

The time course of the inversion effect during individual face discrimination

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Human faces look more similar to each other when they are presented upside down, leading to an increase in error rate and response time during individual face discrimination tasks. This face inversion effect (FIE) is one of the most robust findings in the face processing literature. Recent neuroimaging studies using adaptation to face identity have shown that the “fusiform face area” was the primary neural source of the behavioral FIE. However, the time course of the FIE, that is, when inversion affects the coding of facial identity in the human brain, remains unclear. Here, we addressed this question by recording event-related potentials (ERPs) on the scalp during an adaptation paradigm with upright and inverted faces. Subjects were presented first with an adapting face stimulus for 3,000 ms, followed by a second face of either the same identity or a different identity. Starting at about 160 ms after stimulus onset, the ERP response to the second face stimulus was markedly reduced over occipitotemporal electrode sites when it was identical to the adapting face, during the N170 time window. When the exact same stimuli were presented upside down, the reduction of signal was smaller and took place about 30 ms later, in line with the behavioral effect of inversion. This result shows that face inversion affects the early encoding of face identity in the occipitotemporal cortex at about 160 ms. Because inversion is known to disrupt massively the integration of facial features, these observations provide indirect evidence that individual faces are processed holistically as early as 160 ms after stimulus onset.

Keywords: EEG, ERP, face processing, inversion effect, N170, adaptation

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Introduction

The adult human brain is expert at making fine discriminations between individual faces, whether they are unknown or highly familiar. This ability is thought to rely on a network of occipitotemporal brain areas, predominantly in the right hemisphere (e.g., Haxby, Hoffman, & Gobbini, 2000). However, when pictures of faces are presented upside down, their discrimination at the individual level is dramatically impaired (e.g., Freire, Lee, & Symons, 2000; Yin, 1969), in particular when compared with the same transformation applied to other visual object categories (e.g., Carbon & Leder, 2006; Yin, 1969). The face inversion effect (FIE) is one of the most robust findings in the face literature. There is strong evidence that inverting faces impairs the integration of features into a gestalt, or a so-called holistic face representation (Sergent, 1984; Tanaka & Farah, 1993;

Young, Hellawell, & Hay, 1987). Moreover, most studies show that the perception of the relative position of facial features within the face stimulus is more affected by inversion than the perception of local modifications applied to the facial features (e.g., Barton, Keenan, & Bass, 2001; Freire et al., 2000; Goffaux & Rossion, *in press*; Rhodes, Brake, & Atkinson, 1993).

A number of electrophysiological and neuroimaging studies have been devoted to understand the neurofunctional mechanisms underlying this phenomenon (see Rossion & Gauthier, 2002, for a review, and recent discussions in Mazard, Schiltz, & Rossion, 2006; Yovel & Kanwisher, 2005). However, the time course of the FIE (i.e., the reduced ability to discriminate between inverted faces) in humans is still unclear: At what level of processing are representations of individual faces extracted from the incoming visual stimulus, and when is this process affected by inversion? Behavioral studies have suggested that the impairment in facial identity

coding due to inversion takes place at a perceptual level because it can be observed during simultaneous presentation of unfamiliar faces (e.g., Farah, Wilson, Drain, & Tanaka, 1998) and is unaffected by the length of the interstimulus interval in delayed matching tasks (Freire et al., 2000). Supporting this view, two recent functional magnetic resonance imaging (fMRI) studies using adaptation to facial identity (see, e.g., Gauthier et al., 2000; Grill-Spector, Henson, & Martin, 2006) reported an interaction between the magnitude of the fMRI adaptation for repeated face stimuli and the orientation of the face in face-sensitive areas of the occipitotemporal cortex (Mazard et al., 2006; Yovel & Kanwisher, 2005).

However, given the poor temporal resolution of fMRI measures, particularly with respect to the speed at which visual processes take place (e.g., Thorpe, Fize, & Marlot, 1996), the time course with which inversion affects the coding of facial identity remains unclear. Here, we addressed this question by recording scalp event-related potentials (ERPs) with a millisecond resolution during an identity adaptation paradigm with upright and inverted faces. In each trial, two faces—either both upright or both inverted—were presented successively and were either of the same or of a different identity. The paradigm was inspired by behavioral face adaptation experiments (e.g., Leopold, Rhodes, Muller, & Jeffery, 2005; Webster, Kaping, Mizokami, & Duhamel, 2004) and a recent ERP study (Kovacs et al., 2006) in which the first stimulus is presented for several seconds, acting as an adaptor, followed almost immediately by the second stimulus for a brief duration. Subjects performed a *same/different* matching task on each pair of faces while the ERP response to the second face of the pair was measured.

We defined the onset of the effect of inversion on the processing of facial identity as the earliest time point at which an ERP adaptation effect would be observed for upright but not for inverted faces.

Methods

Subjects

Twenty-one paid volunteers (13 women, 2 left handed, mean $\pm$ SD age = 22.3 $\pm$ 3.4 years) participated in this experiment. All subjects had normal or corrected-to-normal vision.

Stimuli

Thirty different face identities (15 men) were used, with 2 slightly different front views of the same person (thus, 60 face pictures in total). All faces were cropped to remove external features and were equated for mean

luminance. They subtended approximately $2.8 \times 3.7^\circ$ of visual angle.

