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Spatiotemporal analysis of event-related potentials to upright, inverted, and contrast-reversed faces: Effects on encoding and recognition

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Abstract

In an n-back face recognition task where subjects responded to repeated stimuli, ERPs were recorded to upright, inverted, and contrast-reversed faces. The effects of inversion and contrast reversal on face encoding and recognition were investigated using the multivariate spatiotemporal partial least squares (PLS) analysis. The configural manipulations affected early processing (100–200 ms) at posterior sites: Inversion effects were parietal and lateral, whereas contrast-reversal effects were more occipital and medial, suggesting different underlying generators. A later reactivation of face processing areas was unique to inverted faces, likely due to processing difficulties. PLS also indicated that the "old–new" repetition effect was maximal for upright faces and likely involved frontotemporal areas. Marked processing differences between inverted and contrast-reversed faces were seen, but these effects were similar at encoding and recognition.

Descriptors: Configuration, Faces, Partial least squares, Event-related potentials, Inverted, Contrast-reversed, Multivariate analysis, Spatiotemporal analysis

In the past few years, a growing interest in the study of face processing has emerged. One area that has been intensively studied is the "face-inversion effect," the fact that face recognition performance decreases when faces are presented upside down (Farah, Tanaka, & Drain, 1995; Hochberg & Galper, 1967; Rhodes, Brake, & Atkinson, 1993; Yin, 1969) whereas the decrements in performance for inverted objects are not as great. Behavioral investigations of face inversion have focused on what is unique to the processing of upright faces that accounts for recognition decrements when faces are inverted. Converging behavioral results lead to the conclusion that inversion disrupts mainly the relational or configural processing of faces (Bartlett & Searcy, 1993; Leder & Bruce, 2000; Rhodes et al., 1993; Searcy & Bartlett, 1996), that is, the relationships among the features of a face that produce a particular configuration for each face, despite a similar arrangement of features in all human faces. Configural processing can also be disrupted by contrast reversal (Kemp, McManus, & Pigott, 1990; Lewis & Johnston, 1997), which also leads to impaired face recognition (Galper, 1970; Johnston, Hill, & Carman, 1992; Kemp et al., 1990). This disruption occurs despite the fact that all edges, spatial frequencies, and arrangement of facial features are preserved. However, it has been suggested that there are two steps in upright face processing, a holistic processing, enabling the perception of a face as a face, and a configural processing (Hole, George, & Dunsmore, 1999). In this view, inversion would disrupt both steps, whereas only configural processing would be disrupted by contrast reversal, and the perception of a face as a face would be preserved.

Successful face recognition depends on adequate encoding of the faces as well as accurate matching in memory. Disruptions to configural processing of faces during either processing stage could produce recognition deficits. Behavioral studies have consistently shown that inversion disrupts configural processing at the encoding stage (Bartlett & Searcy, 1993; Freire, Lee, & Symons, 2000; Rhodes et al., 1993; Searcy & Bartlett, 1996). The effects of contrast reversal are less consistent, being linked to both encoding (Kemp et al., 1990) and recognition (Liu & Chaudhuri, 1997). Electrophysiological studies have attempted to clarify these discrepancies found in the behavioral literature.

Face processing has been widely investigated using event-related potentials (ERPs), especially the N170 component (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Bötzel, Schulze, & Stodieck, 1995; George, Evans, Fiori, Davidoff, & Renault, 1996) that appears to reflect early face processing (encoding). The findings that the N170 was delayed and larger in amplitude for inverted compared to upright faces (Bentin et al.,

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1996; Eimer, 2000; Itier & Taylor, 2002, 2004; Linkenkaer-Hansen et al., 1998; Rossion et al., 1999, 2000; Taylor, Edmonds, McCarthy, & Allison, 2001) but not for inverted objects (Bentin et al., 1996; Rebai, Poiroux, Bernard, & Lalonde, 2001; Rossion et al., 2000) provided support for an encoding mechanism particular to face processing that could be disrupted by inversion (Eimer, 2000; Itier & Taylor, 2002; Rossion et al., 1999, 2000). N170 was also shown to be delayed and larger for contrast-reversed faces compared to upright faces, in a similar way as for inverted faces (Itier & Taylor, 2002). However, inversion and contrast reversal had different effects on the P1 component (Itier & Taylor, 2002) that seemed associated with initial global processing of faces (Itier & Taylor, 2002, in press; Linkenkaer-Hansen et al., 1998; Taylor, 2002). This suggested that the early face processing steps were differently disrupted by inversion and contrast reversal.

Itier and Taylor (2002) also analyzed long-latency frontal and parietal components that reflect memory processes, and concluded that recognition was also affected differently by face inversion and contrast reversal. However, some differences between contrast reversal and inversion on later components were identified visually, using voltage maps of subtraction waveforms. These and other effects, such as a possible reactivation of face processing areas at ~300 ms in parieto-occipital areas, were observed on these voltage maps but were not assessed statistically. The aim of the present study was to better assess inversion and contrast-reversal impact on face encoding and recognition, using a multivariate analysis technique rather than univariate analyses performed on particular components.

Generally, in classical ERP studies, amplitudes and latencies are measured, focusing on known or prominent components at particular electrodes. This could result in a situation where potentially interesting differences at other electrodes and latencies are missed. One solution is to perform an analysis that takes into account multiple time points and electrodes. Multivariate approaches, such as principal components analysis (Donchin & Heffley, 1978) or independent components analysis (Makeig et al., 1999) begin to address the multivariate nature of ERP data sets by assessing either the temporal or spatial features of the data. Ideally it would be preferable to assess simultaneously the spatial and temporal features that identify face type effects across the scalp. The partial least squares (PLS; Wold, 1975) method does this and was used in the present study. PLS was introduced for the analysis of functional neuroimaging data by McIntosh, Bookstein, Haxby, and Grady (1996), and has had notable success in identifying unique relations between (a) experimental design and brain activity (McIntosh et al., 1996), (b) brain activity and behavioral responses (McIntosh, Lobaugh, Cabeza, Bookstein, & Houle, 1998), and (c) activity in individual brain regions and the rest of the brain (McIntosh, Rajah, & Lobaugh, 1999). PLS has been adapted recently for spatiotemporal data such as ERPs (Duzel et al., 2003; Hay, Kane, West, & Alain, 2002; Lobaugh, West, & McIntosh, 2001; O'Donnell et al., 1999). In this context, PLS identifies the specific combinations of waveform differences that distinguish experimental conditions.

