segmented stimuli, see Rossion and Gauthier, 2002), the impairment of both processes by face rotation may have contributed to the patterns of behavioral results, and thus to the observed correlation between ERPs and behavior in the two successive time windows. ERP variations observed during the first time window (110–145 ms) may reflect at least partly the delayed categorization of the stimulus as a face as a result of face rotation, but not yet the coding of facial identity (for which enough evidence has not yet been accumulated). The latency of this early time window is in line with single-cell recording studies in the monkey inferior–temporal cortex, where neurons responding preferentially to faces have a mean response onset latency of about 100 ms (Kiani et al., 2005; Oram and Perrett, 1992). The onset time of the second time window is compatible with the recent finding that the repetition of same *vs.* different facial identities in a long duration adaptation paradigm leads to a reduced ERP signal at occipito-temporal sites starting at 160 ms (Jacques et al., in press). This suggests that in the present study, information about facial identity may be encoded during this second time window, not earlier (see also Jacques and Rossion, 2006).

Rather than two clearly distinct stages, we consider these modulations due to face rotation as taking place during a

continuous and progressive accumulation of information about the visual stimulus being encountered. This view of visual processing as proceeding in a continuous accumulation of information about a stimulus properties (e.g. Perrett et al., 1998; Tjan, 2001), rather than in a succession of distinct stages suggests that the time to reach a given perceptual decision (e.g. face detection or face individualization) is a function of the amount of information needed to attain the decision threshold and of the format of stimulus presentation. It is compatible with the finding that a large proportion of face responsive neurons are involved in both face detection and face individualization, with information about each categorization level being significantly represented at different time windows of the neurons' responses (Matsumoto et al., 2005; Sugase et al., 1999). According to this model, face neurons would accumulate information about an inverted face at a slower rate as compared to upright faces, leading to increased response time for both face detection and face categorization (Perrett et al., 1998 – see also Logothetis et al., 1995 for non-face stimuli).

Regarding the early (~130 ms) time window, our analyses showed that the ERP amplitude at this latency is predictive of both the behavioral performance and the N170 latency modulation with face orientation. This observation reveals that the correlation between behavior and ERP amplitude at this latency is most probably due to a difference in the latency of the ERP waveforms between conditions that correlates with behavioral face discrimination. More precisely, a latency difference between conditions occurring in a steep slope (here between P1 and N170) artificially creates a large amplitude difference between these conditions when measuring the amplitude at the same time point for all conditions, as in the present case (the amplitude difference would increase and eventually asymptote as the slope become closer to $-\infty$). This suggests that the earliest effect of the face inversion takes the form of a delay in the ERP waveforms after the P1 peak, the amplitude increase in the N170 window starting slightly later. This latency difference observed on ERPs may be due either to a latency difference in the onset of the N170 neural generators between face orientations, or to the addition of a positive-going ERP component starting at ~110 ms, maximal at ~130 ms, and whose amplitude correlates with the N170 latency. However, given that in this time window the ERP amplitude and latency are tightly correlated, the present study cannot distinguish between those two possible alternatives for the latency delay observed at ~130 ms.

We also observed a third pattern of correlation, starting at around 320 ms over occipito-temporal regions, although with a slightly more anterior–temporal distribution than the N170 effect. Similar late ERP effects of face inversion have been found previously on frontal and parietal electrodes (Itier and Taylor, 2002; 2004) or temporal electrodes (Rossion et al., 1999; Carbon et al., 2005). Given its late onset time with respect to early perceptual processes and its similar topography to early effects, this ERP modulation may represent a re-activation of occipito-temporal and anterior temporal regions associated with higher-level processing of faces (Itier and Taylor, 2002, 2004). Here we show that these late effects of inversion are also highly correlated with behavioral output. Yet, correlations were computed on the ERP response to the target stimulus for which no behavioral response was produced. This suggests that that this effect does not reflect decisional processes, but possibly the sustained activation of a face representation to be associated with or discriminated from the incoming probe stimulus.

What do amplitude and latency increases of N170 with face inversion reflect?

