The time course of implicit processing of facial features: An event-related potential study

F. Pesciarelli *, M. Sarlo b, I. Leo c

a Department of Biomedical Sciences, University of Modena and Reggio Emilia, Via Campi 287, 41100 Modena, Italy
b Department of General Psychology, University of Padova, Padova, Italy
c Department of Developmental Psychology, University of Padova, Padova, Italy

A R T I C L E  I N F O

Article history:
Received 24 August 2010
Received in revised form 28 January 2011
Accepted 2 February 2011
Available online 17 February 2011

Keywords:
Event-related potentials
Face processing
Masked priming

A B S T R A C T

In this study, we used ERPs to investigate the time course of implicit face processing. More specifically, we utilized a masked priming paradigm to investigate implicit processing of the eyes and mouth in upright and inverted faces, using a prime duration of 33 ms. Two types of prime–target pairs were used: (1) congruent (e.g., open eyes only in both prime and target); (2) incongruent (e.g., open eyes only in prime and open mouth only in target). The identity of the faces changed between prime and target. Participants pressed one button to indicate whether the target face’s mouth was open, and another if the eyes were open. The behavioral results indicated a congruent priming effect for upright but not for inverted faces. The ERP results indicated a face orientation effect across all ERP components studied (P1, N1, P2, P170, N2, P3) starting at about 80 ms, and a congruency/priming effect on late components (N2, P3), starting at about 200 ms. The functional significance of these ERP effects is discussed in relation to unconscious perception and configural face processing.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

Despite recent theoretical and experimental contributions to the study of face processing, questions about the cognitive mechanisms and the neural substrates subtending the perception of the information in the face are still under debate. Adults are experts in processing faces (e.g., Diamond & Carey, 1986) and can recognize thousands of individual faces rapidly and accurately (e.g., Bahrick, Bahrick, & Wittlinger, 1975). This ability is attributed to enhanced sensitivity to configural information in faces. Configural processing of faces involves processing not just the shapes of individual features (featural or component information) but also the relations among them (relational or configural information) (e.g., Maurer, Le Grand, & Mondloch, 2002). Relative to upright faces, recognizing inverted faces is surprisingly poor, with the decrement far larger than it is for shoes or houses. Indeed, the face inversion effect, much poorer accuracy and longer reaction times when faces are upside down, has been taken as diagnostic of configural processing.

In accordance with the old model of Diamond and Carey (1986), Maurer et al. (2002) have recently suggested that face processing involves three levels of configural processing: an initial stage that encodes the first-order relational information (which refers to qualitative spatial relations among facial features); a second holistic stage that integrates facial features into a whole or a Gestalt, thus rendering individual features less accessible; and a third stage that encodes the second-order relational information (which refers to fine spatial relations between features). The difference between the first two stages is rather subtle because when adults detect the first-order relations of a face, they tend to process the stimulus as a Gestalt (e.g., Maurer et al., 2002). In contrast, recognition of a specific face occurs subsequently on the basis of the second-order relational information (e.g., Carey & Diamond, 1977; Freire & Lee, 2001). Detecting and recognizing faces are two important components of face processing. Current cognitive (e.g., Bruce & Young, 1986) and neural (e.g., Haxby, Hoffman, & Gobbini, 2000) models of face processing propose that face recognition is a sequential process in which an initial stage of structural encoding is necessary. Detecting a facial configuration is fast and efficient and is facilitated by the fact that all faces share the same first-order relational features, with two eyes above a nose, which is above a mouth, leading to holistic processing (e.g., Diamond & Carey, 1986). Adults have a remarkable ability to detect faces among a sample of other visual stimuli on the basis of first-order relational information, even in the absence of normal facial features (e.g., Moscovitch, Winocur, & Behrmann, 1997). The most convincing demonstration that when adults detect the first-order relations of a face they tend to process the stimulus as a Gestalt is the part-whole effect (Farah, Wilson, Drain, & Tanaka, 1998; Tanaka & Farah, 1993). Accuracy in discriminating individual face parts is higher when the entire face is presented than when the parts are presented in isolation, whereas
the same holistic advantage is not found for parts of other objects. Recognition of individual faces refers to the capacity to discriminate between different exemplars of the face category, recognizing a face as familiar. Because all faces share the same first-order relations, face recognition requires the encoding of information about the fine spatial relation among the facial features (i.e., second-order relational information) (e.g., Carey & Diamond, 1977). Surprisingly, recent evidence suggests that at least some rudimentary aspects of face processing expertise are available in early life when the visual experience with faces is small (e.g., Leo & Simion, 2009a, 2009b).