A preliminary spatiotemporal PLS analysis of the Itier and Taylor (2002) data was implemented to identify the specific combinations of waveform differences that distinguished the three face types (Itier, Lobaugh, & Taylor, 2001). In that analysis, encoding and recognition were examined separately, and the results suggested face-type effects were strikingly similar at encoding and recognition. To more fully understand the commonalities and differences in face processing at these two memory stages, a more focused PLS analysis is presented here, in which encoding and the two memory conditions were combined into a single analysis. We predicted that the major results would confirm that face-type effects were similar at encoding and recognition. Additionally we expected that PLS would reveal differences between immediate and delayed recognition among the three face types. Finally, we wished to determine if the longer latency parieto-occipital activity seen for repeated faces (the possible "reactivation" of these areas around 300 ms) varied with task demands and stimuli.

Method

Participants

Thirty-four young adults (17 women) participated in the study; the data from one man and one woman were rejected due to excessive noise at multiple electrodes. The 32 remaining participants (20 to 33 years, mean age 25.3 years) had normal or corrected-to-normal vision. All participants signed informed written consent; the French Comité Opérationnel pour l'Ethique dans les Sciences de la Vie du CNRS approved the experimental procedure.

Stimuli and Procedure

Stimuli were 720 gray-scale pictures of unknown faces (50% female). One third of the 720 faces were presented upright, one third inverted and one third in contrast-reversed format (upright position). Stimuli were divided into 12 series of 60 faces (four series per face type). These 12 series were presented in pseudorandom order. Within each series of 60 faces, 20 faces repeated one time each. Half of the repeated faces were repeated immediately (condition 0-lag) and half were repeated after one intervening face (1-lag). In pilot studies we found that accuracy for recognizing inverted contrast-reversed faces was less than 40% at 1-lag, and recognition of inverted faces fell to 35% at 2-lag. Thus, neither inverted contrast-reversed faces nor lags greater than 1 were included, as they would yield too few trials for reliable ERP measures. Condition "encode" was defined as the first presentation of faces correctly recognized later in the 0- and 1-lag conditions. This ensured that the ERPs reflected processes associated with correct encoding. Similarly, the "memory" conditions consisted of only correctly recognized 0-lag and 1-lag trials. Pictures were presented centrally on a computer screen for 500 ms with an ISI of 1,320 ms. Subjects fixated a centered cross appearing during the ISI to minimize eye movements. They pressed the space bar of a keyboard to repeated stimuli.

Electrophysiology

EasyCaps containing 35 electrodes including three ocular sites were used to record ERPs. One electrode monitored vertical eye movements from the supra-orbital ridge, and horizontal eye movements were monitored with two electrodes at the outer canthi. The EEG was recorded continuously via NeuroScan with a 500-Hz sampling rate and an amplification gain of 500 via SynAmps. Cz was the reference lead during acquisition; an average reference was calculated off-line. EEG was epoched into 1-s sweeps, including a 100-ms baseline. Off-line averaging was performed for each of the face types and memory conditions;

averages were digitally filtered (0.8–60 Hz). Trials contaminated with ocular movements ($\geq 100\,\mu$V) between 0 and 700 ms were rejected. The PLS analysis was conducted on this 700-ms interval (excluding the prestimulus baseline) for the 32 scalp electrodes; the EOG channels were not included.

Partial Least Squares (PLS)

The term *partial least squares* refers to the computation of the optimal *least-squares* fit to *part* of a correlation or covariance matrix. The part is the "cross-block" correlation between sets of exogenous and dependent measures. PLS is similar to PCA or eigenimage analysis (Friston, Frith, Liddle, & Frackowiak, 1993; Moeller, Strother, Sidtis, & Rottenberg, 1987), but one important feature of PLS is that the solutions are constrained to the part of the covariance structure attributable to experimental manipulations.

PLS operates on ERP data matrices containing subjects and conditions in the rows, and the amplitudes for all time points and channels in the columns (Figure 1A). The input matrix for this TaskPLS was obtained by mean-centering the columns of the ERP amplitude data matrix with respect to the grand mean of each memory condition (Encoding, 0-Lag, and 1-Lag). The data points within memory condition are thus expressed as deviations around zero. As the means for the memory conditions are zero, the main effect of memory condition, and its associated variance, is removed from the analysis. This was done to focus the analysis on the main effects of face type (upright, inverted, and contrast-reversed) and Face Type × Memory Condition interactions. The use of deviation matrices produces results identical to what would be obtained through the use of orthonormal contrasts (e.g., Lobaugh et al., 2001; McIntosh et al., 1996).

Singular value decomposition (SVD) was performed on the stacked deviation matrices to identify the structure of the latent variables (LVs). Three outputs derived from the SVD are used to interpret the relationships between ERP amplitudes and task design (Figure 1B). The first is a vector of singular values, which represents the covariance of the experimental effect with the ERP amplitude for each LV, and is also used to calculate the proportion of the cross-block covariance matrix attributable to each latent variable. The second and third outputs contain the structure of the latent variables and are orthogonal pairs of vectors (saliences). One vector defines the contrasts among conditions (design saliences). The other vector (electrode saliences) identifies where, in time and space, the effects in the design saliences for each latent variable are expressed. The magnitude and sign of the electrode saliences indicate the strength and direction of the indentified differences among the conditions at each time point. To provide a summary statistic for each subject, the electrode saliences are multiplied back against the raw waveforms (dot-product) to produce scalp scores for each subject. The significance of the singular values was determined using permutation tests (500 replications) to provide an exact probability of observing the singular value by chance (e.g., $p = .001$); the stability of the electrode saliences at each time point and location in space was established through bootstrap resampling (500 replications; Fabiani, Gratton, Corballis, Cheng, & Friedman, 1998) to provide a standard error for each of the saliences. The ratio of the salience to its bootstrapped standard error is approximately equivalent to a *z* score. Bootstrap ratios greater than 3.0 (roughly equivalent to $p = .001$) were taken to indicate stable saliences, or in other words, time points where the electrode saliences differed from zero. The PLS analysis of this data set was conducted using a Matlab-based (v. 6.5, Mathworks, Inc.) graphical interface (available at www.rotman-baycrest.on.ca:8080). It was completed in about 50 min and required 150 MB RAM on a Pentium III, 1200 MHz CPU.