Procedure

Stimuli were displayed against a light gray background at 100-cm viewing distance. In each trial, two faces were presented sequentially, either both upright or both upside down. A trial started with a fixation point displayed at the center of the screen for 200 ms (Figure 1). Two hundred milliseconds after the offset of the fixation point, a first face (adapting stimulus) appeared for about 3,000 ms (2,800 to 3,200 ms), followed by an interval of random duration (100 to 300 ms), and then the second face for 200 ms. The offset of the second face was followed by an intertrial interval of approximately 1,400 ms (1,300 to 1,500 ms). In half of the trials, the second face stimulus was of the same identity as the first face. To minimize ERP effects due to adaptation to low-level visual features, the second face stimulus was 5% larger than the first stimulus. When the two faces were of the same identity, two slightly different front-view pictures of the same person were used. In trials in which the faces were different, two faces of the same gender were presented. The same pairs of faces were presented in the upright and inverted orientations, and each face appeared equally often in the *same* and *different* conditions. Subjects performed a speeded identity matching task between the first and second faces of each trial and gave their response by pressing one of two keys with their right hand. There were 105 trials per condition, and the order of the conditions was randomized within each block.

EEG recording and analyses

Scalp EEG was recorded from 58 tin electrodes mounted in an electrode cap (Quik-cap, Neuroscan Inc.), with a left earlobe reference, and electrode impedances kept below 10 k Ω . EEG analog signal was digitized at a 1,000-Hz sampling rate, and a digital anti-aliasing filter of $0.27 \times$ sampling rate was applied at recording (at 1,000 Hz sampling rate, the usable bandwidth is 0 to approximately 270 Hz).

EEG data were analyzed using EEprobe 3.2 (ANT, Inc.). After filtering of the EEG with a digital 30-Hz low-pass

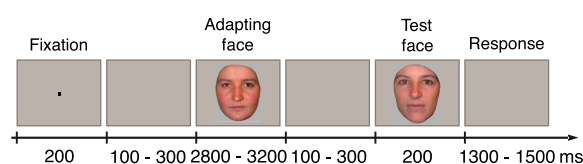


Figure 1. Time line of the stimulus sequence.

filter, time windows in which the standard deviation of the EEG on any electrode within a sliding 200-ms time window exceeded $35 \mu\text{V}$ were marked as either EEG artifacts or blink artifacts. Blink artifacts were corrected by subtraction of a vertical electrooculogram (EOG) propagation factors based on EOG components derived from principal component analyses. Incorrect trials and trials containing EEG artifacts were rejected, and the number of trials was equated between conditions. Subjects' averages were baseline corrected using the 100-ms prestimulus epoch and then re-referenced to a common average reference.

ERP amplitude analyses were performed on the visual components P1 (maximal at approximately 115 ms) and the face-sensitive N170 (maximal at approximately 170 ms; Bentin, McCarthy, Perez, Puce, & Allison, 1996; Botzel, Schulze, & Stodieck, 1995) elicited by the second face of the trial sequence (test face). Amplitude values of the P1 and the N170 were measured at five pairs of occipito-temporal electrodes in the left and right hemisphere where both components were the most prominent. Amplitudes were quantified for each condition as the mean voltage measured within 30-ms windows centered on the grand average peak latencies of the components' maximum. The amplitude values of each component were then submitted to separate repeated measures analyses of variance (ANOVA) with the factors orientation (upright vs. inverted), adaptation (same face vs. different faces), hemisphere (right vs. left), and electrode (five levels). The mean amplitude of the N250r (Figure 3), which has been found to index face identity repetition effects consistently (e.g., Schweinberger, Huddy, & Burton, 2004), was also measured in the interval from 260 to 320 ms after stimulus onset. Greenhouse-Geisser adjustments to the degrees of freedom were used when appropriate, and polynomial contrasts were performed for post hoc comparisons.

To characterize precisely the timing of the identity adaptation effect on ERPs, we compared the waveforms obtained in the *same* versus *different* conditions at each time point (from -100 to 400 ms)—separately for the upright and inverted orientations (Figures 3 and 4). The significance of the difference between *same* and *different* trials was assessed using a permutation test based on the method from Blair and Karniski (1993). Specifically, at each time point, the data from all subjects in the two conditions (*same* vs. *different*) were pooled and then randomly assigned to one of two bins of equal sizes as the original conditions (i.e., sampling without replacement). Because resampling in this way shuffles the assignment of conditions, the difference between the means of the two bins reflects the difference between conditions under the null hypothesis (i.e., that no difference exists between the ERP waveforms). This was repeated 3,000 times to create a distribution of “artificial” differences that can be used to estimate the probability that the observed difference between ERPs in the two conditions is due to chance (i.e., a p value).

Moreover, the time course of the interaction between face orientation and identity adaptation effects was characterized by subtracting the waveforms obtained in the *same* from those obtained in the *different* condition, separately for upright and inverted conditions (upright [different – same] vs. inverted [different – same]; see Figure 3). Permutation tests were performed to compare each time sample of the resulting waveforms (Figure 4).

Results

Behavior

Error rates and response times at the identity matching task were submitted to repeated measures ANOVAs with the factors Orientation (upright vs. inverted) and Adaptation (same vs. different identities).

