

Research report

Event-related brain potential evidence for a response of inferior temporal cortex to familiar face repetitions

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Abstract

We investigated immediate repetition effects in the recognition of famous faces by recording event-related brain potentials (ERPs) and reaction times (RTs). Participants recognized celebrities' faces that were preceded by either the same picture, a different picture of the same celebrity, or a different famous face. Face repetition caused two distinct ERP modulations. Repetitions elicited a strong modulation of an N250 component (~200–300 ms) over inferior temporal regions. The N250 modulation showed a degree of image specificity in that it was still significant for repetitions across different pictures, though reduced in amplitude. ERPs to repeated faces were also more positive than those to unprimed faces at parietal sites from 400 to 600 ms, but these later effects were largely independent of whether the same or a different image of the celebrity had served as prime. Finally, no influence of repetition was observed for the N170 component. Dipole source modelling suggested that the N250 repetition effect (N250r) may originate from the fusiform gyrus. In contrast, source localisation of the N170 implicated a significantly more posterior location, corresponding to a lateral occipitotemporal source outside the fusiform gyrus.

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1. Introduction

Faces are a unique type of stimulus in that they provide very rich social information, not only about identity but also, for example, about affect, age, or gender. It is therefore not surprising that cognitive neuroscience has put considerable effort into characterising the functional and neuroanatomical organization of human face processing. With respect to face recognition (i.e. the processing of face identity), research on brain-lesioned patients with prosopagnosia has highlighted the role of inferior temporal cortex, including the fusiform and lingual gyri and the inferior longitudinal fascicle, a major occipitotemporal fiber bundle [11,35]. Moreover, event-related potentials

(ERP) research has suggested that the brain may produce a specific response to faces that is absent or attenuated for other visual stimuli [26]. Intracranial ERP recordings from the ventral surface of the temporal lobe have extended these findings, and have demonstrated a face-specific N200 wave originating from fusiform cortex [1,2]. Based on evidence from functional magnetic resonance imaging (fMRI), a fusiform face area (FFA) was described by Kanwisher and colleagues [27] as a region that is activated by a variety of face stimuli (including cartoons and animal faces), but is not activated, or activated to a reduced extent, by non-face objects. They argued that the mid-fusiform gyrus is selectively involved in the perceptual analysis of faces, although it should be noted that other areas, such as the occipital face area [21], also exhibit a weaker selectivity for faces.

While earlier studies with scalp-recorded ERPs used only very few electrodes [26], more recent ERP studies

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used more electrodes encompassing posterior temporal scalp areas. Many of these studies have focussed on the N170, an electrically negative wave over occipito-temporal areas ~170 ms after the onset of a face. The N170 is prominent for faces but absent, or attenuated for visual stimuli other than faces [5] (for controversial issues about its specificity for faces see Refs. [14,44]). Subsequent research has shown that this component is not influenced by the familiarity of faces [6,15,42]. Repetition priming (the change in response to an face based on previous exposure to that face) is thought specifically to probe the operation of the face *recognition* system [19]. The N170 appears to be largely insensitive to repetition priming [4,49], although it has to be said that very small amplitude face repetition effects have occasionally been reported both for N170 and the preceding P1 component [9,23,49]. Overall, most of the available evidence therefore suggests that the N170 is related to early structural encoding of faces, rather than to the individual recognition of familiar faces [6,16,17,22,43,45].

One important question is therefore whether ERPs can be identified that may be more directly related to the recognition of faces. Another important issue is how the findings obtained with different techniques can be related to one another. For example, are the generators for the scalp-recorded N170 [5] the same as those for the intracranial N200 [2], and how are these phenomena related to the FFA activation reported in fMRI studies [27]? While it is clear that an intracranial N200 can be recorded from fusiform areas [1] and a relationship to the FFA is therefore at least plausible, it has been suggested that the N170 has a more lateral and posterior generator in the inferior temporal gyrus or the occipitotemporal sulcus [5]. However, both inferior temporal and fusiform gyri may contribute to the N170 [32], and with respect to the intracranial N200, more recent recordings have shown that face-specific N200 response can also be obtained from more lateral sites over the inferior and middle temporal gyri [3].

Of particular interest for the present study, recent research has identified a distinct ERP modulation as a result of the immediate repetition of faces in the time range just following the N170¹. Specifically, an increased negativity was observed between 180 and 290 ms at inferior temporal sites [49]. This ERP repetition effect peaked ~250 ms ('N250r'), had a more anterior and inferior distribution compared to the N170 (with a maximum at TP₁₀ rather than at T₆), and was lateralized to the

right hemisphere (for similar results, see also Ref. [4]). The effect was also seen for unfamiliar faces, though with reduced amplitude. Subsequent research showed that when between two and four other faces intervened between repetitions, repetition priming still caused increased negativity at right inferior temporal sites, but only for repeated *familiar* faces [39]. Relative to immediate repetitions, this effect was smaller in amplitude and had a slightly longer peak latency (~280 ms).

Repetition of written personal names also caused increased negativity at inferior temporal electrodes for familiar but not unfamiliar names. The effect for names was observed predominantly over *left* hemisphere temporal areas. The attenuation of the N250r for unfamiliar stimuli suggests that it does not just reflect face repetition, or a general facilitation of perceptual encoding as a result of repetition. Moreover, its different topography for faces and names would seem to indicate that it does not reflect a stimulus-independent facilitation of semantic processing. Therefore, the N250r may reflect the perceptual recognition of the individual stimuli [39,49].

While no attempt at source localisation has been made to date, the more inferior and anterior distribution of the N250r relative to the N170 [49] could suggest that this ERP correlate of face repetition might be more closely related to activity in the fusiform gyrus. The aim of this study was to replicate the N250r as an ERP correlate of repetition priming, and to investigate a number of open questions. Firstly, what is the degree of image-specificity of the N250r? Is this component only seen for repetitions of faces that use the same image as prime and target, or is it also seen for the repetition of faces across different images? One possibility is that the N250r reflects the recognition of individual faces at the level of face recognition units, which according to Bruce and Young [8] are defined as abstract, image-independent representations of familiar faces. If this is the case, a similar N250r should be seen regardless of whether repetitions of faces involve the same or different images of the same face. In contrast, to the extent that the N250r would reflect more image-specific aspects of face recognition, a larger effect should be seen for repetitions across the same images. Secondly, using dipole source analysis, can it be demonstrated that the generators of the N250r are different from those for the N170? Specifically, is there evidence that the N250r is generated in ventral temporal areas, and possibly in the fusiform gyrus?