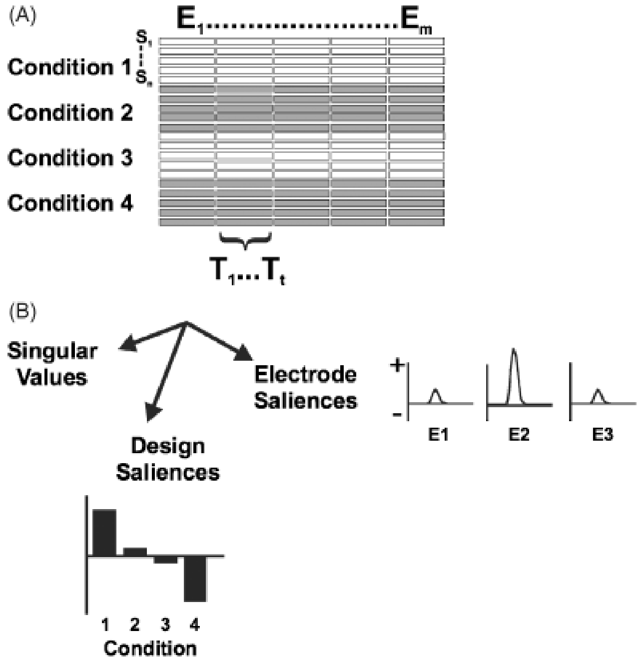

Figure 1. Steps in the PLS analysis of ERP data. A: A data matrix is created. The data matrix is organized such that a single row contains all datapoints (T_1 ... T_t) for a single subject for all electrodes (E_1 ... E_m) within a condition. This matrix is converted to a deviation matrix by subtracting the grand mean from each datapoint. B: Singular value decomposition on the deviation data matrix generates two sets of vectors for each latent variable (LV): *design saliences* and *electrode saliences*, as well as the singular values for the LV. The spatiotemporal distribution of the electrode saliences for a LV is plotted here for three electrodes.

Results

Behavioral Results

A main effect of face type on reaction times (RTs), $F(2,63.4) = 14.52$, $p < .0001$, was due to RTs to upright faces being faster than to inverted, $p < .0001$, and contrast-reversed, $p < .0001$, faces, which did not differ. A condition main effect, $F(1,31) = 67.68$, $p < .0001$, was due to immediately repeated faces (0-lag condition) eliciting faster RTs than 1-lag faces.

Accuracy was higher for upright than inverted or contrast-reversed faces, *p*s < .0001, with no difference between the latter two; face type effect, $F(1.6,52.5) = 43.09$, $p < .0001$. Higher hit rates were found for 0-lag (94.9%) compared to 1-lag (67.8%) faces; condition effect, $F(1,31) = 159.1$, $p < .0001$. A Type × Condition interaction, $F(1.8,56.4) = 13.38$, $p < .0001$, was due to greater decreases in performance in the 1-lag condition for inverted and contrast-reversed faces compared to upright faces.

PLS Results

PLS identified three major effects, three latent variables, which were significant by permutation test, *p*s $\leq .002$. The first two effects indicated that ERP amplitude differences among the three face types were similar across all memory conditions. The dominant effect reflected the distinction between upright and inverted faces. The second identified differences between contrast-reversed faces and the other two face types. The third effect was a Face Type × Memory Condition interaction. These are described in detail below.

Face-type effects independent of memory condition

Inversion effect. The design saliences for the first latent variable (LV1) indicated that the largest difference among the face types was between upright and inverted faces; it represented 49.4% of the cross-block covariance. As can be seen in Figure 2 (top left panel) upright-inverted differences were similar in magnitude for all memory conditions. The electrode saliences indicate where the differences are being expressed, and the electrodes with the strongest saliences are shown in the right panel of Figure 2 (blue lines). The stable differences, as assessed by bootstrap tests, are shown by the blue markers at the top of each channel plot. Although the inversion effect was found at almost all electrodes, a close look at the saliences revealed that the effect was primarily posterior and seen polarity reversed at frontal sites (clearly seen on Figure 3, left panels). It is largest where the saliences are maximal, and this occurred over the posterior parietal and parietal-occipital electrodes (P7/P8, PO9/PO10). The face-inversion effect was biphasic at early latencies, with positive saliences emerging around 110 ms (but stable from 140 ms and maximal at 150 ms), followed by strong negative saliences peaking around 190 ms. This was followed by sustained negative saliences from 300 to 600 ms. To better appreciate the topography of face-inversion effects, the peak saliences are plotted in Figure 3 (left panel). The topographies of the early and late differences are quite similar, both being strongest over posterior lateral electrodes.

Contrast-reversal effect. The design saliences for LV2 (34.8% of the cross-block covariance) indicated that this LV distin-