Studies using functional magnetic resonance imaging (fMRI) and event-related potentials (ERPs) have identified neural correlates of detecting a face. fMRI activation in regions of the ventral occipitotemporal cortex, the inferior occipital gyrus and the lateral fusiform gyrus, i.e., the fusiform face area (FFA), is larger for faces than for a variety of non-face objects (including houses, cars and hands) (Aguirre, Singh, & D’Esposito, 1999; Haxby et al., 2000). Face-specific modulations of ERPs provide a source of evidence for specialized brain process subserving face detection, involving the characterization of facial structure, and recognition, which involves processing facial features and their second-order spatial relations. ERP studies of face processing have focused on several face-sensitive components. These components are also sensitive to face information such as internal features (e.g., spacing and orientation). Several recent ERP studies have examined early face processing and reported that occipital P1/N1 responses occurring between 120 and 180 ms contributed to the detection of facial features. More specifically, some authors have found that the P1/N1 responses are different for faces than for other objects (e.g., Herrmann, Ehls, Ellgring, & Fallgatter, 2004). There is evidence that the P1/N1 are sensitive to violation of the first-order configuration of a face, such as orientation (Itier & Taylor, 2002; Taylor, Batty, & Itier, 2004), thatcherization (Milivojevic, Clapp, Johnson, & Corballis, 2003) and Mooney faces defined by shape-from-shading (Latinus & Taylor, 2005). ERP studies have also pinpointed another early negative component peaking around 170 ms (the N170), distributed consistently over the posterior temporal regions, and an early positive component peaking in the same latency range distributed over the frontocentral regions (VPP), which are highly sensitive to faces (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000; Rossion et al., 1999). The N170 is also sensitive to inversion, with greater amplitude elicited for inverted compared to upright faces. Some authors have found that the N170 is not affected by stimulus familiarity, and have suggested that this component is more likely to reflect structural encoding of face stimuli rather than identity recognition (Bentin & Deouell, 2000; Eimer, 2000). However, it remains unclear what exactly is encoded at the stage of the N170. Several other ERP components have also been recorded at different time points that appear to be related to face processing and in particular to face recognition, such as the P2, the N250 and the P3. The P2, a positive component that peaks around 200 ms in posterior temporal sites, is sensitive to the first-order configuration (thatcherization; Boutsen, Humphreys, Praamstra, & Warbrick, 2006), but also to the second-order configuration (elongation; Halit, de Haan, & Johnson, 2000) of a face. Several works suggest that the P2 may reflect a later stage of local processing of configurational information in a face (Boutsen et al., 2006; Itier & Taylor, 2004), but this issue is still a matter of debate. The N250, a negative component that peaks around 250 ms, is sensitive to repetition and familiarity of faces. The N250 repetition effect is delayed when the face is inverted, suggesting a sensitivity to configurational relations of features (Itier & Taylor, 2004). Some studies have also pinpointed a late positive component at around 500–800 ms. This component has been identified as the P3 or late positive complex (LPC). More specifically, some authors have found a larger late posterior positivity for repeated faces (Bentin & McCarthy, 1994; Guillem, Bicu, & Debruiulle, 2001), while some other authors have observed a reduced late posterior positivity for repeated pictorial stimuli (Münite et al., 1997; Trenner, Schweinberger, Jentzsch, & Sommer, 2004). However, this issue is discussed controversially.

Despite much research, the types of configural processing and the stages that underpin face perception are still under debate. Recently, Williams, Moss, and Bradshaw (2004) investigated the early processes involved in face recognition. More specifically, the authors investigated implicit face processing of the eyes and mouth in upright and inverted faces, using a masked priming paradigm in which the prime was presented for 33 ms. Based on their results, the authors suggested that an upright face is processed by analysis of its configuration based on second-order relational processing, while an inverted face is first processed using first-order information, and then by configural analysis.

The present study took the work of Williams et al. (2004) as a useful starting point to explore the temporal characteristics of subliminal face priming through ERP measures. Although response times and accuracy rates can be used to make inferences on the sequence with which cognitive processes occur, these inferences are limited. In order to avoid this limitation, the present work used ERPs since they provide a more direct measure of intervening processes. Because ERPs provide an instantaneous assessment of underlying neural activity, they allow for easier identification and isolation of individual cognitive processes.