2. Method

2.1. Participants

A total of 12 participants (eight women and four men) aged between 17 and 24 years (mean 21.2 years, S.D. 2.0 years) were paid to contribute data to this study. All

¹There are several studies that report face repetition effects at latencies earlier than the N170 [7,12,51]. One difficulty with these effects is that they appear to be rather different from study to study. Also, many of these early face repetition effects were obtained by comparing ERPs to the first stimulus with ERPs to the second stimulus [7,51]. Such ERP modulations may vanish when comparing ERPs to a repeated versus non-repeated second face [7], and may thus reflect differential habituation or attentional processing, rather than priming of individual faces.

participants reported normal or corrected-to-normal visual acuity.

2.2. Stimuli and apparatus

Photographs of faces of 90 famous people from various areas (e.g. politics, entertainment, sports, TV) were used as target faces in the present experiment. Two different photographs were available for each celebrity. The celebrities were selected out of a list of more than 600 celebrities on the basis of highest ratings for ease of face recognition. Photographs of 90 unfamiliar faces were also used as target faces in order to create the task demands, and were matched to famous counterparts with respect to gender and approximate age. Faces were obtained from different sources (magazines, various websites, face databases made available by other researchers) and were all software-edited using Adobe Photoshop™. They were converted to grayscale, all background was removed, and each face was framed within an area 170 pixels wide × 216 pixels high (6.0 × 7.6 cm). A fixed chin rest was used to maintain a constant viewing distance of 100 cm. An attempt was made to homogenise the stimuli with respect to average luminance (for both familiar and unfamiliar faces, mean 50.9 cd/m²) and contrast.

The 90 familiar faces were further subdivided into three sets (with 30 faces each). The assignment of face set to experimental condition (unprimed, primed same, primed different; see below) was completely counterbalanced across participants.

2.3. Procedure

After the EEG electrodes were applied and prior to the experiment, participants received written task instructions. A total of 16 trials preceded the critical trials for practice reasons; the faces shown in these practice trials were not shown subsequently.

Each trial consisted of the presentation of a prime face and a target face in succession. At the beginning of each trial, a white fixation cross appeared for 500 ms and was then replaced by a prime face, presented for 500 ms and followed by a green fixation circle for 1300 ms. This was replaced by a target face, presented for 1500 ms. The inter-trial interval was 2500 ms. Participants were told to decide by speeded two-choice key presses whether the second face in each trial was famous or unfamiliar. Speed and accuracy were emphasized. Half of the participants responded with their right index finger to indicate a famous person, and with their left index finger to indicate an unfamiliar person. For the other half of the participants, this assignment was reversed. Incorrect or missing responses were indicated by a feedback tone (500 Hz, 250 ms).

A total of 180 critical trials were presented, with 90 familiar target faces and 90 unfamiliar target faces. One

third of familiar target faces were preceded by a different familiar face (*unprimed* condition). One third of familiar target faces were preceded by the same picture (*primed same* condition). One third of familiar target faces were preceded by the same face, but a different photograph was used for the prime (*primed different* condition). Primes in the prime different conditions could differ from the target face in a number of ways including facial expression, eye gaze, head orientation, hairstyle, and age when photographed, so that the visual similarity between the prime and target faces was minimal.

Unfamiliar faces were only included to create task demands; they were not subject to the same priming manipulations as familiar faces, and therefore the data for unfamiliar faces were not analyzed in detail. However, in order to prevent any predictive value of the prime with respect to the forthcoming response, the same prime stimuli that were used for familiar target faces were used for the 90 unfamiliar target faces as well. Moreover, all 180 trials of the block were shown in completely randomized order. Throughout the experiment, short breaks were allowed after every 60 critical trials. In an additional block of trials, participants performed blinks (20 trials), as well as horizontal and vertical eye movements of predefined visual angle (ten trials each). These served as an individual calibration for later correction of ocular contributions to the EEG (see below).

2.4. Performance

Responses were scored as correct if the correct key was pressed within a time window lasting from 200 to 1500 ms after stimulus onset. Errors of omission (no key press) and of commission (wrong key) were recorded separately. Mean reaction times were calculated for correct responses only.

2.5. Event-related potentials

The EEG was recorded with sintered Ag/AgCl electrodes mounted in an electrode cap (Easy-Cap™) at the scalp positions F_z, C_z, P_z, I_z, Fp₁, Fp₂, F₃, F₄, C₃, C₄, P₃, P₄, O₁, O₂, F₇, F₈, T₇, T₈, P₇, P₈, FT₉, FT₁₀, P₉, P₁₀, PO₉, PO₁₀, C₃', C₄', F₉', F₁₀', TP₉ and TP₁₀ [40]. The C₃' electrode was positioned 0.75 cm anterior to the midpoint of a straight line between C₃ and C₁, and the C₄' electrode was positioned 0.75 cm anterior to the midpoint of a straight line between C₄ and C₂. The F₉' electrode was positioned 2 cm anterior to F₉ at the outer canthus of the left eye, and the F₁₀' electrode was positioned 2 cm anterior to F₁₀ at the outer canthus of the right eye. The positions TP₉ and TP₁₀ refer to inferior temporal locations over the left and right mastoids, respectively. The TP₁₀ electrode served as initial common reference, and a forehead electrode (AF_z) served as ground. Electrode impedances were kept below 10 kΩ and were typically below 5 kΩ. The horizontal electrooculogram (EOG) was recorded from F₉'

and F'_{10} at the outer canthi of both eyes, and the vertical EOG was monitored from an electrode above the right eye against an electrode below the right eye. All signals were recorded in DC mode, with low-pass filters set to 40 Hz (−6 dB attenuation, 12 dB/octave), and sampled at a rate of 250 Hz.

