Research Report

Misaligning face halves increases and delays the N170 specifically for upright faces: Implications for the nature of early face representations

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ABSTRACT

The N170 is an occipito-temporal visual event-related potential that is larger in response to faces than other nonface object categories and has been associated with the early activation of visual face representations in the human brain. It has been recently showed that spatially misaligning the bottom and top halves of a face stimulus–a manipulation used in behavioural studies to disrupt the processing of the whole face configuration (i.e. holistic processing)–increases the latency and the amplitude of the N170, particularly in the right hemisphere. Here we show that these observations cannot be accounted for by a general effect of spatial misalignment of visual patterns. A first experiment showed that the effect of misalignment on the N170 was larger when both top and bottom halves of the stimulus were made of face parts (i.e. a full face) compared to when one of the two halves was made of visual noise. The N170 delay and increase for misaligned faces is similar to the effect of upside-down face inversion, a manipulation thought to disrupt holistic processing. Supporting this view, in a second experiment in which we presented upside-down versions of the stimuli used in the first experiment, we did not observe such a larger effect of misalignment on the N170 for a full face compared to the control conditions. These observations support the view that the early face representation activated in the human brain at the level of the N170, is that of a global upright face pattern. Specifically, when the global configuration of a face is modified by inverting it or spatially misaligning its top and bottom halves, the activation of its representation is delayed in cortical areas coding preferentially for faces. Moreover, when the global face configuration is disrupted, the face stimulus appears to recruit additional neural processes compared to normal face processing, leading to an increase of the N170 amplitude on the scalp.

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1. Introduction

It is widely acknowledged that a face is processed primarily as a global pattern or holistically, both at the basic category level (i.e., categorizing the visual stimulus as "a face") and at the individual level (categorizing the stimulus as an individual face). Evidence for holistic perception of faces at the category level comes from the ability of the visual system to see a global outline or an organization of non-facial elements as a face, for instance as in two-tone "Mooney" face stimuli (e.g., McKone,

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2009; Mooney, 1957; Moore and Cavanagh, 1998) or in paintings of Arcimboldo where "features" are made of organic and non-organic nonface elements (Hulten, 1987). Evidence that an individual face is processed holistically comes from the finding that the perception of the identity of a facial feature in an individual face (e.g. the eyes) is strongly influenced by the position and identity of other face features in the whole facial configuration (e.g., the mouth, see Sergent, 1984; Tanaka and Farah, 1993; Young et al., 1987).

Two stimulus manipulations that are commonly used in studies of face perception to disrupt holistic processing of a face are (1) upside-down inversion of the stimulus, and (2) spatial dissociation of the facial features. An excellent illustration of the disruption of holistic face perception by these 2 manipulations comes from the so-called composite face illusion (CFI) (Fig. 1, top row). That is, identical top parts of faces appear different if they are aligned with different bottom parts, because the face processing system cannot help to fuse
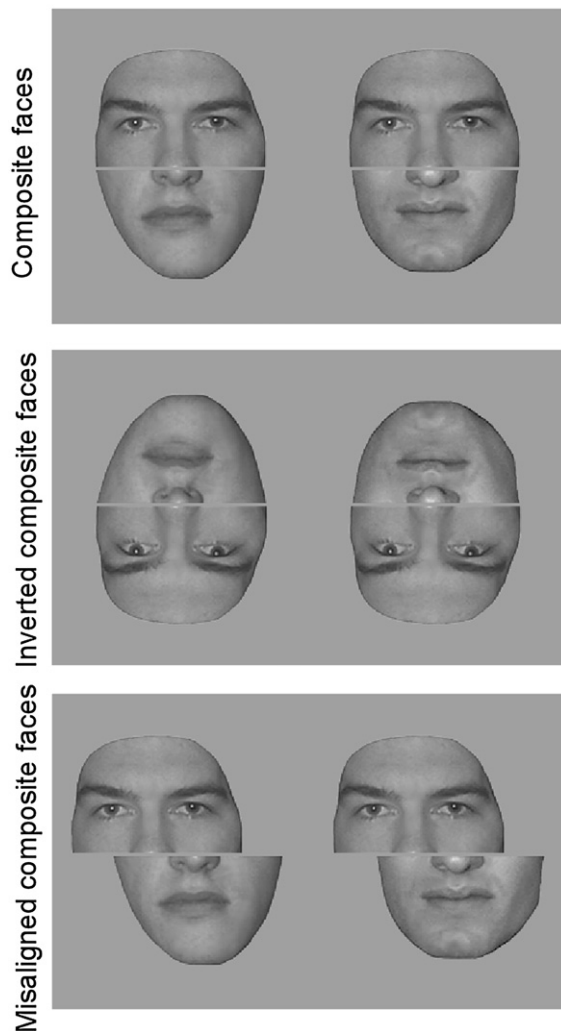

Fig. 1 – Illustration of the composite face illusion (upper row), whereby two identical top face halves appear slightly different if they are paired with different bottom face halves, and disruption of this illusion by upside-down inversion (middle row) and spatial misalignment of the bottom face halves (bottom row).

the top and bottom parts into whole faces (Young et al., 1987). Strikingly, this illusion vanishes if the faces are presented upside-down or if the two parts of the faces are spatially misaligned (middle and bottom rows of Fig. 1), indicating that these manipulations disrupt our ability to perceive the face as a whole or a "gestalt" (see Rossion, 2009).

At the neural level, the effect of inverting a face stimulus has been investigated extensively over the past 10 years (see Rossion and Gauthier, 2002 for a review, and below for more recent references), in order to isolate the responses to expert face (i.e. holistic) processes. Functional magnetic resonance imaging (fMRI) studies in humans indicate that presenting an inverted face causes a reduction of activity in the brain areas responding preferentially to faces in the human occipito-temporal cortex, such as in the lateral part of the middle fusiform gyrus (the fusiform face area, "FFA"), in the posterior part of the superior temporal sulcus (pSTS), and to a lesser extent in the inferior occipital gyrus ("occipital face area," OFA) (e.g., Goffaux et al., 2009; Kanwisher et al., 1998; Mazard et al., 2006; Yovel and Kanwisher, 2005). The reduction of fMRI signal following inversion varies strongly between studies, with some studies showing little or no effect in the "FFA" for instance (e.g. Aguirre et al., 1999; Epstein et al., 2006; Haxby et al., 1999), and other studies showing relatively strong decreases in the same area (Goffaux et al., 2009; Kanwisher et al., 1998; Mazard et al., 2006; Yovel and Kanwisher, 2005). These discrepancies between studies have been attributed to the fact that, in a block design, inverted faces lead to a reduced release from adaptation to identity in the "FFA" compared to upright faces (Mazard et al., 2006; Yovel and Kanwisher, 2005). In contrast to these decreases of neural response, inverting a face stimulus rather *increases* the activation in visual areas that do not respond preferentially to faces overall, such as in the lateral occipital complex (LOC; Grill-Spector et al., 1999; Malach et al., 1995) or in a region in the medial fusiform gyrus/parahippocampal gyrus (e.g. Aguirre et al., 1999; Epstein et al., 2006; Goffaux et al., 2009; Haxby et al., 1999; Yovel and Kanwisher, 2005).

The effect of face inversion has also been studied in humans by recording electrical and magnetic responses on the scalp, in order to investigate the time-course of expert face processes; inverted faces being often used as an ideal control stimulus. The first event-related potential (ERP) or event-related magnetic field (ERMf) component that responds preferentially to faces in a consistent manner, the occipito-temporal N170/M170 (e.g., Bentin et al., 1996; Botzel et al., 1995; Itier and Taylor, 2004; Rossion et al., 2000; Rousselet et al., 2008; M170: e.g., Halgren et al., 2000; Liu et al., 2000; see Rossion and Jacques, 2008 for a review), is delayed in response to the presentation of upside-down compared to upright faces (e.g., Eimer, 2000; Itier and Taylor, 2004; Jacques and Rossion, 2007a; Linkenkaer-Hansen et al., 1998; Rossion et al., 1999; Rousselet et al., 2004). This delay is compatible with the delayed response to inverted faces of populations of face-selective neurons in the monkey infero-temporal cortex (Perrett et al., 1988). Paradoxically, the same studies have also found that the N170/M170 is substantially enhanced in amplitude when a face is presented upside-down.