As in previous studies, we observed large latency and amplitude increases of the N170 to inverted faces. The latency delay of the N170 is compatible with the delay found in single-cell responses to faces presented upside-down (Perrett et al., 1988, 1998), and with intracranial recordings on the cortical surface (the N200, McCarthy et al., 1999). This latency effect may reflect a delay in the onset of activation of face representations due to the unusual conditions of stimulation, or a slower build up of neural activity in population of neurons for faces presented at unusual views (Perrett et al., 1998). However, the increase of N170 amplitude with inversion is more puzzling because face-selective cells respond equally strongly or even slightly *less* to inverted than upright faces (Perrett et al., 1988), the intracranial N200 is *smaller* in amplitude to inverted faces (McCarthy et al., 1999), as is the response of the 'FFA' to inverted faces (Mazard et al., 2006; Rossion and Gauthier, 2002; Yovel and Kanwisher, 2005). Thus, the larger N170 amplitude to inverted faces has been related to indirect factors such as the increase in the difficulty of processing inverted stimuli (Rossion et al., 1999), or an enhanced contribution of the STS region coding for eyes features (Bentin et al., 1996; Itier et al., 2006b). It has also been suggested (Rossion et al., 1999) that the N170 increase could be related to the activation of additional sources for inverted faces in the object perception system as evidenced in fMRI studies (Haxby et al., 1999). Yet these proposals are still speculative at this state of knowledge: the reason why inversion increases the N170 amplitude on the scalp is still unclear. The interest of the present study is not in clarifying the neurophysiological origin of these effects, but in providing evidence that they are meaningful from a functional point of view: they are directly correlated with behavioral performance during an individual face discrimination task.

Do amplitude and latency effects on the N170 reflect the same phenomenon? Here we found a strong positive correlation between these two parameters: both increased as a function of face orientation, following the same pattern. At first glance, this may suggest that the increase of amplitude and latency with face inversion reflects the same phenomenon: perhaps an increased difficulty in detecting and encoding a face template, leading to a delay in the onset of the N170 and an increased processing time for inverted faces. Yet, while a commonality of underlying cause(s) may be true for plane-rotation of the face stimulus, one should be aware that other stimulus manipulation may affect differently the relationship between these two parameters. For instance, Jemel et al. (2003) found that progressively increasing the amount of visual noise onto a face image leads to a linear *decrease* of the N170 amplitude and a linear *increase* in N170 latency, thus yielding a correlation of opposite sign to that found here. Because these two parameters are differentially affected by different stimulus manipulations, they may reflect partly distinct functional processes involved in face categorization.

The perceptual nature of the face inversion effect

The strong correlation patterns between electrophysiological and behavioral measures found during the N170 time window clearly demonstrates the perceptual encoding basis of this effect, as suggested by behavioral evidence (e.g. Farah et al., 1998; Freire et al., 2000), and more recently by neuroimaging studies showing significant correlation between the behavioral inversion effect and fMRI signal in the fusiform gyrus (Yovel and Kanwisher, 2005; see also Mazard et al., 2006).

It is generally acknowledged that inverting a face impairs mainly, but not exclusively, the perception of facial configuration, i.e. the integration of features into a holistic representation (Sergent, 1984; Tanaka and Farah, 1993; Young et al., 1987) and the perception of metric distances between features (e.g. Barton et al., 2001; Collishaw and Hole, 2000; Freire et al., 2000; Le Grand et al., 2001; Leder and Bruce, 2000; Rhodes et al., 1993), in particular in the vertical direction (Goffaux and Rossion, in press). The respective time-course of the encoding of facial configuration and facial parts is currently unknown, but the present data suggest that at least some aspects of facial configuration are coded early on during face processing.

At the behavioral level, several previous studies have investigated and characterized the patterns of response to faces presented at different orientations. Valentine and Bruce (Valentine and Bruce, 1988) reported several experiments using faces presented at 45° increments (0°, 45°, 90°, 135°, and 180°) and found a linear relationship between response time at face identification and the degree of misorientation. However, the 45° steps rendered invisible any non-linearity in the data. Furthermore, linearity was described only for RTs, while error rates were larger at 135° than at 180°, suggesting a non-linear component. More recently several investigators have presented faces at more than two (upright and inverted) orientations in conjunction with other face manipulations, such as blurring, featural and configural changes, or 'Thatcherization' of the face (Bruyer et al., 1993; Collishaw and Hole, 2002; Lewis, 2001; McKone, 2004; Murray et al., 2000; Sjoberg and Windes, 1992; Sturzel and Spillmann, 2000). Even though different tasks and behavioral measures were used in these studies, most of them showed that subjects' performances as a function of face orientation significantly deviate from linearity at orientations around 90°–120°, similarly to our behavioral findings. These non-linear effects of rotation are generally interpreted as further evidence for a qualitative impact of inversion on face processes, and against the presence of an early linear normalization perceptual mechanism (e.g. mental rotation).

Importantly, the present study shows for the first time that these patterns of behavioral modulations with picture-plane rotation are highly similar to the ERP responses at the level of the early encoding of face representations in the visual system (N170). In addition, the present results encourage relying on parametric designs during active behavioral tasks in future human electrophysiological studies to clarify the time-course of robust behavioral effects at a global scale.

Acknowledgments

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