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Neural correlates of perceptual contributions to nondeclarative memory for faces

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Face priming is a nondeclarative memory phenomenon that can be observed when recognition is facilitated for a recently encountered face. This data-driven form of priming is distinct from conceptually driven priming. Moreover, it includes two dissociable components, the facilitated access to pre-existing representations and facilitation in perceptual processing of faces. In the present study, we measured neural correlates of perceptual contributions to face priming with event-related brain potentials. Faces appeared two times (separated by 7–17 s), while participants discriminated familiar from unfamiliar faces. Half of the initial face stimuli were inverted, thereby disrupting perceptual face processing and making possible an assessment of perceptual contributions to face priming. Whereas none of the brain waves previously linked to perceptual processing of faces showed indications of priming, such effects were observed between 200 and 600 ms at left occipito-parieto-temporal recording sites. This electrical activity was present for both unfamiliar and familiar faces. The scalp topography of this effect was consistent with sources within the temporal and occipital cortices of the left hemisphere (based on a LORETA source localization). These findings suggest that priming of perceptual face processing is subserved by prolonged neural activity from 200 to 600 ms primarily in the left hemisphere. We propose that this priming reflects facilitated selection based on second-order relations among facial features.

Introduction

An improved ability to identify a face occurs when the same face had been encountered recently (Bruce and Valentine, 1985; Burton, 1998). Such experience-induced changes develop quickly, can be very long lasting, and can occur even in the absence of remembering the recent encounter. This repetition priming is a prime example of nondeclarative memory, which differs from other forms of memory in its functional properties and its neural implementation as revealed with functional imaging and lesion studies (for reviews, see Gabrieli, 1998; Richardson-Klavehn and Bjork, 1988; Roediger and McDermott, 1993; Squire and Knowlton, 2000). For example, nondeclarative memory is often preserved in neurological patients with dramatically impaired declarative memory abilities.

Improved identification of visual objects depends critically on the match of perceptual factors between initial and subsequent encounter and is therefore sometimes called 'perceptual priming'. It is important to distinguish this *data-driven* form of priming from *conceptually driven* forms of priming, which depend on conceptual knowledge spanning multiple modalities or domains. In keeping with these ideas, data-driven priming of recognizing faces is interrupted by a shift of modality or domain (Burton et al., 1998; Ellis et al., 1996; for a review, see Burton, 1998). However, data-driven priming need not reflect only a single process. Recent findings from our laboratory showed that this priming for faces can have two dissociable components, the facilitated access to pre-existing representations and facilitation in perceptual processing of faces (Boehm et al., in press). The representations responsible for data-driven priming of faces are usually considered to comprise (a) representations of familiar faces, or *face recognition units* (Bruce and Young, 1986; Goshen-Gottstein and Ganel, 2000), or (b) face recognition units in combination with multimodal representations of familiar persons, or *person identity nodes* (Burton, 1998; Valentine et al., 1996). Facilitated access to pre-existing representations occurs only for familiar faces, whereas facilitation in perceptual processing of faces was found to be independent of face familiarity. Here, we attempted to measure neural correlates of this perceptual contribution to priming.

Much remains to be learned about the neural underpinnings of face priming. Useful perspectives on the neural implementation of memory can be provided via event-related potentials (ERPs) recorded from the human brain. ERPs are time-locked signals within the electroencephalogram, which is thought to reflect neuronal activity primarily produced by spatially aligned cortical neurons activated synchronously (Münte et al., 2000). In contrast to many other methods for measuring human brain activity, ERPs

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allow a precise description of the time course of neural events. In general, ERP correlates of memory retrieval can be observed as differences between ERPs to repeated and new stimuli (Friedman and Johnson, 2000; Rugg, 1995) and associations between retrieval subprocesses and specific ERPs are currently under investigation. For repetitions of faces after short intervals in the time range of approximately 10 s, as in the current study, a so-called early repetition effect or N250r (ERE/N250r) and a centro-parietal so-called late repetition effect or N400 (LRE/N400) have been reported (Boehm and Sommer, 2005; Boehm et al., 2005; Pfütze et al., 2002; Schweinberger et al., 1995; for a review, see Schweinberger and Burton, 2003). The ERE/N250r is a frontal/fronto-polar positivity peaking around 300 ms when measured against a linked-mastoid reference (Boehm et al., 2005). Because the ERE/N250r has usually not been found for unfamiliar faces when immediate face repetitions were excluded, it has been concluded that it relates to changes in the access to facial representations (face recognition units) due to short-term repetition (Pfütze et al., 2002; Schweinberger and Burton, 2003; Schweinberger et al., 1995). The LRE/N400 appears as a centro-parietal positivity (or reduced centro-parietal negativity) between about 400 and 600 ms and is usually interpreted as reflecting changes in the access to semantic knowledge about the depicted person (for a review, see Schweinberger and Burton, 2003).