The aim of the current work was twofold: (1) to investigate the time course of implicit face processing and the associated ERP components, and (2) to explore the types of configural processing involved in face perception. To do this, we used a method highly similar to that employed by Williams et al. (2004; Experiment 3). More specifically, we utilized a masked priming paradigm to investigate implicit processing of the eyes and mouth in upright and inverted faces. In one variant of this type of paradigm, the prime stimulus was briefly presented and immediately replaced by a pattern mask (e.g., a series of letters or symbols occupying the same spatial location as the prime) or, in some cases, by the target stimulus itself. Participants were most often unable to report having seen the prime stimulus. Nonetheless, unmasked target stimuli in these cases were typically associated with faster response times (RTs) and fewer errors when they followed an identity or semantically related masked prime. There was a large consensus around the hypothesis that in the masked priming paradigm, the mask interferes with the consolidation of long-lasting episodic memories and, therefore, it offers a good methodological tool (a) to investigate the neural correlates of the processing of facial features prior to awareness and (b) to investigate early stages of face processing.

Thus, there are to date few and controversial studies that have investigated the different roles of early and late ERP components reflecting different stages of configural face processing, and no study has used a masked priming paradigm. Thus, in this study, we investigated the time course of implicit face processing of facial features on early (P1, N1, P2, N170) and late (N2, P3) ERP components. Specifically, the goal of our study was to examine the role of orientation and priming at both early and late stages of processing. Based on the literature, we hypothesized the existence of an orientation effect in the early components and a priming effect in the late components. However, given the controversial results provided by the literature, it was possible that, for some of the considered components, the orientation and priming effects could emerge in additional time windows.

2. Methods

2.1. Participants

Fourteen University of Padova undergraduate and graduate volunteers, between the ages of 19 and 31 (mean = 20 years) participated in the experiment. All partic-
Participants were right-handed, with no history of neurological disorders and reported having normal or corrected-to-normal visual acuity.

2.2. Stimuli

Black and white pictures selected from the NimStim face stimulus set (Tottenham et al., 2009) were used. The background was black and the mean luminance was approximately the same for all pictures. The forward mask and prime stimuli were identical faces, while the target face was different from both the forward mask and prime face. The prime was 25% smaller (visual angle 8.5°) than the forward mask and target (visual angle 11.3°) to avoid any apparent movement between the forward mask and prime stimuli.

The forward mask face had both eyes and mouth closed, the prime face had either eyes, mouth, or both open. The target face had open mouth or open eyes, except on 50% of the trials in which both eyes and mouth were closed (catch trials). These catch trials were included to prevent response habituation, to control for attention and to make sure that the participants examined the whole face. As in Williams et al. (2004), we used a high number of catch trials in order to have an equal number of trials in which the participant had to respond (50% target trials) and to withhold the response (50% catch trials). Unlike Williams et al. (2004), however, only two types of prime–target pairs were used: (1) congruent (e.g., open eyes only in both prime and target) and (2) incongruent (e.g., open eyes only in prime and open mouth only in target). The dual condition (i.e., both eyes and mouth open in prime and either eyes or mouth open in target) was omitted in order to reduce the number of variables and to avoid fatigue. Half of the trials were rotated by 180° to produce inverted mask, prime and target faces.

Participants performed four blocks of 160 trials each, two blocks with upright faces and two blocks with inverted faces resulting in a total of 640 trials (40 trials per condition). It should be noted that the same two faces were used throughout the experiment.

2.3. Design and procedure

The stimulus presentation procedure is graphically reported in Fig. 1. All stimuli (faces) were displayed in the center of a black CRT at a viewing distance of 100 cm. Each trial began with a termination of a fixation stimulus in the middle of the screen. Five hundred milliseconds later, a 200-ms black screen that was replaced by a 1500-ms forward mask was presented. The forward mask was replaced at the same location on the screen by the prime item for 33 ms. The prime was then immediately replaced by the target, which lasted until a response was given. The next trial began 1 s after response onset.

Participants were instructed to press a button as quickly as possible when the target face had the eyes open, another button when the target face had the mouth open and to withhold the response when the target face had neither eyes nor mouth open. The participant’s responses controlled the onset and termination of the target on the screen. When the participant pressed one of the response buttons, the stimulus was erased from the screen. Participants were asked to maintain fixation on the center of the screen and to refrain from blinking and moving their eyes except when the fixation stimulus appeared on the screen. At the end of the experiment, participants were asked to describe what they perceived between the forward mask and target. They were then informed of the presence of the prime and were asked if they could describe the face. None of the participants explicitly reported that the prime face was the same as the forward mask face.