Offline, epochs were generated, lasting 1700 ms and starting 216 ms before stimulus onset. Automatic artifact detection software was run for an initial sorting of trials, and all trials were then visually inspected for artifacts of ocular (e.g. blinks, saccades) and non-ocular origin (e.g. channel blockings or drifts). Trials with non-ocular artifacts, saccades, or with incorrect behavioural responses were discarded. For all remaining trials, ocular blink contributions to the EEG were corrected [18]. ERPs were averaged separately for each channel and for each experimental condition. Each averaged ERP was low-pass filtered at 10 Hz with a zero phase shift digital filter, and recalculated to average reference [29], excluding the vertical EOG channel.

2.6. Dipole source analysis

Dipole source models were determined by using the Brain Electromagnetic Source Analysis program (BESA2000 [47]) with the four-shell spherical head model (i.e. brain, bone, cerebrospinal fluid, and scalp). Primarily, a source model is derived by fitting the source model iteratively to the data until a minimum in residual-variance (RV) is reached, i.e. the percentage of variance in the recorded potential distribution not accounted for by the source model is minimized. Symmetry constraints with respect to location were applied to lateral dipole pairs in order to limit the number of parameters estimated. No other constraints with respect to localisation were used.

3. Results

3.1. Performance

Mean error rates and reaction times to familiar target faces are shown in Table 1. No omissions were observed. Table 1 shows that error rates were very low (mean 3.7%) and any differences between priming conditions followed a

Table 1
Mean RTs (in milliseconds) and percentages of errors (PE) for target faces

| | RT | PE |
|------------------------|-----|-----|
| <i>Famous faces</i> | | |
| Unprimed | 712 | 6.4 |
| Primed different | 619 | 2.8 |
| Primed same | 549 | 1.9 |
| Famous faces, mean | 627 | 3.7 |
| Unfamiliar faces, mean | 711 | 4.7 |

similar pattern as that for RTs, with no evidence for a speed-accuracy trade-off. Therefore, error rates were not analyzed further.

Mean correct RTs to familiar faces were submitted to analyses of variance (ANOVA) with repeated measures on priming condition (unprimed vs. primed different vs. primed same). Where appropriate, we performed epsilon corrections for heterogeneity of covariances, using the Huynh-Feldt method [25] throughout.

The ANOVA on RTs revealed a significant effect of priming, $F(2, 22)=67.9$, $P<0.001$, mean 712, 619 and 549 ms, for the unprimed, primed different, and primed same conditions, respectively. Bonferroni-corrected paired contrasts revealed that, relative to the unprimed condition, priming was significant both by the same, $F(1, 11)=84.2$, $P<0.001$, and by different pictures of the target face, $F(1, 11)=49.1$, $P<0.001$. Moreover, there was more priming in the primed same condition relative to the primed different condition, $F(1, 11)=49.3$, $P<0.001$.

3.2. Event-related potentials

ERPs to target faces were quantified by mean amplitude measures in the time segments 110–130, 160–196, 200–300, 300–400, 400–500 and 500–600 ms. The first segment was chosen to correspond to the occipital P1, and the second segment corresponded to the occipito-temporal N170 peak in the waveforms, with a peak latency of ~180 ms in the grand-average ERPs. The onset latency of N250r was ~200 ms, and although peak latency was ~280–290 ms in the present study (Table 2), the 200–300-ms segment was chosen because it was relatively free from temporal overlap with later ERP modulations. The subsequent 100-ms segments were arbitrarily chosen. All amplitude measures were taken relative to a 200-ms baseline preceding the target stimulus.

For every time segment, ANOVAs were then performed analogous to those for the RT data, except for the inclusion of an additional repeated measurements factor electrode (32 levels). Note that because the average reference sets the mean activity across all electrodes to zero, any condition effects in these ANOVAs are only meaningful in interaction with electrode site. Therefore, any condition effect reported below is in interaction with electrode site.

For both the 110–130-ms (P1) and the 160–196-ms

Table 2
Mean peak latency (in milliseconds) and amplitude (area measures in μV) for N170 (unprimed condition) and N250r (primed same minus unprimed difference) for selected posterior electrode sites

| | N170 latency | N170 amplitude | N250r latency | N250r amplitude |
|-----------|-----------------|-------------------|------------------|--------------------|
| P_9 | 180 | −2.1 | 292 | −2.7 |
| P_{10} | 180 | −1.6 | 280 | −2.6 |
| TP_9 | 180 | −2.0 | 288 | −2.5 |
| TP_{10} | 182 | −1.6 | 288 | −2.9 |