Though these ERPs reflect differences in processing between repeated and new faces, it is unlikely that these processing differences relate to data-driven priming for the following reasons. In case of the ERE/N250r, this effect has not been found at a repetition lag of 15 min (Schweinberger et al., 2002a), whereas face priming generally can be measured at this lag. In order to describe neural correlates of data-driven priming in general, specific conditions can be employed to discriminate priming from declarative memory and other repetition-related changes; manipulations such as a shift of modality or domain and varying the level of processing are especially useful because they selectively affect one type of memory (for a review, see Roediger and McDermott, 1993). Whereas data-driven priming for faces is sensitive to a domain-shift from names to faces, the LRE/N400, in contrast, has been found to be similar for different stimulus domains; moreover, the LRE/N400 can also be elicited when the prime and target faces belong to different but related famous persons (Boehm et al., 2005; Pfütze et al., 2002; Schweinberger, 1996; Schweinberger et al., 1995). Some recent studies have applied conditions that dissociate priming from other types of memory and demonstrated ERP correlates of priming for words, reporting small positivities of 1–2 μV around 400 ms that were most pronounced at parieto-central or occipital sites (Boehm et al., 2005; Joyce et al., 1999; Paller and Gross, 1998; Paller et al., 1998; Rugg et al., 2000; Rugg et al., 1998; Rugg and Nieto-Vegas, 1999). For priming of unfamiliar faces, small negativities around 350 ms at central or parietal electrode sites have been reported, which contrast to fronto-temporal positivities at ~500 ms described for priming of familiar faces (Boehm et al., 2005; Henson et al., 2003; Nessler et al., 2005; Paller et al., 2003).

The quest for neural correlates of priming of face perception can be informed further by considering specific processes of face perception, often referred to as structural encoding (Bruce and Young, 1986; Burton, 1998). Structural encoding entails a particular facility in processing configural information within faces, and three distinct types of configural processing have been distinguished, namely processing of first-order relations, holistic processing, and processing of second-order relations (Maurer et al., 2002). First-order relations, such as the spatial arrangement of a pair of eyes above a nose with a mouth below, define faces as a unique class of visual stimuli. Holistic processing groups individual facial features to a gestalt-like whole, making processing of individual features more difficult than when presented alone. Second-order relations (i.e., distances and angles between eyes, nose, and mouth) are considered critical for distinguishing between individual faces.

The extent to which these three types of configural processing contribute to priming of structural encoding is currently unknown. This question can be partially addressed by analyzing several ERP components that have been purported to bear close relationships to structural encoding—P100, vertex positivity (VPP) or P150, and N170 (Bentin et al., 1996; Itier and Taylor, 2002; Jeffreys, 1996; Linkenaer-Hansen et al., 1998); magnetic counterparts of these ERP components may also be considered, with some caveats (Liu et al., 2002). The functional significance of these components, however, is still under some debate. For example, some investigators hypothesized that P100 relates to processing of first-order relations and N170 to processing second-order relations (Itier and Taylor, 2002; Liu et al., 2002), but others failed to establish a link between N170 and processing specific to the individuality of faces (Bentin and Deouell, 2000; Eimer, 2000a). By determining which ERPs reflect priming of structural encoding, valuable information may be gained concerning both the contribution of types of configural processing to face priming and the functional significance of these ERPs.

In order to measure ERP correlates of priming at the level of structural encoding, we recorded electrical brain activity from scalp electrodes, while participants were asked to discriminate familiar from unfamiliar faces (Fig. 1). Each individual face was presented twice with one to four intervening faces. Repeated faces were always presented upright, whereas half of the familiar and half of the unfamiliar faces were initially presented inverted (Yin, 1969). We chose to use a shift from inverted to upright presentation because all three types of configural processing are disrupted by such face inversion, resulting, for example, in reduced recognition accuracy

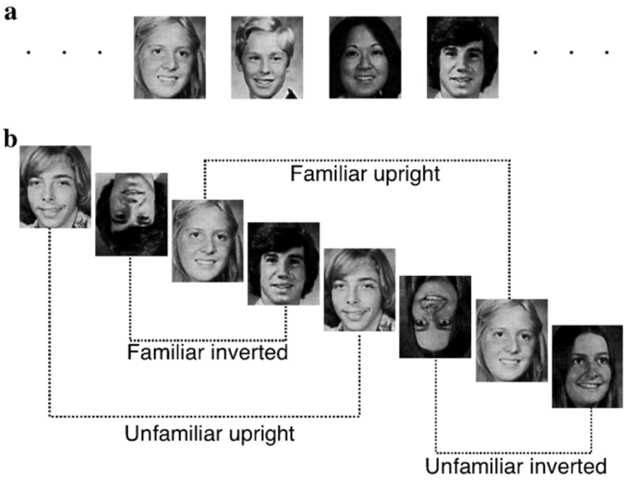

Fig. 1. Experimental paradigm. (a) Participants familiarized themselves with 80 pre-experimentally unknown faces. (b) One to three days later, memory for these familiar faces was tested. In a continuous task, familiar and unfamiliar faces were presented consecutively, and participants made a familiarity decision on each face. Each face was presented twice with 1–4 intervening faces. All repeated faces were presented upright; half of the familiar and half of the unfamiliar faces were initially presented inverted. (Different faces are shown here only to represent the paradigm schematically.)

