

Electrophysiological neural mechanisms for detection, configural analysis and recognition of faces

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Despite ample explorations the nature of neural mechanisms underlying human expertise in face perception is still undetermined. Here we examined the response of two electrophysiological signals, the N170 ERP and induced gamma-band activity (>20 Hz), to face orientation and familiarity across two blocks, one in which the face identity was task-relevant and one in which it was not. N170 amplitude to inverted faces was higher than to upright faces and was not influenced by face familiarity or its task relevancy. In contrast, induced gamma activity was higher for upright than for inverted faces and for familiar than unfamiliar faces. The effect of face inversion was found in lower gamma frequency band (25–50 Hz), whereas familiarity affected amplitudes in higher gamma frequency band (50–70 Hz). For gamma, the relevance of face identity to the task modulated both inversion and familiarity effects. These findings pinpoint three functionally dissociated neural mechanisms involved in face processing, namely, detection, configural analysis, and recognition.

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Face identification poses a challenge to the visual system since all human faces share a similar spatial arrangement of the eyes, nose and mouth within an oval contour. Given this homogeneous global structure, the evident human expertise in identifying individual faces must involve an intricate visual mechanism that is tuned to analyze the configuration and features of the face in order to individuate faces within their category. Although previous studies identified several temporal and neuroanatomical characteristics of this tuning, the distinction among sub-components of the face processing mechanism is still under debate. Using ERP and neural synchronicity measures we distinguish here among neural

manifestations of (a) initial face categorization, (b) configural analysis of the face, and (c) its recognition.

An established neural correlate of face processing is the lateral–posterior temporal N170 component, which consistently shows greater amplitudes in response to faces than to stimuli from other categories (the “N170-effect”; Bentin et al., 1996; George et al., 2003; Rossion et al., 2000). However, famous and unfamiliar faces elicit identical N170s (Bentin and Deouell, 2000; Eimer, 2000a,b; Schweinberger et al., 2002), suggesting that the mechanism associated with the N170 is not sensitive to face identity. Nevertheless, the N170 peak is delayed and enhanced by inversion (Bentin et al., 1996; Rossion et al., 2000), a manipulation that impairs face identification probably by disrupting configural processing (Yin, 1969). Similarly, the N170 peak is enhanced and delayed by presenting inner face components outside the face contour, regardless of their configuration (Bentin et al., 1996; Itier et al., 2006). Together, the inversion and the features’ isolation effects on the N170 component suggest that the ERP difference between faces and non-face stimuli is induced by the global detection of the face and might be associated with the additional analysis of facial features. Importantly, the neural mechanism eliciting the N170 is probably not directly involved in the computation of configural face metrics or in its semantic identification (Bentin et al., 2006; Sagiv and Bentin, 2003; but see Jacques and Rossion, 2006; Rossion and Gauthier, 2002).

In contrast to the N170, a recent study suggested that configural processes and the activation of face perceptual representations might be reflected in enhanced neural synchronicity, as indexed by the amplitude of EEG activity, particularly in the gamma band (>20 Hz). Induced gamma activity reflects local neural synchronization which is not necessarily phase-locked to the stimulus onset as it may jitter in latency from trial to trial and is evident during an epoch ranging between 200 and 400 ms after stimulus onset (Herrmann et al., 2004; Tallon-Baudry and Bertrand, 1999). In that study, the amplitude of induced gamma activity in a bandwidth between 20 and 50 Hz was larger in response to globally well configured faces than to scrambled faces (Zion-Golumbic and Bentin, 2007). While this finding suggests that the

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faces' global structure may influence EEG activity in the gamma band, it does not provide conclusive evidence for a relationship between gamma activity and configural processes that are presumed to be invoked during the within-category discrimination of faces. This is because a scrambled face does not only prevent configural processing but also distorts the global face shape. In addition, although previous studies established a relationship between induced gamma activity and the activation of pre-existent representations (e.g., Gruber and Müller, 2005), little attempt was made to explore whether the amount of semantic information associated with a pre-existing perceptual representation affects their amplitude. To bridge the gap we manipulated configural processes by face inversion, without destroying the perception of the stimulus as a face, and compared the amplitude of gamma elicited by upright and inverted faces. If gamma activity is associated with the processing of face configuration larger amplitudes would be found in the gamma bandwidth for upright faces, where configural processes could be applied, than in response to inverted faces, in which the computation of the configural metrics is obstructed.

In addition, we manipulated the familiarity of the presented faces and compared gamma activity elicited by famous and unfamiliar faces. On the premise that gamma amplitude is affected by pre-existing memory representations (Klimesch, 1996; Gruber et al., 2001, 2004; Düzel et al., 2005; Guderian and Düzel, 2005) larger gamma amplitudes would be elicited by familiar than unfamiliar faces.

Finally, we explored in this study whether the neural events associated with face processing are automatic or could be modulated by the task demands. Specifically, if within-category face recognition is the default modus operandi of the face perception system, the effect of face familiarity on gamma should be similar regardless of whether familiarity is or is not relevant to the task at hand. To this end participants were presented with two blocks, one in which a famous/non-famous task was administered and a second in which they were asked to monitor for a target (flowers) embedded within the faces.

Methods

Participants

Twenty-four undergraduate students (11 females, 5 left-handed) of the Hebrew University participated in the study. Their age ranged from 19 to 30 ($M=25$), and all reported normal or corrected to normal visual acuity with no history of psychiatric or neurological disorders. They signed an informed consent according to the institutional review board of the Hebrew University and received either course credit or money payment for their participation.

Stimuli

The stimuli consisted of 360 faces, half of them famous, which were selected from various public-accessed websites. The 180 famous pictures were selected, in a pilot study, from a pool of 400 faces in which 90% of the participants ($n=20$) identified them either by name or by supplying specific information about their identity. The pictures did not contain any external cues of the identity of the figure (e.g., throne, national flag in the background). All pictures were converted to a 256 gray-level

format and rescaled proportionally to a size of $5.33^\circ \times 6.84^\circ$ (5.6×7.2 cm).