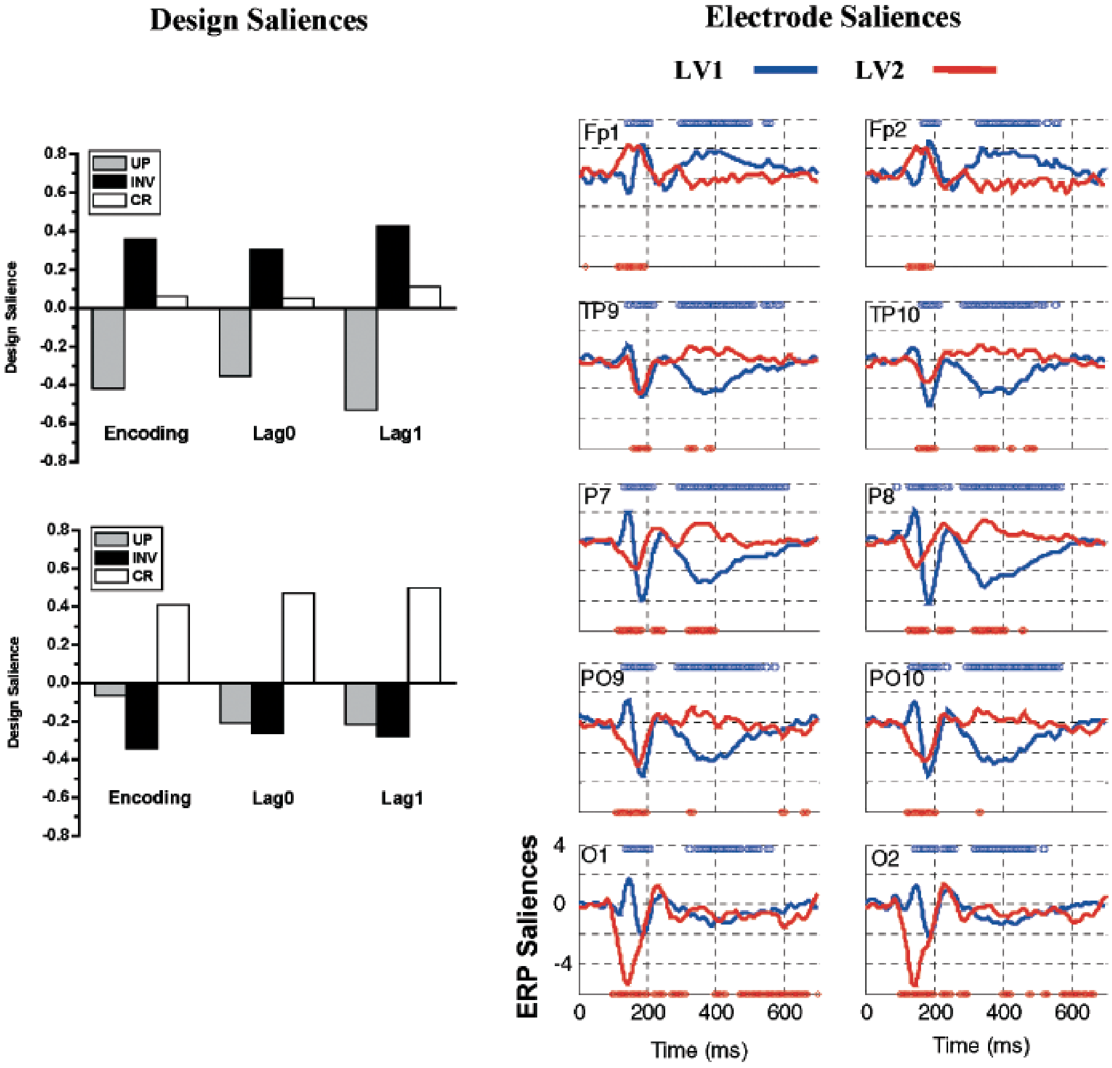

Figure 2. Left panels: Design saliences showing the distinctions between upright and inverted faces (LV1, face-inversion effect) and contrast-reversed and the other face types (LV2, contrast-reversal effect). Design saliences provide a visual depiction of the experimental effects, showing which conditions are maximally distinguished. Right panel: Electrode saliences for LV1 (blue) and LV2 (red). The blue markers above the traces indicate saliences stable by bootstrap estimation for LV1 and the red markers below the traces, on the *x*-axis, indicate stable saliences for LV2. The strongest saliences for both LVs are over posterior occipital and parietal electrodes shown here, seen weaker and polarity reversed at frontal electrodes (e.g., Fp1/Fp2).

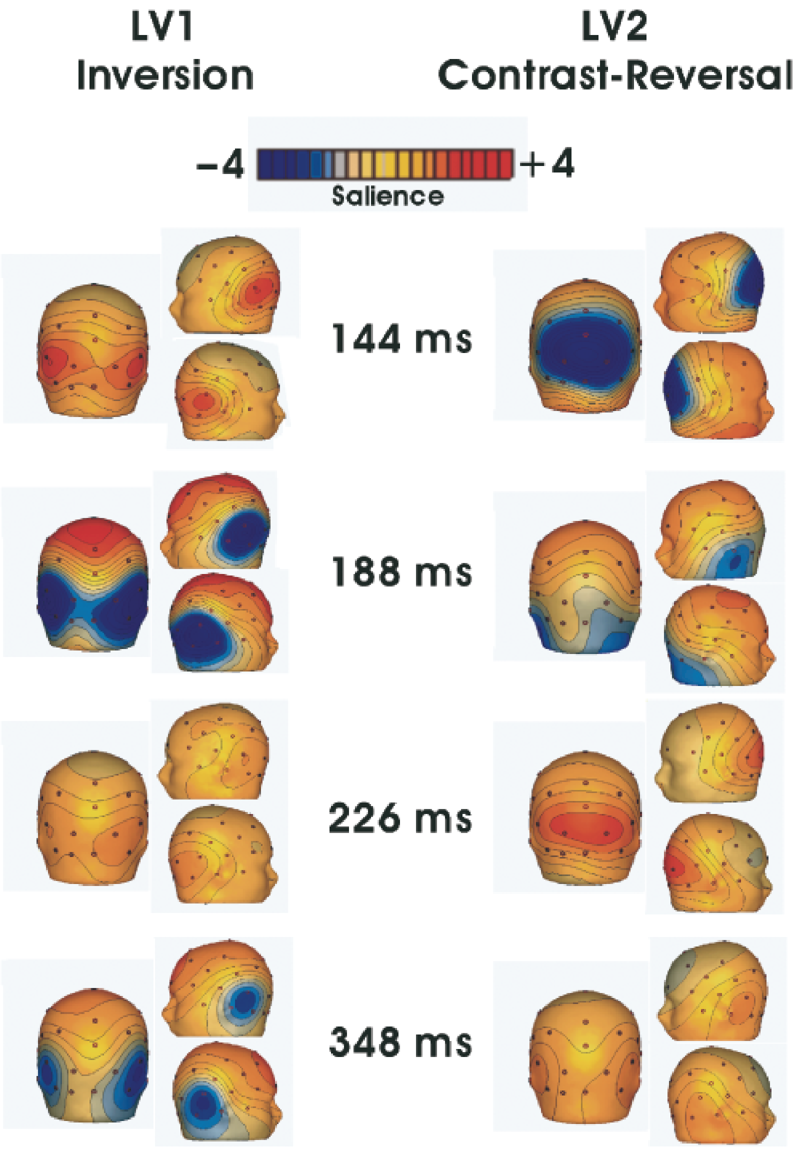

Figure 3. Topographies of the electrode saliences for the inversion effects (left panels, LV1) and for the contrast-reversal effects (right panels, LV2). The topographies are presented at four latencies: (1) 144 ms corresponds to the maximal negative saliences for LV2 at occipital sites and to the first positive peak salience at parietal sites for LV1; this latency corresponds to the P1–N170 transition on actual ERPs; (2) 188 ms corresponds to the largest negative peak salience for LV1, after the N170 on the ERPs; (3) 226 ms corresponds to positive saliences for both LVs and to the P2 on actual ERPs; (4) 348 ms corresponds to the maximum of the long-latency negative saliences for inversion effects at parietal sites; this latency corresponds to the "reactivation" of face parietal lateral areas for inverted faces only. Note the marked difference in the topographies of the two effects at all times except at 348 ms, where both effects are at the same posterior parietal electrodes.