(Leder and Bruce, 2000; Leder et al., 2001; Maurer et al., 2002). A common assumption is that inverted faces are processed to a relatively higher degree on the basis of their isolated features (Maurer et al., 2002), as indexed by increased activity in brain areas usually more involved in processing other visual objects (Aguirre et al., 1999; Haxby et al., 1999). Given the great divergence between how upright versus inverted faces are processed, priming of structural encoding can occur with upright-to-upright repetition but not with inverted-to-upright repetition (Boehm et al., in press). A pure indication of priming of structural encoding can thus be obtained by computing the difference between ERPs to repeated faces that had been presented upright at initial encounter and ERPs to repeated faces that had been presented inverted at initial encounter.

Methods

Participants

Twenty-four young adults (16 females, 8 males) participated for payment. The mean age was 21 years (range 18 to 26); all participants had normal or corrected-to-normal vision and were right-handed as assessed by a handedness questionnaire. Informed consent from all participants was obtained, and the study was approved by the Institutional Review Board at Northwestern University.

Stimuli

The set of faces consisted of 195 grayscale photographs of nonfamous faces (Endl et al., 1998). Five faces were used as filler faces during the test phase, ten famous faces were used together with 10 nonfamous faces during practice, and 20 nonfamous faces were used only during the learning phase. The other 160 nonfamous faces were divided into two groups of 80 faces. One group of 80 faces was assigned to the 'familiar' condition, the other to the 'unfamiliar' condition (assignment counterbalanced across participants).

Procedure

During the 1-h learning session, participants first familiarized themselves with 40 faces selected randomly from a total group of 80. These faces were presented individually or in sets of 10 on a computer screen. Participants were then given a short recognition test, using five new and five learned faces each, in order to provide feedback about learning. Next, the participants were given a set of 40 cards containing each of the faces they had been studying and were asked to sort the faces into male/female couples. Once this task was completed, participants took a second recognition test with a different set of five new and five learned faces. Participants were then given the same set of cards in a random order and were asked to sort them into the same couples as before. This whole learning procedure was then repeated for the second 40 faces, so that participants became familiar with all 80 faces.

Memory for these newly learned faces was tested 1–3 days later (mean 2 days). For the test session, participants sat in front of a computer monitor in a dimly lit, sound-attenuated, and electrically shielded chamber. They were asked to discriminate familiar (learned) from unfamiliar (new) faces by pressing buttons with their left or right index fingers. The assignment of hands to responses (learned/new) was counterbalanced across participants. Instructions emphasized both speed and accuracy. In a continuous task, each face (height 4.0°, width 2.8° visual angle) was presented on a computer screen for 600 ms, separated by a 2800-ms fixation cross; the refresh rate of the monitor was 67 Hz. All 80 familiar and 80 unfamiliar faces were presented twice with one to four intervening faces. The 5 (unfamiliar) filler faces were presented only once. Half of the familiar and half of the unfamiliar faces were initially presented inverted, whereas all repeated faces were presented upright. The order of conditions was unpredictable to the participants. The specific faces presented upright versus inverted were counterbalanced across participants. Reaction time and response accuracy were measured. Missing responses were treated as errors. Analysis of priming effects included trials with repeated faces only if a correct response had been given at both presentations.

The test session was subdivided by short breaks into four blocks. Including breaks, the test session lasted about 25 min. Prior to the test session, a practice run was conducted, using a different set of 10 nonfamous faces, intermixed with 10 famous faces (instead of learned faces); all faces were presented multiple times.

EEG recording, ERP methods, and source modeling

The continuous electroencephalogram (EEG) was recorded from 30 scalp positions [Fp1, Fp2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, Oz, O2, Iz, M1, and from electrodes close to PO5, PO1, PO2, PO6, PO9, PO10, OI9, OI10 (Pivik et al., 1993)] from tin electrodes mounted in an elastic cap, referenced against M2 as initial common reference and digitized with a frequency of 250 Hz. The band-pass was set to 0.1 to 100 Hz. Horizontal and vertical electrooculograms (EOG) were also recorded. Electrode impedances were kept below 5 kΩ.

The EEG was separated offline into epochs of 1000 ms, starting 100 ms before stimulus onset. All epochs free of ocular artifacts and with responses that were correct according to the behavioral analysis were averaged into ERPs for each experimental condition and each channel. A 100-ms prestimulus interval served as baseline.

For the analysis and display of face-related ERP components P100, vertex positivity/P150, and N170, ERPs were rereferenced to the average reference in order to remove possible effects resulting from the choice of the reference electrode. (For N170, ERPs were also obtained with an average of Fp1 and Fp2 reference and the pattern of results was the same.) Peaks for P100 were determined within the time segment from 80 to 110 ms after face onset at Oz, for vertex positivity within the time segment from 120 to 230 ms at Cz, and for N170 between 120 and 230 ms at P7 and P8. For all components, both peak latency in relation to face onset and peak amplitude relative to baseline were measured. All peaks were detected automatically as the most positive or most negative local extrema within the corresponding time segment defined as follows. Local maxima (and minima) were taken as the maximum (or minimum) point in the ERP waveform that showed a higher (or lower) amplitude than both the average of the preceding 20 ms and the average of the succeeding 20 ms. Note therefore that the local maxima (and minima) do not correspond necessarily to the most positive (or negative) point of the waveform in the given interval. Peaks were verified by visual inspection and the parameters adjusted in a few cases. Prior to peak detection, the relevant ERP waveforms were filtered with a low-pass filter at 18 Hz to reduce the influence of high-frequency noise (Picton et al., 2000). Three participants were excluded from the P100 analysis because P100 peaks were not detectable in one or two conditions.