All the faces, famous and non-famous alike, were also inverted to form in total four stimulus conditions, with 90 stimuli in each condition: upright famous faces, inverted famous faces, upright non-famous faces, and inverted non-famous faces. The famous and non famous faces were equated for luminance and contrast.

Tasks, design and procedure

Participants performed two tasks in separate blocks during the session. In each block 360 faces were presented, equally divided between the different experimental conditions. A face which was presented in upright orientation in one block was presented upside-down in the second block and vice versa.

In one block the task was an oddball target-monitoring in which participants were requested to press a button each time a flower appeared on the screen. Note that the face identity was irrelevant to this task. Forty flowers (half of them inverted) were presented among 360 faces. In the other block the task was face identity relevant. It required categorization between familiar and unfamiliar faces using different buttons for each category. In each block the stimuli were fully randomized with a short (up to a minute) break between blocks for refreshment. Each stimulus was presented for 350 ms with an inter-trial interval of 2000 ms. Every 40 trials a short break was introduced.

The experiment was run in an acoustically treated and electrically isolated booth. Following the mounting of the electrode-cap the participants were seated in a comfortable reclining chair and the monitor was raised at their eyes' level. Half of the participants performed the block of the familiarity categorization task first, while the others received the face identity irrelevant monitoring task as the first block.

EEG recording

The EEG analog signals were recorded continuously by 64 Ag-AgCl pin-type active electrodes mounted on an elastic cap (ECI) according to the extended 10–20 system (American EEG Society Guidelines, 1994), and from two additional electrodes placed at the right and left mastoids, all reference-free. Eye movements as well as blinks were monitored using bipolar horizontal and vertical EOG derivations via two pairs of electrodes, one pair attached to the external canthi, and the other to the infraorbital and supraorbital regions of the right eye. Both EEG and EOG were sampled at 1024 Hz using a Biosemi Active II digital 24-bit amplification system with an active input range of -262 mV to $+262$ mV per bit with a low-pass filter of 258 Hz. The digitized EEG was saved and processed off-line.

Data processing and analysis

Raw data were 1.0 Hz high-pass filtered (24 dB) and referenced to the tip of the nose. Eye movements were corrected using an ICA procedure, and remaining artifacts exceeding ± 100 μ V in amplitude or containing a change of over 100 μ V in a period of 50 ms were rejected. Artifact-free data were then segmented into epochs ranging from -300 ms before to 800 ms after stimulus onset for all conditions.

N170 analysis

ERPs resulted from averaging the segmented trials separately in each condition. The averaged waveforms were smoothed by applying a low-pass filter of 17 Hz (24 dB) and were baseline-corrected by subtracting the mean amplitude during an epoch ranging between -200 and 0 ms before stimulus onset. For each subject the peak of the N170 was determined (based on the filtered waveform) as the most negative peak between 150 and 190 ms. Subsequent visual scrutiny ensured that the most negative values represented real peaks rather than end points of the epoch. Based on previous studies and on scrutiny of the present N170 distribution, the statistical analysis was restricted to posterior lateral regions. The amplitudes and latencies of the N170 at sites P8, PO8, and P10 over the right hemisphere and the homologous sites over the left were averaged within each hemisphere separately to yield the dependent variables for ANOVA. The characteristic scalp distribution of the N170 in each condition was estimated by spherical spline interpolations with 4 levels.

ANOVAs with repeated measures were applied on N170 amplitudes and latencies. The factors were Familiarity (famous, non-famous), Orientation (upright, inverted), and Hemisphere (right, left). To examine the influence of face identity relevance the two blocks were compared adding a fourth factor, Block (face identity relevant/irrelevant task). For factors with more than two levels, P -values were corrected for non-sphericity using the Greenhouse–Geisser correction (for simplicity, the uncorrected degrees of freedom are presented). In the familiarity categorization task correct responses (HIT and CR) were included in the analysis (see Results for details).

Induced gamma-band activity analysis

Wavelet analysis was used in order to obtain the amplitude of induced EEG activity in the gamma band, based on the procedure suggested by Tallon-Baudry et al. (1997). Data were convolved with a complex Gaussian Morlet wavelet: $w(t, f) = A \exp(-t^2/2\sigma_t^2) \exp(2i\pi ft)$ using a constant ratio of $f/\sigma_f = 8$ where $\sigma_f = 1/(2\pi\sigma_t)$ and normalization factor $A = (\sigma, \sqrt{\pi})^{-1/2}$. This procedure was applied to frequencies ranging from 20 Hz to 80 Hz in steps of 0.75 Hz. Induced activity was calculated by applying wavelet analysis to individual trials and averaging the time frequency matrices. The results were baseline-corrected based on the time between -200 and -50 ms before stimulus onset. At each frequency level, the mean activity during the baseline epoch was subtracted from the activity during the entire epoch. Time–frequency plots were created based on the absolute value of the wavelet outcome for each frequency.

Visual inspection of the time–frequency plot of the induced gamma activity averaged across all conditions combined revealed a prominent increase in amplitude peaking at 200 ms. Based on this unbiased average the analysis region of interest (ROI) was chosen as a window of 150 – 250 ms for two frequency bands: 25 – 50 Hz (low gamma) and 50 – 70 Hz (high gamma; see also Zion-Golumbic and Bentin, 2007 for a similar division of ROI). The scalp distribution of the induced gamma-band activity was widely spread. Therefore, our analysis compared left, midline and right clusters at anterior, center and posterior regions (see demarcation of regions in Fig. 4; the gray labeled sites in the figure were included in the statistical analysis). The mean amplitude of the gamma activity within each frequency range was calculated separately for each ROI “box” by averaging the amplitude of the relevant wavelets during the above specified time range.

Statistical significance of the modulation of the amplitudes of induced activity in each gamma frequency range was determined by ANOVA with repeated measures. The factors were Familiarity (famous, non-famous), Orientation (upright, inverted), Anterior–Posterior distribution (anterior, center, posterior), and Laterality (left, medial, right). For assessing the influence of face relevancy an additional factor, Block (face identity relevant/irrelevant task), was added.

