Electrophysiological correlates of the composite face illusion: Disentangling perceptual and decisional components of holistic face processing in the human brain

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ABSTRACT

When the bottom halves of two faces differ, people's behavioral judgment of the identical top halves of those faces is impaired: they report that the top halves are different, and/or take more time than usual to provide a response. This behavioral measure is known as the composite face effect (CFE) and has traditionally been taken as evidence that faces are *perceived* holistically. Recently, however, it has been claimed that this effect is driven almost entirely by decisional, rather than perceptual, factors (Richler, Gauthier, Wenger, & Palmeri, 2008). To disentangle the contribution of perceptual and decisional brain processes, we aimed to obtain an event-related potential (ERP) measure of the CFE at a stage of face encoding (Jacques & Rossion, 2009) in the absence of a behavioral CFE effect. Sixteen participants performed a go/no-go task in an oddball paradigm, lifting a finger of their right or left hand when the top half of a face changed identity. This change of identity of the top of the face was associated with an increased ERP signal on occipito-temporal electrode sites at the N170 face-sensitive component (∼160 ms), the later decisional P3b component, and the lateralized readiness potential (LRP) starting at ∼350 ms. The N170 effect was observed equally early when only the unattended bottom part of the face changed, indicating that an identity change was perceived across the whole face in this condition. Importantly, there was no behavioral response bias for the bottom change trials, and no evidence of decisional biases from electrophysiological data (no P3b and LRP deflection in no-go trials). These data show that an early CFE can be measured in ERPs in the absence of any decisional response bias, indicating that the CFE reflects primarily the visual perception of the whole face.

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1. Introduction

The efficiency with which human adults are able to recognize hundreds or perhaps even thousands of faces has been proposed to depend on the ability to process faces in a *holistic* manner. To process a face holistically means that rather than processing local facial features (eye, nose, mouth, ears...) independently, the face is processed as a single global perceptual representation, i.e. as a whole. This implies that a modification to a subset of features, or even to one feature, is capable of altering the perception of the overall face (Galton, 1883). This dependant relationship between the processing of local features and of the entire face has been demonstrated in a number of classical behavioral experiments (e.g., Sergent, 1984; Tanaka & Farah, 1993; Tanaka & Sengco, 1997). However, the most compelling evidence favoring the idea

that faces are processed holistically comes from the composite face effect (CFE, Young, Hellawell, & Hay 1987).

The CFE was first described (Young et al., 1987) as an increase in the time needed to name the top part of a familiar face (cut below the eyes) when it is aligned with the bottom part of another face, relative to the time needed to name the top part when the same top and bottom parts are laterally offset (i.e. misaligned). With respect to unfamiliar faces, this effect emerges as a result of a visual illusion: identical top halves of faces are perceived as being slightly different when they are aligned with different bottom halves (see Fig. 1; see also Rossion, 2008; Rossion & Boremanse, 2008). This visual illusion nicely demonstrates that facial features (here the two halves of the face) cannot be perceived independently from one another, but rather that the face is perceived as a whole.

Since originally being reported, the CFE has been observed consistently in matching tasks that require discrimination of individual, unfamiliar, composite faces (see Hole (1994) for a first demonstration). In these tasks, participants are more likely to judge two identical top halves of a face as being different when they are presented with different bottom parts that are aligned with the top parts, in comparison to when the top and bottom