guished contrast-reversed faces from the other face types (Figure 2, bottom left panel). Although the differences were largest between contrast-reversed and inverted faces, the separations between contrast-reversed and upright faces also contributed to this LV, especially in the recognition conditions. The electrode saliences indicated the contrast-reversal effect was strongest over posterior channels (POz, O1/O2, Iz, PO9/PO10), and was maximal at occipital sites (Figure 2, right panel, red lines, stable saliences indicated by red markers on the x-axis). The effect was seen polarity reversed at frontal electrodes (e.g., Fp1/Fp2 in Figure 2; Figure 3, right panel). Unlike the face-inversion effect (LV1), which was maximal at parietal lateral sites, the contrast-reversal effect was maximal at medial occipital electrodes (O1/2), and it emerged much earlier, at 100 ms. A period of late, stable differences, over parietal (P7/8) electrodes only, was also noted on this LV, but the duration was shorter (300–400 ms) than the face-inversion effect. Very long-latency differences (>500 ms) were focused over occipital electrodes, but saliences were weaker than the earlier effects. The salience topography of the contrast-reversal effect is shown in the right panel of Figure 3, at the same latencies as for LV1. Here, the earlier onset, and more occipital location of differences for the contrast-reversal effect can be seen quite clearly (144 ms and 188 ms). Interestingly, the topography of the late differences (348 ms) is similar to that seen for the face-inversion effect, although with smaller magnitude.

Inversion and contrast-reversal effects expressed on ERPs. To more fully appreciate the nature of the differences in ERP

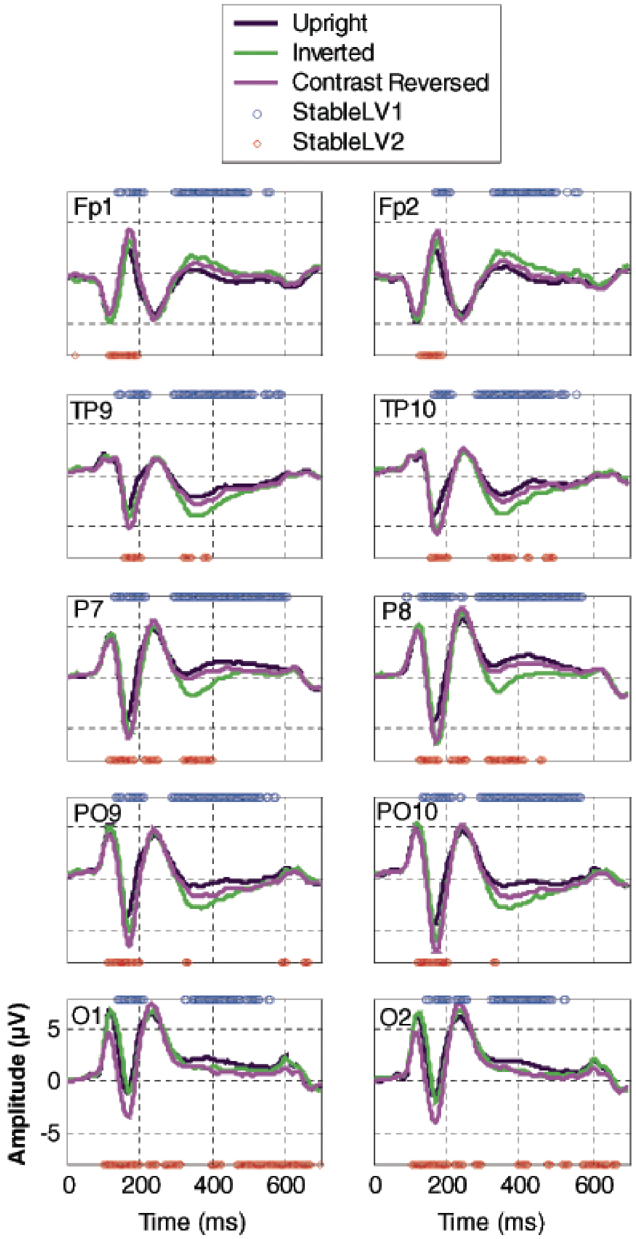

Figure 4. ERP waveforms, collapsed across encoding and recognition, displayed at the same electrodes as in Figure 2 for upright (black), inverted (green), and contrast-reversed (magenta) faces. The stable differences are indicated for each electrode as in Figure 2 (blue, top = LV1/inversion effects; red, bottom = LV2/contrast-reversal effects).

amplitude related to face type, the ERPs are shown in Figure 4, collapsed across memory conditions (as the effects were similar across memory conditions), for the channels showing the largest differences. Markers at the top (blue) and bottom (red) indicate the time points of stable differences for the face inversion and contrast-reversal effects, respectively. Because the frontal sites reflected only a polarity reversal, we describe only the posterior electrodes.

The inversion effect started around 150 ms, that is, right after the peak of P1, and encompassed the transition between P1 and N170, the N170 peak itself, as well as the transition between N170 and the P2 component (and including the P2 on right hemisphere electrodes). The effect reflected slightly larger amplitudes for inverted compared to upright faces between P1 and N170 and between N170 and P2, due to a latency delay between the two face types. The negative saliences seen in Figure 2 and reaching a maximum around 190 ms reflected the larger amplitudes obtained for inverted faces at the peak of N170. Thus, at early time points (<250 ms), the inversion effect was expressed as a delay of the triphasic complex P1-N170-P2 for inverted faces, in addition to larger N170 amplitudes for inverted compared to upright faces.

The contrast-reversal effect started earlier than the inversion effect, at around 100 ms, and included the P1 peak in addition to the P1-N170-P2 transitions/complex. Contrast-reversed faces showed smaller P1 amplitudes at occipital electrodes with a faster transition to a more negative N170 peak compared to upright and inverted faces. The N170 was largest for contrast-reversed faces at occipital and parieto-occipital sites (Figure 4), whereas at parietal sites, it was equally large for inverted and contrast-reversed faces, both of them being larger than upright faces. Similar to the inversion effect, the N170-P2 transition was later for contrast reversed than for upright faces.

The inversion effect at temporo-parietal, parietal and parieto-occipital sites from 300 to 600 ms reflected more negative amplitudes posteriorly for inverted than upright faces; this was seen in opposite polarity at frontal sites (more positive amplitudes for inverted faces). The contrast-reversal effect at parietal sites between 300 and 400 ms reflected the difference between contrast-reversed and inverted faces, with again more negative amplitudes for inverted than contrast-reversed faces. The comparison of salience head plots (Figure 3, at 348 ms) shows that the two effects were found at the same posterior lateral sites. Thus, at these parietal electrodes, inverted faces yielded more negative amplitudes than both upright and contrast-reversed faces, the latter eliciting amplitudes similar to upright faces.