For factors with more than two levels, P -values were corrected for non-sphericity using the Greenhouse–Geisser correction (for simplicity, the uncorrected degrees of freedom are presented). Significant main effects and interactions were followed up by subsequent 2-way ANOVAs for each level of the interacting factors or by post hoc Bonferroni-corrected contrasts.

Results

Behavioral findings

Accuracy in the oddball flower monitoring task was at ceiling (99%) as participants did not encounter any difficulties monitoring the appearance of a non-face target. In the familiarity categorization task non-famous faces were categorized correctly as unfamiliar 91% of the time while famous faces were categorized correctly as familiar in 73% of the trials ($F_{1,23} = 54.52$, $P < .001$). Participants performed the familiarity categorization task more accurately when faces were upright (93%) than inverted (72%; $F_{1,23} = 120.40$, $P < .001$). In addition, inversion affected the categorization of famous faces considerably more than of that of the unfamiliar face (91% vs. 57% for upright and inverted famous faces, and 95% vs. 73% for upright and inverted unfamiliar faces; $F_{1,23} = 55.70$, $P < .001$).

Reaction times (RTs) to correct responses were trimmed for latencies higher or lower than 2.5 SD and subjected to Familiarity \times Orientation ANOVA. Mean RTs to familiar faces were longer than to unfamiliar faces (480 and 429 ms, respectively, $F_{1,23} = 10.24$, $P < .005$), and RTs to upright faces were faster than to inverted faces (404 and 504 ms, respectively, $F_{1,23} = 56.08$, $P < .0001$). In addition, an interaction between Inversion and Familiarity was found ($F_{1,23} = 13.54$, $P < .001$); whereas in the upright conditions the decision latencies were similar for familiar and unfamiliar faces (411 and 398 ms respectively, $F_{1,23} < 1$), in the inverted condition responses for familiar faces (550 ms) were slower than unfamiliar faces (460 ms) ($F_{1,23} = 24.52$, $P < .0001$). This finding corroborates the reduced accuracy for inverted familiar faces, probably reflecting the additional processes required to recognize a familiar face when it is inverted. A signal detection analysis further strengthens this hypothesis by demonstrating reduced sensitivity to upright than inverted faces ($d' = 3.17$ and $d' = 1.44$ for upright and inverted faces respectively, $t_{23} = 13.47$, $P < .0001$). Interestingly, however, the reduced accuracy and prolonged RT could be attributed to participants' bias to judge faces as unfamiliar when inverted than when upright ($\beta = .11$ and $\beta = .55$, for upright and inverted faces respectively, $t_{23} = -6.13$, $P < .0001$).

N170 effects

The N170 analysis was performed in two stages. First we examined the effect of face inversion and familiarity in the face familiarity task, including in the analysis only trials yielding correct response, in order to better isolate familiarity effects, if they exist. The mean number of correct responses in each condition was 82,

85, 52, and 66, for the upright familiar, upright unfamiliar, inverted familiar and inverted unfamiliar conditions, respectively. This analysis showed that face inversion enhanced the amplitude of the N170 and delayed its peak latency ($-7.00 \mu\text{V}/164 \text{ ms}$ and $-5.73 \mu\text{V}/159 \text{ ms}$ for inverted and upright faces, respectively; Fig. 1a). In contrast, familiarity did not affect either the N170 amplitude or its latency, neither in the upright nor in the inverted condition. The topographical distribution of the N170 was posterior–temporal, predominantly over right hemisphere sites, and similar for inverted faces and upright faces (Fig. 1b).

These observations were confirmed by three-way ANOVA with repeated measures (Orientation \times Familiarity \times Hemisphere) conducted separately for N170 amplitude and its peak latency. The amplitude analysis yielded a main effect of Orientation resulting from a larger N170 for inverted than upright faces ($F_{1,23}=8.88$, $P<.007$), and a main effect of Hemisphere ($F_{1,23}=14.5$, $P<.001$) resulting from a larger N170 amplitude over the right ($-7.30 \mu\text{V}$) than the left ($-5.40 \mu\text{V}$) hemisphere. The main effect of Familiarity was not significant ($F_{1,23}<1$) and did not interact with other variables. None of the interactions were significant.

The N170 latency analysis showed a main effect of Orientation ($F_{1,23}=6.06$, $P<.022$); the N170 peaked later for inverted than upright faces. A significant interaction between Orientation and Hemisphere ($F_{1,23}=6.00$, $P<.02$) revealed that orientation effect was larger over the left (7 ms) than over the right hemisphere

(4 ms). Indeed, the inter-hemispheric difference in latency was significant when faces were inverted ($F_{1,23}=5.47$, $P<.03$) but not when they were upright ($F_{1,23}<1$).

In a second stage we analyzed the influence of task relevance on face identity effects comparing the N170 latency and amplitude elicited in each condition across blocks. Since in the oddball task all the responses were correct, in these analyses we included all the artifact-free trials in both blocks, regardless of response accuracy in the familiarity categorization task. The four-way ANOVA with repeated measures (Orientation \times Familiarity \times Hemisphere \times Block) conducted separately for N170 amplitude and its peak latency showed that neither the amplitude nor the latency of the N170 was influenced by the task relevance of face identity [i.e., no main effect of Block (-5.75 and $-6.52 \mu\text{V}$ for face-irrelevant task and face-relevant, respectively, $F_{1,23}=1.07$, $P>.31$; 161.30 and 160.52 ms for face-irrelevant and -relevant task, respectively, $F_{1,23}<1$)]. The Block variable did not interact with any of the other variables, and the significant main effects and interactions obtained in these analyses for the other three factors were identical to those reported above.

Induced gamma-band activity

Induced gamma activity was apparent in a time window between 150 and 250 ms post stimulus onset in all conditions.