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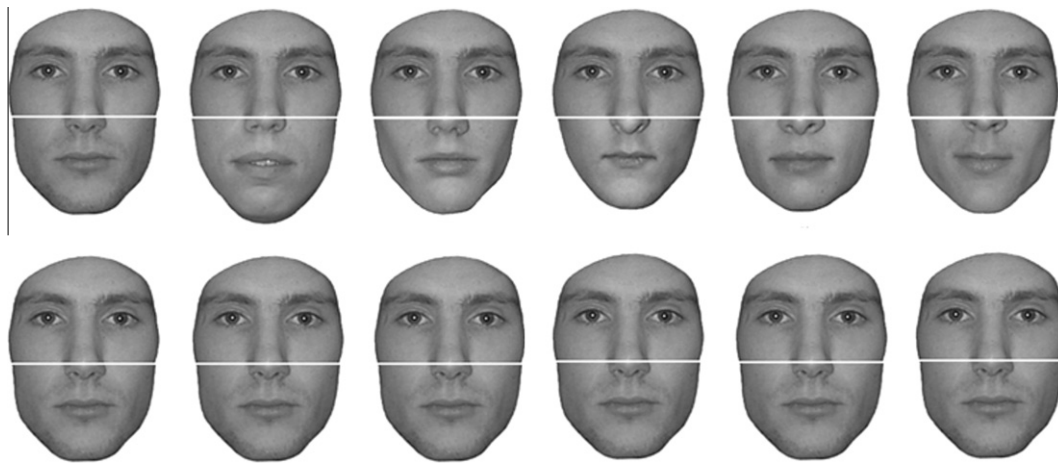E-mail address: dana.kuefner@uclouvain.be (D. Kuefner).

Fig. 1. Illustration of the composite face illusion. All top halves (above the white line) are identical, but when aligned with distinct bottom parts (top row), they appear slightly different. This illusion reflects the perception of the face stimulus as an integrated whole. When the two halves of the face are aligned with identical bottom parts (bottom row), it becomes obvious that the top parts are the same.

parts are misaligned. This happens despite the fact that the bottom parts of the face are irrelevant for the task, (e.g., Goffaux & Rossion, 2006; Le Grand, Mondloch, Maurer, & Brent, 2004; Michel, Rossion, Han, Chung, & Caldara, 2006; Robbins & McKone, 2007; Taubert & Alais, 2009) and that eye gaze remains fixed on the top parts of the faces (de Heering, Rossion, Turati, & Simion, 2008). When faces are inverted, the composite effect either disappears or is strongly attenuated (e.g., Goffaux & Rossion, 2006; Hole, 1994; Hole, George, & Dunsmore, 1999; Rossion & Boremanse, 2008; Young et al., 1987).

1.1. Is the composite face effect driven by decisional response biases?

Overall, the existing evidence demonstrating interdependent processing of the top and bottom halves of composite faces has led researchers to propose that the functional locus of the CFE is perceptual (Farah, Wilson, Drain, & Tanaka, 1998; Rossion, 2008, 2009). That is, that faces are *perceived* holistically. However, the perceptual nature of holistic face processing in general (Wenger & Ingvalson, 2002), and of the CFE in particular, has recently been challenged (Richler, Gauthier, Wenger, & Palmeri, 2008; see also Cheung, Richler, Palmeri, & Gauthier, 2008; Richler, Tanaka, Brown, & Gauthier, 2008). Specifically, Richler, Gauthier, et al. (2008) used the multidimensional generalization of signal detection theory known as *general recognition theory* (GRT; e.g., Ashby & Townsend, 1986; Kadlec & Townsend, 1992; Thomas, 1995) to analyze data from a behavioral same/different discrimination task with composite faces. Using GRT, the authors inferred that the composite effect is driven both by perceptual, as well as decisional (i.e. response related) factors, with the most consistent evidence pointing to a decisional locus of the effect. Although the authors admitted that signal detection theory could not speak to *how* decisional factors may influence the outcome of a composite face task, they suggested that decisional biases may be gained through experience. In particular, the authors postulated that extensive experience with faces may cause people to develop a deeply ingrained assumption that face parts change together. The strength of this assumption would make it difficult to override during an experiment, even when participants are instructed to selectively attend only to the top half of the face. This bias, in turn, would affect the percept of the face, as measured by the composite face task. Richler, Gauthier and colleagues (2008) suggested that such a decisional bias, because it relates to a domain of expertise, may be deeply ingrained and relatively immune to task influences.