Error rates

Subjects performed better with upright (96.5%) than inverted (91.6%) faces, $F(1, 20) = 35.79$, $p < .00001$ (Figure 2). The main effect of adaptation, $F(1, 20) = 0.03$, $p = .9$, and the Orientation $\times$ Adaptation interaction were not significant, $F(1, 20) = 3.54$, $p = .075$.

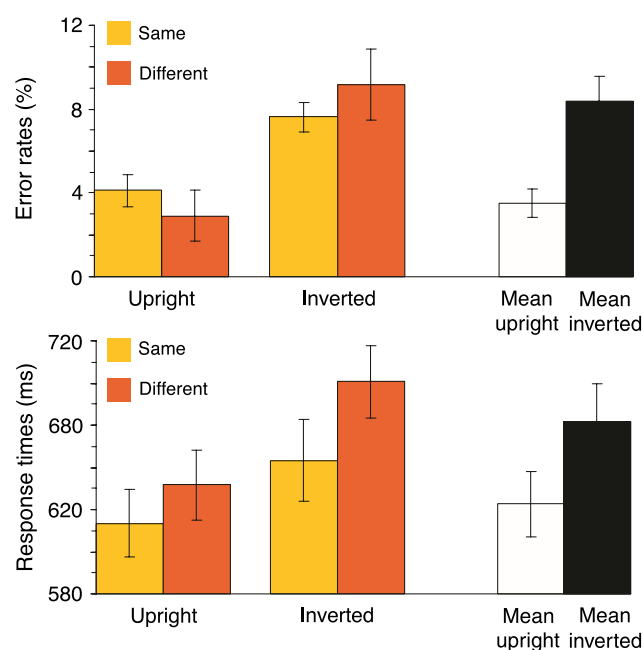


Figure 2. Behavioral results. Error rates and response times ($\pm$ standard error) separately for *same* and *different* conditions. Rightmost histograms show the behavioral results for upright and inverted conditions averaged across *same* and *different* trials.

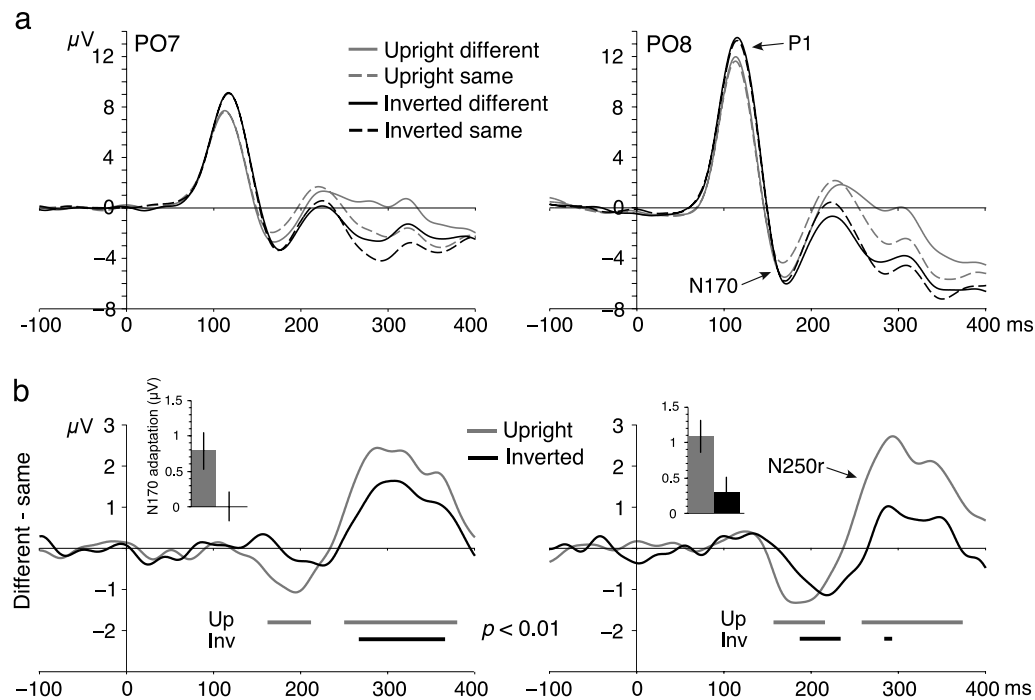


Figure 3. Grand average ERP waveforms elicited by the second face of the trial sequence (test face) at two occipitotemporal electrodes (PO7, left hemisphere; PO8, right hemisphere). (a) ERPs are shown as a function of orientation (upright vs. inverted) and adaptation (same vs. different). (b) Subtraction ERP waveforms (ERPs elicited in the *different* condition minus ERPs elicited in the *same* condition) separately for upright and inverted faces for PO7/8 electrodes. Histograms in the insets represent the amount of adaptation (amplitude in *same* minus *different* conditions) at the N170 level for upright (gray) and inverted (black) orientations. Below the waveforms, results of the permutation tests for the two occipitotemporal electrodes are depicted (PO7/8). Significant differences ($p < .01$) between waveforms recorded in the *same* versus *different* conditions are indicated as horizontal gray bars for upright faces (Up) and as black bars for inverted faces (Inv). The figure shows P1, N170, and N250r ERP components. Note that N250r appears here as a positive component because it was computed by subtracting *same* from *different* conditions.