In an independent step, ERPs were rereferenced to an average mastoid reference in order to display and analyze memory-related ERP modulations and to enable comparability to prior ERP studies of memory. In contrast to the peak analyses, no additional filtering took place.

Localization of brain generators for the main ERP effect was done with LORETA-KEY software (Pascal-Marqui, 1999; Pascal-Marqui et al., 1994). For a given EEG signal measured at the scalp, LORETA estimates the underlying structure of generators as spatially distributed sources in cortical grey matter and hippocampus in a standardized brain. Note that for the inverse problem of finding a generator solution for a given EEG signal, an infinite number of solutions are possible. To achieve a unique solution, specific assumptions have to be employed. In the case of LORETA, smoothness in activity between neighboring voxels is maximized. In order to reduce the influence of residual noise, the localization was done on the basis of the average signal from all participants (Picton et al., 2000).

Statistical analysis

Mean reaction times, error rates, and ERP measures were subjected to repeated-measure analyses of variance or paired *t* tests. All comparisons were two tailed. The level of significance was set to $\alpha = 0.05$.

Results

Behavioral results

Recognition accuracy was assessed by comparing hit rates to false alarm rates, as shown in Table 1. High accuracy for upright faces on initial presentation signaled reliable memory for learned faces, $F(1,23) = 1162.19$, $P < 0.0001$. Recognition accuracy for inverted faces was well above chance, $F(1,23) = 149.80$, $P < 0.0001$, but it was reduced compared to upright faces, as reflected by a lower hit rate, $F(1,23) = 43.87$, $P < 0.0001$, and a higher false alarm rate, $F(1,23) = 32.74$, $P < 0.0001$, resulting in reduced recognition sensitivity (d-prime). Additionally, response times for initial presentations were longer for inverted than for upright faces by 196 ms for familiar faces, $F(1,23) = 69.10$, $P < 0.0001$, and by 168 ms for unfamiliar faces, $F(1,23) = 36.18$, $P < 0.0001$. These results demonstrate reliable memory for learned faces and replicate the well-known disruptive influence of face inversion.

To assess priming, reaction times for repeated faces (which were always presented upright) were compared to reaction times to upright faces at initial presentation (see Fig. 2). Reaction times were analyzed only for correct trials, and data from repeated faces were included only if the same face was also recognized correctly on initial presentation. In the upright condition, a priming effect of 131 ms was observed for familiar faces, $F(1,23) = 71.47$, $P < 0.0001$, and a priming effect of 47 ms for unfamiliar faces, $F(1,23) = 19.37$, $P = 0.0002$. The much smaller priming effect for unfamiliar than familiar faces, $F(1,23) = 21.26$, $P < 0.0001$, replicates previous reports of reduced priming effects for unfamiliar faces.

Table 1
Recognition accuracy across presentation conditions

Measure	Initial presentation		Repetition (upright)	
	Upright	Inverted	Initially upright	Initially inverted
Hit rate	0.86 (0.02)	0.65 (0.04)	0.90 (0.02)	0.88 (0.02)
False alarm rate	0.06 (0.01)	0.22 (0.03)	0.08 (0.01)	0.08 (0.01)
d-prime	2.61	1.15	2.67	2.59

Note. Mean hit rate (proportion of familiar faces correctly recognized) and false alarm rate (proportion of unfamiliar faces incorrectly endorsed as familiar) shown with standard error in parentheses. A hit rate higher than the false alarm rate indicates above-chance recognition, as indicated by a positive value for d-prime, an index of recognition sensitivity. d-prime was derived from mean hit and false alarm rates.

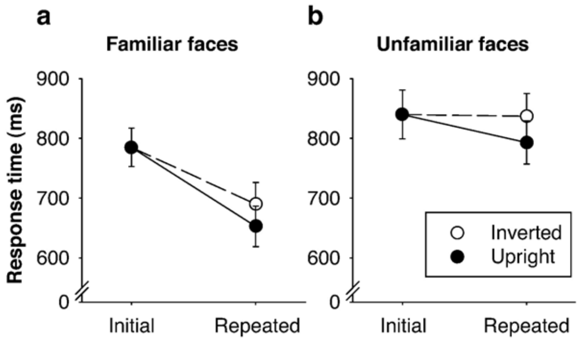

Fig. 2. Mean response times with standard errors for (a) familiar faces and (b) unfamiliar faces. The given stimulus orientation refers to initial stimulus presentation; all repeated stimuli were presented upright. Note that for the assessment of face recognition priming, reaction times of repeated faces were compared to the reaction times of initial presentations of upright faces. Mean response times for initial presentation of inverted faces (not shown) were 980 ms (SE = 49) for familiar faces and 1008 ms (SE = 49) for unfamiliar faces.

Priming effects were smaller with inverted than with upright initial presentations for both familiar, $F(1,23) = 14.61$, $P = 0.0009$, and unfamiliar faces, $F(1,23) = 18.97$, $P = 0.0002$ (see Fig. 2). This priming reduction due to stimulus inversion at initial presentation was of comparable size for familiar and unfamiliar faces, $F(1,23) = 0.23$. For the inverted condition, the priming effect of 94 ms for familiar faces was significant, $F(1,23) = 91.16$, $P < 0.0001$, whereas the difference of 3 ms for unfamiliar faces was negligible, $F(1,23) = 0.53$.