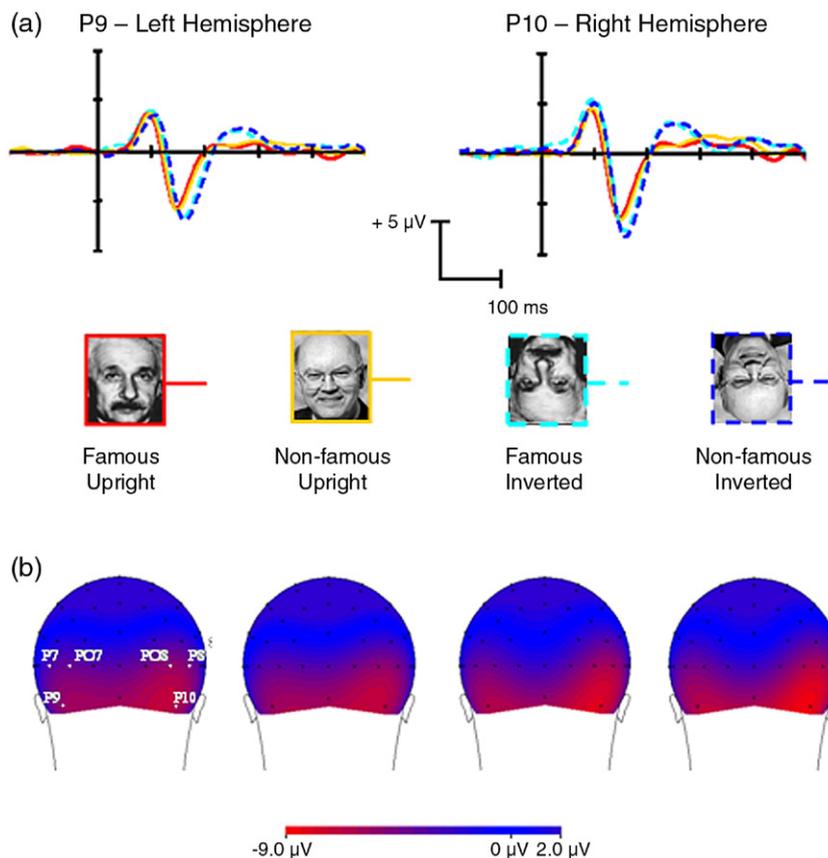


Fig. 1. The modulation of the N170 ERP by face familiarity and orientation at posterior lateral scalp sites. (a) The basic N170 effect showing considerably higher amplitudes for inverted faces than to upright faces. Note that the familiarity of faces has absolutely no effect on either the amplitude of the latency of the ERP elicited. (b) Posterior lateral distribution of the N170; note right hemisphere lateralization for all stimuli and the enhanced amplitude for inverted faces regardless of familiarity.

During this time window two different bands of induced gamma activity were discernible, one in a lower frequency band (25–50 Hz) and one in a higher frequency band (50–70 Hz). These two bands were analyzed separately (Fig. 2).

Low-band-induced gamma activity (25–50 Hz)

The low-band-induced activity between 25 Hz and 50 Hz in the face familiarity task (based on correct responses only) showed lower gamma amplitudes for inverted faces (0.22 μV) than upright faces (0.89 μV ; Figs. 2 and 3). The amplitudes were higher at central and posterior sites than at anterior sites, and higher at midline than lateral sites. Importantly, the familiarity of the faces did not seem to influence lower gamma oscillatory activity.

The above observations were supported by ANOVA (Familiarity \times Orientation \times Laterality \times Anterior–Posterior) that showed a significant effect of Orientation manifested by higher gamma amplitudes for upright than inverted faces ($F_{1,23}=9.93$, $P<.005$). However, the Familiarity effect was not significant in this frequency range ($F_{1,23}<1$). The main effects of Anterior–Posterior as well as Laterality distributions were also significant ($F_{2,22}=8.59$, $P<.002$; $F_{2,22}=6.66$, $P<.005$, respectively). Pair-wise comparisons with Bonferroni corrections performed for the Anterior–Posterior and Laterality variables revealed that the amplitudes were higher at central and posterior sites (0.67 μV and 0.71 μV , respectively) than at anterior sites (0.28 μV ; both P 's $<.01$), and higher at midline (0.66 μV) than at any of the lateral sites (0.49 and 0.51 μV for left

and right clusters, respectively; both P 's $<.05$). No interactions were significant.

Similar to the N170 analysis, relevance of face identity to the task was examined in a separate analysis by comparing the mean low-band gamma amplitude elicited by all artifact-free trials in both blocks. The most interesting finding was a larger face inversion effect in the detection task block than in the familiarity categorization task block. This enhanced difference was exhibited at central and posterior sites but not at anterior sites (Fig. 4, left). This observation was supported by a Block \times Orientation \times Anterior–Posterior three-way interaction ($F_{2,22}=5.37$, $P<.02$). Post hoc analyses performed separately for the three clusters revealed greater differences between upright and inverted faces in the detection task block than in the familiarity categorization task block in central (0.83 μV and 0.31 μV , respectively; $F_{1,23}=3.92$, $P=.055$) and posterior (0.80 μV and 0.21 μV , respectively; $F_{1,23}=3.99$, $P<.05$) sites, but not in anterior sites (0.57 μV and 0.26 μV , respectively; $F_{1,23}=1.74$, $P>.20$). The significant main effects obtained were identical to those reported above, in the familiarity task analysis.