Response times

There was a significant inversion effect for correct response times, $F(1, 20) = 38.81$, $p < .00001$ (623 and 662 ms for upright and inverted faces, respectively), and an effect of adaptation, $F(1, 20) = 10.13$, $p < .005$ (Figure 2), with subjects being slower for *different* (656 ms) than for *same* (628 ms) trials. A significant Orientation $\times$ Adaptation interaction, $F(1, 20) = 6.9$, $p < .02$, revealed that subjects were slower for *different* compared with *same* trials in the inverted orientation only (37 ms slower for *different* trial; $p < .001$). In the upright orientation, the response time difference between *same* and *different* trials (18 ms) was only close to significance ($p = .063$).

Electrophysiology

P1 amplitude

The P1 was larger in the inverted compared with the upright face orientation (Figure 3), $F(1, 20) = 59.34$, $p < .00001$. The significant Orientation $\times$ Electrode interaction, $F(2.6, 52.7) = 18.38$, $p < .00001$, further

qualified by an Orientation $\times$ Electrode $\times$ Hemisphere interaction, $F(2.6, 53.4) = 3.91$, $p < .02$, indicate that the orientation effect was larger on posterior electrodes (PO7/8, PO5/6, and O1/2; all p 's $< .0001$) compared with more anterior electrodes (P7/8 and P5/6; all p 's $< .005$) and that this was especially true in the right hemisphere. There was no effect of Adaptation, $F(1, 20) = 0.75$, $p = .34$, and, importantly, no Orientation $\times$ Adaptation interaction, $F(1, 20) = 0.104$, $p = .75$, at the level of P1.

N170 amplitude

The amplitude of the N170 was larger for inverted than for upright faces, $F(1, 20) = 9.72$, $p = .0054$, and for *different* than for *same* faces, $F(1, 20) = 12.93$, $p = .0018$. The effect of identity adaptation was slightly larger on lower electrodes (P7/8, PO7/8, and O1/2) than on occipitoparietal electrodes (P5/6 and PO5/6), $F(2.9, 59.3) = 3.9$, $p = .014$ (Figure 5). Most importantly, there was a significant interaction between Orientation and Adaptation, $F(1, 20) = 9.67$, $p = .0055$, due to a larger N170 in response to *different* than to *same* faces in the

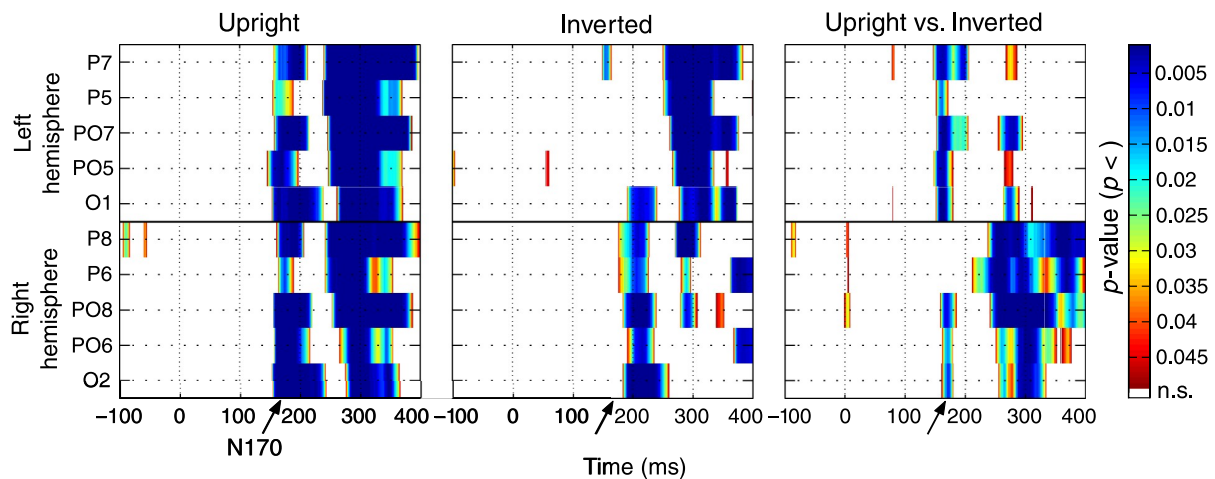


Figure 4. Time course of the inversion effect on facial identity processing. The plots depict permutation tests comparing *same* to *different* conditions for the upright orientation (left column) and for the inverted orientation (middle). Rightmost column shows the time course of the significant interactions between identity adaptation and orientation. Analyses were performed on each time sample for 10 occipitotemporal electrodes and significant differences are plotted in color as a function of the p value. The arrow below each plot indicates the latency of the N170 peak.

upright orientation ($p = .00016$), but not in the inverted orientation ($p = .37$; Figures 3 and 5). A significant Orientation $\times$ Adaptation $\times$ Electrode interaction, $F(2, 40.7) = 3.48$, $p < .039$, indicated that the Orientation $\times$ Adaptation interaction was significant at all electrodes (all p 's $< .011$), except at P5/6, where there was only a nonsignificant trend ($p = .056$). Further analyses revealed that the interaction was significant at P5 ($p < .05$) but not at P6 ($p = .82$). Moreover, the adaptation effect was significant on all electrodes in the upright orientation and nonsignificant on all electrodes in the inverted orientation (all p 's $> .27$). Finally, the N170 was larger in the right hemisphere, $F(1, 20) = 6.43$, $p = .02$.