Face orientation was blocked whereas prime–target congruency was randomized within each block. All factors were fully crossed. Behavioral RT data were submitted to an analysis of variance (ANOVA) that considered face orientation (upright and inverted), prime–target congruency (congruent, incongruent) as within-subject factors. To test specific effects or interactions, additional ANOVAs were employed.

2.4. EEG recording

The electroencephalogram (EEG) was recorded from 19 tin electrodes mounted in an elastic cap according to the International 10–20 System (Jasper, 1958) at sites Fp1, Fp2, F3, Fz, F4, F7, F8, C3, Cz, C4, T3, T4, T5, T6, P3, P4, O1, O2 and right mastoid. The signals were recorded using a left mastoid reference, and then re-referenced offline to the average of the left and right mastoids. For the purpose of artifact scoring, vertical and horizontal electro-oculograms (EOGs) were recorded. Electrode pairs (bipolar) were placed at the supra- and suborbit of the right eye and at the external canthi of the eyes. All electrode impedances were kept below 10kΩ. The EEG and EOG signals were amplified with Neuroscan Synamps (El Paso, TX, USA), bandpass filtered (0.1–70 Hz), digitized at 500 Hz (16 bit AD converter, accuracy 0.08 uV/bit) and stored on a Pentium IV computer.

Continuous EEG data were corrected for eyeblinks using a regression-based correction algorithm (Scan 4.1 software). The EEG was then segmented off-line into 900-ms epochs from 100 ms before to 800 ms after target onset. The EEG epochs were baseline-corrected against the mean voltage during the 100-ms prestimulus period. All EEG epochs were visually scored for eye movement and other artifacts, and each portion of data containing artifacts greater than ±70 uV in any channel was rejected for all the recorded channels prior to further analysis. Artifact-free trials with correct behavioral responses were separately averaged for each subject in each experimental condition.
2.5. ERP data analysis

On the basis of the inspection of grand average ERP waveforms, the following components were identified for target onset at frontal (F3, Fz, F4), central (C3, Cz, C4) and parietal (P3, Pz, P4) scalp sites: N1, specified as the most negative peak between 60 and 115 ms from target onset; P2, specified as the most positive peak between 120 and 210 ms from target onset; N2, specified as the most negative peak between 165 and 265 ms from target onset and P3, specified as the most positive peak between 350 and 510 ms from target onset. At posterior electrode sites (T5, T6, O1, O2), the following ERP components were considered: P1, specified as the most positive peak between 40 and 100 ms and N170, specified as the most negative peak between 100 and 180 ms.

For target onset, separate repeated-measures analyses of variance (ANOVAs) were conducted on mean ERP peak amplitudes with face orientation (upright, inverted), prime–target congruency (congruent, incongruent) and EEG site (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4) as within-subject factors. At posterior electrode sites, the ANOVA included the following within-subject factors: face orientation, prime–target congruency and EEG site (T5, T6, O1, O2).

Post-hoc mean comparisons (Newman–Keuls) were employed to further examine significant effects (using a $p < .05$ criterion for significance).

3. Results

3.1. Behavior

Participants were unable to identify the prime. Catch trials were excluded from further analyses. These RT means are reported in Fig. 2.

The two-way within-subject ANOVA conducted on the RT data yielded a significant main effect of prime–target congruency [$F(1,13)=15.07$, $p < .002$, $\eta^2_p = .54$, observed power = .95]. There was no significant main effect of face orientation [$F(1,13)=1.82$, $p > .2$, $\eta^2_p = .12$, observed power = .24]. Moreover, the analysis revealed a reliable orientation by congruency interaction [$F(1,13)=4.81$, $p < .047$, $\eta^2_p = .27$, observed power = .53]. Separate analysis of prime–target congruency showed a congruency priming effect for upright faces [$F(1,13)=14.84$, $p < .002$, $\eta^2_p = .53$, observed power = .94], with faster RTs for the congruent than incongruent condition, and not for inverted faces [$F(1,13)=.56$, $p > .46$, $\eta^2_p = .04$, observed power = .11]. Hit rates were not formally analyzed because of ceiling effects, with all conditions averaging 98% correct.