The analysis revealed two additional interactions which were not found when the familiarity task was analyzed separately. An Orientation \times Laterality interaction ($F_{2,22}=5.48$, $P<.02$) indicated that the inversion effect revealed in the lower gamma band is greater at central sites (0.60 μV) than left (0.45 μV , $t_{23}=2.46$, $P<.05$) or right sites (0.45 μV , $t_{23}=3.22$, $P<.004$). In addition, an Anterior–Posterior \times Laterality interaction ($F_{4,20}=3.14$, $P<.05$)

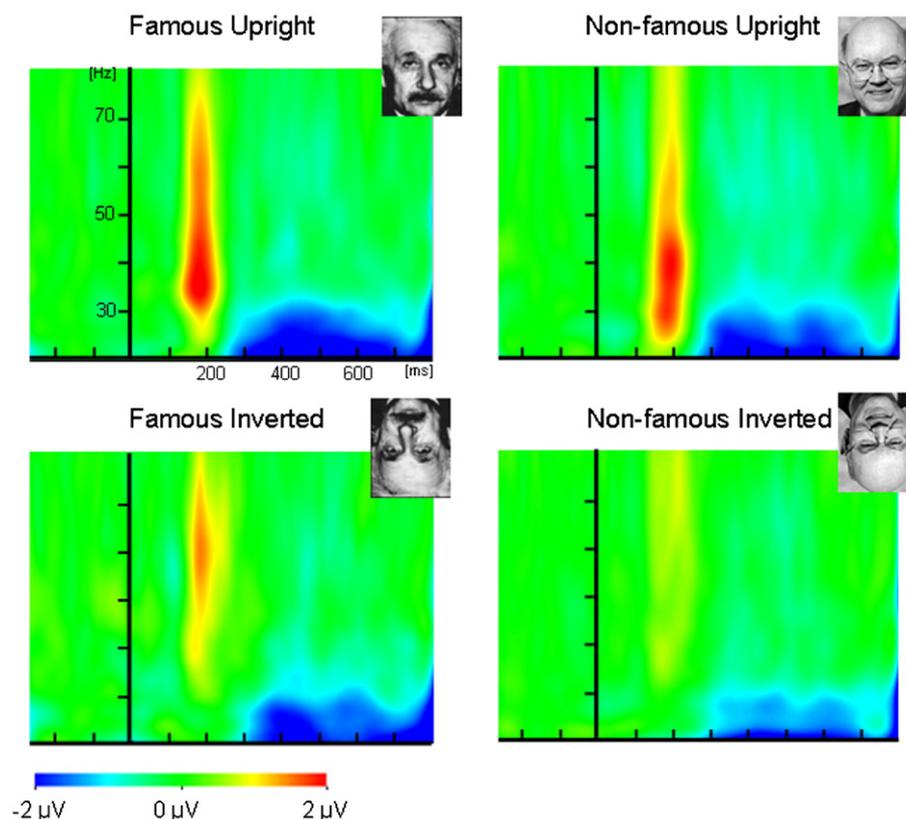


Fig. 2. Time–frequency plots depicting the amplitude of induced gamma-band activity at electrode CPz elicited by famous and non-famous faces presented in upright and inverted orientation. Note the pervasive effect of orientation, expressed by the reduced gamma amplitude for inverted faces regardless of familiarity, in the low frequency band (25–50 Hz). In contrast, an enhancement in induced gamma activity was observed for famous faces relative to non-famous faces in the high frequency band gamma bandwidth (50–70 Hz).

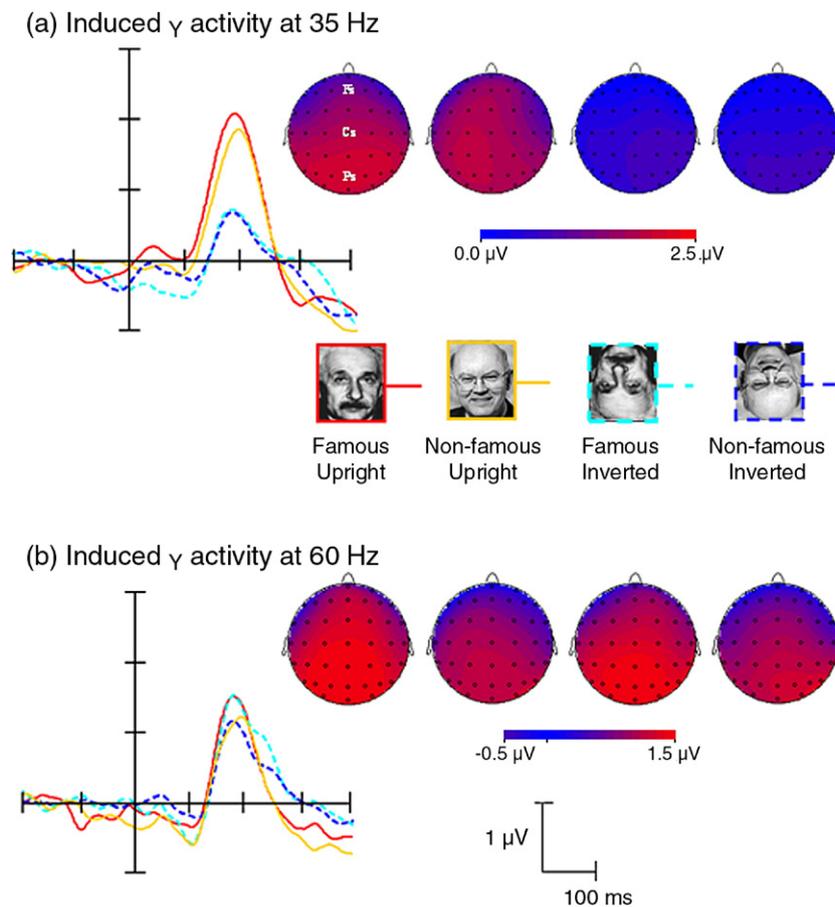


Fig. 3. (a) *Left*. Time course of induced amplitude at 35 Hz recorded from electrode CPz. A significant reduction in amplitude was observed when faces, regardless of familiarity, were inverted, relative to upright faces. *Right*. Distribution of induced activity at 35 Hz measured at the peak of activity (~ 180 from stimulus onset) at electrode CPz. (b) *Left*. Time course of induced amplitude at 60 Hz recorded from electrode CPz. Gamma amplitude was larger for familiar faces relative to unfamiliar faces, especially in anterior sites. *Right*. Distribution of induced activity at 60 Hz measured at the peak of activity (~ 185 from stimulus onset) at electrode CPz.

was found reflecting the fact that, although gamma activity was significantly stronger at medial than lateral sites, this was more pronounced at anterior and central regions than posterior regions.