In short, the most compelling observation was the reduced N170 amplitude in *same* compared with *different* trials for upright faces only, not for inverted faces.

N250r amplitude

The N250r component was measured on the waveforms obtained by subtracting ERP waveform obtained in the *same* condition to the ERP obtained in the *different* condition. The amplitude of the N250r was submitted to a repeated measures ANOVA with factors orientation, hemisphere, and electrode. The N250r measured in the upright orientation was much larger than that measured in

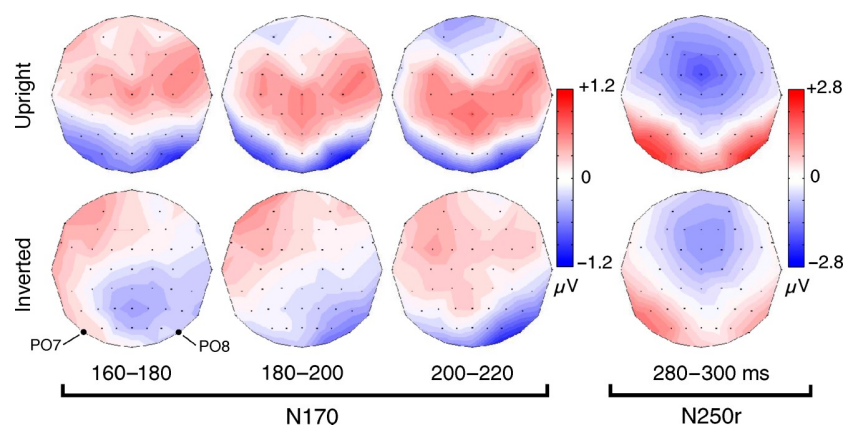


Figure 5. Topographical maps of the adaptation effect in the N170 and N250r time windows. The maps represent the scalp distribution of the difference between *different* and *same* conditions separately for upright and inverted face orientations. The view is from above the scalp with frontal sites at the top and posterior sites at the bottom.

the inverted orientation, $F(1, 20) = 16.18$, $p < .001$ (Figures 3 and 5). Although the amplitude difference between upright and inverted faces tended to be larger in the right hemisphere than in the left hemisphere, the Orientation $\times$ Hemisphere interaction was not significant, $F(1, 20) = 2.06$, $p = .17$.

Time course of the inversion effect on facial identity processing

Permutation tests performed on each time point of the ERP waveforms allowed us to characterize the time course of the identity adaptation effect independently for upright and inverted faces. Results from these analyses are depicted in Figure 4. For upright faces, ERP waveforms in *same* and *different* conditions started to differ significantly ($p < .01$; two-tailed test) at around 160 ms, both in the left and right hemispheres (Figures 3 and 4, leftmost column). Critically, in the inverted orientation, the difference waves between *same* and *different* conditions attained significance ($p < .01$) at a later (approximately 30 ms) time point than in the upright orientation (190–195 ms; Figures 3 and 4, middle column). The latency difference in the onset of a significant adaptation effect can be visualized in Figure 3 for electrodes PO7 and PO8. A second significant difference between *same* and *different* conditions corresponded to the occurrence of the N250r. For upright faces, the N250r started at 245 and 250 ms in the left and right hemispheres, respectively. Again, there was a delay of about 20 to 30 ms in the onset time of the N250r for the inverted orientation (265 and 280 ms for the left and right hemispheres, respectively).

We also used point-by-point permutation tests to characterize the time course of the interaction between identity adaptation and face orientation. As shown in Figure 4 (rightmost column), the first significant interaction between adaptation and face orientation started at a similar latency as the adaptation effect for upright faces (approximately 160 ms). A second significant interaction started at about 230 ms, slightly before the occurrence of the N250r (difference between *same* and *different* trials) in the upright orientation.

Discussion

Presenting faces upside down in an individual face matching task led to an increase in error rates and response times with respect to the upright condition, replicating numerous behavioral studies (e.g., Freire et al., 2000; Yin, 1969; see Rossion & Gauthier, 2002, for a review). Here, we identified the time point at which this effect takes place in the human brain: For upright faces, the ERP response to a repeated compared with an

unrepeated face identity was reduced starting in the N170 time window (at approximately 160 ms), whereas for inverted faces, this adaptation effect occurred with a delay of about 30 ms. A second ERP adaptation effect (N250r) started at around 250 ms for upright faces. Again, it was smaller and with a delay of 30 ms for inverted faces.