Considering fMRI and electromagnetic studies altogether, these observations suggest that an inverted face stimulus is processed more slowly and less efficiently in areas responding preferentially to faces in the human brain, while leading to an

increase of activation in areas that do not respond preferentially to faces such as the LOC. While keeping in mind that indirect hemodynamic (fMRI) and direct electromagnetic neuroimaging methods (EEG/MEG) may reflect distinct neural signals, the increase of amplitude recorded on the scalp during the N170 time-window by the latter methods may thus at least partly originate from the activation increase in other visual areas such as the lateral occipital complex or the medial fusiform/parahippocampal gyrus.

If the delayed and enhanced N170 to inverted faces reflect at least partly an impairment in holistic face encoding (Rossion et al., 1999), one would expect other manipulations known to disrupt holistic face processing behaviourally, such as spatial misalignment of face parts, to cause a similar increase and delay of the face N170. Indeed, a recent ERP study reported this observation: faces which were horizontally cut in two halves (i.e., with parts misaligned see Fig. 1, bottom row) elicited a larger and delayed N170 as compared to faces presented with aligned halves, in particular in the right hemisphere (Letourneau and Mitchell, 2008; see also Jacques and Rossion, 2009). However, the two conditions compared in that study did not allow clarifying whether the effect of spatial misalignment of the face on the N170 amplitude and latency was strictly related to faces, or reflected a more general effect of misalignment of visual patterns.

The goal of the present study was to clarify this issue. That is, we measured the ERP response to top and bottom face parts that were either aligned (i.e. forming a complete face) or spatially misaligned (i.e. horizontally splitting the face in two separate halves) as in previous behavioural studies of holistic face processing with composite faces (e.g., Goffaux and Rossion, 2006; Hole, 1994; Le Grand et al., 2004; Michel et al., 2006; Young et al., 1987). We aimed at sorting out effects of integration of top and bottom face halves from a general effect of spatial alignment, an issue that was not addressed by Letourneau and Mitchell (2008). To do so, we used two control conditions in which the top (or the bottom) part of a face was combined with visual noise presented at the bottom (or the top). These control conditions were displayed both in the aligned and misaligned stimulus configuration[1] (Fig. 2). We hypothesized that the visual noise presented together with either the top part of a face or the bottom part of the face should prevent the top and bottom parts of the stimuli being perceived as a whole (i.e. holistically). According to this hypothesis, the difference between aligned and misaligned conditions at the level of the face-sensitive N170 should be observed exclusively, or at least maximally, when

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[1] For simplicity throughout the text we used the terms "aligned" and "misaligned" even when the stimuli contain only the top or the bottom part of a face and the other half is made out of visual noise. For these two control conditions, the terms aligned and misaligned refer to the fact that the two parts that make up the stimulus are either positioned in a vertically aligned configuration or are positioned in a vertically misaligned configuration, with the bottom part being displace to the right side of the top part. Thus, we use these terms because they offer a convenient way to refer to our manipulation of the vertical arrangement of the top and bottom parts of the stimulus with the same terms (i.e. aligned and misaligned) in the three face format (i.e. top=face/bottom=face, top=face/bottom=noise and top=noise/bottom=face).
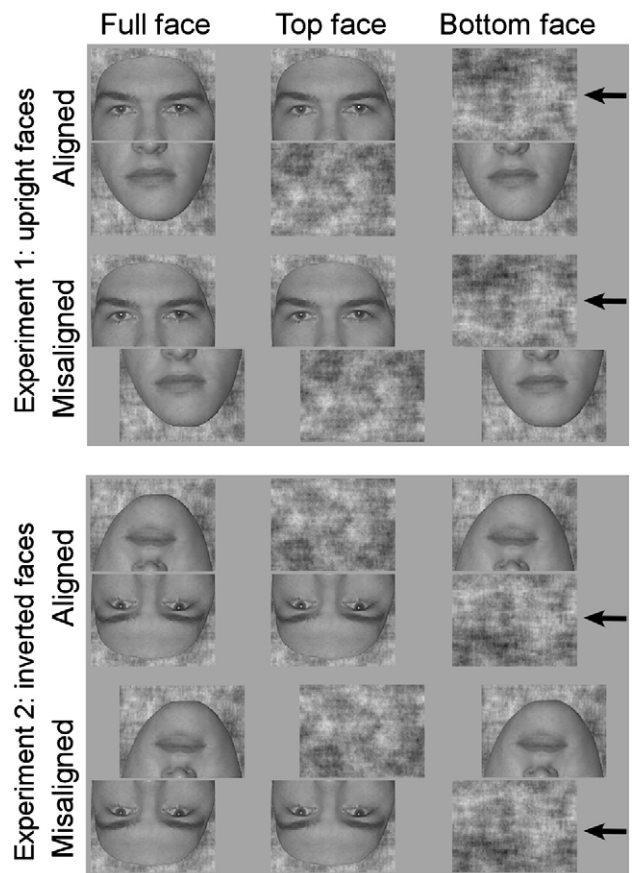

Fig. 2 – Experimental conditions (format × alignment) and examples of stimuli used in experiment 1 with upright stimuli (upper part) and experiment 2 with inverted stimuli (lower part). The arrows on the right side indicate the part of the stimulus where participants were instructed to fixate.

both the top and the bottom parts of the stimulus were face parts, but not when either the top or the bottom part was made out of visual noise.

In addition, we conducted a second experiment that was identical in all respect to the first experiment expect for the use of vertically flipped versions (i.e. inverted) of the stimuli used in experiment 1. As indicated above, holistic processing of a face is impaired when the face is inverted. We thus reasoned that if any effect of misalignment found on the N170 with upright full faces was genuinely related to a disruption of the integration of top and bottom face halves (i.e. holistic processing), such effect should not be observed or at least be strongly reduced with inverted faces. The use of inverted faces also provides an adequate control for physical (i.e. low-level) differences between our conditions.

2. Results

2.1. Experiment 1: upright faces

2.1.1. Behaviour
Participants were instructed to fixate the top part of the stimulus and to press a key whenever the top part was

colorized in red (see methods). Participants detected 99.5% (±2%) of the targets (false alarms: 0.05%), with a mean response time of 461 ms (±64 ms). There was no difference between aligned and misaligned for hits (99.5% in both conditions) and response times (461 ms in both conditions).

2.2. Electrophysiology

Grand average ERP waveforms recorded at two occipito-temporal electrodes (PO7/8, left and right hemisphere respectively) for all six conditions are depicted in Fig. 3. Two separate sets of analyses were performed on the ERP signal recorded at the scalp in response to the stimuli. First, we performed conventional analyses on the amplitudes and latencies of specific visual potentials, as classically done in studies of face