Electrophysiological results

For familiar faces, ERPs to repeats differed from ERPs to initial presentations in an ERE/N250r between 250 and 400 ms at frontopolar electrode sites and a subsequent LRE/N400 between 300 and 600 ms at parietal electrode sites (Fig. 3a). Such differences were negligible for unfamiliar faces (Fig. 3b). In order to investigate priming of structural encoding, we contrasted ERPs to repeated faces that had been initially presented upright with ERPs to repeated faces that had been initially presented inverted.

The relationship between priming of structural encoding and the face-related ERP components P100, vertex positivity/P150, and N170 was evaluated by analyzing peak amplitudes and latencies at electrodes where each component usually shows highest amplitudes, with an average reference montage (see Table 2 and Fig. 4). For P100, data were included for only 21 participants who showed detectable peaks in all conditions. As can be seen from Table 2, none of these components showed significant differences in peak amplitude or latency to repeated faces initially presented upright versus inverted.

These negative findings contrast with clear effects of face inversion in both behavior (as described above) and in ERPs.

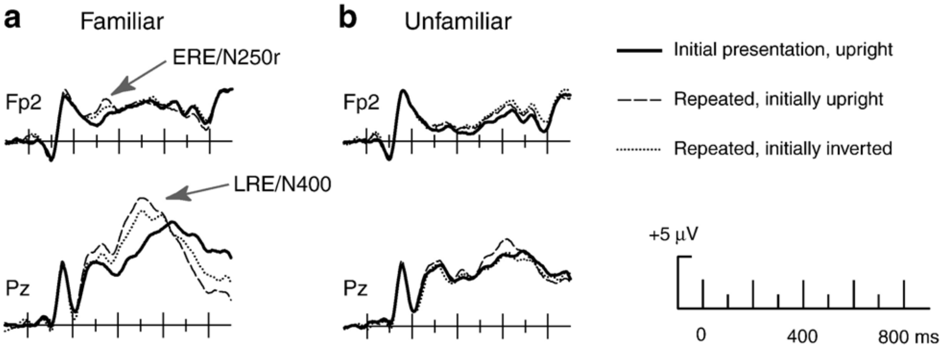

Fig. 3. ERP repetition effects. (a) ERE/N250r for familiar faces between 250 and 400 ms at a fronto-polar and LRE/N400 between 300 and 600 ms at a parietal electrode site. (b) Same contrasts for unfamiliar faces. ERE/N250r and LRE/N400 were not observed.

Inversion effects in ERPs were significant in latency and amplitude at all electrodes and for all components as differences between ERPs to initial presentations of upright faces and ERPs to initial presentations of inverted faces, Fs(1,23)/Fs(1,20) $\geq$ 4.49, Ps $\leq$ 0.0450, except for latency effects on P100, Fs(1, 20) $\leq$ 2.84, Ps $\geq$ 0.1074, and a latency effect on N170 at P8 for unfamiliar faces, $F(1,23) = 2.24$, $P = 0.1483$.

In order to describe a neural correlate of priming of structural encoding, we further analyzed the data by computing the difference between ERPs to repeated faces initially presented upright and ERPs to repeated faces initially presented inverted. This ERP difference included a steady left posterior positivity from about 200 to 600 ms for both familiar and unfamiliar faces (Fig. 5a). The mean amplitude difference at the P3 electrode measured 0.80 µV, $t(23) = 3.48$, $P = 0.0020$ (collapsed across familiar and unfamiliar faces). Amplitude differences from 200 to 600 ms at all electrodes were transformed into topographic P-value maps. Because P values take into account both size and variability of amplitude differences between conditions, these P-value maps provide a better measure than amplitude differences alone. The map for unfamiliar faces showed a left occipito-temporal topography (Fig. 5b). Following the rationale that this ERP difference reflects priming of structural encoding, a similar ERP was predicted for familiar faces. As is evident from Fig. 5c, the location of the corresponding ERP for familiar faces was somewhat different. This difference may be related to concurrent changes in processing specific to familiar faces, for example, access to face recognition units (Bruce and Young, 1986; Burton, 1998). As is evident from Fig. 5a, the ERP waveform for familiar faces was fairly similar to the ERP waveform for unfamiliar faces between 200 and 600 ms. Accordingly, when data for unfamiliar and familiar faces were collapsed, the t values of the left occipito-temporal positivity increased in comparison to the uncollapsed conditions, suggesting that this ERP is common to both unfamiliar and familiar faces (Fig. 5d).