These observations show that information about facial identity is available at about 160 ms after stimulus onset in the N170 time window, in line with the temporal dynamics of neuronal responses involved in face identification in the monkey's inferior-temporal cortex (e.g., Tovee & Rolls, 1995). It is also in keeping with the recent evidence that individual faces presented alternatively in a pattern-reversal paradigm yield an ERP component over occipitotemporal scalp regions peaking at about the same latency (Jacques & Rossion, 2006). Most importantly, the present data show that when faces are presented upside down, the effects of adaptation to identity, both at the N170 and N250r levels, are strongly delayed (about 30 ms) and reduced, mirroring behavioral output taking place almost half a second later. This occurred despite the fact that the very same stimulus pairs were presented in both orientations, suggesting that the neurons that participate in generating the N170 respond, at least partly, to the perceived difference rather than to the actual physical difference. Given that the N170 represents an early stage of face visual processing originating from multiple areas in the inferior occipital and temporal cortices (e.g., Henson et al., 2003; Herrmann, Ehlis, Muehlberger, & Fallgatter, 2005), these findings indicate that the behavioral impairment in discriminating individual inverted faces takes place during the early perceptual coding of faces in the occipitotemporal cortex. To our knowledge, this is the first evidence that the origin of the substantial decrease in performance and the increase in response times in discriminating individual inverted faces takes place during the early activation of face processes in the human brain. As such, our data complement the observations of two recent fMRI-adaptation studies in which the "fusiform face area" (FFA; Kanwisher, McDermott, & Chun, 1997) in both hemispheres showed stronger identity adaptation to upright than inverted faces (Mazard et al., 2006; Yovel & Kanwisher, 2005), but without any precise information about the time course of these effects.

The finding of an early (approximately 160 ms) interaction between adaptation and orientation cannot be accounted for by low-level visual features because low-level information (luminance, contrast, size, and spatial frequency power spectrum) is equal between upright and inverted faces. In addition, the adaptation effects in the same-identity condition were obtained by using different pictures presented at different sizes. In this paradigm, subjects could anticipate the orientation of the target face based on the orientation of the adapting stimulus. However, the N170 adaptation effect cannot be explained by a higher attention level to either one of the face orientation because this effect arises in interaction with

the identity of the target stimulus (same or different), which was unpredictable.

Independently of adaptation effects, the P1 and the N170 were larger to inverted faces (Figure 3), replicating the findings of a number of ERP and magnetoencephalographic studies comparing upright and inverted face stimuli in single mode presentation, especially for the N170 (e.g., Itier & Taylor, 2002; Rossion et al., 2000; Rousselet, Mace, & Fabre-Thorpe, 2004; Sagiv & Bentin, 2001). The factors contributing to the larger P1 and N170 to inverted faces are currently unclear. They are inconsistent with the small decreases in signal to inverted faces that are observed in fMRI studies ("fusiform face area"; see Rossion & Gauthier, 2002), single-cell recordings in the monkey brain (Perrett et al., 1988), and intracranial recordings of field potentials in humans (McCarthy, Puce, Belger, & Allison, 1999). P1 effects in previous studies (e.g., Itier & Taylor, 2002) and in this study may be due to low-level differences between upright and inverted faces, such as the location of the high-contrast regions of the face (eyes and eyebrows) in the upper or lower visual field, respectively. Regarding the N170, the larger amplitude for inverted faces could be due to an additional recruitment of non-face object processes (Haxby et al., 1999), to an increased processing time (see Rossion & Gauthier, 2002, and Sagiv & Bentin, 2001, for a discussion of these issues), or both. However, these main effects of amplitude alone cannot be directly related to the reduced ability to discriminate individual faces presented upside down, contrary to the new observation here of a strong interaction between orientation and identity adaptation.

A few ERP studies have investigated the timing with which inversion modulates the ERP correlates of facial identity repetition, but they yielded conflicting results on the time course of such modulations: either small identity repetition effects on the N170, with no interaction with inversion (Itier & Taylor, 2002), or repetition effects and interactions with inversion taking place at the level of the N250r (Itier & Taylor, 2002; Schweinberger et al., 2004). When considering upright faces only, previous ERP experiments have found that the N170 is either insensitive (e.g., Henson et al., 2003) or slightly reduced (e.g., Guillaume & Tiberghien, 2001) by immediate or delayed repetition of the same face. The lack of consistent face identity repetition effect at the N170 level in these previous studies is likely to be due to the use of short stimulus presentation time (typically <1 s), as suggested by the finding that behavioral identity aftereffects induced by adaptation to a face strongly depend on the presentation duration of the adapting stimulus (Leopold et al., 2005). In this study, we used a long adaptation time (approximately 3 s) and short interstimulus interval (approximately 200 ms), as in recent studies of successful face adaptation effects on the N170 at the category level (Kovacs et al., 2006; Kovacs, Zimmer, Harza, Antal, & Vidnyanszky, 2005). Our study also departs from previous

work by investigating the precise temporal dynamics of the interaction between identity adaptation and face orientation (using sample-by-sample analyses) while subjects performed an active identity matching task on each trial.

What could be the neurophysiological mechanisms underlying the differential time course of the adaptation effect for upright and inverted faces? Most neurons in the monkey inferior-temporal cortex respond to both upright and inverted faces (e.g., Perrett et al., 1988). Studies recording the response of single neurons in the monkey's inferior-temporal cortex have suggested that facial identity may be coded by partly overlapping sparse populations of neurons (Rolls & Tovee, 1995; Young & Yamane, 1992). One plausible hypothesis is that the neural response patterns to different identities overlap more for two different inverted faces than for two upright faces, leading to an adaptation effect even when different identities are presented (according to this view, one may have expected a larger amplitude in the upright-different condition only, relative to the three other conditions, as is observed in fMRI; see Mazard et al., 2006; Yovel & Kanwisher, 2005). However, as discussed in an earlier paragraph, the overall N170 amplitude is larger for inverted faces, whereas the fMRI signal in the FFA is not, thereby counterbalancing the adaptation effect). As a result, the time for populations of face-selective neurons to reach a decision threshold for an accurate individual discrimination may be shorter for upright faces, leading to a faster behavioral output relative to inverted faces (see Perrett, Oram, & Ashbridge, 1998).