perception (e.g. Bentin et al., 1996; Itier and Taylor, 2004; Jacques and Rossion, 2007a; Rossion et al., 1999): the P1 and N170 components, recorded at posterior sites. Statistical analyses on the P1 and the N170 were performed using repeated measures analyses of variance (ANOVA) with the factors *alignment* (aligned, misaligned), *format* (full-face, top-face, bottom-face), *hemisphere* (left, right) and *electrode* (5 levels) for amplitude analyses and the factors *alignment*, *format* and *hemisphere* for the latency analyses. Fig. 4 shows the scalp topographies of the N170 component in all conditions. Amplitude and latency values of the N170 measured at occipito-temporal electrodes PO7 and PO8 are depicted in Fig. 5. A second set of analyses was performed to characterize more precisely the time-course of the effect of misaligning the bottom part of the stimulus on the ERP response. Specifically, we
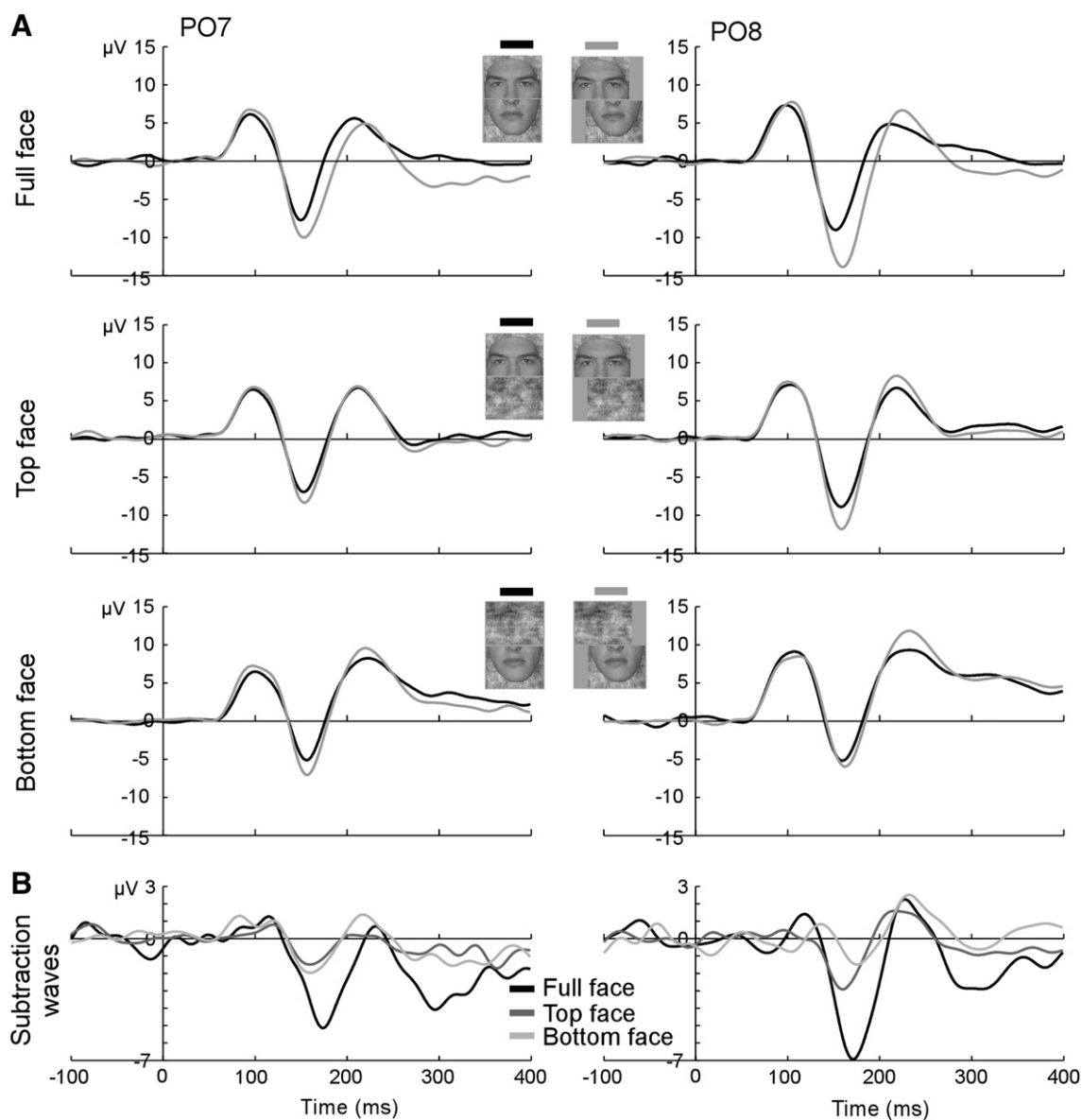

Fig. 3 – Grand average ERP waveforms (from –100 to 400 ms relative to stimulus onset) elicited in the 6 conditions of experiment 1 (upright stimuli) at two occipito-temporal electrodes (PO7 in left hemisphere; PO8 in right hemisphere). (A) ERPs are shown as a function of format (full-face vs. top-face vs. bottom-face) and alignment (aligned vs. misaligned). (B) Subtraction waveforms (misaligned minus aligned) for the 3 format conditions.
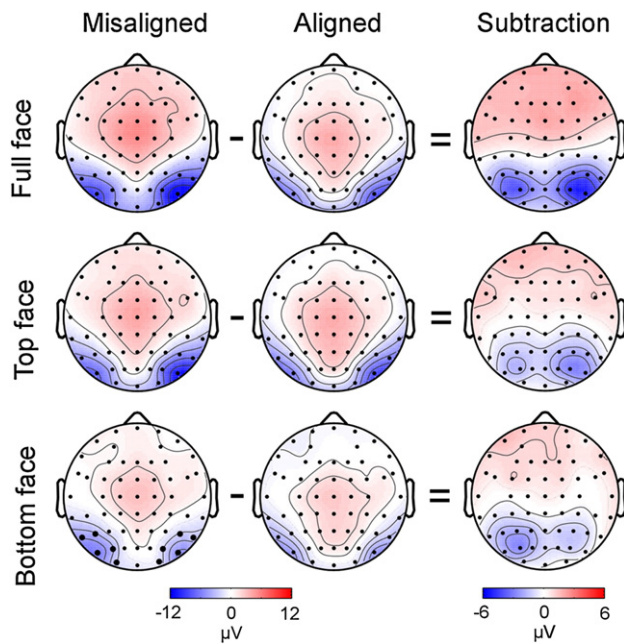
Fig. 4 – Topographical maps of the N170 (signal averaged in the 150–170 ms time-window) in the aligned and misaligned conditions of experiment 1, as well as of the difference between these 2 conditions, for full face, top face and bottom face separately. The view is from above the scalp with frontal sites at the top and posterior sites at the bottom. Note the difference in topography for aligned and misaligned condition. Bottom-left map shows the location of the 5 pairs of occipito-temporal electrodes (larger dots) used in the ERP amplitude analyses. Topographical maps were created using EEGLAB (Delorme and Makeig, 2004).

analyzed the ERP data at each electrode and each time-point in a series of pair-wise comparisons between aligned and misaligned conditions for the three different face formats.

2.2.1. P1 amplitude
Analyses performed on the amplitude of the P1 component revealed a significant effect of *format* [$F(1.9,22.4)=4.19$, $p<0.05$], the amplitude of the P1 in the bottom-face condition being significantly larger than in the full-face condition (5.8 μV vs. 5.1 μV respectively, $p<0.01$; other comparisons were non significant). The effect of *format* was significant on all electrodes tested except on occipital electrodes O1/2 as revealed by a significant *format×electrode* interaction [$F(3.4,41)=2.97$, $p<0.05$]. The effect of *alignment* [$F(1,12)=1.2$, $p=0.3$] and the interaction between *format* and *alignment* [$F(1.8,21.8)=0.32$, $p=0.7$] were not significant. There was a trend for a significant interaction between *alignment* and *hemisphere* [$F(1,12)=4.44$, $p=0.057$], the P1 amplitude being slightly larger in the misaligned condition only in the left hemisphere. This effect was probably due to the difference in the visual field position of the bottom part of the face between aligned and misaligned (bottom part in the right visual field) conditions. A significant *alignment×hemisphere×electrode* [$F(2.6,31.4)=4.5$, $p<0.05$] revealed that this was only the case on electrode PO5 ($p<0.05$).

2.2.2. P1 latency
A significant effect of *format* on the P1 latency [$F(1.4,17.3)=8.64$, $p<0.005$] indicated that the P1 was delayed in the bottom-face condition compared to the full-($p<0.01$) and top-face ($p<0.01$) conditions which did not differ in terms of P1 latency ($p=0.11$). The P1 latency however did not differ between aligned and misaligned conditions [$F(1,12)=0.02$, $p=0.91$], and there was no significant interaction between *alignment* and *format* [$F(1.8,21.4)=1.15$, $p=0.33$]. All other interactions were non-significant.

2.2.3. N170 amplitude
A significant main effect of *format* [$F(1.6,18.8)=43.63$, $p<0.0001$] indicate a larger N170 amplitude in the full-face than in the top-face ($p<0.005$) and the bottom-face conditions ($p<0.0001$), and a larger amplitude for top-face than for bottom-face ($p<0.0005$). There was also a main effect of *alignment* [$F(1,12)=66.34$, $p<0.0001$] reflecting larger N170 amplitude when the top and bottom parts of the stimulus were presented misaligned as compared to aligned. Most importantly there was a significant *format×alignment* interaction [$F(1.3,16.2)=6.38$, $p<0.02$] because the amplitude difference between aligned and misaligned stimuli was larger in the full-face condition compared to the other two conditions (aligned minus misaligned for full-face: 2.56 μV, $p<0.0001$; for top-face: 1.09 μV, $p<0.0005$; for bottom-face: 0.86 μV, $p<0.05$; Figs. 3 and 5). Further comparisons of the alignment effect across face format revealed that the alignment effect was significantly larger for full-face compared to top-face (effect of alignment for full-face vs. for top-face: $p<0.01$) and bottom-face (effect of alignment for full-face vs. for bottom-face: $p<0.05$). The alignment effect did not differ between the top-face and the bottom-face conditions ($p=0.58$), although it was marginally larger for top-face in the right hemisphere only ($p=0.06$). In addition, a significant *format× alignment×hemisphere* interaction [$F(2,23.5)=15.7$, $p<0.0001$] reflected that while the effect of alignment was largest in the
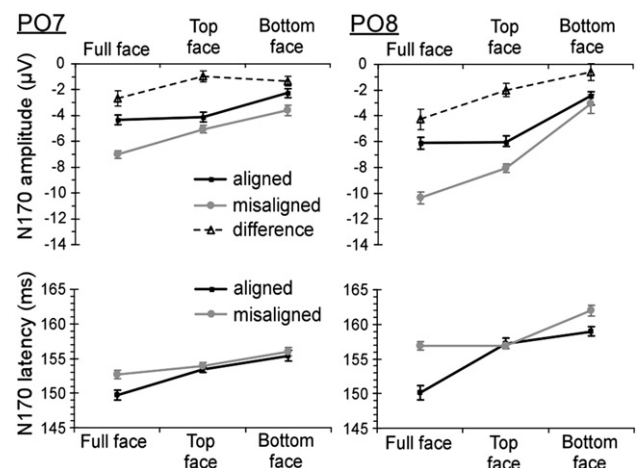