Interaction of face type with memory condition

The third (and last) significant LV accounted for 6.8% of the crossblock covariance and reflected an interaction between face types and memory conditions. The design saliences (Figure 5, top panel) showed that 0-lag amplitudes varied as a function of face type, the effects being in opposite directions between upright and the other two face types. For the contrast-reversed faces, the primary difference was between 0- and 1-lag. The electrode saliences (Figure 5, bottom left panel) showed that these differences were expressed at two time periods: from ~220 to 320 ms at posterior sites (right lateralized, TP10 and P8), and from ~370 to 470 ms at fronto-temporal electrodes (FT9/FT10). This second effect was smaller and shorter at temporo-parietal (TP9/TP10) sites and was seen polarity reversed at parietal (P3/P4/Pz) electrodes. These two time intervals are highlighted in the electrode salience topographies, shown in the lower right panel of Figure 5.

The early effect at P7/P8 between 220 and 320 ms was related to the smaller P250 component and faster return to baseline for 0-lag upright faces (Figure 6, top left traces), which was not seen for the other two face types. More interestingly, at 370–470 ms, 0-lag ERPs for upright faces at FT9/FT10 were more negative compared to the other memory conditions (Figure 6, top right traces) and were most negative of all conditions. At 1-lag,

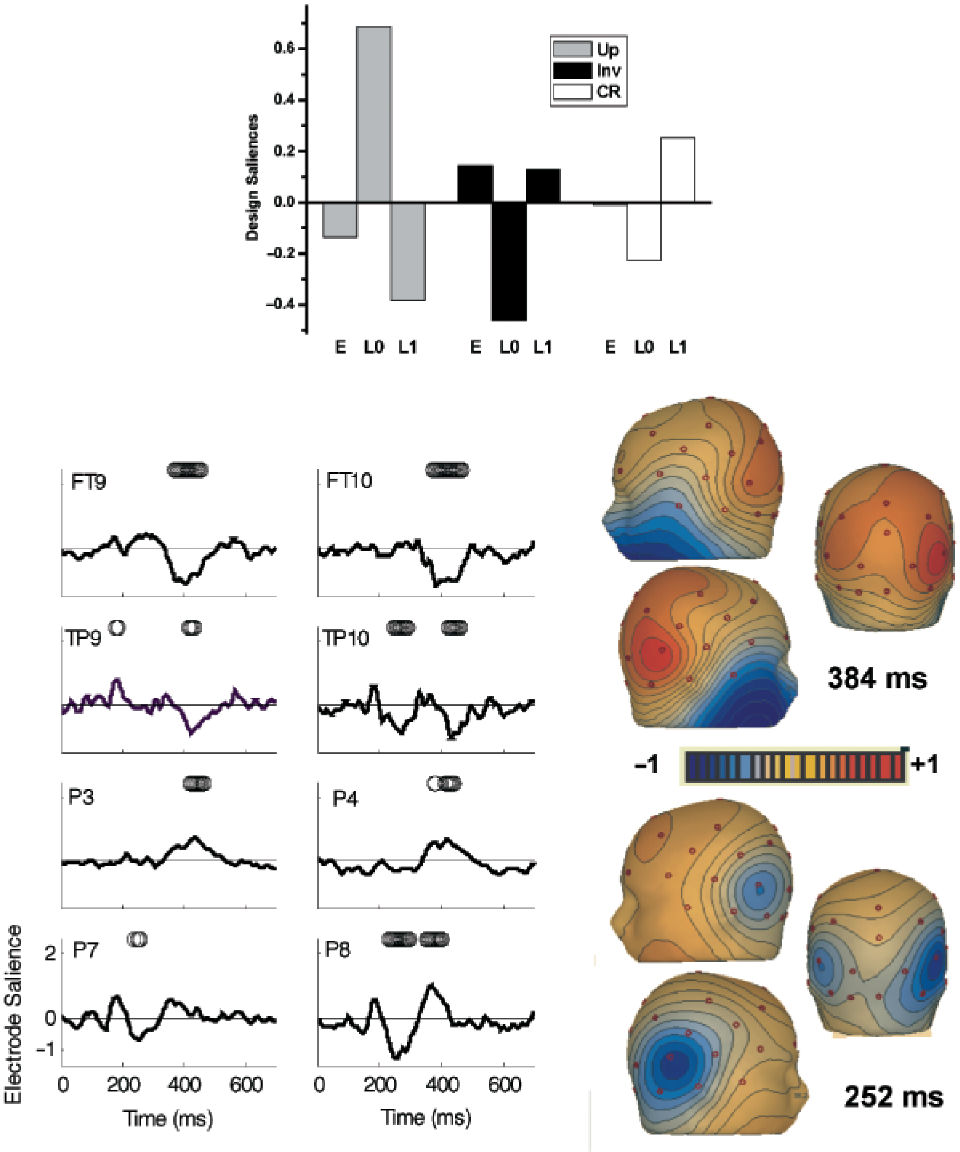

Figure 5. Top panel: Design saliences for LV3, showing a face type by condition interaction. For the upright and inverted faces, the differences are between the 0-lag and the other conditions, but are in opposite directions. Contrast-reversed faces show maximal distinctions between 0- and 1-lag conditions. Bottom left panel: Electrode saliences for LV3 displayed at the electrodes where saliences were maximal. The markers at the top indicate saliences stable by bootstrap estimation. The strongest saliences are over right parietal electrode P8 and over fronto-temporal electrodes, seen polarity reversed over P3/P4 sites. Bottom right panel: Scalp topography of the electrode saliences for the late fronto-temporal effects, (384 ms, top) and for earlier parietal effects (252 ms, bottom).

inverted and contrast-reversed faces led to more negative amplitudes than upright faces, as at encoding. This indicated a marked difference between face types, memory, and encoding conditions being similar for inverted and negative faces whereas 0-lag was very different from encoding and 1-lag conditions for upright faces only (Figure 6).

Discussion

PLS "pulls out" the experimental effects in order of magnitude, and in the present study, it identified three primary effects across the whole 700-ms epoch: (1) an inversion effect (inverted vs. upright faces), (2) a contrast-reversal effect (contrast-reversed vs. upright and inverted faces), and (3) an interaction between face types and memory conditions. The first two effects were independent of processing stage (encoding or memory) as they were similar for both, while the third effect differentiated face types in the encoding, 0-lag, and 1-lag conditions.