A number of studies have found that previous exposure to a given face stimulus leads to distortion in the perceptual space in which faces are encoded, the so-called face aftereffects (e.g., Leopold, O'Toole, Vetter, & Blanz, 2001; Leopold et al., 2005; Watson & Clifford, 2003; Webster & MacLin, 1999). Even though we could not measure such aftereffects in this study, our results suggest that these effects may partly originate in the occipitotemporal cortex, during the time window of the N170 or N250r. However, we found delayed and reduced adaptation effects for inverted faces here, whereas most behavioral studies reveal equally strong aftereffect for upright and inverted faces (e.g., Leopold et al., 2001; Watson & Clifford, 2003; Webster & MacLin, 1999). This suggests that slightly different perceptual mechanisms and/or neural populations may be involved in these phenomena. Behavioral studies have also found that face aftereffects are partly invariant to various stimulus manipulations such as changes in size (Zhao & Chubb, 2001) or in visual field position (Leopold et al., 2001). Investigating how such manipulations modulate ERP identity adaptation as observed in the present paradigm may help clarify the spatiotemporal course of these face aftereffects.

Finally, numerous studies have shown that presenting faces upside down disrupts holistic processing (e.g., Sergent, 1984; Tanaka & Farah, 1993; Young et al.,

1987). In addition, the processing of the metric distances between features in inverted faces (e.g., mouth–nose distance) is generally more impaired than the processing of local features (see e.g., Barton et al., 2001; Freire et al., 2000; Goffaux & Rossion, *in press*; Le Grand, Mondloch, Maurer, & Brent, 2001; Rhodes, Brake, & Atkinson, 1993). Our findings of an early effect of inversion on individual discrimination thus indirectly supports the view that holistic processes leading to the extraction of an individual face representation take place as early as 160 ms in the occipitotemporal cortex.

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References

- Barton, J. J., Keenan, J. P., & Bass, T. (2001). Discrimination of spatial relations and features in faces: Effects of inversion and viewing duration. *British Journal of Psychology*, 92, 527–549. [PubMed]
- Bentin, S., McCarthy, G., Perez, E., Puce, A., & Allison, T. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8, 551–565.
- Blair, R. C., & Karniski, W. (1993). An alternative method for significance testing of waveform difference potentials. *Psychophysiology*, 30, 518–524. [PubMed]
- Botzel, K., Schulze, S., & Stodieck, S. R. (1995). Scalp topography and analysis of intracranial sources of face-evoked potentials. *Experimental Brain Research*, 104, 135–143. [PubMed]
- Carbon, C. C., & Leder, H. (2006). The Mona Lisa effect: Is ‘our’ Lisa fame or fake? *Perception*, 35, 411–414. [PubMed]
- Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. N. (1998). What is “special” about face perception? *Psychological Review*, 105, 482–498. [PubMed]
- Freire, A., Lee, K., & Symons, L. A. (2000). The face-inversion effect as a deficit in the encoding of configural information: Direct evidence. *Perception*, 29, 159–170. [PubMed]
- Gauthier, I., Tarr, M. J., Moylan, J., Skudlarski, P., Gore, J. C., & Anderson, A. W. (2000). The fusiform “face area” is part of a network that processes faces at the individual level. *Journal of Cognitive Neuroscience*, 12, 495–504. [PubMed]
- Goffaux, V., & Rossion, B. (in press). Face inversion disproportionately impairs the perception of vertical but not horizontal relations between features. *Journal of Experimental Psychology: Human Perception and Performance*.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: Neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, 10, 14–23. [PubMed]
- Guillaume, F., & Tiberghien, G. (2001). An event-related potential study of contextual modifications in a face recognition task. *Neuroreport*, 12, 1209–1216. [PubMed]
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4, 223–233. [PubMed]
- Haxby, J. V., Ungerleider, L. G., Clark, V. P., Schouten, J. L., Hoffman, E. A., & Martin, A. (1999). The effect of face inversion on activity in human neural systems for face and object perception. *Neuron*, 22, 189–199. [PubMed] [Article]
- Henson, R. N., Goshen-Gottstein, Y., Ganel, T., Otten, L. J., Quayle, A., & Rugg, M. D. (2003). Electrophysiological and haemodynamic correlates of face perception, recognition and priming. *Cerebral Cortex*, 13, 793–805. [PubMed] [Article]
- Herrmann, M. J., Ehlis, A. C., Muehlberger, A., & Fallgatter, A. J. (2005). Source localization of early stages of face processing. *Brain Topography*, 18, 77–85. [PubMed]
- Itier, R. J., & Taylor, M. J. (2002). Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: A repetition study using ERPs. *Neuroimage*, 15, 353–372. [PubMed]
- Jacques, C., & Rossion, B. (2006). The speed of individual face categorization. *Psychological Science*, 17, 485–492. [PubMed]
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, 17, 4302–4311. [PubMed] [Article]
- Kovacs, G., Zimmer, M., Banko, E., Harza, I., Antal, A., & Vidnyánszky, Z. (2006). Electrophysiological correlates of visual adaptation to faces and body parts in humans. *Cerebral Cortex*, 16, 742–753. [PubMed] [Article]