Fig. 5 – Amplitude (top row) and latency (bottom row) of the N170 in each condition of experiment 1 (upright stimuli). Line graphs in the top row also show the amplitude of the difference between aligned and misaligned conditions. Error bars are standard errors of the mean computed after normalizing the data to remove subject variability (Loftus and Masson, 1994).

full-face condition both in the left and right hemispheres, the effect of alignment was larger in the top-face than in the bottom-face in the right hemisphere and the reverse was true (i.e. alignment effect larger for bottom-face than for top-face) in the left hemisphere.

To further explore the effect of *format* and because there was a 4-way interaction between all factors [$F(3.8,45.6)=3.5$, $p<0.05$], we performed two separate ANOVAs; one on each level of the *alignment* factor. Each ANOVA thus included the factors *format*, *hemisphere* and *electrode*.

The first ANOVA, performed on the N170 amplitude measured in the aligned condition only, revealed a significant effect of *format* [$F(1.9,22.9)=18.9$, $p<0.00005$]; the N170 being larger in the full-face and the top-face compared to the bottom-face ($p<0.00005$ and $p<0.0005$ respectively). The amplitude of the N170 in the full-face and top-face did not differ ($p=0.5$). A significant *format × hemisphere* interaction [$F(1.4,16.7)=7.8$, $p<0.01$] indicated that the difference between the bottom-face condition and the two other conditions was larger in the right than in the left hemisphere. A significant *format × electrode* interaction [$F(3.3,39.8)=5.9$, $p<0.005$] further indicated that the effect of format was smaller at electrodes P5/6 compared to the other more posterior and inferior electrodes.

The second ANOVA, performed in the misaligned condition only, revealed a significant effect of *format* [$F(1.9,22.9)=18.9$, $p<0.00005$]; the N170 amplitude being larger in the full-face compared to top-face ($p<0.00005$) or bottom-face ($p<0.00001$) conditions. The N170 measured in the top-face condition was also larger than in the bottom-face condition ($p<0.005$). Altogether, significant interactions between *format* and *hemisphere* [$F(1.3,15.2)=23.76$, $p<0.0001$], *format* and *electrode* [$F(3.3,40)=9.95$, $p<0.0001$] and *format*, *hemisphere* and *electrode* [$F(3,36.3)=4.44$, $p<0.01$] revealed that the difference between top-face and bottom-face conditions was significant at all electrodes in the right hemisphere (all p's <0.0023), but only at PO7 ($p=0.044$) and O1 ($p=0.015$) in the left hemisphere. In addition, the full-face condition elicited a significantly larger N170 than the top-face condition at all measured electrodes in both hemispheres (all p's <0.002).

To summarize, the N170 was larger in the misaligned condition in all face format, but the effect of alignment was significantly larger when a full face was presented compared to the other 2 face formats. Moreover, additional ANOVAs performed separately for aligned and misaligned conditions indicate that the interaction between alignment and format was mostly driven by the increased N170 amplitude for the *misaligned* full face compared to the other 2 face format. In the aligned condition, the N170 amplitude for full face and top face did not differ.

2.2.4. N170 latency
The N170 peaked on average between 150 and 160 ms (Fig. 3 and 5). The significant main effect of *format* [$F(1.6,19.8)=30.86$, $p<0 .0001$] revealed that the N170 latency significantly increased from the full-face condition to the top-face condition ($p<0.001$), and was the highest in the bottom-face condition ($p<0.001$). The latency of the N170 was also higher in the misaligned than in the aligned condition [$F(1,12)=24.12$, $p<0.0005$]. The significant *format × alignment* [$F(1.8,21.6)=13.6$, $p<0 .001$] qualified by a significant *format × alignment × hemisphere* [$F(1.8,21.2)=6.05$, $p=0 .01$] revealed that the latency of

the N170 was larger in the misaligned compared to the aligned condition in both hemispheres for the full-face condition ($p<0.005$ and $p<0.0001$ for left and right hemisphere respectively) and only in the right hemisphere for the bottom-face condition ($p=0.5$ and $p=0.005$ for left and right hemisphere respectively). In the top-face condition, the latency of the N170 did not differ between aligned and misaligned conditions ($p=0.3$ and $p=0.7$ for left and right hemisphere, respectively).

2.2.5. N170 topographies
We also tested whether the spatial distribution of N170 amplitude values on the scalp (i.e. topographies) in the aligned and misaligned conditions were equal in shape or not. A difference in topography between two conditions, independently of an overall amplitude difference, indicates a difference in the patterns of activation of the neural sources generating the two topographies. Scalp topographies of the N170 are shown in Fig. 4. Normalized N170 scalp topographies (McCarthy and Woods, 1985) were compared between the aligned and the misaligned conditions independently for each format using 2-way *alignment × electrode* ANOVAs. These analyses revealed that the shape of the N170 topographies to aligned vs. misaligned conditions were significantly different in all face formats (*alignment × electrode* interaction in full-face: $F(2.7,35.5)=4.92$, $p=0.006$; in top-face: $F(4.8,58)=5.66$, $p=0.0002$ and in bottom-face: $F(3.3,40.1)=3.43$, $p=0.02$). An additional ANOVA comparing the full-face aligned to the top-face aligned conditions did not reveal any significant difference between the topographies (*alignment × electrode* interaction: $F(2.7,32.5)=1.28$, $p=0.3$).

2.2.6. Time course of misalignment effects
Time by electrodes plots of the significant alignment effect for each face format as well as the corresponding scalp topographies are depicted in Fig. 6. The earliest consistent effect of alignment started at around 130 ms in the full face condition and around 140 ms in the top-face and bottom-face condition. The alignment effect was larger and of longer duration in the full-face compared to the other two formats. These analyses further revealed that the differential alignment effect for full-face (i.e. full-face vs. top-face and bottom-face) was largest after the N170 peak (although still within the N170 time-window). This observation is similar to the finding that the largest increase of the N170 for inverted compared to upright faces is observed slightly after the N170 peak (e.g. see Jacques and Rossion, 2007a). Interestingly, during the N170 time window the maximal difference between aligned and misaligned conditions was located over lateral occipital sites (around PO5/6), with a different topography compared to the one observed for the N170 elicited by aligned full-faces, which was maximal over inferior occipito-temporal electrodes (P7/8, PO7/8; see Fig. 4). The effect of alignment reversed its polarity at frontal and pre-frontal sites. Over posterior sites, the effect of face alignment for the full-face and top-face format was the largest in the right hemisphere, while it was significant in the left hemisphere only for the bottom-face format.