1.2. Neuroimaging and electrophysiological evidence for a perceptual locus of the composite face effect

It is reasonable to assume that decisional response biases may arise as a consequence of the perception of the composite face illusion. That is, when observers are presented with two identical top halves of faces each paired with a different bottom half, they tend to make more errors (i.e. respond "different") and/or take more time when having to match the face halves. However, the claim that holistic face processing is *driven* by decisional factors (Richler, Gauthier, et al., 2008) seems difficult to reconcile with the available neuroimaging and electrophysiological evidence from studies of the CFE. For example, fMRI studies have shown that following adaptation to an aligned composite face, there was a significantly larger response to the same top part of a face when it was aligned with a different bottom part as compared to when it was aligned with the same bottom part. This "neural CFE" was found particularly in the right middle fusiform gyrus (rMFG), as well as less strongly in the right inferior occipital gyrus (IOG) (Schiltz, Dricot, Goebel, & Rossion, 2010; Schiltz & Rossion, 2006) two areas of the human visual cortex that have been shown to respond preferentially to faces ("FFA" and "OFA" respectively; Gauthier et al., 2000; Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy 1995; Sergent, Ohta, & Macdonald 1992). These results, which were not found when faces were spatially misaligned or inverted, suggests that neurons in these visual areas integrate information from the two aligned face halves into a single representation of the whole face.

Most recently, evidence from scalp event-related potentials (ERPs) showed that following adaptation, top halves of faces with different aligned bottoms produced larger responses than the same top halves of faces with the same bottoms, as early as 160 ms post-stimulus onset (Jacques & Rossion, 2009),[1] on the face-sensitive N170 component (Bentin, McCarthy, Perez, Puce, & Allison, 1996; see Rossion & Jacques, 2008, 2010). Again, this was not the case when the faces where spatially misaligned. Since the face-sensitive N170 component at occipito-temporal recording sites is independent of

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[1] Other recent studies have reported modulations of the N170 to aligned and misaligned halves of faces as in the composite face effect (Ishizu, Ayabe, & Kojima, 2008; Jacques & Rossion, 2010; Letourneau & Mitchell, 2008). These studies reported an increased and delayed N170 when face halves were spatially misaligned. However, they did not test the composite face effect in face individualization, by measuring how a perceived change of identity in the top part of the face affects the ERP signal, the N170 amplitude in particular, during face identity adaptation/repetition.

decision making (e.g., Philiastides & Sajda, 2006) and reflects the earliest stage at which individual face representations are accessed (Jacques, d'Arripe, & Rossion, 2007; Jacques & Rossion, 2006), these findings suggest that the initial perceptual representation of an individual face in the human brain is inherently holistic.

1.3. Goals of the current study

Together, fMRI and ERP evidence suggest that information from the two face halves are integrated quite early following stimulus onset, and that this operation is performed by areas of the visual cortex that are known to respond preferentially to faces. However, although the recent ERP findings (Jacques & Rossion, 2009) seem to indicate that there is little room for decisional factors to come into play before a face is processed holistically in face-sensitive areas of the visual cortex, this issue deserves further consideration. Importantly, in the critical condition of the ERP composite face effect, i.e. when the unattended bottom half of the face changes in the aligned condition, observers make errors and are slower to make their behavioral decision than when the same face halves are spatially misaligned (Jacques & Rossion, 2009). This implies that the ERP effects related to the composite face illusion have been observed in a paradigm in which behavioral decisional biases are also, concomitantly, observed. The unresolved question is thus whether electrophysiological evidence for holistic perception of faces can be found in the absence of any kind of decisional bias. Importantly, should this be the case, it would refute the idea that decisional biases give rise to the perceptual effect and are the driving factor in the manifestation of the CFE. Addressing this issue was the focus of the present study.

For this study, we adapted a face identity adaptation paradigm in the context of a visual oddball ERP paradigm. High-density electroencephalogram (EEG) was recorded as participants viewed sequentially presented aligned composite faces. A face with same top and bottom halves was presented on 78% of the trials. On 11% of the trials, the top half of the face was changed, and on the remaining 11% of the trials the bottom half of the face was

changed. Participants attended to the top of the face and responded by lifting their finger only when the top half of the face changed (Go response; see Fig. 2).

With this new paradigm, we expected first to replicate the findings of Jacques and Rossion (2009). That is, we expected to observe an increase of N170 amplitude on trials in which the top half of the face changed (relative to no change), and crucially, we also expected to find the same modulation for trials in which the bottom half of the face changed, reflecting the perception of the composite illusion.