High-band-induced gamma activity (50–70 Hz)

The pattern of results observed in the higher gamma band was different than the pattern observed in the lower gamma band. In contrast to the robust inversion effect found in the lower band, the orientation of the face did not have a conspicuous effect in the higher gamma range. Conversely, unlike the lower band, in the higher band familiar faces elicited higher gamma amplitudes than unfamiliar faces, regardless of face orientation. The scalp distribution of gamma activity in the higher gamma band was similar, although not identical, to that observed in the lower band (Fig. 3); this activity was more prominent at posterior than central and anterior sites. In addition, the amplitudes were higher over medial and right clusters than over left clusters.

ANOVA corroborated these observations. There was no effect of Orientation in the higher gamma range ($F_{1,23} < 1$). However, familiar faces elicited higher amplitudes than unfamiliar faces, across face orientation ($F_{1,23} = 4.23$, $P < .05$). In addition, the main effects of Anterior–Posterior and Laterality distributions were also significant ($F_{2,22} = 8.32$, $P < .002$, and $F_{2,22} = 7.72$, $P < .003$, respectively). Bonferroni-corrected pair-wise comparisons performed for

the Anterior–Posterior variable showed lower amplitudes at anterior site (0.36μ V) than central sites (0.71μ V), which in turn were lower than posterior sites (0.89μ V; all P 's $< .006$). A similar comparison performed for the Laterality variable revealed that the amplitudes were higher over medial clusters (0.75μ V), than over the left (0.56μ V; $P < .002$), but not right clusters (0.66μ V; $P < .10$).

Face relevancy of the task influenced the high-gamma amplitude differences between familiar and unfamiliar faces but mainly in anterior sites, as revealed by a three-way interaction between Block \times Familiarity \times Anterior–Posterior [$F_{2,22} = 3.81$, $P < .02$; Fig. 4, right]. In additional two-way ANOVAs (Block \times Familiarity) performed separately for anterior, central and posterior sites we found that the familiarity effect was larger in the face-relevant task than in the face-irrelevant task but only in anterior sites (0.15μ V and -0.05μ V difference score for face-relevant and face-irrelevant tasks, respectively; $F_{1,23} = 3.89$, $P = .06$). In contrast, in central and posterior sites the amplitude difference between familiar and unfamiliar faces did not differ between the two tasks (central sites: -0.02μ V and 0.08μ V for face-relevant and face-irrelevant, respectively, [$F_{1,23} < 1$]; posterior sites: 0.06μ V and 0.05μ V for face-relevant and face-irrelevant, respectively, [$F_{1,23} < 1$]). The significant main effects obtained were identical to those reported above in the familiarity task analysis.