Additional modulations of the ERP response due to our manipulation of face alignment occurred at slightly later time-points, partially replicating findings from Letourneau
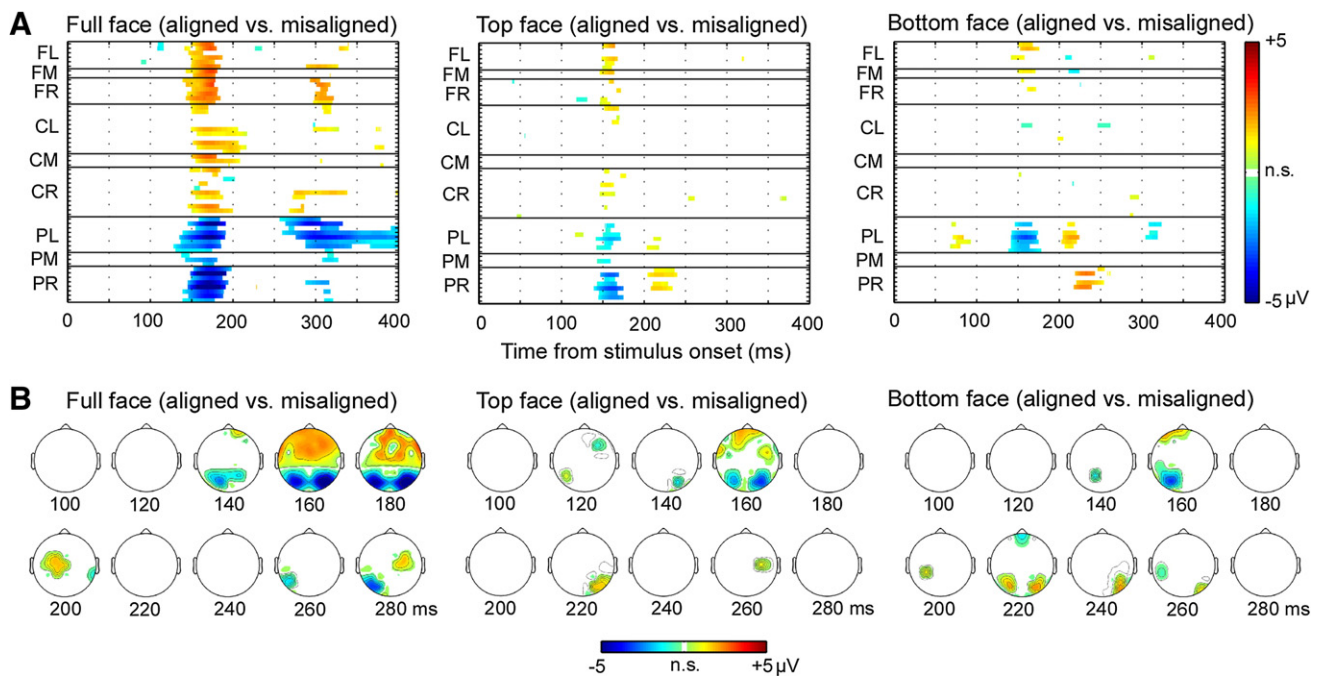
Fig. 6 – Time course of the ERP alignment effect in experiment 1. (A) Time by electrode statistical plots of the significant ERP alignment effect ($p < 0.01$; two-tailed; 8000 permutations) in each face format (Full face, Top face and Bottom face). Only significant differences are color-coded as a function of the amplitude of the ERP difference between misaligned and aligned conditions. The 58 electrodes are represented on the y-axis and grouped as a function of their location in frontal (F), central (C) and posterior (P) scalp region, as well as left hemisphere (L), midline (M) and right hemisphere (R). (B) Topographical maps (view from above the head) of the significant ERP alignment effect in the 3 face format between 100 and 280 ms after stimulus onset in 20 ms steps. Topographical maps were created using EEGLAB (Delorme and Makeig, 2004).

and Mitchell (2008) when comparing aligned to misaligned whole faces. First, the ERP response was more positive to misaligned compared to aligned stimuli during the P2 component time-window (220–250 ms) in all face formats (but largest in the bottom-noise condition), mostly over the right hemisphere. Interestingly, such an effect on the P2 component was not described in Letourneau and Mitchell's study. This difference of result between the two studies could possibly be due to differences in the tasks used in our (detection task) and their experiment (matching task), to differences in the type of stimuli (e.g. presence vs. absence of visual noise in the background) or the design (aligned and misaligned stimuli presented randomly vs. blocked by alignment). Second, a large ERP effect of alignment specific to the full-face format started around 270 ms after stimulus onset (i.e. in the time window of the N250 component, e.g. Schweinberger et al., 2002) more strongly over the left hemisphere[2] and lasted for about 300 ms. The timing and polarity of this effect (increased negativity for misaligned faces) effect was again similar to what is observed when comparing the ERP response to upright and inverted faces (see Carbon et al., 2005; Jacques and Rossion, 2007a) or to aligned and misaligned faces (Letourneau and Mitchell, 2008).

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[2] A similar trend was observed over the right hemisphere (see Fig. 3) but did not reach the $p < 0.01$ significance threshold used for the permutation tests.

2.3. Experiment 2: inverted faces

2.3.1. Behaviour
Participants detected 99.5% (±1.4%) of the targets (false alarms: 0.03%), with a mean response time of 457 ms (±69 ms). There was no difference between aligned and misaligned for hits (99.3% and 99.6% for aligned and misaligned respectively) and response times (460 ms and 454 ms).

2.4. Electrophysiology

Grand average ERP waveforms recorded at two occipito-temporal electrodes (PO7/8, left and right hemisphere respectively) for all six conditions in experiment 2 are depicted in Fig. 7. Because experiment 2 was intended as a control for the N170 findings with upright faces (experiment 1), we performed analyses only on the amplitude and the latency of the N170 component.

2.4.1. N170 amplitude
A significant main effect of *format* [$F(1.1, 13.6) = 77.3$, $p < 0.001$] indicate that the amplitude of the N170 was larger in the full-face than in the top-face ($p < 0.002$) conditions and larger for top-face than for bottom-face ($p < 0.0001$). Although these differences were significant in both hemispheres, the amplitude difference between face formats were larger in the right hemisphere as revealed by a significant *format× hemisphere* interaction [$F(1.4, 16.7) = 11.51$, $p < 0.005$]. Moreover,
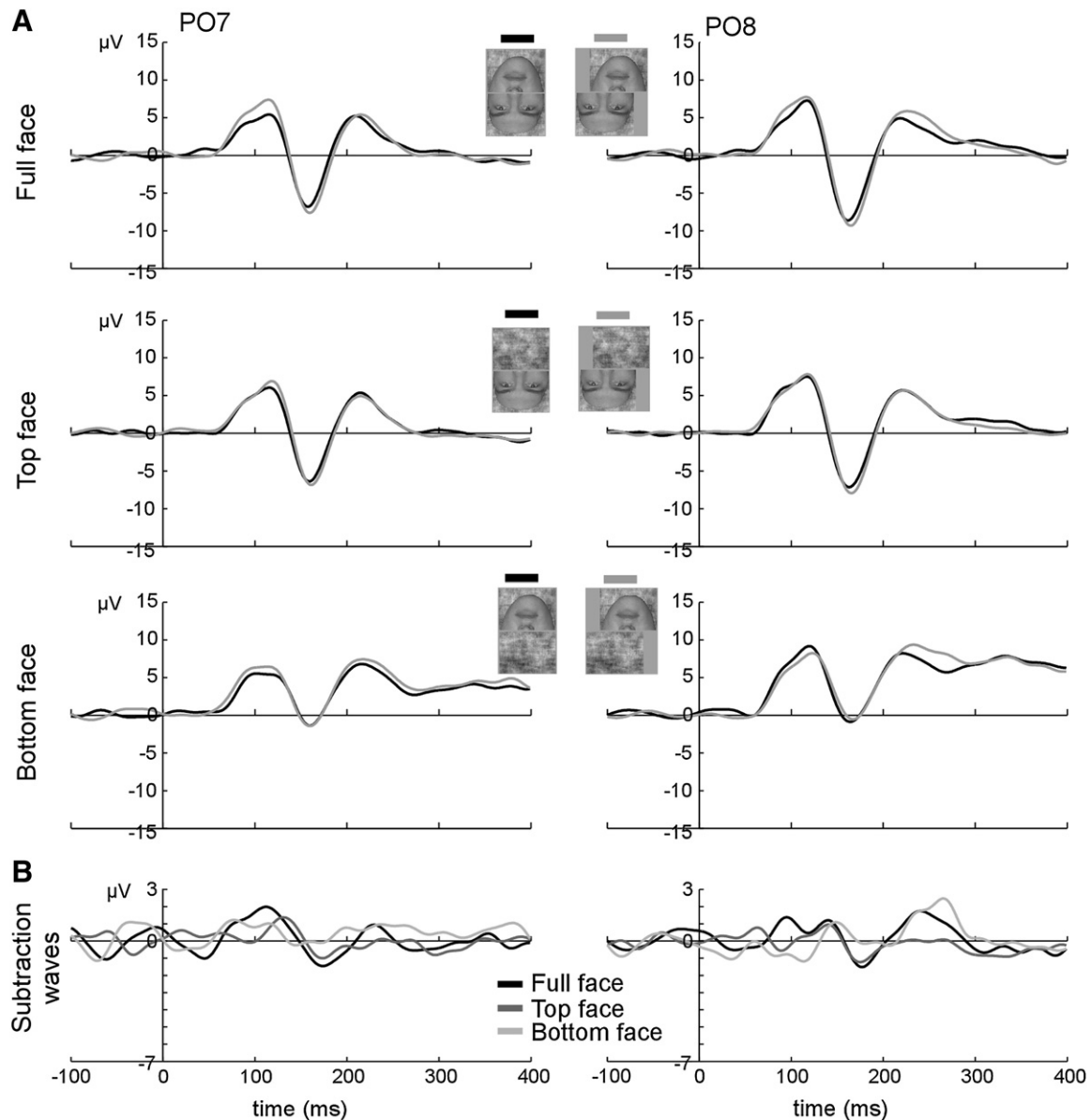
Fig. 7 – Grand average ERP waveforms (from −100 to 400 ms relative to stimulus onset) elicited in the 6 conditions of experiment 2 (inverted stimuli) at two occipito-temporal electrodes (PO7 in left hemisphere; PO8 in right hemisphere). (A) ERPs are shown as a function of format (full-face vs. top-face vs. bottom-face) and alignment (aligned vs. misaligned). (B) Subtraction waveforms (misaligned minus aligned) for the 3 format conditions.

a significant $format \times electrode$ interaction [$F(2.9, 35.07) = 13.28$, $p < 0.001$] indicated that the effect of format was largest at electrodes PO7/8 and smallest on the more anterior electrodes P7/8 and P5/6.