Table 2
Priming of structural encoding in face-related ERP components

Measure [electrode, detection interval (ms), N]	Familiar faces F	Familiar faces P	Unfamiliar faces F	Unfamiliar faces P
P100 [Oz, 70–110, 21]				
Amplitude	2.61	0.1218	0.04	0.8397
Latency	0.13	0.7245	0.74	0.3984
VPP/P150 [Cz, 120–230, 24]				
Amplitude	0.14	0.7162	2.87	0.1037
Latency	0.26	0.6177	0.03	0.8676
N170 [P7, 120–230, 24]				
Amplitude	0.02	0.8960	0.03	0.8536
Latency	1.30	0.2667	0.16	0.6899
N170 [P8, 120–230, 24]				
Amplitude	0.57	0.4579	0.80	0.3816
Latency	0.16	0.6921	0.73	0.4001

The time course of this collapsed ERP difference was analyzed in more detail using nonoverlapping time segments of 50 ms over the interval from 200 to 600 ms. This analysis was done at the left-parietal electrode P3, which showed the highest t value in the 200- to 600-ms time period. With the exception of one time segment (450 to 500 ms, $t(23) = 1.96$, $P = 0.0616$), ERP differences were significant, ts(23) $\geq$ 2.15, Ps $\leq$ 0.0422, thus verifying that the ERP correlate of priming of structural encoding was reliably present between 200 ms and 600 ms.

To substantiate that this ERP correlate of priming of structural encoding could have been generated mainly by neural sources within the left hemisphere, a source localization was conducted with LORETA (Pascal-Marqui, 1999; Pascal-Marqui et al., 1994). The ERP difference in the time segment from 200 to 600 ms, combined for familiar and unfamiliar faces, and averaged over all participants, was used. LORETA indicated sources in the left and right occipitotemporal cortices with stronger sources in the left than the right hemisphere. The main source was located in the left inferior temporal cortex, centered in the inferior temporal gyrus (Figs. 5e–f). A second source was located in the left inferior occipital gyrus. When analyzed in more detail for the individual 50-ms time segments, the occipital source was only found between 450 and 600 ms, whereas the source in the inferior temporal gyrus remained active centered at the same location over the whole time range.

Discussion

The behavioral results replicated findings from our prior study and indicate two distinct components of data-driven face priming (Boehm et al., in press). As in the prior study, one priming component represents facilitated access to pre-existing representations, as generally described in models of face recognition (Bruce and Young, 1986; Burton, 1998; Valentine et al., 1996). This priming component was measured as priming from inverted faces and was present only for familiar faces. The second priming component, a perceptual contribution to data-driven face priming, was apparent as the difference in priming between faces initially presented upright

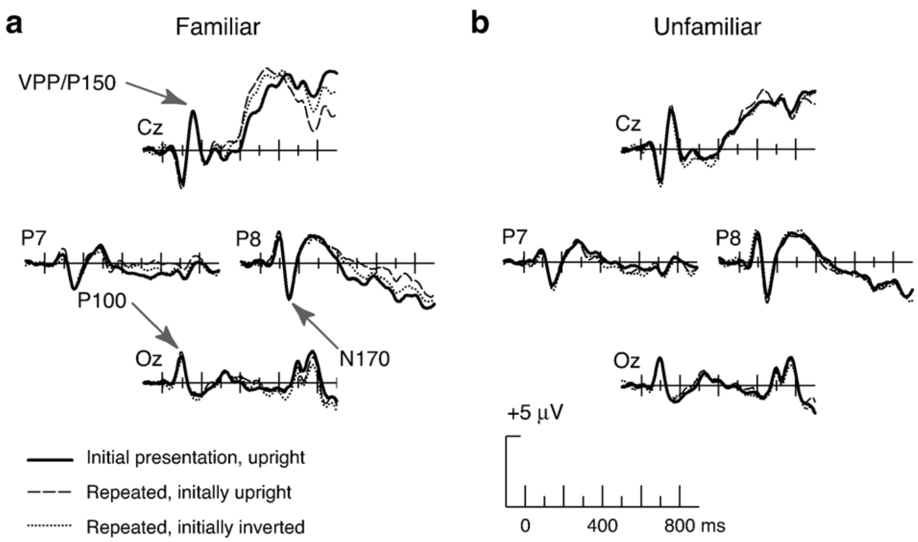

Fig. 4. Face-related ERP components; an average reference was used. (a) For familiar faces: P100 around 100 ms at Oz; VPP/P150 around 160 ms at Cz; N170 around 150 ms at P7, P8. (b) The same three face-related ERP components for unfamiliar faces.

and faces initially presented inverted. This priming of structural encoding was present for both familiar and unfamiliar faces, and its magnitude was independent of face familiarity.

This behavioral index of priming of structural face encoding was associated with a left occipito-temporo-parietal positivity between 200 and 600 ms. This ERP correlate of priming of structural encoding was common to both familiar and unfamiliar faces and has not been reported earlier. Note that all findings concerning ERP correlates of face priming are mixed in some respects, which may be explained by task factors, pre-experimental familiarity of faces used, and multiple priming components for familiar faces (Boehm et al., 2005, in press; Henson et al., 2003; Nessler et al., 2005; Paller et al., 2003). One strength of our approach is that it takes advantage of experimental contrasts as a function of whether the prior presentation of the same face was inverted or upright, such that the resulting ERP difference can be interpreted unequivocally as related to priming of perceptual processing of faces (Boehm et al., in press).