- Kovacs, G., Zimmer, M., Harza, I., Antal, A., & Vidnyanszky, Z. (2005). Position-specificity of facial adaptation. *Neuroreport*, *16*, 1945–1949. [PubMed]
- Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2001). Neuroperception. Early visual experience and face processing. *Nature*, *410*, 890. [PubMed]
- Leopold, D. A., O'Toole, A. J., Vetter, T., & Blanz, V. (2001). Prototype-referenced shape encoding revealed by high-level aftereffects. *Nature Neuroscience*, *4*, 89–94. [PubMed] [Article]
- Leopold, D. A., Rhodes, G., Muller, K. M., & Jeffery, L. (2005). The dynamics of visual adaptation to faces. *Proceedings of the Royal Society B: Biological Sciences*, *272*, 897–904. [PubMed] [Article]
- Mazard, A., Schiltz, C., & Rossion, B. (2006). Recovery from adaptation to facial identity is larger for upright than inverted faces in the human occipito-temporal cortex. *Neuropsychologia*, *44*, 912–922. [PubMed]
- McCarthy, G., Puce, A., Belger, A., & Allison, T. (1999). Electrophysiological studies of human face perception. II: Response properties of face-specific potentials generated in occipitotemporal cortex. *Cerebral Cortex*, *9*, 431–444. [PubMed] [Article]
- Perrett, D. I., Mistlin, A. J., Chitty, A. J., Smith, P. A., Potter, D. D., Broennimann, R., et al. (1988). Specialized face processing and hemispheric asymmetry in man and monkey: Evidence from single unit and reaction time studies. *Behavioral Brain Research*, *29*, 245–258. [PubMed]
- Perrett, D. I., Oram, M. W., & Ashbridge, E. (1998). Evidence accumulation in cell populations responsive to faces: An account of generalisation of recognition without mental transformations. *Cognition*, *67*, 111–145. [PubMed]
- Rhodes, G., Brake, S., & Atkinson, A. P. (1993). What's lost in inverted faces? *Cognition*, *47*, 25–57. [PubMed]
- Rolls, E. T., & Tovee, M. J. (1995). Sparseness of the neuronal representation of stimuli in the primate temporal visual cortex. *Journal of Neurophysiology*, *73*, 713–726. [PubMed]
- Rossion, B., & Gauthier, I. (2002). How does the brain process upright and inverted faces? *Behavioral and Cognitive Neuroscience Reviews*, *1*, 62–74.
- Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S. et al. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: An electrophysiological account of face-specific processes in the human brain. *Neuroreport*, *11*, 69–74. [PubMed]
- Rousselet, G. A., Mace, M. J., & Fabre-Thorpe, M. (2004). Animal and human faces in natural scenes: How specific to human faces is the N170 ERP component? *Journal of Vision*, *4*(1):2, 13–21, <http://journalofvision.org/4/1/2/>, doi:10.1167/4.1.2. [PubMed] [Article]
- Sagiv, N., & Bentin, S. (2001). Structural encoding of human and schematic faces: Holistic and part-based processes. *Journal of Cognitive Neuroscience*, *13*, 937–951. [PubMed]
- Schweinberger, S. R., Huddy, V., & Burton, A. M. (2004). N250r: A face-selective brain response to stimulus repetitions. *Neuroreport*, *15*, 1501–1505. [PubMed]
- Sergent, J. (1984). An investigation into component and configural processes underlying face perception. *British Journal of Psychology*, *75*, 221–242. [PubMed]
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology A: Human Experimental Psychology*, *46*, 225–245. [PubMed]
- Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, *381*, 520–522. [PubMed]
- Tovee, M., & Rolls, E. T. (1995). Information encoding in short firing rate epochs by single neurons in the primate temporal visual cortex. *Visual Cognition*, *2*, 35–58.
- Watson, T. L., & Clifford, C. W. (2003). Pulling faces: An investigation of the face-distortion aftereffect. *Perception*, *32*, 1109–1116. [PubMed]
- Webster, M. A., & MacLin, O. H. (1999). Figural aftereffects in the perception of faces. *Psychonomic Bulletin & Review*, *6*, 647–653. [PubMed]
- Webster, M. A., Kaping, D., Mizokami, Y., & Duhamel, P. (2004). Adaptation to natural facial categories. *Nature*, *428*, 557–561. [PubMed]
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology: Human Perception and Performance*, *81*, 141–145.
- Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception*, *16*, 747–759. [PubMed]
- Young, M. P., & Yamane, S. (1992). Sparse population coding of faces in the inferotemporal cortex. *Science*, *256*, 1327–1331. [PubMed]
- Yovel, G., & Kanwisher, N. (2005). The neural basis of the behavioral face-inversion effect. *Current Biology*, *15*, 2256–2262. [PubMed] [Article]
- Zhao, L., & Chubb, C. (2001). The size-tuning of the face-distortion after-effect. *Vision Research*, *41*, 2979–2994. [PubMed]