Second, and most importantly, we aimed to disentangle perceptual from decision-related processes of the CFE. With respect to this goal, the strength of the present paradigm lies in the fact that active responses were recruited for *top change* trials but not for *bottom change* or *same* trials. Therefore, in addition to the early ERP components associated with perceptual face processes, we expected to observe response-related components, but only for *top change* trials. In particular, we expected to observe a P3b, an event-related evoked potential peaking on parietal sites that has been proposed to reflect a bridge between perceptual processing and response processing (Verleger, Jaskowski, & Wascher, 2005). Amplitude of the P3b has been described as having an inverse relationship with the probability of the target stimulus (Duncan-Johnson & Donchin, 1977). We thus expected to observe a sizable P3b in the present study, due to the quite low probability of the occurrence of a top change stimulus. Although the exact function of the P3b is not entirely clear, it has been suggested that this component reflects a process of monitoring whether or not the decision to classify some stimulus is appropriately transformed into action (Verleger et al., 2005).

The P3b overlaps with the electrophysiological correlate of the overt go response, i.e. the lateralized readiness potential (LRP) associated with unilateral hand movement (Verleger, Paehge, Kolev, Yordanova, & Jaskowski, 2006). In the present experiment we used a go/no-go paradigm with half of the responses being provided by each hand. This allowed for the ERP effects related to perception to be separated from later processes, including decisional
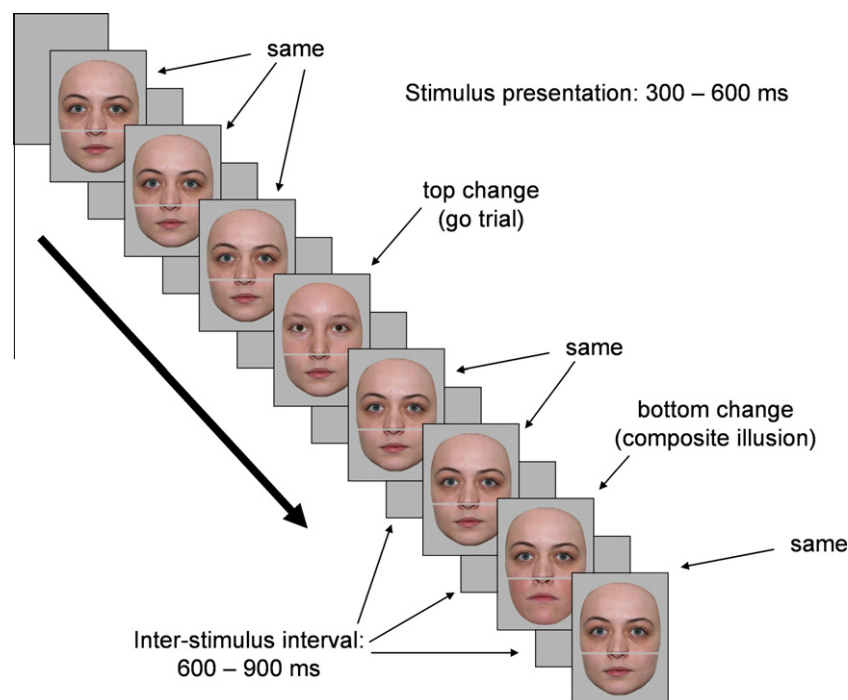

Fig. 2. The experimental paradigm. Top change and bottom change faces were presented pseudo-randomly within a stimulus train of same faces. Participants were instructed to lift their finger only on trials in which the top part of the face was different with respect to the frequent face.