3.2. Event-related potentials

Grand-averaged ERPs elicited by target faces as a function of prime–target congruency and face orientation are represented in Figs. 3 and 4.

![Fig. 3. Grand-averaged event-related potentials recorded at frontal, central and parietal sites to target faces as a function of prime–target congruency and face orientation.](image-url)
Fig. 4. Grand-averaged event-related potentials recorded at occipito-temporal and occipital sites to target faces as a function of prime–target congruency and face orientation.

3.2.1. P1
As supported by the significant face orientation × EEG site effect [$F(3,39) = 4.06$, $p < .01$, $\eta_p^2 = .24$, observed power = .80], P1 amplitudes were larger for inverted than upright faces in the left hemisphere ($p < .04$), whereas no significant difference was found in the right hemisphere. Overall, P1 was larger in the occipital than in the occipito-temporal area, and on the right than on the left hemisphere [EEG site main effect: $F(3,39) = 10.52$, $p < .00003$, $\eta_p^2 = .45$, observed power = .99].

3.2.2. N1
Overall, the N1 amplitude was largest at midline sites and in the fronto-central than parietal regions [EEG site main effect: $F(8,104) = 6.36$, $p < .000001$, $\eta_p^2 = .33$, observed power = 1.0]. The significant face orientation × EEG site interaction [$F(8,104) = 1.99$, $p < .05$, $\eta_p^2 = .13$, observed power = .79] showed that the N1 amplitude was larger for inverted than upright faces on the parietal sites ($p < .05$), whereas no significant differences were found on the fronto-central sites.

3.2.3. N170
The analysis of this face-specific component revealed only the significant main effect of face orientation [$F(1,13) = 4.32$, $p < .05$, $\eta_p^2 = .25$, observed power = .48], showing larger amplitudes for inverted than upright faces.

3.2.4. P2
The significant face orientation × EEG site interaction [$F(8,104) = 3.35$, $p < .001$, $\eta_p^2 = .20$, observed power = .97] showed that upright faces tended to elicit larger amplitudes than inverted faces on the P3 and P4 electrodes ($p < .07$), whereas no significant differences were found on the frontal and central sites. Overall, larger positivity was found at the midline than on the left and right hemispheres and on the central than frontal and parietal sites [EEG site main effect: $F(8,104) = 3.09$, $p < .003$, $\eta_p^2 = .19$, observed power = .95].

3.2.5. N2
The significant main effect of face orientation [$F(1,13) = 15.07$, $p < .001$, $\eta_p^2 = .54$, observed power = .95] showed larger N2 amplitudes for upright than inverted faces. A significant main effect of prime–target congruency was also obtained [$F(1,13) = 7.81$, $p < .01$, $\eta_p^2 = .38$, observed power = .73], reflecting an overall greater negativity for incongruent than congruent targets (Fig. 5).

As highlighted by the significant face orientation × EEG site interaction [$F(8,104) = 3.61$, $p < .0009$, $\eta_p^2 = .22$, observed power = .98], upright faces elicited larger N2 amplitudes than inverted faces at all sites ($p < .02$). In both conditions of face orientation, lower negativity was found in the midline centro-parietal regions.

3.2.6. P3
The significant prime–target congruency × face orientation × EEG site effect [$F(8,104) = 3.70$, $p < .0007$, $\eta_p^2 = .22$, observed power = .98] indicated that, in the parietal area, larger P3 amplitudes were elicited by congruent than incongruent targets when faces were presented both upright and inverted ($p < .04$). Furthermore, a larger P3 was found for upright than inverted faces for the congruent condition ($p < .0001$). In the frontal area, no significant differences were found between congruent and incongruent conditions. Inverted faces elicited an enhanced P3 as compared to upright faces for both congruent and incongruent targets ($p < .0001$) (Fig. 6). Overall, as supported by the significant main effect of EEG site [$F(8,104) = 35.43$, $p < .00001$, $\eta_p^2 = .73$, observed
power $= 1.0$], the largest P3 amplitudes were obtained in the midline parietal area ($p < .00001$).