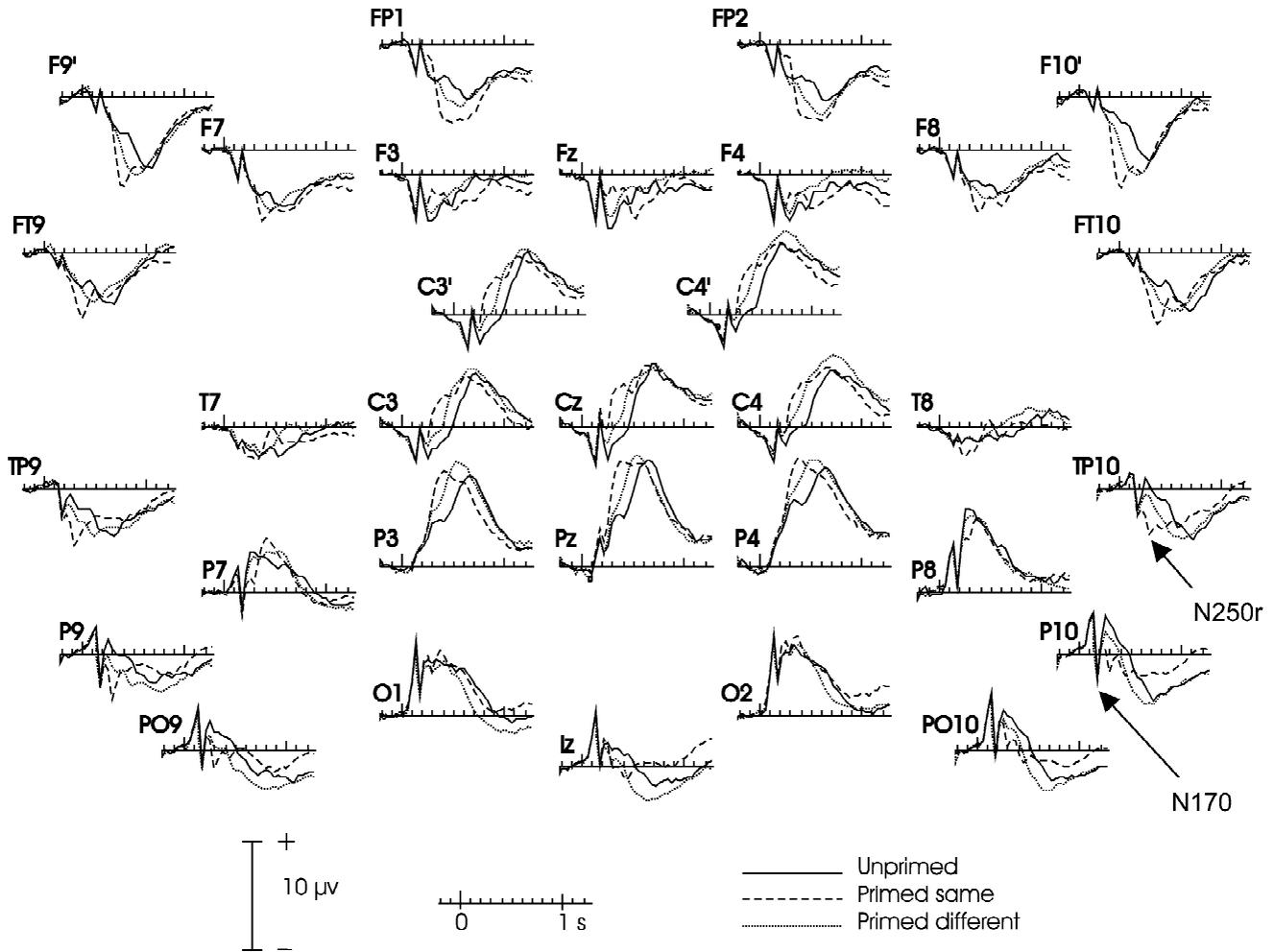


Fig. 1. ERPs recorded for familiar faces that were unprimed (solid lines) or that had been preceded by the same (dashed lines) or a different image (dotted lines) of the same familiar person. Recordings are shown for all 32 channels used. Arrows indicate the N170, and the N250r repetition effect around 200–300 ms.

segment (N170), no significant effects of priming were observed, all F -values $< 1^2$.

Fig. 1 shows the priming effects for famous faces. Effects of priming started in the 200–300-ms segment and continued in the 300–400-ms segment, F 's(62, 682)=5.4 and 9.3, P 's <0.001 . Bonferroni-corrected paired contrasts revealed that, relative to the unprimed condition, priming was significant both by the same, F 's(31, 341)=8.4 and

13.6, P 's <0.001 , and by different pictures of the target face, F 's(31, 341)=3.6 and 3.3, $P<0.05$ and $P=0.05$, for the 200–300- and 300–400-ms segments, respectively. Moreover, stronger priming was observed in the primed same condition relative to the primed different condition, F 's(31, 341)=3.4 and 8.3, $P<0.05$ and $P<0.001$, for the 200–300- and 300–400-ms segments, respectively. Fig. 2 shows both the N170 and these N250r repetition effects at inferior and posterior temporal recording sites.

Effects of priming were also significant in the 400–500- and 500–600-ms segments, F 's(62, 682)=7.7 and 3.2, $P<0.001$ and $P<0.01$, respectively. However, in contrast to the earlier time segments, Bonferroni-corrected paired contrasts revealed no differences between the primed same condition and the primed different condition, F 's(31, 341)=1.3 and 2.4, P 's >0.10 , respectively. Priming by different pictures of the target face was significant, F 's(31, 341)=13.4 and 5.8, $P<0.001$ and $P<0.01$, respectively. Priming by the same picture of the target face was also significant in the 400–500-ms segment, $F(31, 341)=9.8$,

²Previous studies [6,15,42] have indicated that the N170 is insensitive to the familiarity of faces. In the present study, unfamiliar target faces were only included to create task demands, but were not subject to the same priming manipulations as were familiar faces. Nevertheless, we made an attempt to evaluate familiarity effects on the N170 by comparing ERPs to unprimed familiar target faces with ERPs to unfamiliar target faces (in order to make these conditions as comparable as possible with respect to trial numbers and pre-stimulus baseline, we used the subset of unfamiliar faces that was preceded by the same familiar prime stimuli). This analysis suggested comparable N170 amplitudes for familiar and unfamiliar faces, $F(31, 341)<1.2$, $P>0.10$, supporting the conclusions reached by the above-mentioned studies.