and motor responses, via an analysis of the LRP along the time-course of holistic face processing. The LRP is an electrophysiological potential, measured over central cites corresponding to motor cortex, that reflects the preparation of motor processes prior to the ballistic point of no return (Coles 1989; Miller & Hackley, 1992; for its use in face processing experiments see e.g., Martens, Leuthold, & Schweinberger, 2010). Prior to a movement made in response to a stimulus, EEG activity becomes more negative at electrodes over motor cortex contralateral to the hand that will be used to respond. This excess contralateral negativity in the EEG is reflected in the LRP. Crucially, the LRP is also sensitive to low levels of response activation that are not associated with the ultimate overt behavior. This means that the LRP can develop based on an initial indication that a response may be needed, even if the response is subsequently aborted and never actually executed (e.g., de Jong, Wierda, Mulder, & Mulder, 1988; Hackley & Miller, 1995; Miller, 1998). Thus, the generation of response preparation, as reflected by the LRP, when a response is not required and ultimately not made, indicates that participants are initially biased to act in a particular way based on a particular decisional strategy, even though the actual response is ultimately made on the basis of a different strategy (Coles, 1989; Gratton, Coles & Donchin, 1992; Miller & Hackley, 1992). In other words, the presence of an LRP on no-go trials would indicate that there is a discrepancy between a decision based on initial stimulus analysis, which may activate a response preparation, and the final decision regarding the response that is executed following the completion of stimulus analysis.

By measuring the LRP we were able to test for the existence of a response bias based on a deeply ingrained assumption that all face parts change together (Richler, Gauthier, et al., 2008). Specifically, we hypothesized that if adults inherently assume that all face parts change together, in the current experiment they should begin to prepare a manual response as soon as they detect any change within the face. However, on trials in which the bottom (i.e. the irrelevant, unattended) part of the face changes, to arrive at a correct response (i.e. no response), participants would need to override this bias, and abort their response preparation. The preparation and subsequent abortion of the response on ultimately correct trials should be reflected by the onset and subsequent return to baseline of an LRP on bottom change trials. Rather, if the composite effect is not driven by this type of decisional bias, no LRP should be observed at all on bottom change (composite illusion) trials. The absence of an LRP on bottom change trials would indicate that subjects do not need to overcome any decisional bias to arrive at a correct (non) response when the bottom of the face changes.

To summarize, there were three possible outcomes in the present study. First, an early sensitivity to a change in the bottom half of the face (N170 time-window) could be observed at occipito-temporal sites despite no behavioral response bias, no evidence of a decision-related component (P3b), and no effect of response hand lateralization (LRP) in this condition. This would demonstrate that holistic processing of a face is profoundly perceptual in nature and exists even in the absence of decisional/response biases. Second, the early perceptual effect may be absent, and P3b and LRP may be observed for the no-go bottom change trials. This outcome would support the view that holistic face processing, as assessed in the composite task, has a primarily decisional locus (Richler, Gauthier, et al., 2008). Finally, one may observe both an early effect at occipito-temporal sites associated with a perceptual locus, and P3b, LRP responses for the no-go bottom change trials. The presence of these decision-related components in the bottom change condition would not contradict the view that the origin of the effect is perceptual, provided that the effect is also clearly observed at posterior occipito-temporal sites starting at an earlier time-window. In this case, one could then measure and attempt to relate the

perceptual and decision-related components, in order to better understand the cause and consequence of the holistic processing effect measured by the composite face paradigm.

Finally, there were two other novel aspects of the present study worth mentioning. First, in the study by Jacques and Rossion (2009), the condition in which the whole face was repeated (i.e. "same") was analyzed in comparison to two conditions, one in which only the bottom half of the face changed, and another in which both the top and bottom halves changed simultaneously. In the present study, rather, whenever there was a change in the face, it was only either the top (attended) half or the bottom half which was modified. Hence, the comparison between the top change and bottom change conditions was more adequately balanced in terms of the overall amount of physical change (compared to the "same" condition). Second, we recorded EEG from a much higher density array of electrodes (128 vs. 58) with a more complete sampling of the visual regions of the brain, allowing us to make more precise topographical maps of the effects of interest.

2. Materials and methods

2.1. Participants

The final sample consisted of 16 paid volunteers (8 males; mean age = 21.6, range 18–29 years). EEG was also recorded from four additional participants whose data was removed from further analysis due to excessive artifact contamination. All but two of the participants in the final sample were right handed and all had normal or corrected-to-normal vision.