Effects of inversion were essentially seen over posterior electrodes, from 120 to 250 ms then from 300 to 600 ms, seen polarity reversed at frontal sites. Effects were maximal at lateral parietal electrodes P7/P8 for both time periods. Interestingly, inversion had no impact on the very early processing leading up to the peak of the P1, contrary to what was found in the P1 peak analysis (Itier & Taylor, 2002). However, right after the P1, the

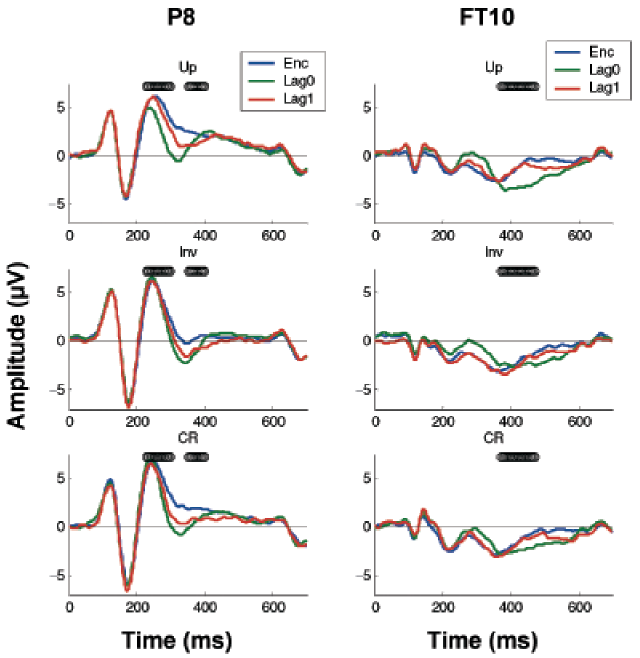

Figure 6. Grand average ERP waveforms at parietal (P8) and fronto-temporal (FT10) electrodes for upright (top panels), inverted (middle panels), and contrast-reversed (bottom panels) faces. The face type by memory condition effect emerged because upright faces showed larger differences between 0-lag (green) and encoding (blue) and 1-lag (red). Time points of stable differences are indicated by the black markers at the top of each trace.

pattern of differences suggested that inverted faces were processed more slowly than upright faces until the P2.

Contrast-reversal effects were also found at posterior electrodes and seen polarity reversed at frontal sites. However, unlike the laterally localized inversion effect, this effect was maximal at occipital electrodes, with a medial distribution (Figure 3, 144 ms). Furthermore, contrast-reversal effects started earlier, around 100 ms, encompassing the P1, which was smallest for contrast-reversed faces. The transition to the N170 was also faster for contrast-reversed compared to inverted and upright faces (Figure 4). Larger N170 amplitudes were seen for inverted and contrast-reversed compared to upright faces over all posterior sites, with a maximal difference at P7/P8 electrodes for inverted faces. However, the N170 was also larger for contrast-reversed than inverted faces at parieto-occipital and occipital sites, reinforcing the more occipital localization of the contrast-reversal effects. Thus, the same face type differences as those identified in Itier and Taylor (2002) were found on the N170 component, as well as on P1 for contrast-reversed faces, but PLS identified a marked difference in the distribution of the two effects that was not identified with the classical analyses.

Both inversion and contrast-reversal effects were found over parietal and temporo-parietal cortices, areas previously shown to be sensitive to face processing (Bentin et al., 1996; George et al., 1996). In fMRI studies, upright faces have been shown to reliably activate the fusiform gyrus, a ventral temporo-occipital area, more than other object categories (Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Puce, Allison, Gore, & McCarthy, 1995). Studies of face inversion have found that inverted faces also activate the fusiform gyrus, to the same extent or slightly less than upright faces (Aguirre, Singh, & D'Esposito, 1999; Haxby et al., 1999; Kanwisher, Tong, & Nakayama, 1998), whereas contrast-reversed faces activate this brain area less than their normal-contrast counterparts (George et al., 1999). This latter finding is in accordance with single-cell recordings in monkeys showing that although the selectivity for shapes of infero-temporal neurons is preserved when contrast is reversed (Baylis & Driver, 2001; Kovacs et al., 2003), the response of these face-selective cells to contrast-reversed faces decreases in magnitude (Ito, Fujita, Tamura, & Tanaka, 1994; Perrett et al., 1984).

The fMRI data are in contradistinction to our ERP data, which showed larger N170 amplitude for both inverted and contrast-reversed faces compared to upright faces. It has recently been shown that the N170 was generated to a large extent by lateral generators (Shibata et al., 2002; Watanabe, Kakigi, & Puce, 2003), likely in the superior temporal sulcus region (Itier & Taylor, 2004). Our present results suggest that inverted and contrast-reversed faces activate this lateral area more than upright faces, and that the two configural manipulations delay this lateral activity. However, the N170 was equivalent for contrast-reversed and inverted faces at parietal lateral sites but largest for contrast-reversed at parieto-occipital and occipital sites. This finding suggests additional medial generators were active for contrast-reversed faces. This hypothesis is supported by work in monkeys showing that some cells are selective to contrast polarity in macaque areas V1, V2, and V3 (Baumann, van der Zwan, & Peterhans, 1997).

Another new set of findings was that amplitudes during the P1–N170 transition played an important role in distinguishing the three face types. At 150 ms, the signal for contrast-reversed faces was more negative than for upright and inverted faces, reflecting a faster transition to N170 for contrast-reversed faces. One hundred fifty milliseconds is also the latency of the first peak of salience for the inversion effects localized laterally and is also found in the P1–N170 transition. It reflects a delay of processing inverted faces compared to both upright and contrast-reversed faces.

It is difficult to define precisely the nature of the underlying neural activity responsible for differences in "transitions" between two ERP components. Peak transitions could reflect component overlap or perhaps transitions between unique distributions of active neuronal generators (microstates; for a review, see Michel et al., 2001). In a recent study comparing ERPs for upright and inverted faces and seven object categories, Itier and Taylor (2004) showed that an extra microstate, corresponding to activity related to the N170, differentiated faces from objects. For upright faces, the onset of this microstate was during the transition between P1 and N170, which was similar to the timing of the onset of stable differences in the PLS inversion effect. However, at this same latency, the microstate for inverted faces was one related to P1 activity. Thus, both sets of findings indicate the P1–N170 transition is important in distinguishing upright from inverted faces. Irrespective of the actual neural basis for differences during peak transitions, PLS showed that these periods accounted for *more* of the distinction between face types than the peaks themselves, a result that could not have been found with peak analyses alone.