4. Discussion

The main focus of the current work was to explore the temporal characteristics of configural face processing. To this end, implicit processing of the eyes and mouth of upright and inverted faces was investigated. ERPs were recorded while participants were exposed to a masked priming paradigm in which prime–target pairs were congruent or incongruent. Priming was inferred from both reaction times for congruent versus incongruent targets, and ERP amplitude differences at various latencies post-target onset for the same comparison. Different face-sensitive modulations of ERPs are likely to reflect different stages of face processing from the perceptual analysis and structural encoding of face components up to the identification and recognition of face stimuli. Behavioral and electrophysiological findings revealed a consistent pattern of results.

Our behavioral results showed a congruency priming effect for upright faces and not for inverted faces. This result, however, is partially at odds with those of Williams et al. (2004), who did find a priming effect for both upright and inverted faces. One likely explanation for this discrepancy is that Williams et al. used familiar faces while we used novel faces. This possible explanation is consistent with the results of Kouider, Eger, Dolan, and Henson (2009; see also Henson, Mouchlianitis, Matthews, & Kouider, 2008) in which they found reliable face priming effects with masked primes for familiar faces, although this was small and not reliable for unfamiliar faces, and with the literature on masked word priming (Forster, 1998). On this basis, it can be argued that the lack of statistical significance of prime–target congruency for inverted faces is a reflection of the low observed power ($r^2 = .04$), indicating limited effectiveness to detect a small effect in such a relatively small sample size. However, further analyses of our data revealed that the addition of subjects is unlikely to have resulted in a significant difference for the congruency condition for inverted faces. If we treat our behavioral results as ‘pilot data’, the congruency condition for inverted faces showed a small effect size ($r^2 = .04$), and approximately 239 subjects would have been needed to obtain a 0.8 power level, which is considered desirable (or 119 subjects, for 0.5 power, which is considered medium).

4.1. ERP effects of face orientation

Although no effect of face orientation was found behaviorally, such an effect was seen in all the analyzed ERP components. The earliest effect of orientation in the ERPs was observed in the P1 time window. The P1 was larger for inverted faces compared to upright faces. These results are in agreement with the unmasked literature (Halit et al., 2000; Itier & Taylor, 2002, 2004), showing that the inversion effect arises as early as the P1 also for subliminal face stimuli and confirming an early face processing stage around 100 ms sensitive to face configuration. Thus, the present result contributes to further support the suggestion that facial configuration processing starts around the time window of the P1 and that could reflect the disruption of configural changes on very early processes. The subsequent component affected by face orientation was the N1. The N1 was larger for inverted than upright faces at the midline and on the right hemisphere. There is only very little evidence that the

Fig. 5. Histogram of the amplitude of the N2 component in the congruent (gray bar) and incongruent (black bar) conditions averaged over the nine electrodes. As this component was recorded in the positive field, less positive values indicate greater negativity.

Fig. 6. Histograms of the amplitude of the P3 component as a function of upright vs. inverted faces and congruent (gray bar) vs. incongruent (black bar) conditions averaged over three electrodes in each region.
N1 may be sensitive to facial characteristics, and this is limited to emotional faces (Dennis, Malone, & Chen, 2009; Eimer & Holmes, 2002). These implicit and early effects reflected by the P1 and N1, reported in the present study, demonstrate that face configuration is analyzed rapidly and can affect cortical processing at very short latencies. Moreover, the data suggest an automatic neural mechanism underlying the perception of configurual changes of the face. The present data suggest that this process is likely to be a relatively low-level visual process. In line with previous studies (Bentin et al., 1996; Eimer, 2000; Rossion et al., 1999, 2000), the N170 amplitude, when compared to upright faces, was enhanced in response to inverted faces. This sensitivity of N170 to inverted faces has been interpreted as reflecting a disruption of configurual information at the encoding stage of face processing (Rossion et al., 1999, 2000).