2.2. Stimuli

Stimuli were created using full-front view photographs of young, Caucasian, adult faces. Each of the four blocks of the experiment contained nine different stimuli. One of the stimuli in each block was the frequent face, four different stimuli made up the *top change* trials, and four different stimuli made up the *bottom change* trials. Top change stimuli were created by replacing the top part of the frequent face stimulus with the top parts of different, previously unseen faces (the bottom of the face was identical). Likewise, the bottom change trials were each created by replacing the bottom half of the frequent face stimulus of each block with the bottom halves of previously unseen faces. Using Adobe Photoshop, we separated the top and the bottom parts of each stimulus by inserting a small gap of approximately 2 mm (0.12° of visual angle) above the nostrils (Fig. 2). This small gap was used so that the border separating the top and bottom halves could easily be identified, and to ensure that participants knew exactly what was meant when referring to "the top part of the face" in the task instructions (e.g., Michel et al., 2006; Rossion & Boremanse, 2008). The size of the stimuli was alternated with each presentation between two possible sizes, the smaller a 10% reduction of the larger, so as to avoid ERP repetition effects due to pixelwise comparison of images. The larger stimuli subtended vertical and horizontal visual angles of 6.9° and 4.5°, respectively. Two of the experimental blocks consisted of male faces, and two of female faces. All faces were free of glasses and facial hair and posed a neutral expression. Faces were cropped to remove background, clothing and hairline, and the resulting full-color images were equated for mean pixel luminance using Adobe Photoshop.

2.3. Validation of stimuli in a behavioral task

In order to ensure that the stimuli used in the present study would generate a classic behavioral CFE, we ran a complementary

behavioral experiment with an independent group of subjects. Seventeen paid volunteers (4 males; mean age = 20.7, range 18–32 years) participated in the behavioral experiment, of which five were left handed. The stimuli for this experiment included the stimuli for the ERP experiment. However, in order to determine if our stimuli would generate a traditional behavioral CFE we also included misaligned versions of the stimuli. Finally, the behavioral study called for more stimuli in each condition compared to the ERP study, so additional stimuli were created. A total of 52 aligned and 52 misaligned stimuli were constructed from the tops and bottom parts of 26 faces. Aligned faces were created identically to those for the ERP study. Misaligned faces were created by slightly offsetting the bottom part of the face to the right of the top part (30 pixels = 0.6° of visual angle). Importantly, like those used in the ERP study, the top and bottom halves of these stimuli were also separated by a small gap of approximately 2 mm (0.12° of visual angle) above the nostrils. The aligned stimuli subtended vertical and horizontal visual angles of approximately 6.0° and 4.0°, respectively and the misaligned stimuli approximately 6.0° and 4.7°.

Stimuli were displayed against a light gray background using *E*-prime 1.1 (PST) at 100 cm viewing distance. On each trial, two face stimuli were presented sequentially, at the center of the screen, either both in the aligned or both in the misaligned format. A trial started with a fixation point displayed at the center of the screen for 250 ms. Then, the first face appeared for about 200 ms with the top part being presented at fixation. The offset of the first face was followed by a blank interval of 300 ms and then the second face (test face) was presented for 200 ms. An inter-trial-interval of about 1000 ms separated the offset of the test face from the next trial. Identity of the top and the bottom parts was manipulated between the first and the test face in three conditions. In one third of the trials, both the top and bottom parts of the test face stimulus were identical to those of the first face ("same" condition). In a second third of the trials, only the bottom part of the test face stimulus was different from that of the first face, the top part being identical ("bottom change" condition). This condition was critical as it leads to the perception of a new identity in the aligned and not in the misaligned format. For the last third of the trials, the top part of the test face stimulus was different from that of the first face ("top change" condition). Importantly, the same pairs of faces were presented in the aligned and misaligned orientations, so that any effect cannot be attributed to the particular pairing of first and test faces. Participants were instructed to attend only to the top part of the face (appearing at fixation) and to press one of two response keys corresponding to whether the top parts of the first and test faces were the same or different. Participants performed 52 trials per condition, resulting in 312 trials. The order of conditions was randomized within each block.