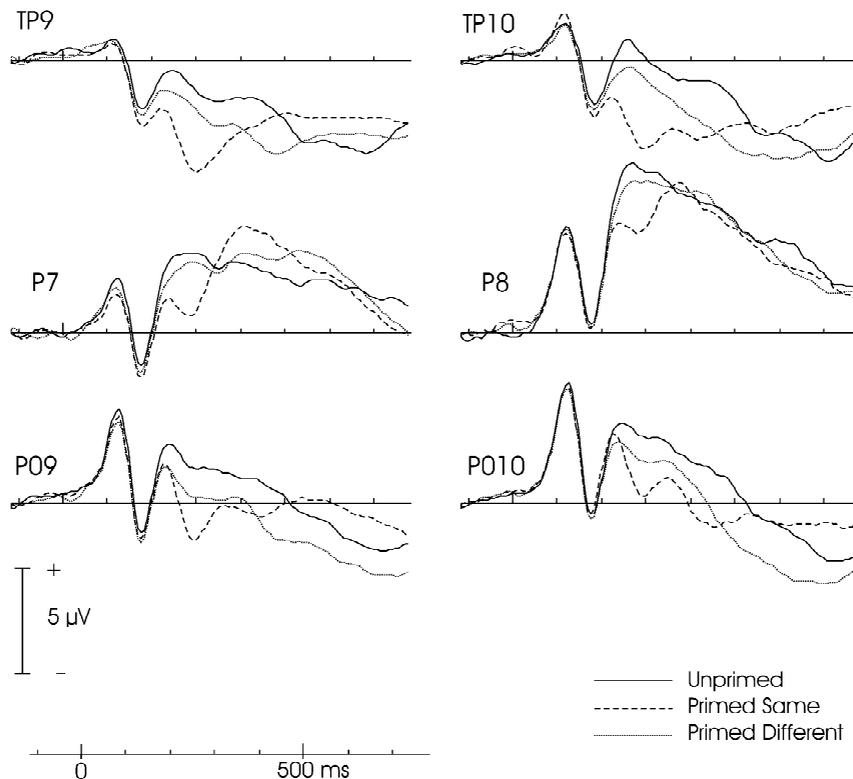


Fig. 2. ERPs at inferior and posterior temporal electrodes (TP₉, TP₁₀, P₇, P₈, PO₉, PO₁₀). It can be seen that repetition does not affect the N170, but starts to influence ERPs from ~200 ms onwards, and this effect is most prominent at more anterior and inferior locations (e.g. TP₁₀).

$P < 0.001$, but not in the 500–600-ms segment, $F(31, 341) = 2.3$, $P > 0.10$.

3.3. Topographic analyses

Fig. 1 suggests at least two qualitatively different priming effects between 200 and 600 ms. Specifically, between 200 and 300 ms priming caused increased negativity at inferior temporal electrodes (TP₉, TP₁₀, P₉, P₁₀, PO₉, PO₁₀) and increased positivity at midfrontal electrodes (e.g. F_z). In contrast, between 400 and 600 ms priming caused increased positivity at parietal and central sites (C_z, P_z, C₃, C₄, P₃, P₄) and increased negativity at prefrontal sites (Fp₁, Fp₂, F'₉, F'₁₀). These two effects correspond precisely to the results of a previous study [49]. To determine whether the ERP effects of repetition in the 200–300-ms segment were topographically dissociable from those seen in the 400–500-ms segment, we first calculated two difference waveforms (primed same minus unprimed, primed different minus unprimed; Fig. 3). For both time segments, we then scaled mean amplitudes for each participant across all electrodes, with the average distance of the mean, calculated from the grand-mean ERPs, as the divisor [34]. Finally, for each difference wave we performed an ANOVA on these scaled amplitude differences, with one factor time segment (two levels) and

a second factor electrode site (32 levels). It turned out that the topography of the primed same minus unprimed difference changed qualitatively from the 200–300- to the 400–500-ms segment, $F(31, 341) = 9.0$, $P < 0.001$. Similarly, the topography of the primed different minus unprimed difference changed across these time segments, $F(31, 341) = 2.6$, $P < 0.05$. Finally, in the 200–300-ms segment the primed different minus unprimed difference was topographically indistinguishable from the primed same minus unprimed difference, $F(31, 341) = 1.7$, $P > 0.10$, consistent with the assumption that the former difference is just a weaker version of the latter. These two differences were also topographically indistinguishable in the 400–500-ms segment, $F(31, 341) = 1.4$, $P > 0.10$, but this was less surprising because the unscaled data (see above) had not revealed differences between the primed same and primed different conditions.

3.4. Dipole analyses

3.4.1. P1 and N170

To derive the source model for the early ERP components we used grand-average ERPs. Because the statistical analyses of the ERPs had revealed no priming-related differences for both P1 and N170, we used the data from the unprimed condition for the purpose of modelling.

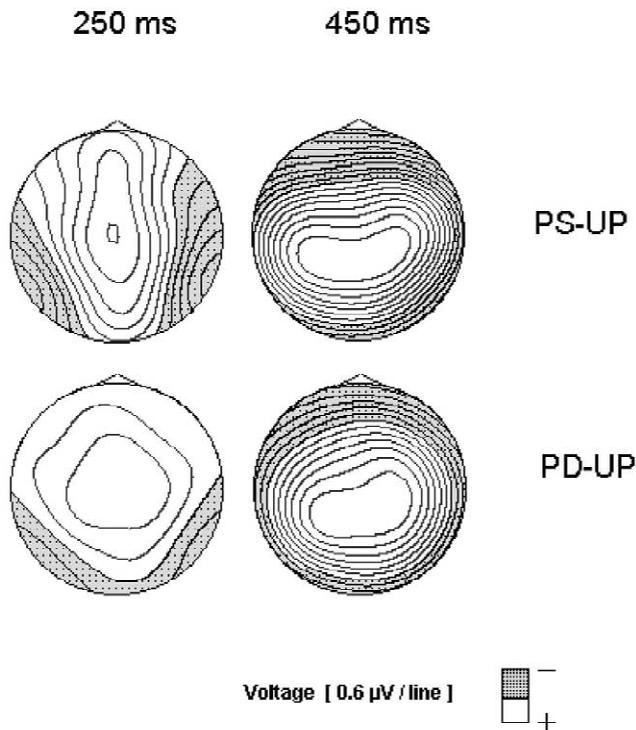


Fig. 3. Topographical maps of ERP differences between primed and unprimed conditions show the two qualitatively different priming effects at 250 ms (left) and 450 ms (right). Top maps show the difference primed same minus unprimed, and bottom maps show the difference primed different minus unprimed. Maps were obtained by using spherical spline interpolation.

A dipole source analysis was performed for the time interval from 100 to 200 ms. Spatial principal component analysis (PCA) was employed to estimate the minimum number of dipoles that should be included in the model. A PCA of the 100-ms epoch indicated that two principal components explained 99.7% of the variance in the data (PC1: 87.9%; PC2: 11.8%). However, when the interval was reduced to 100–130 ms, one PC explained more than 99% of variance. We therefore decided to use a sequential fitting strategy [46]. A first dipole pair was fitted in an interval from 100 to 130 ms. This single pair of dipoles accounted for nearly all variance ($RV=1.2\%$). When the fit interval was extended, RV began to increase rapidly, suggesting the growing influence of a second source. Therefore, a second pair of dipoles was added and fitted in the time interval from 100 to 200 ms, with the first pair of dipoles held fixed. The resulting dipole model with two dipole pairs accounted for 97.7% of the variance in the 100–200-ms interval. The first source showed a peak in the P1 time range whereas the second source had a later peak in the N170 time range.