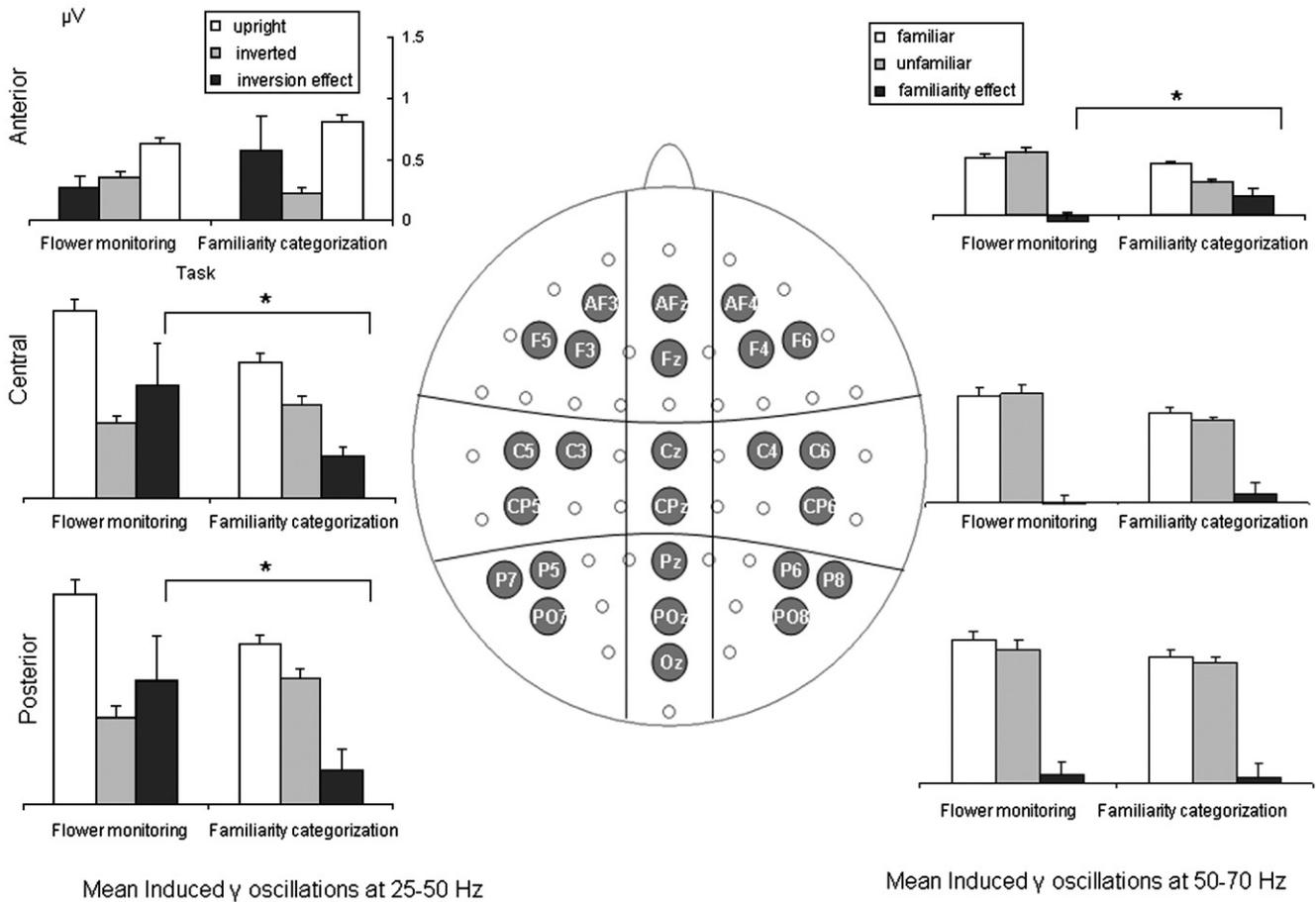


Fig. 4. Mean induced gamma amplitude across all recording sites in anterior, central, and posterior regions (up, middle, and bottom, respectively) for upright/inverted faces (left; lower gamma band [25–50 Hz]) and familiar/unfamiliar faces (right; higher gamma band [50–70 Hz]) in the different tasks (flower monitoring/familiarity categorization). The inversion effect was greater in the monitoring task especially in central and posterior sites ($P < .05$). The familiarity effect was greater in the face categorization task especially in anterior sites ($P < .05$).

The analysis revealed an additional interaction not seen in the familiarity task analysis, an Anterior–Posterior \times Laterality interaction ($F_{4,20} = 3.10, P < .05$). Similar to what was found in the lower band gamma this interaction stemmed from differences in gamma activity at medial rather than lateral sites, which were more conspicuous in anterior and central than posterior regions.

Discussion

The present study examined neural mechanisms involved in the detection, configural analysis, and recognition of faces as reflected by two electrophysiological manifestations, the N170 ERP component, and induced EEG activity in the gamma band (20–70 Hz). Manipulating the orientation and the familiarity of faces, we found dissociations between different forms of neural activity suggesting that different neural mechanisms account for each type of process. The amplitude of the N170 was higher to inverted faces than upright faces and was not influenced by face familiarity. Moreover, the N170 amplitude was not affected by the relevance of the face identity to the task. In contrast, induced gamma-band activity was influenced by both orientation and familiarity, but in different frequency bands. The gamma amplitudes between 25 and 50 Hz were higher for upright than inverted faces, regardless of

familiarity. Familiar faces elicited higher gamma amplitudes than unfamiliar faces in the 50–70 Hz band, regardless of orientation. In addition, unlike the N170, gamma amplitudes were influenced by the relevance of face identity to the task. Face inversion had a bigger effect in the lower band when face identity was not task-relevant, while familiarity had a bigger effect in the higher band when faces were categorized by familiarity.

The absence of familiarity effects on the N170 is consistent with the idea that this component is associated with a face detection mechanism (Bentin et al., 1996, 2006; Sagiv and Bentin, 2003). According to this view the detection of a face in the visual field triggers by default additional processes required for within-category discrimination and recognition of the face. These processes might include additional analyses of the face features as well as their spatial metric relations. Coupled with the previous data we suggest that the N170 amplitude might reflect the analysis of features following (or as part of) face detection (Bentin et al., 2006; Zion-Golumbic and Bentin, 2007). In contrast, the modulations of gamma amplitude in the present study suggest that this activity reflects a mechanism of configural encoding (manifested by lower gamma-band activity) and accessing previously acquired knowledge associated with the face (in the higher gamma band).

The dissociation between the N170 and gamma effects implied by these results replicates a previous report from our laboratory (Zion-Golombic and Bentin, 2007). However, the current time range of the gamma effect is earlier than that observed previously (as well as the time range usually found for gamma effects in the literature, see below). Note though, that while earlier than usual, there is no complete overlap between the time course of the N170 effect (peaking around 160 ms) and that of the gamma activity (150–250 ms with a peak at around 180 ms). Nevertheless, the earlier than usual time course of the gamma effects in this study is noteworthy. Although the timing of induced gamma activity is not phase-locked with the stimulus and any conclusion based on this time should be considered with care, this difference merits additional investigations.

Induced gamma activity reflects local neural synchronization which is not necessarily phase-locked to the stimulus onset and is most conspicuous during an epoch ranging between 200 and 400 ms after stimulus onset (Herrmann et al., 2004; Tallon-Baudry and Bertrand, 1999). Specifically, it has been suggested that this activity might be associated with a neural mechanism involved in forming and/or activating coherent perceptual representations (e.g., Busch et al., 2006). Supporting this view, meaningful objects were found to elicit higher induced gamma activity than meaningless stimuli (Tallon-Baudry et al., 1997; Gruber and Müller, 2005). The gamma band modulated by meaningfulness in these studies was similar to the lower band in which we found the face inversion effect in the present study. Other studies have shown that gamma activity is associated with memory mechanisms and reflects the matching process performed between memory contents and the perceived stimulus (e.g., Gruber and Müller, 2006). Importantly, the gamma band affected by memory retrieval in the above Gruber and Müller study was high, corresponding to the higher band modulated by face familiarity in the present study (see also Vidal et al., 2006 for additional fractionation coupled with functional dissociations within the gamma bandwidth).

Although induced gamma activity in the lower band has been observed in response to a wide variety of visual stimuli, a handful of studies have investigated its possible involvement in face perception. For example, upright “Mooney” faces (which are black-and-white photographs of faces taken in a dark-contrasted environment) elicited a higher induced gamma response than inverted “Mooney” stimuli (Rodríguez et al., 1999; see also Keil et al., 1999 for a manipulation of orientation with schematic faces). Yet, since inverted Mooney faces are meaningless objects it is impossible to conclude whether the higher gamma activity exhibited for upright Mooney stimuli reflected sensitivity to the global shape of the face, to featural aspects of the face, or to configural relations which allow individuation. In fact, the Mooney-face inversion effect could be just another demonstration of the meaningful/meaningless distinction. Based on the well established literature linking the face inversion effect to the disruption of configural processing (Freire et al., 2000; Maurer et al., 2002) we suggest that the inversion effect on lower band-induced gamma activity in the present study is associated with the configural computations performed during the structural encoding of the face. Specifically, we suggest that when the face is inverted configural computations are less likely to be attempted. This conclusion is further supported by the reduced inversion effect in the familiarity categorization task (where configural computations, albeit difficult, are nevertheless attempted in order to recognize the face), as well as by findings showing no face

inversion effects on gamma in autistic individuals in whom configural processing abilities are impaired (Grice et al., 2001). This argumentation also suggests that the amplitude of induced gamma activity is not related to the difficulty of applying configural computation during face processing but it is a marker of the extent of utilizing these computations.