There was no significant main effect of $alignment$ [$F(1,12) = 1.29$, $p = 0.28$], reflecting the fact that when presented upside-down, the amplitude of the N170 did not significantly differ when the top and bottom parts of the stimuli were presented misaligned as compared to aligned. The amplitude difference between aligned and misaligned conditions varied slightly across electrodes [$alignment \times electrode$: $F(1.7, 20.6) = 5.89$, $p < 0.001$] but was not significant at any electrode (all p's > 0.2) except at PO5/6 where it was close to significance ($p = 0.08$). However and most importantly for our point, there was no significant $format \times alignment$ [$F(1.7, 20.1) = 0.43$,

$p = 0.62$], $format \times alignment \times electrode$ [$F(4, 48.1) = 1.05$, $p = 0.38$], or $format \times alignment \times hemisphere$ [$F(1.3, 15.6) = 1.79$, $p = 0.2$] interactions.

2.4.2. N170 latency

There was no significant main effect of format [$F(1.09, 13.08) = 2.02$, $p = 0.18$] on the N170 peak latency. However, a significant $format \times hemisphere$ interaction [$F(1.17, 14.11) = 8.84$, $p < 0.01$] indicate that, in the left hemisphere, the N170 elicited in the top-face condition peaked slightly later (at 160.8 ms) than in the full-face and the bottom-face conditions which did not differ (158.7 and 158.2 ms, respectively). In the right hemisphere, the N170 measured in the top-face condition (162.8 ms) peaked later than in the full-face condition (161.4) and not significantly earlier than in the bottom-face condition (165 ms). In addition,

there was a significant effect of *alignment* [$F(1,12)=6.17$, $p<0.05$] indicating that the N170 peaked slightly later in the misaligned (161.8 ms) than in the aligned (160.5 ms) condition. The *format × alignment* interaction was close to significant [$F(1.3,16)=6.17$, $p=0.1$] and was due to the presence of an effect of *alignment* both in the full-face (effect of alignment: $p<0.005$) and in the top-face (effect of alignment: $p<0.005$) formats but not in the bottom-face format (effect of alignment: $p=0.7$).

3. Discussion

The main observation of our study is that the N170 is substantially increased and delayed when the two halves of a face stimulus are spatially misaligned, so that the whole face stimulus is broken into two separate parts. This effect is bilateral but particularly large in the right hemisphere. As such, these results replicate the recent observations of Letourneau and Mitchell (2008), with a denser and more extended coverage of the whole head in the present study. We also note the similarity between this previous study and the present observations; even though here we used a task that did not explicitly called upon holistic face processing. Importantly, here we were able to disentangle this ERP effect from general effects of spatial misalignment of visual patterns by adding a condition in which the aligned/misaligned unattended bottom part of the stimulus was made of visual noise (i.e. top-face), and a condition in which the fixated top part was made of visual noise (i.e. bottom-face). We observed that the increase in the amplitude and latency of the N170 due to misalignment was the largest when *both* the top and the bottom halves of the stimulus were made of face parts compared to when one half of the stimulus was made out of visual noise. We also observed a smaller increase of N170 latency and amplitude in the latter two conditions when the two parts of the stimulus were misaligned. However, these effects were much smaller, especially in the bottom-face condition, and no hemispheric lateralization was found[3]. These observations indicate that the effect of misalignment on the N170 for whole faces is not merely due to a general effect of misalignment of visual patterns. Moreover, this suggests that the latency and amplitude increases of the N170 component in the right hemisphere following the disruption of the normal face configuration by misalignment, is specific, to a large extent, to whole face stimuli. Since the N170 represents a reliable marker of early activation of facial representations in the human brain (Rossion and Jacques, 2008), this observation suggests that breaking a face stimulus in two separate halves delays the activation of these representations and increases the neural representation of the face stimulus.

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[3] An increase in the latency of the N170 was however found for misaligned bottom face condition in the right hemisphere. This is probably due to the fact that in this condition, the only face information present in the image appears in the hemifield ipsilateral to the right hemisphere (i.e. the right visual field), which may have delayed the N170 (see Jacques and Rossion, 2007b). Indeed, in this condition, no latency effect was found in the left hemisphere in contrast to the full face condition.

As noted previously (Letourneau and Mitchell, 2008), the effect of misalignment of two face halves on the N170 shows a striking similarity to the effect of face inversion. Since these two kinds of manipulations are commonly used in behavioural studies to disrupt holistic face processing (see Fig. 1), this observation reinforces the view that this N170 amplitude and latency increase is directly related to a disruption of holistic processing (Rossion et al., 1999). Along the same lines, changing the position of the inner facial features also delays and increases the N170 (Caharel et al., 2006; George et al., 1996; but see Zion-Golumbic and Bentin, 2007), as other manipulations that disrupt the usual configuration of a face do ("thatcherization," Carbon et al., 2005; Milivojevic et al., 2003; contrast reversal, Itier et al., 2007). The present observation of a larger increase of the N170 latency and amplitude due to spatial misalignment for full faces compared to top-face or bottom-face also parallels the finding of a larger N170 inversion effect for faces compared to non-face categories, which has been described as a signature of the face processing system (Itier et al., 2006; Rossion et al., 2000; Rousselet et al., 2004). Hence, somewhat paradoxically, when a visual face stimulus cannot be processed as a whole entity but remains nevertheless visible and interpretable by the visual system as a face, the neural representation of this stimulus, at a global scale, is not only slowed down, but also increased. Recent observations indicate that, at least for inversion, these early electrophysiological increases of amplitude and latency are not an epiphenomenon: they are directly correlated to the efficiency with which observers are able to process faces (Jacques and Rossion, 2007a). Overall, these observations support the view that the early activation of facial representations in the human brain is inherently global, or holistic.

In addition to the main experiment with upright stimuli, we performed a control experiment with inverted stimuli. This experiment aimed at providing further support to the hypothesis that the large N170 effects of misalignment observed for whole faces are related to a disruption of holistic processing. We used inverted faces in this control experiment for two reasons. First, inverted and upright faces have identical low-level visual properties, except for their 180° difference of orientation in the picture plane. Second, as already mentioned, face inversion disrupts the ability to perceive a face as a whole template (i.e. holistic perception). For these reasons inverted faces have been widely used in the face processing literature as an adequate control stimulus to study holistic face processing. In a nutshell, results of this control experiment are twofold. First, the N170 component was not larger for misaligned compared to aligned stimuli in any of the three face format conditions. Second and most importantly, unlike with upright stimuli, we did not observe a larger effect of misalignment on the N170 amplitude and latency for whole face stimuli compared to stimuli containing half of a face and visual noise. These findings further reinforce the view that the effects of misalignment on the N170 are due to the disruption of holistic processing for misaligned whole faces. That is, the absence of a differential effect of misalignment on the N170 for whole faces was expected given that inversion already disrupts holistic face processing. Similarly to this observation, a massive reduction in the magnitude of the composite face illusion (i.e. a manifestation of holistic processing of individual

faces) is usually reported in behavioural experiments following upside-down inversion of the face stimuli (Goffaux and Rossion, 2006; Hole, 1994; Le Grand et al., 2004; Michel et al., 2006; Rossion and Boremanse, 2008). Moreover and importantly, upright and inverted stimuli from our original and control experiments were identical in terms of visual complexity and other low-level visual properties. Therefore, the findings from the control experiment ensure that the differential effects of misalignment across face formats observed for upright stimuli cannot be accounted for by such differences in visual properties across face formats. They also ensure that alignment effects found for upright stimuli are not due to differences in low-level visual properties (i.e. overall size, spatial frequency distribution, …) between aligned and misaligned stimuli.