The ERP correlate of priming of structural encoding mainly appeared at electrode sites over the left hemisphere, which contrasts to the right-hemisphere dominance demonstrated for face perception on a variety of measures. Because ERPs measured on one side of the scalp do not necessarily relate to brain generators in the same hemisphere, we conducted a source localization. This analysis using the LORETA method provided evidence that priming of structural encoding as indicated by scalp ERPs could be supported by brain regions in inferotemporal cortex. One speculation is that face priming may be mediated in part by processing in the middle fusiform gyrus, which has been shown to be of special relevance for face perception (Haxby et al., 2001; Kanwisher et al., 1997; McCarthy et al., 1997), but future research with functional imaging is needed to further pinpoint the exact brain regions that support this function (e.g., Pourtois et al., 2005). Importantly, the localization demonstrated stronger sources within the left hemisphere, thus suggesting that this facilitated processing of faces occurred primarily in the left hemisphere. Priming of structural encoding may increase the contribution of left-hemispheric processing to face perception, or such priming may reflect better synchronization between face-processing networks in the two hemispheres.

The differences in perceptual processing of upright compared to inverted faces suggest that priming of structural encoding may depend critically on configural processing (Boehm et al., in press). An intriguing question is whether priming of structural encoding depends equally on all three distinct types of configural processing, that is, processing of first-order relations, holistic processing, and processing of second-order relations (Maurer et al., 2002). The discussion of this question is closely related to currently debated relationships between configural processing and face-related ERP components P100, vertex positivity/P150, and N170 (Bentin et al., 1996; Itier and Taylor, 2002; Jeffreys, 1996; Linkenaer-Hansen et al., 1998).

Notably, none of these ERP components showed any indication of systematic changes associated with priming of structural encoding here. These negative findings would be uninformative if priming of structural encoding had not occurred, but we obtained clear evidence of such priming in response times and at later latencies in ERPs. Also, face inversion effects were clearly demonstrated behaviorally and electrophysiologically, showing that face-related ERP components were quite sensitive to the inversion manipulation. These negative findings thus cannot be ascribed to either ineffectiveness of the face inversion manipulation or general insensitivity of these components. Although repetition-related changes in one or more of these components have been reported occasionally for immediate repetitions or short-term repetitions within a few seconds (Campanella et al., 2000; Guillaume and Tiberghien, 2001; Itier and Taylor, 2002, 2004), other experiments have failed to find such changes (Boehm and Sommer, 2005; Eimer, 2000b; Pfütze et al., 2002), in accordance with the present findings. Importantly, at a repetition lag of 15 min or more at which priming still prevails, the N170 component has been found to not show repetition-related changes (Schweinberger et al., 2002a). It is also important to note that the present study examined these components for the first time under conditions that permit ERP results to be attributed specifically to priming of structural encoding as opposed to other repetition-related changes. Whereas further exploration seems needed to understand the reasons for these divergent results (e.g., factors like the specific task employed might be found to play a crucial role), it is

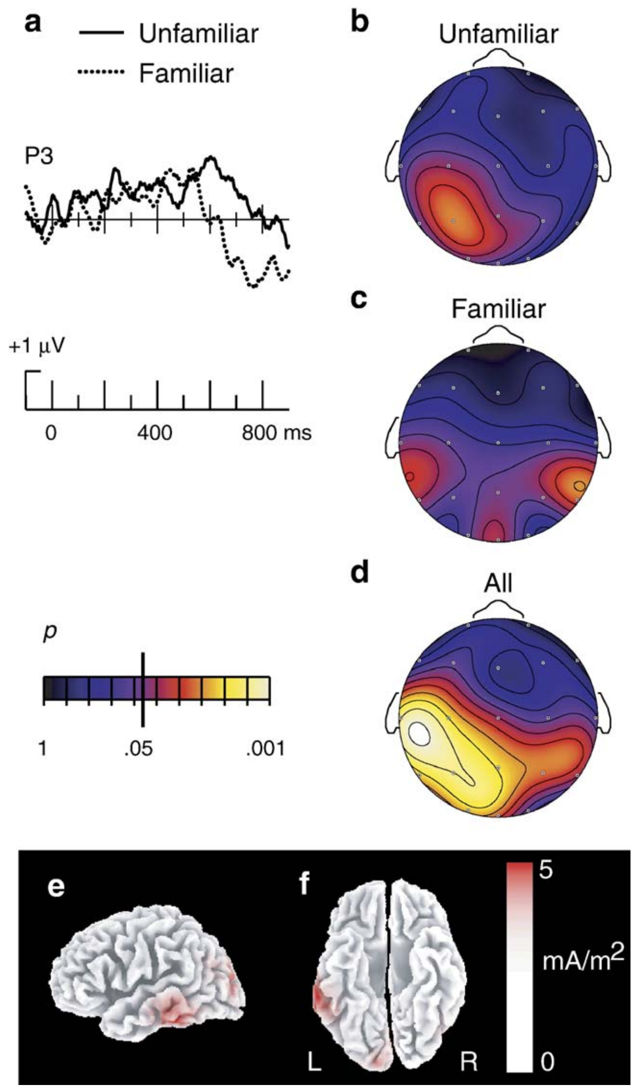

Fig. 5. ERP correlate of priming of structural encoding (mean amplitude difference between ERPs to repeated faces initially presented upright and ERPs to repeated faces initially presented inverted) for unfamiliar and familiar faces and source localization. (a) ERP waveforms at the left-parietal electrode site P3. (b–d) Topographic *P* value maps displaying the ERP correlate of priming of structural encoding between 200 and 600 ms. (b) Unfamiliar faces. (c) Familiar faces. (d) Unfamiliar and familiar faces collapsed. (e–f) Source localization of the ERP correlate of priming of structural encoding. Location of the left-hemispheric sources in the inferior temporal gyrus with the center at BA 20, Talairach coordinates $x = -59$, $y = -39$, $z = -20$ and inferior occipital gyrus, centered at BA 17, $x = -10$, $y = -94$, $z = -13$. The brain is partially inflated. Because LORETA estimates distributed sources, the scale is adjusted to display the center of the sources. (e) Lateral view of the left hemisphere. (f) View of both hemispheres from below; the left hemisphere is on the left.

reasonable to infer that none of these components likely index perceptual processes that gain by prior exposure in the way that supports the perceptual component of face priming.