One could argue that inverted faces are less familiar than upright faces, hence to assume that the face inversion effect on gamma in the present study, like for Mooney faces, actually reflects a distinction between meaningful and meaningless stimuli. Although this account cannot be completely rejected by the present data there are at least three reasons that speak against it. The first is that in a previous study we found that normally configured faces and face components outside the face contour elicited similar gamma amplitudes in the lower gamma band (Zion-Golombic and Bentin, 2007). Clearly full faces are more familiar stimuli than components outside the face, even if the configuration of the latter is normal. The second reason is that familiarity effects were found in the present study at a higher band than the face inversion effects were found. Thus, there is clear frequency dissociation between the inversion and the familiarity effects affecting gamma in the present study. The final reason is that studies showed that observers are able to detect inverted faces almost as fast as upright faces (Rousselet et al., 2003). If inverted faces are unfamiliar they should have been detected as faces slower than upright faces. Together these arguments support the view that the impact of face inversion on lower band gamma amplitude reflects the modulation of a different process than retrieval of long-term representations.

The larger induced gamma amplitudes in the high-frequency band (50–70 Hz) found for familiar compared to unfamiliar faces may be associated with the retrieval of face familiarity information from the semantic system. This view is supported by other studies showing that retrieval of information from memory modulates induced gamma activity in the higher frequency band (Gruber et al., 2004; Osipova et al., 2006). However, the previous studies exploring the role of induced gamma activity in memory encoding and retrieval have focused primarily on short-term, episodic-based memory for items studied during the experimental session. The current study is the first to probe the involvement of gamma activity in retrieval of detailed within-category face-related information from long-term semantic memory. Although the task did not require explicit identification, familiarity decisions must also be based on previous knowledge stored in long-term semantic and/or perceptual memory. In addition, if indeed the high-band gamma activity reflects the activation of face information at the subordinate level, it indicates that neural processes involved in face identification are much earlier than has been thought before. The previously conceived time course for face identification was influenced by the absence of a face identity effect on the N170. Indeed, to our knowledge, the current results are the first direct evidence that face identity could influence face processing during the first 250 ms from stimulus onset (cf. Tanaka et al., 2006).

Interestingly the time range of the higher band gamma modulations, which presumably reflect the process of associating perceptual input with previous knowledge, were not delayed relative to the time range of the lower band gamma modulation, presumably reflecting the structural encoding and face individuation. This time course suggests that these two processes occur in parallel during face processing. Albeit post hoc, this conceptualization is compatible with previous behavioral data suggesting that

for faces, the subordinate individuation processes are default and as fast as base-level categorization (Tanaka, 2001).

It is noteworthy that the RTs in the familiarity decision task were more than 100 ms later than the end of the relevant gamma activity, and, indeed, later for inverted than upright faces. This is conceivable because the RTs are probably influenced by decision-related aspects of the process, decisions that are actually based on the output of the structural encoding and the availability of previous knowledge about faces, reflected by gamma in both the lower and the higher band. Note that in addition to an overall increase in RTs for inverted faces, we also found an interaction showing that the RTs were similar for familiar and unfamiliar faces in the upright condition, while longer for correctly recognized inverted familiar faces than for correctly rejected inverted unfamiliar faces. Whereas the main effect of inversion on RTs could reflect decision uncertainty when the structural encoding system provides insufficient information, the longer RTs to familiar than unfamiliar inverted faces also reflect a bias for unfamiliar decisions induced by inversion.

Finally, the induced gamma activity but not the N170 was influenced by relevancy of the face identity to the task. This pattern suggests that induced gamma activity is more sensitive to strategic decisions during task performance while the N170 reflects a more rigid, automatic process (Carmel and Bentin, 2002; Eimer, 2000b).

In the lower gamma band the amplitude difference between upright and inverted faces was smaller in the familiarity categorization task than in the detection task. As suggested above, the attenuation of the inversion effect in the familiarity categorization task might be accounted for by the intentional attempts to identify inverted faces when identity was task-relevant. This strategy could have initiated attempts of configural computations even when the face was inverted, a process that might have not been attempted when identity was irrelevant. Some support for this suggestion is provided by the posterior distribution of task influence on the inversion effect, which fits the assumption that the task influenced perceptual processing.

In the higher frequency band the difference between the induced gamma activity elicited by famous and non-famous faces was larger when face identity was task-relevant. This effect could be associated with the nature of the familiarity categorization task, which, in the present study could only be based on the ability to retrieve previously stored knowledge for famous but not for unfamiliar faces. It is possible that the larger effect of familiarity on higher band gamma amplitude when familiarity was task-relevant reflects the successful retrieval of semantic information linked to famous faces and the failure of retrieval for non-famous faces. The above hypothesis is tentative, but also fits the more anterior distribution of these effects.

In summary, the present study points to the existence of three functionally dissociated neural mechanisms involved in different aspects of face processing in humans. The N170 ERP component is an early marker which indexes the initial detection of a face in the visual field and possibly additional subordinate categorization processes triggered by this detection. Note that the current study demonstrates, again, that these processes are immune to attentional or strategic manipulations. Induced gamma activity, on the other hand, reflects higher level perceptual processes such as forming the specific perceptual representation of the face as well as the retrieval of face familiarity information relevant to it. These latter neural processes are modulated by attention and distinguished from each other by different frequency bands.

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