The faster P1–N170 transition found for contrast-reversed faces could suggest a faster onset of the activity related to the generation of N170 and thus faster P1 processing. Hole et al. (1999) proposed that contrast reversal disrupts configural but not holistic information—the perception of a face as a whole (Tanaka & Farah, 1993). Other behavioral studies further suggest that contrast reversal affects face recognition by disrupting three-dimensional shape-from-shading information (Kemp, Pike, White, & Musselman, 1996), which in turn disrupts configural/relational processing (Kemp et al., 1990; Lewis & Johnston, 1997). In contrast, the behavioral literature suggests that inverted faces disrupt both holistic and configural processing. Using these behavioral findings in addition to their P1 effects, Itier and Taylor (2002) hypothesized that P1 could reflect a global, "holistic" face processing, while N170 could reflect a more relational/configural processing stage that could enable later identity recognition. Following the same logic with the present PLS results, the configural processing would start where inversion and contrast-reversal effects overlap, that is, around 120 ms, after the P1 (Figure 4, see occipital sites), and the global processing of faces would thus occur between 100 and 120 ms. Configural and holistic processing are unlikely to be as clearly distinguishable as this, but the 100–120-ms latency is in accordance with single cell recordings in infero-temporal cortex of monkeys showing that global information about faces is conveyed by neurons in the first 100 ms, whereas the details of the faces (e.g., features enabling identity recognition) are conveyed by the same neurons about 60 ms later (Sugase, Yamane, Ueno, & Kawano, 1999). This latter latency corresponds roughly to the middle of the P1–N170 transition period and to the N170 latency in some studies.

The smaller P1 amplitude to contrast-reversed faces compared to other face types could be due to the decreased luminance of the faces; neurons in visual areas V1 and V2 that contribute to P1 are sensitive to luminance and contrast differences. However, the reason why the transition to N170 would be faster for contrast-reversed faces is unclear. We speculate that by disrupting the surface information of faces, contrast reversal leaves the general arrangement of faces even more obvious, rather like schematic faces, resulting in even faster global face processing. This hypothesis would need further investigation.

Another interesting finding of the present study is the posterior long-latency effect found as sustained negative saliences from 300 to 600 ms in the inversion effect that was also found in the contrast-reversal effect as positive saliences from 300 to 400 ms. The comparison of head plots (Figure 3, at 350 ms) revealed that both effects were situated at the same parietal posterior electrodes. The actual ERPs revealed that in both cases, the effect was driven by more negative amplitudes at these sites for inverted faces compared to upright and contrast-reversed faces. Because this localization is very similar to that of the N170 component, this effect appeared to be a reactivation of temporo-parietal face areas by inverted faces only. As LV1 and LV2 represented similar face type effects at encoding and recognition, these reactivations were not memory driven but were dependent on the inverted stimuli, likely reflecting additional processing for inverted faces.

Finally, PLS demonstrated the involvement of fronto-temporal electrodes from ~370 to 470 ms in the face type by memory condition interaction (LV3). Relative to encoding, the amplitudes to upright faces were more negative at 0- than 1-lag; this effect was polarity reversed at parietal sites. There were much smaller differences for inverted and contrast-reversed faces. This is similar to a parietal repetition effect found for upright but not inverted faces (George, Jemel, Fiori, & Renault, 1997). The latency of the "old–new repetition effect" presented here, and its localization, suggest the parietal old–new repetition effect may also involve frontal cortices. PLS showed that this effect was maximal for upright faces and minimal for the other two face types, supporting the view that its magnitude can be sensitive to the quality of episodic information that is retrieved (Rugg, Cox, Doyle, & Wells, 1995; Wilding, 2000). Accordingly, we can infer that immediately repeated faces were qualitatively better recognized than 1-lag faces, which is supported by behavioral results. The lateral frontal sites likely reflected the recruitment of areas such as the lateral prefrontal cortex, consistently activated in neuroimaging studies on recognition memory (for a review, see Fletcher, Frith, & Rugg, 1997), or the inferior frontal gyri, areas shown to be more involved in recognition than encoding for both verbal and nonverbal materials (Cabeza & Nyberg, 1997; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999). The inferior frontal gyri, in or near the boundaries of Brodman areas 6/44, are well situated to generate signals recordable on the scalp by frontal-temporal electrodes.

The PLS results thus confirmed and extended the findings of Itier and Taylor (2002) on peak amplitudes and latencies. Both sets of analyses identified the increased latency and amplitude of N170 for inverted and contrast-reversed faces, and smaller P1 amplitudes for contrast-reversed faces, restricted to occipital electrodes. PLS did not identify the peak of the P1 as part of the face-inversion effect, although Itier and Taylor (2002) found inversion effects at this latency. These kinds of discrepancies can arise because the PLS analysis is over the entire 700-ms period. PLS pulled out the *major* effects over that period and showed that face inversion mainly involved the N170 and the later parietal effects (300–600 ms). In a separate analysis, PLS was run across a shorter interval (0–250 ms, data not shown here), and the P1 was part of the face-inversion effect. One factor that contributes to whether or not effects are identical between classical and PLS analyses is whether an effect identified at a single peak is the best reflection of the global ERP differences involved in the experimental effect.

Interestingly, PLS found that facial manipulations affected not only the components' peaks, but also the transitions between peaks, a result that could not emerge using classic analyses. This is important, as it suggests that dynamics and underlying neuronal generators differ between conditions during that transition (120–170 ms). The original long-latency analysis was performed only on frontal and central electrodes, and the posterior differences were not identified. PLS showed that long-lasting posterior reactivations of face areas were unique to processing of inverted faces. Thus, the present analysis extends the original findings by showing that face inversion affected transitions surrounding the N170, followed by a reactivation of face processing areas, whereas contrast-reversal effects involved primarily earlier time periods. Importantly, PLS identified a marked localization difference; the inversion effect was found at posterior lateral sites whereas contrast-reversal effects were essentially occipital and medial, probably reflecting activity from additional generators in extrastriate visual areas. Finally, PLS identified the involvement of fronto-temporal areas in differentiating the old–new repetition effect across face types, the effect being minimal for inverted and contrast-reversed faces and maximal for upright faces, between 370 and 470 ms. It also suggested that in the present study, this old–new effect arose from fronto-temporal rather than parietal areas.

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