3.1. Amplitude and latency variations of the N170 following inversion/misalignment

When comparing the N170 amplitude and latency over the six conditions in the present experiment, we found that these two parameters did not show the same response profiles, reinforcing the view that they may reflect partly distinct functional processes involved in face processing (see Jacques and Rossion, 2007a). Indeed, while variations of N170 latency and amplitude may be highly positively correlated when varying face orientation (Jacques and Rossion, 2007a), these N170 parameters may also be negatively correlated when manipulating the amount of visual noise added to a face image (Jemel et al., 2003). In the present experiment we also observed dissociations between N170 latency and amplitude modulations. On the one hand, we observed an increased N170 *latency* as soon as we replaced half of the face with visual noise, even without misaligning the face parts (Figs. 3 and 5). On the other hand, replacing half of the face with visual noise did not reduce the N170 amplitude when the noise replaced the *bottom* part of the face (top-face), and it strongly reduced the N170 amplitude when the noise replaced the *top* part of the face and the remaining bottom part of the face was out of fixation (bottom-face). Similarly, while misalignment increased both the N170 latency and amplitude in the full-face condition, only the amplitude was increased in the top-face condition. The latency delay of the N170 is generally found whenever a full face is transformed, not only by inversion, misaligning face halves or replacing them with visual noise as performed here, but also by scrambling inner features (Caharel et al., 2006; George et al., 1996; Zion-Golumbic and Bentin, 2007), presenting the eyes alone or the face without the eyes (e.g., Bentin et al., 1996; Eimer, 1998; Itier et al., 2006; Itier et al., 2007). The most straightforward interpretation of this latency effect is that populations of neurons in the visual cortex accumulate evidence that a face is present in the visual environment more slowly if the face stimulus is transformed, i.e. does not fit with a full face template (Perrett et al., 1998). The N170 latency increase is also in line with the observation of a delay in the response of populations of face-selective neurons to inverted faces in the monkey infero-temporal cortex (Perrett et al., 1988; see also supplementary material in Tsao et al., 2006). These observations reveal that different manipulations

of a face stimulus yield dissociable patterns of modulation of the amplitude and the latency of the N170. This suggests that despite the similarity of electrophysiological effects on the N170 following face manipulations it should not be concluded that all these transformed stimuli are processed the same way overall. A misaligned face stimulus is certainly not processed like an inverted face for instance, even though in both cases the normal full configuration of the face is disrupted. Moreover, while inverting a face leads to a modification both in the global and local face configuration and in the orientation of the local facial features (e.g. eyes, nose), breaking up the face in two halves mostly affect the global face configuration while preserving *most* of the local information (i.e. the nose is *not* preserved by spatial misalignment).

In contrast to the latency effect due to face inversion or misalignment, the amplitude increase of N170 to inverted faces is more puzzling because it is incompatible with the reduced response to inverted faces of most single neurons coding for faces in the monkey infero-temporal cortex (Tanaka et al., 1991; Tsao et al., 2006), with the absence of amplitude difference between upright and inverted faces at face-specific intracranial N170 over the fusiform gyrus (McCarthy et al., 1999; Rosburg et al., 2010), or with the finding that the BOLD signal in fMRI in the brain areas responding preferentially to faces in the middle fusiform gyrus ("FFA"), the inferior occipital gyrus ("OFA") and the posterior portion of the STS is either similar (Aguirre et al., 1999; Epstein et al., 2006; Haxby et al., 1999) or reduced (Goffaux et al., 2009; Kanwisher et al., 1998; Mazard et al., 2006; Yovel and Kanwisher, 2005) in response to inverted compared to upright faces.

In contrast to these fMRI findings, the presentation of an inverted compared to an upright face generally *increases* the activation in visual areas that either show a non-specific preference for complex visual stimuli (i.e. either face or non-face) or that respond more to non-face compared to face stimuli, such as in the lateral occipital complex (LOC; Grill-Spector et al., 1999; Malach et al., 1995) or in the medial fusiform/parahippocampal gyrus (Aguirre et al., 1999; Epstein et al., 2006; Goffaux et al., 2009; Haxby et al., 1999; Yovel and Kanwisher, 2005). Hence, if a face is explicitly broken in two parts, or cannot be handled as a whole because of its inverted orientation, not only does it activate face sensitive brain regions, but it would also activate brain regions containing populations of neurons not specific to faces more strongly than would a normal face. Altogether, these findings support the view that the increase in N170 amplitude to inverted and misaligned faces comes at least partly from the fact that both face preferring and non-face preferring regions in the occipito-temporal cortex are activated, leading to a larger overall signal when recorded at scalp level (Rossion et al., 1999; Rossion and Gauthier, 2002). This suggestion is largely supported by a recent study that combined scalp and intracranial EEG recordings in the human brain of epileptic patients (Rosburg et al., 2010). While the scalp vertex positive potential (VPP: counterpart of the N170 recorded at the vertex; Joyce and Rossion, 2005) was larger for inverted faces, as usually found (e.g. Itier and Taylor, 2004; Joyce and Rossion, 2005), the concomitant intracranial face-sensitive response (i.e. intracranial N170)

over the middle fusiform gyrus was *not* larger, but it was significantly delayed in response to inverted faces (see also McCarthy et al., 1999). In contrast, the intracranial N170 recorded over lateral occipital electrodes was significantly larger for inverted faces. Most interestingly, this amplitude increase to inverted faces on the surface of the lateral occipital cortex was found both at electrodes positioned over face-sensitive patches of neurons and at electrodes positioned over patches of neurons that responded more to objects than faces, with the amplitude increase to inverted faces appearing proportionally much larger and of longer duration at object-sensitive electrode locations (Rosburg et al., 2010).

Based on these observations, and in line with a similar proposal to account for the increased N170 for inverted faces (Rossion et al., 1999; Rossion and Gauthier, 2002) we suggest that the increase of amplitude of the N170 when misaligning faces may at least partly be related to an increase of activation in populations of neurons that do not show a face-selectivity of response. Such a proposal is compatible with the present observation of a difference in the topographies of the N170 for full faces between the aligned and the misaligned conditions (Figs. 4 and 6). Specifically, such a difference of topography is an indication either that (at least partly) different neural sources are involved in generating the topographies in the aligned and misaligned conditions, or that identical neural sources are active in the two conditions but the pattern of activation of the sources are different. Moreover, in the full face condition, the maximal difference between aligned and misaligned faces was observed after the N170 peak (around 170 ms, see Fig. 3) over lateral occipital electrodes, further reinforcing the view that a source normally not active for normal faces may be activated when face parts are misaligned.

3.2. N170 *effects of misalignment for upright top-face and bottom-face conditions*

Even though the effect of misalignment on the N170 amplitude for upright stimuli was larger in the full face condition, there was still a strong effect of misalignment in the top-face and the bottom-face conditions. This alignment effect when visual noise was present either in the bottom or the top part of the stimulus cannot be solely attributed to spatial misalignment *per se* given that no such effect of misalignment was observed for inverted stimuli even though identical stimuli and conditions were used. These misalignment effects in the upright top-face and bottom-face conditions suggest that the aligned version of these stimuli containing some remaining visual properties of a face (i.e. either the eye region or the mouth region, a coherent vertical configuration and the spatial frequency amplitude spectrum of a face in the visual noise), can at least partly activate a face representation, although with a small delay compared to a normal face. Indeed, the increased amplitude of the N170 for the misaligned versions may indicate that misalignment further disrupted the processing of these "face-like" stimuli. The observation that the N170 topographies differ between aligned and misaligned formats even in the top-and bottom-face conditions supports this proposal. The misalignment effect was particularly large in the top

face condition, and especially so in the right hemisphere. In this condition the N170 amplitude and topography was similar to that measured for full faces, with a slight latency delay. This larger misalignment effect for the top face condition could be generated by the fact that, in this condition, participants fixated the part of the stimulus where the face information was present, whereas the face information (i.e. mouth region) was out of fixation for the bottom face condition. However, this is unlikely given the absence of such a differential effect of alignment on the N170 amplitude between the top face and the bottom face conditions in the inverted orientation. More interestingly, this larger effect of misalignment for the top face condition could reflect the overall dominant role of the eye region in face perception (e.g. Haig, 1985; Sadr et al., 2003). These observations further support the view that the initial basic-level face categorization in the occipito-temporal cortex is based on a global and relatively coarsely defined representation (possibly centred around the eye region) (Sergent, 1986; Sugase et al., 1999). It also highlights the importance of the global face shape/contour in the activation of an early face representation during the N170 time-window, in agreement with previous evidence that the latency and amplitude of the N170 are highly sensitive to the presence of a face contour (Shibata et al., 2002; Zion-Golumbic and Bentin, 2007). The highlighted importance of the global face shape in the activation of face representation during the N170 could also account for the absence of a larger N170 in the top face (which contains mainly the eyes) compared to the full face condition, whereas previous studies have consistently reported that the N170 is larger for eyes presented in isolation compared to a normal face (e.g. Bentin et al., 1996; Itier et al., 2007).