Fig. 4 shows the two-dipole pair solution obtained for the grand-average ERP waveforms for the unprimed condition. The first dipole-pair (P1 source) was located in lateral extrastriate areas ($x=\pm 46$ mm, $y=-47$ mm, $z=48$

mm)³. This location is similar to what has been observed by others [10]. The second dipole pair (N170 source) also corresponded to lateral extrastriate areas, but more inferior to the P1 source ($x=\pm 44$ mm, $y=-42$ mm, $z=29$ mm). This location is also broadly in line with previous suggestions for generators of the N170, and may correspond to the posterior inferior temporal gyrus [5].

3.4.2. N250r

In a next step difference waves were calculated to localize the generators of the N250 repetition effect. Three difference waves were calculated for primed same minus unprimed, primed different minus unprimed, and primed same minus primed different conditions. For each of these difference waves grand-averages across subjects were calculated and separate dipole models derived as described in the following. In a first step a PCA was applied to estimate the minimum number of dipoles needed to explain activity in a 50-ms interval, starting 250 ms after stimulus onset. In all three difference waves, a single PC could explain more than 97.5% of the mean variance. Thus, one dipole pair was fitted to each difference wave. For all three difference waves, the best-fitting dipole pairs were located in inferior temporal areas anterior to the location that had been identified for N170. The best fits (in terms of variance explained) were obtained for the primed same minus unprimed difference ($RV=2.8\%$), and the primed same minus primed different condition ($RV=4.8\%$); in the subsequent analyses we focus on these conditions. RV was somewhat higher for the primed different minus unprimed condition ($RV=7.6\%$), possibly due to the reduced signal amplitude as suggested by Fig. 2.

3.4.3. Location differences between N170 and N250r

Although the present approach has certain limitations with the identification of the exact anatomical location of sources, relative differences in location of sources are nevertheless illustrative. For example, the location of the N170 sources ($x=\pm 44$ mm, $y=-42$ mm, $z=29$ mm) can be used as a landmark for the comparison with the location of sources revealed for the N250r ($x=\pm 42$ mm, $y=-26$ mm, $z=31$ mm). To test statistically for such location

³Dipole locations are expressed in the spherical coordinates of the BESA program, for which the cortical surface is approximately at 70 mm from the centre. The centre of the head model used in the BESA program is located at a point where the line that connects scalp locations T_7 and T_8 is bisected by a perpendicular line going through the nasion. The spherical coordinates of the BESA software are therefore not identical to the centre of the brain in the Talairach atlas [53]. The BESA versus Talairach and Tournoux coordinate systems differ mainly with respect to locations along the y -axis. This is because the line between anterior (A) and posterior (P) commissures defines the principal A–P axis for the Talairach and Tournoux coordinate system. As a result, the zero point in the BESA coordinate system is located at ~ 20 – 25 mm anterior to those in Talairach coordinates.

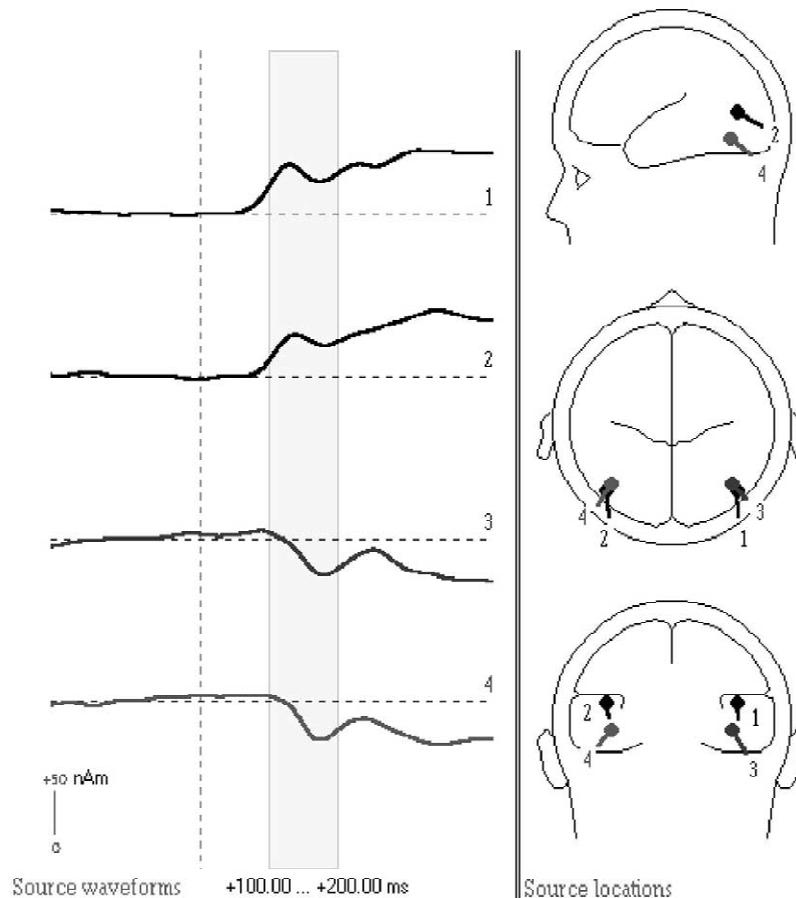


Fig. 4. Dipole model for P100 (dipoles 1 and 2) and N170 (dipoles 3 and 4) for the unprimed faces only. Source waveforms are shown on the left and the source locations on the right. The grey bar in the source waveforms indicates the fitting interval (+100 to +200 ms).

differences, separate model fits for each subject would be required. Here the problem of lower signal-to-noise ratio in individual data arises. Therefore, we decided to compare source locations using a jackknife procedure, which has been demonstrated to increase the power in the analysis of LRP onset [36] and was recently introduced to test for differences in dipole locations [31]. Using the jackknife procedure, 12 subsamples of grand-average waveforms for each difference wave (primed same minus unprimed and primed same minus primed different), as well as the ERPs for the unprimed condition were computed by omitting from each subsample the data of another participant. The average waveform of each subsample was fitted separately as described for grand-average data, and the locations of the dipole sources were determined. The mean location differences in dipole coordinates (x : lateral–medial, y : anterior–posterior, and z : superior–inferior) for both difference waves and for the N170 were calculated for the grand-average waveforms. Finally, one-tailed t -tests were performed, with the jackknife-based standard error replacing the usual standard error calculated from individual location differences (cf. Refs. [31,36]).