Face orientation also modulated later components such as the P2, N2 and P3. The P2 was more positive for upright compared to inverted faces in the parietal region. What processes the P2 indexes is not clear in the literature; nevertheless, our results agree with the studies suggesting that this component is sensitive to facial configuration and is involved in processing configurual relations between features (Boutsen et al., 2006; Itier & Taylor, 2004). Face orientation also affected the N2, with upright faces eliciting larger negativity than inverted faces at all sites. This N2 effect is in accordance with previous ERP evidence suggesting that the N2 component is modulated consistently by face stimuli (Bentin, Sagiv, Mecklinger, Friedrici, & Von Cramon, 2002; Liddell, Williams, Rathjen, Shevrin, & Gordon, 2004; Schweinberger & Burton, 2003). The last component affected by face orientation was the P3. A larger P3 amplitude was found with inverted than upright faces in the frontal area. Interestingly, a different pattern emerged in the parietal region, where upright faces elicited an enhanced P3 as compared to inverted faces, but only for congruent targets. This difference can be explained by the distinction proposed by Squires, Squires, and Hillyard (1975), identifying a frontally maximal P3a component and a parietally maximal P3b component. Several studies have shown that novel, unexpected, or unusual stimuli elicit a frontal P3 (e.g., Courchesne, Hillyard, & Galambos, 1975), supporting the hypothesis that such a component reflects the activation of a frontal neural network responding to deviant events (Friedman, Cycowicz, & Gaeta, 2001). Such an interpretation seems to account for our results at frontal sites, as P3 was larger for inverted (i.e., with unusual orientation) than upright faces. Here, the processing of face orientation appears to prevail over the detection of prime–target congruency, possibly because of the novelty effect produced by face inversion. On the other hand, the P3 effect observed at parietal sites seems to reflect the processes of memory access and attentional resource allocation evoked by the evaluation of target stimuli (e.g., Kok, 2001), as P3 was primarily modulated by prime–target congruency.

4.2. ERP effects of masked priming

Priming effects were seen only on late ERP components (N2, P3) and not on early components (P1, N1, P2, N170). It is interesting to note that the N170 in both upright and inverted faces was not affected by face congruency. This result is in line with previous findings (Bentin & Deouell, 2000; Eimer, 2000), demonstrating that the N170 is not affected by familiarity, thus indicating, as suggested by Eimer (2000), that this component reflects processes prior to the recognition and identification of individual faces. The N170 seems therefore to reflect the perceptual encoding of face components rather than the processing stages involved in face identification. The N2 was the first component to be affected by congruency. The amplitude of the N2 was affected by the relation between prime and target, being larger when the stimuli were incongruent in both upright and inverted faces. The explanation that the N2 reflects detection and holistic perceptual analysis of facial configuration (Bentin et al., 2002) accounts only partly for our (priming) results, where the N2 was modulated by the distinctive configurations that defined each face. Interestingly, this N2 modulation suggests an automatic neural mechanism underlying the recognition and identification of faces and seems in accordance with previous neurophysiological studies that consider the N2 component to be a reflection of an automatic, non-conscious attention-orienting response (Liddell et al., 2004). The last component affected by priming was the P3. The enhanced P3 observed in the parietal area for congruent relative to incongruent targets might indicate facilitated encoding and retrieval of stimuli that matched an active memory representation. In other words, evaluative categorization of face targets was more pronounced when it was pre-activated by a congruent prime.

It is worthy of note that the discrepancy between the behavioral and the ERP results for the prime–target congruency condition for inverted faces is most likely due to a difference in sensitivity between the two measures. It is widely acknowledged that ERPs can be a more sensitive measure and reveal subtle effects that are not evidenced in response latencies. In particular, the RT measures are considered as less sensitive to small effects (e.g., Snodgrass, 1993). Therefore, it may be the case, at least when using unfamiliar faces as prime stimuli, that ERPs were more sensitive than RTs to the inversion effect, since they can index the time course of covert information processing. Taken together, the results of the present work suggest that face orientation is processed in an automatic mode using the first-order information. After the first 200 ms, the face processing system creates an upright face representation by second-order relational information and is affected by congruency. These conclusions seem to be in line with the pattern of behavioral results obtained in the study of Williams et al. (2004).

As a remark, it is important to determine to what extent the obtained ERP effects are specific to face processing. Future studies should address this issue in a masked priming paradigm by including stimuli other than faces.

4.3. Conclusion

The results indicated a face orientation effect across all the analyzed ERP components, starting around 80 ms, and a congruency/priming effect on late components, starting around 200 ms. The present ERP data suggest that facial identity can be processed unconsciously in the brain to some degree of abstraction. This study has shed light on these processes by revealing at least two disassociable effects that emerge over time. One onsets early (as reflected by P1, N1, P2, N170), implicating rapid perceptual processing. The other occurs later (as reflected by N2 and P3) and may reflect identification and recognition processing. This pattern of results suggests that these late ERP components are generated by brain processes underlying the recognition and semantic analysis of faces, while early components are linked to the perceptual analysis of faces. According to Bruce and Young’s (1986) model of face processing, recognizing individual faces is a sequential process in which an initial stage of structural encoding, prior to face identification, is necessary.

References