In summary, we found that the N170 is increased and delayed when the two halves of a face stimulus are spatially misaligned and cannot be processed holistically. Moreover, this effect cannot be accounted for by a general effect of spatial misalignment of visual patterns. These observations support the view that a face is processed globally or as a whole template during its initial visual encoding as reflected by the N170.

4.   Experimental procedures

4.1.   *Participants*

Thirteen paid volunteers (12 females, 2 left-handed, mean age = 22 ± 1.7 years) participated in both experiments. All participants had normal or corrected-to-normal vision.

4.2.   *Stimuli and procedure*

A set of 25 greyscale face photographs were used in the experiments. Faces were cropped to remove background, hair and everything below the chin. Each face was horizontally cut in two halves above the nostrils. The 25 top and bottom halves were then embedded in visual noise created by randomizing the phase of each original top and bottom halves of the 25 faces. The phase randomization procedure

yields images that preserve the global low-level properties of the original image (i.e. luminance, contrast, spatial frequency amplitude spectrum), while completely degrading shape information. The top and bottom face parts embedded in visual noise were then used to create 25 top and bottom noise stimuli using the same phase randomization procedure. Top and bottom halves of the faces were embedded in visual noise before phase randomization so that face and noise stimuli were matched for global low-level visual properties and subtended equal shape and size. These top and bottom halves were then combined to create 6 different stimulus conditions (Fig. 2) defined by crossing the factors *alignment* (2 levels: aligned vs. misaligned top and bottom halves) and *format* (3 levels: "full-face": top = face and bottom = face; "top-face": top = face and bottom = noise; "bottom-face": top = noise and bottom = face). Top and bottom parts were always separated by a 3 pixel gap as commonly done in behavioural studies to allow the observers to identify the top parts to match/discriminate equally easily in the aligned and misaligned conditions (e.g., Michel et al., 2006). At 100 cm viewing distance, aligned stimuli subtended $2.9° \times 4.5°$ of visual angle (top and bottom halves: each $2.9° \times 2.2°$; gap between top and bottom: 0.07°). For experiment 1 with upright stimuli, in the misaligned condition the *bottom* part of the stimulus was displaced by 0.7° toward the right visual field. For experiment 2 with inverted stimuli, in the misaligned condition the *top* part of the stimulus was displaced by 0.7° toward the right visual field. Therefore the distance between the centre of the top part and the centre of the bottom part was about 2.22° in the aligned condition and about 2.34° in the misaligned condition.

Stimuli were displayed against a light grey background using E-prime 1.1 (PST). In each trial a stimulus was presented for 300 ms followed by a blank-screen interval of random duration (1200–1800 ms). In experiment 1 with upright stimuli, participants were instructed to fixate the top part of the stimulus and to press a response key with their right hand whenever the top part appeared colorized in red. In experiment 2 with inverted stimuli, participants performed the same task while fixating the bottom part of the stimulus. This task was used to maintain participants' fixation on the top (for experiment 1) or the bottom (for experiment 2) part of the face, without eliciting differences in difficulty of processing between conditions (orthogonal task). These rare targets appeared randomly during each experiment in 28 out of 328 trials and were removed from further ERP analyses. Both experiments contained 4 blocs of 82 trials, the order of the 6 conditions (50 trials per condition) within each block being randomized. All subjects first performed experiment 1 followed by experiment 2.

4.3. 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 kΩ. Vertical and horizontal eye movements were monitored using 4 additional electrodes placed above and below the left eye orbit and on the outer canthus of each eye. EEG analog signal was digitized at a 1000 Hz sampling rate and a digital anti-aliasing filter of 0.27 * sampling rate was applied at recording

(therefore, at 1000 Hz sampling rate, the usable bandwidth is 0 to ∼270 Hz).

EEG data were analyzed using EEprobe 3.2 (ANT, Inc.). After filtering of the EEG with a digital 30 Hz low-pass filter, time windows in which the standard deviation of the EEG on any electrode within a sliding 200-ms time window exceeded 35 μV were marked as either EEG artefacts or blink artefacts. Blink artefacts were corrected by subtraction of a vertical electro-oculogram (EOG) propagation factors based on EOG components derived from principal component analyses. For each subject, EEG epochs containing no EEG artefacts were averaged for each condition separately and baseline corrected using the 200-ms pre-stimulus time window. Participants' averages were then re-referenced to a common average reference, as recommended for N170 studies (Joyce and Rossion, 2005).

For experiment 1, two separate sets of analyses were performed on the ERP signal recorded at the scalp in response to the stimuli. First, we performed conventional analyses on specific visual potentials, as classically done in studies of face perception (e.g. Bentin et al., 1996; Itier and Taylor, 2004; Jacques and Rossion, 2007a; Rossion et al., 1999): the P1 and N170 components, recorded at posterior sites. Amplitude values of the P1 and N170 components were measured at 5 pairs of occipito-temporal electrodes in the left and right hemisphere (Fig. 4) where both components were the most prominent (P7/8, P5/6, PO7/8, PO5/6, O1/2). Amplitudes were quantified as the mean voltage measured within time-windows centred on the peak latencies of the grand averages measured for each condition and hemisphere separately. We used windows of 30 ms duration for the P1 and windows of 50 ms duration for the N170. In addition, analyses were performed on the latency of the P1 and N170 components measured in one pair of occipito-temporal electrodes (PO7: left hemisphere; PO8: right hemisphere). Statistical analyses were performed using repeated measures analyses of variance (ANOVA) with the factors *alignment* (aligned, misaligned), *format* (full-face, top-face, bottom-face), *hemisphere* (left, right) and *electrode* (5 levels) for amplitude analyses and the factors *alignment*, *format* and *hemisphere* for the latency analyses.

We also tested whether the spatial distribution of N170 amplitude values on the scalp (i.e. topographies) in the aligned and misaligned conditions were equal in shape or not. First we normalized the amplitude values of the N170 using McCarthy and Wood's vector scaling procedure (McCarthy and Wood, 1985). Next we carried out 3 different 2-ways ANOVAs with the factors *alignment* (2 levels) and *electrode* (58 levels) on the normalized N170 amplitude values; one ANOVA being performed for each *format* condition. Greenhouse–Geisser adjustments to the degrees of freedom were used when appropriate in all ANOVAs and polynomial contrasts were performed for *post-hoc* comparisons.

A second set of analyses was performed to characterize more precisely the time-course of the effect of misaligning the bottom part of the stimulus on the ERP response. Specifically, we analyzed ERP data at each electrode as a function of time in a series of pair-wise comparisons between aligned and misaligned conditions for the three different face formats. To statistically identify the onset latency of the differential ERP responses between the conditions compared, a permutation

test (see Blair and Karniski, 1993; Nichols and Holmes, 2002) was performed on each scalp electrode and each time sample. In a given permutation sample, the ERP data (consisting of the whole electrode × time-point matrix) for the two conditions compared are randomly permuted within each subject (i.e. paired comparisons) to obtain two new bins of size N. Because permutation shuffles the assignment of the conditions, the difference between the means of the two new bins reflects the difference between conditions under the null hypothesis. We performed 8000 permutations to generate a distribution of ERP differences expected under the null hypothesis. The p-value corresponded to the fraction of the randomly generated differences (i.e. the permutation distribution) which were greater than or equal to the observed ERP difference between the two conditions. The results of this analysis are displayed as time by electrode statistical plots in which significant effects of alignment are color-coded as a function of the amplitude of ERP difference between aligned and misaligned (see Fig. 6). To minimize the probability of false positives due to the large number of comparisons performed, only significant differences at the $p < 0.01$ (two-tailed), that lasted for at least 20 consecutive time-samples and included a cluster of at least two neighbor electrodes were considered.

For experiment 2, only repeated measures ANOVAs were performed on the amplitude and latency of the N170 component (with identical parameters as in experiment 1) as this experiment was mostly intended as a control for the N170 observations of experiment 1.

Acknowledgments

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