In a next step the two difference waves were fitted. Fig. 5 shows the dipole locations for the primed same minus

unprimed difference. It can be seen that dipoles were located in inferior temporal brain areas, possibly corresponding to the fusiform gyrus. A very similar location (slightly more anterior and medial) was obtained for the difference between primed same and primed different. Statistical tests for location differences were applied using the jackknife procedure. The N170 source was located posterior to the sources of both the difference primed same minus unprimed (mean -42 vs. -26 mm, $t_c(11)=2.84$, $P<0.05$) and the difference primed same minus primed different (mean -18 mm, $t_c(11)=3.19$, $P<0.01$). Additionally, the N170 source was located more laterally than the source of the difference primed same minus primed different (mean ± 44 vs. ± 28 mm, $t_c(11)=3.19$, $P<0.01$). There were no significant differences in the inferior–superior direction. Fig. 6 shows the comparison of locations obtained for the N170 and the N250 repetition effect.

4. Discussion

The immediate repetition of familiar faces caused an ERP modulation at ~ 250 ms (N250r) with an inferior temporal maximum, in line with earlier findings [4,49].

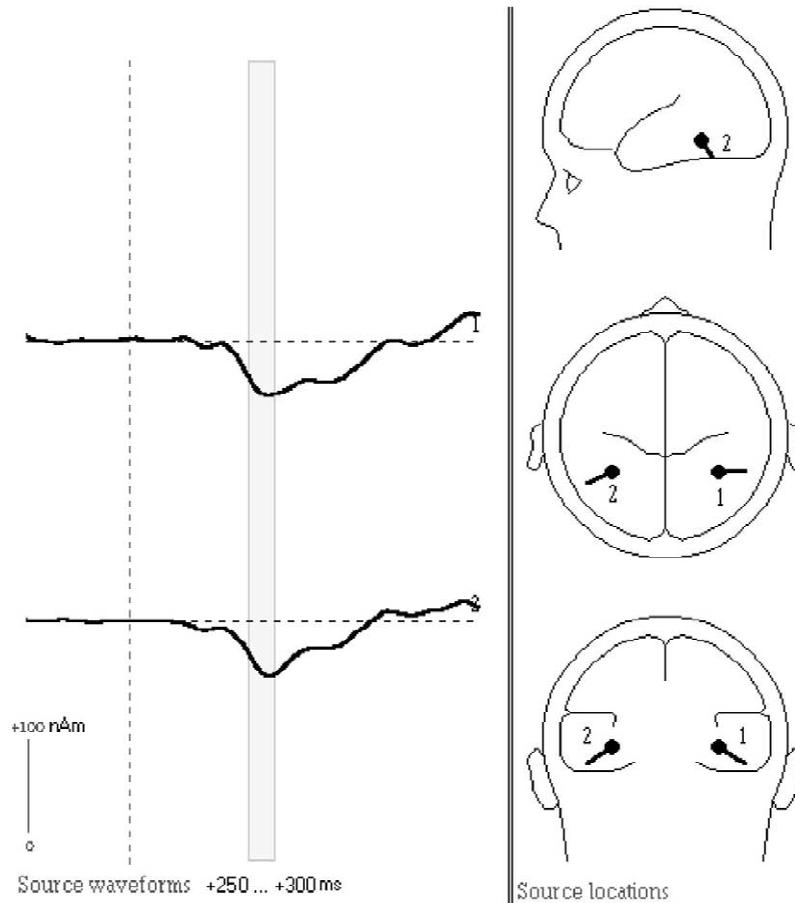


Fig. 5. Dipole model for the three difference waves (primed same minus unprimed). Source waveforms are shown on the left and source locations on the right. The grey bar in the source waveforms indicates the fitting interval (+250 to +300 ms).

Face priming also caused a topographically different ERP modulation at ~400–600 ms. This later effect probably reflects semantic rather than perceptual processing of

faces, has been related by various authors to N400 or ‘old/new’ effects [24,37,50], and will not be discussed in detail here. The main aim of this study was to explore the N250r component further, and to compare it to the N170 both with respect to functional significance and putative generating structures.

The sensitivity to repetition of the N250r strongly contrasted with the N170, which was completely uninfluenced by face repetitions. Another difference between the N170 and the N250r appears to be its sensitivity to the recognition of individual faces: the N170 is insensitive to face familiarity, and has therefore been suggested to reflect structural encoding of faces prior to recognition [6,17,42] (but see also Ref. [9,51]). In contrast to the N170, the N250r appears to be reduced [4,49] or even abolished [39] for unfamiliar relative to familiar faces. This would seem to suggest that the N250r depends, at least to some extent, on the access to stored representations of familiar faces. However, it is important to note that the N250r also showed a degree of image specificity: although this component was still seen for repetitions of the same face across different images, its amplitude was reduced relative to repetitions of the same image. Moreover, other recent

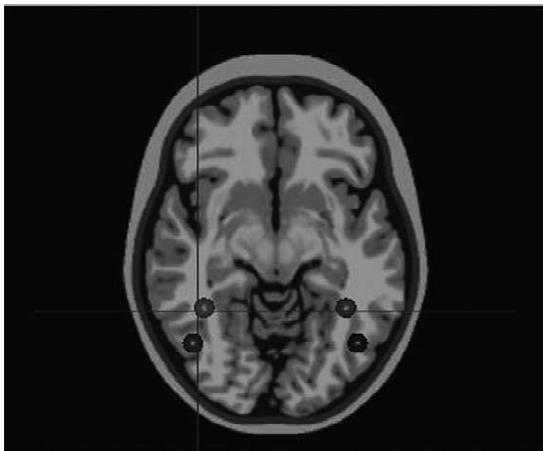


Fig. 6. Dipole locations for the N170 (posterior dipole pair, in dark gray, based on the ERPs to unprimed faces) and for the N250r (anterior dipole pair, in light gray, based on the difference between primed same and unprimed conditions), as projected on a standard brain anatomy.

data suggest that the N250r face repetition effect is of a relatively transient nature. For instance, the effect is considerably reduced when between two and four faces intervene between repetitions [39], and is completely abolished for intervals of more than 15 min and more than 100 intervening stimuli [50]. The N250r effect is also not observed for associative priming, indicating that it does not reflect a facilitation of the semantic processing of a person's identity [48,49]. The degree of image-specificity and the transient nature of N250r would seem to indicate that this component is not an electrophysiological correlate of the activity of face recognition units, at least not when defined according to Bruce and Young [8], who conceptualize FRUs as abstract, image-independent representations.