A suitable way to accommodate these and related findings concerning the functional significance of those components is to propose that P100 and vertex positivity/P150 reflect at most two aspects of configural processing, processing of first-order relations and holistic processing. These processes, together with other low-level visual processing, may show no priming or priming of only marginal magnitude, too small to be detected in our experiment. Most processing of second-order relations may occur after processing of first-order relations and holistic processing. It has been recently shown that the putative magnetic counterpart of the N170, the M170, reflects processing necessary for identifying individual faces, which is based on second-order relations, but not for detecting faces as stimulus category, which relies on first-order relations (Liu et al., 2002). The present results argue in favor of the idea that N170 might reflect an initial stage of processing second-order relations but not the core of this processing. We suggest that processing of second-order relations, in contrast to first-order relations and holistic processing, can be facilitated by prior face exposure and was thus measured here as the ERP correlate of priming of structural encoding, starting at 200 ms (which corresponds to the offset of the N170). Hence, a reasonable hypothesis is that structural encoding per se occurs during the interval from P100 to the end of the ERP correlate of priming of structural encoding, or roughly from 100 to 600 ms. Although structural encoding has a right-hemispheric dominance, structural encoding seems to involve both hemispheres with a higher contribution for repeated faces from the left hemisphere.

Our results have some further implications for the literature on face recognition. Firstly, we discuss timing issues. Structural encoding was arguably in progress at 300–500 ms, the time when the ERE/N250r and the LRE/N400 for familiar faces have been observed (Pfütze et al., 2002; Schweinberger et al., 1995; Schweinberger et al., 2002b; for a review, see Schweinberger and Burton, 2003). Both effects were also evident here between the ERPs of repeated and initially presented familiar faces. The overlap in time of structural encoding and both the ERE/N250r and the LRE/N400 thus demonstrates that structural encoding and face recognition processes co-occur. This result implies that information flows in a cascade style across multiple face recognition processes, as opposed to a transmission that takes place only after processing at the earlier stage is finished.

A second implication of our results is related to the priming effect that was evident only for familiar faces, as also found in our previous behavioral study (Boehm et al., in press). This priming is considered to be related to access to semantic–memory representations (face recognition units or face recognition units in combination with person identity nodes), as usually described in models of face recognition (Bruce and Young, 1986; Burton, 1998). When compared across the two studies, the size of this priming effect here was numerically smaller than in the prior study by about 33% (141 versus 94 ms). Interestingly, there were 80 familiar faces in the current study in comparison to 50 in the prior study. Although study procedures differed, the duration of the learning session was the same in both studies, so that the individual exposure time for faces at learning here was reduced by about 36%. The reduction in priming magnitude and the parallel reduction in time of exposure to each face across studies lead us to propose a close relationship between the amount of prior experience during face learning and priming magnitude. The amount of priming that arises from semantic–memory representations may thus be determined by the strength of the representations themselves. Hence, priming may be a promising tool for studying how faces are learned such that enduring representations are established for familiar persons—this face learning process is essential for social communication but still largely unexplained.

The finding that face priming is greater for well-learned faces compared to other faces contrasts with priming results with words.

Priming is typically reduced for high- compared to low-frequency words (for a review, see Roediger and McDermott, 1993). This divergence between words and faces is consistent with the view that priming is domain specific and arises within perceptual and semantic–memory processes involved in perceiving and identifying visual objects (Boehm et al., in press).

Lastly, we have argued that data-driven priming for familiar faces comprises two distinct components, facilitated access to pre-existing representations and facilitated perceptual processing (Boehm et al., in press). On the other hand, electrophysiological data as described here suggest that only a part of structural encoding is associated with face priming. These findings bring up a central question: why do some processes show facilitation, whereas others do not? We hypothesize that these facilitated processes might share a common functional feature, which is the requirement to select an individual entity among similar entities. Indeed, selection has been described in the language domain as a process contingent on specific processing capabilities of the left hemisphere (Jung Beeman and Chiarello, 1998). For the two components of face priming discussed here, according to the model of face recognition (Bruce and Young, 1986; Burton, 1998; Valentine et al., 1996), the facilitation may correspond to selecting a specific face and to selecting a specific familiar person, respectively. Priming thus may be the result of facilitation of the most important processes within face perception and person recognition.

To conclude, although the perception of faces is comprised of several distinct subprocesses, not all of them are associated with behavioral face priming. The perceptual processes most likely to show such facilitation deal with second-order relations of facial features, which define the individuality of faces, either familiar or unfamiliar. This facilitation in perceptual face processing, indexed by a behavioral priming effect, occurred between 200 and 600 ms after face onset and may happen primarily in the left hemisphere.

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