However, it is possible that image-specific processes may have some transient influence on familiar face recognition. Of particular interest, Leopold et al. [30] showed recognition biases induced by adaptation to a face. In their study, familiar faces were morphed to their respective 'anti-identities' along a trajectory which passed through an average face. Previous adaptation to a particular anti-identity caused a bias to perceive the average face as containing the respective identity. It also selectively facilitated the recognition of a familiar test face on this trajectory, while impairing recognition of other faces. These biases were very short-lived, suggesting that very recent perceptual experience may influence the recognition of familiar faces. Druzgal and D'Esposito [13] recently demonstrated that activity in the fusiform face area increases as a function of working memory load for faces. Source localisation of the N250r suggests that this component may also relate to fusiform activity. The degree of image specificity and the transient nature [39,50] of the N250r suggests that this component may reflect the stimulus-triggered access to stored facial representations in inferior temporal cortex as influenced by very recent visual experience.

It is noteworthy that ERP differences between familiar and unfamiliar faces have been described recently [6,15,38]. Familiar faces have been reported to either elicit larger *negativity* than unfamiliar faces between ~300 and 500 ms [6,15], or to elicit larger *positivity* between ~300 and 600 ms [38]. The reason for this discrepancy is not completely clear, although task and stimulus differences between studies may have played a role. It is also unclear whether these ERP differences relate to the familiarity of *faces*, or instead reflect different degrees of semantic processing invoked by familiar and unfamiliar people. In line with a role for semantic processing, Paller et al. [38] showed that compared to faces which were only learned visually, faces for which additional semantic information had been learned evoked an additional anterior ERP positivity. The present study was designed to investigate priming rather than familiarity effects, and it must therefore remain unclear at present how the N250r relates to the

above-mentioned ERP differences between familiar and unfamiliar faces. However, because previous research has suggested that the N250r is increased for familiar faces [4,39,49] this will be an important question for future research.

The present dipole source location approach also suggests clear differences in the brain generators of N170 and N250r. Consistent with earlier suggestions [5], the N170 source appeared to correspond to posterior lateral temporal areas, possibly in the inferior temporal gyrus. The N250r source corresponded to a more anterior area in the ventral temporal lobe, with the best fit obtained for a source corresponding to the fusiform gyrus⁴. Recent intracranial recordings have also indicated several ERP components between 200 and 300 ms at the same or nearby areas in the ventral temporal cortex [3], some of which may be related to the present findings. Specifically, whereas there appears to be at best a very small sensitivity to face repetitions of the intracranial N200, the intracranial P290, recorded at very similar ventral temporal sites, appeared to be more strongly affected by repetitions [41]⁵.

The degree to which the present N250r may be related to activations of the fusiform face area as described in recent functional imaging research [27] warrants further exploration [20,28]. This is particularly so because both activity in the fusiform face area [21], and activity in more anterior temporal areas [52] have been reported to be sensitive to face repetitions. In summary, we have demon-

⁴It is possible that the scalp-recorded N170 to faces actually originates from two generators in posterior temporal cortex. McCarthy et al. [33] recently demonstrated at least two generator sites for the intracranial face-specific N200, and based on these findings Sagiv and Bentin [45] hypothesized that a holistic encoding of face representations may be carried out in the lateral fusiform gyrus, whereas a component analysis of faces may be carried out in posterior lateral temporal areas nearby. It cannot be excluded that more than one generator contributed to the N170 in the present study, although two different generator sites for N170 have never been directly demonstrated on the basis of scalp-recorded ERPs. It is unclear whether two putative adjacent generators could have been discriminated reliably, given the limitations of the present source localization methods. Thus, whereas the present data do not provide evidence with respect to whether the N170 is generated by one or several brain sources, the present methods could reliably discriminate the generators of the N170 and the N250r.

⁵A minor point is that previous studies reported that the N250r modulation was larger over the right hemisphere, particularly at TP₉ versus TP₁₀ locations [39,49]. In the present study, the N250r was also slightly smaller over LH as compared to RH sites (2.5 vs. 2.9 μ V, respectively, at TP₉ vs. TP₁₀ for the primed same minus unprimed difference, 200–300-ms segment). However, this hemispheric difference failed to reach significance, $F(1, 11) < 1$. The N170 was slightly larger over LH as compared to RH sites (2.1 vs. 1.6 μ V, respectively, at P₉ vs. P₁₀ for the unprimed condition, 160–196-ms segment). Again, this hemispheric difference failed to reach significance, $F(1, 11) < 1$. Inspection of individual data suggested some variation in hemispheric asymmetry of both N170 and N250r. Thus, it is possible that individual variability in the lateralization of face processing, together with the relatively small sample of 12 participants, accounts for the failure to find significant asymmetries in the present study.

strated that an N250 ERP component over inferior temporal regions was strongly sensitive to repetitions of familiar faces. This N250 repetition effect was particularly clear for repetitions across the same images, but was still present for repetitions across different images of the same face. At the same time, it was demonstrated that the N170 was unaffected by repetitions. Source localization implicated a lateral occipitotemporal source for the N170, consistent with earlier suggestions. In contrast, the N250r source was located significantly more anterior in ventral temporal areas, possibly corresponding to the fusiform gyrus. It is proposed that while the N170 reflects structural encoding of faces, the N250r may signify the stimulus-triggered access to stored facial representations.

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