2.4. ERP procedure

After placement of the electrode cap, participants were seated at a table 100 cm from a computer monitor. They placed the index finger of either their right or left hand on a light-sensor response box positioned on the table in front of them. They were instructed that pictures of faces would be shown in rapid succession, and that their task was to attend to the top part of the face and to lift their finger only when the top half of the stimulus was different from that of the first, and frequent, stimulus of each block. Stimuli were displayed using *E*-prime 2.0 on a light grey background. Participants completed four blocks with one hand, and then repeated the same four blocks, in the same order, with the other hand. Half of the participants began the experiment using their right hand, the other half began with their left hand. Each stimulus remained on the screen for about 450 ms (randomized between 300 and 600 ms), and was followed by an inter-stimulus-interval of approx-

imately 750 ms (randomized between 600 and 900 ms). Participants completed 200 trials per block, resulting in a total of 1600 trials. Fig. 2 depicts an example of a possible sequence of events with this paradigm. Seventy-eight percent of trials in each block were presentations of the frequent stimulus. Top change and bottom change stimuli each accounted for 11% of the trials in each block. The order of trials in each block was pseudo-random, with at least two, and a maximum of five, presentations of the frequent stimulus between each top or bottom change trial. In addition to the small change in the size of the stimuli on each trial, to avoid ERP repetition effects due to pixelwise comparison of images, the position of the stimulus on the screen changed slightly from one trial to the next. The range of possible vertical/horizontal offset relative to the center of the screen was set to 0.7°.

2.5. EEG recording

Scalp EEG was recorded from 128 Ag/AgCl electrodes mounted in an electrode cap (Wavegard, ANT Inc.), with a left mastoid reference. Electrodes were positioned according to the standard 10–20 system with additional intermediate positions. Two pairs of bipolar electrodes were used to record vertical and horizontal eye movements. Electrode impedances were maintained below 10 k during recording. EEG analog signal was digitized at a 1000-Hz sample rate and a digital analog-aliasing filter of 0.27* sampling rate was applied at recording (at 1000 Hz sampling rate the usable bandwidth is 0 to approximately 270 Hz).

EEG data were analyzed using ASA 4.6 (ANT, Inc.) and custom-made routines in Matlab 7.0. EEG was filtered with a bandpass filter of .1–30 Hz for all analyses except for that of the LRP. Do to the slow nature of the LRP we used a bandpass filter of .01–8 Hz for the analysis of this component. Time points in the filtered data at which the absolute amplitude of the EEG exceeded ±75 µV were marked as EEG artifact or blink artifacts. Blink artifacts were corrected, when necessary (performed on data from five subjects), by subtraction of a vertical electroculogram (EOG) propagation factors based on EOG components derived from principal component analysis. Trials containing EEG artifacts were rejected from further analyses, as were trials containing an incorrect behavioral response. Data were then averaged in epochs from 200 ms pre-stimulus onset to 800 ms post-stimulus onset. Averages were baseline corrected using the 200 ms pre-stimulus epoch and re-referenced to a common average reference. In order to ensure that the average for the frequent stimulus condition was calculated using a comparable number of trials to the averages of the top or bottom change conditions, we constructed two different averages for the frequent stimulus condition. The first average was created using the frequent stimuli that immediately preceded each top change trial (same pre-top trials). The second average was created using the frequent stimuli that immediately preceded each bottom change trial (same pre-bottom trials). For the purposes of the analyses, the average of the top change trials was compared to the average of the same pre-top trials, and the average of the bottom change trials was compared to the average of the same pre-bottom trials.

2.6. ERP analyses

We performed three types of analyses on the averaged ERP signals. First, as typically done in studies of face perception, we performed analyses on the peak amplitude values for the two first well identified visual components: the P1 (maximal at approximately 100 ms over the lateral occipital sites) and the N170 (maximal at approximately 160 ms on occipito-temporal sites for faces). Amplitude values were measured at six pairs of occipito-temporal electrodes in the right and left hemisphere for the P1, and at five pairs of occipito-temporal electrodes for the N170. Measures for

each component were taken from electrodes at which each component was most prominent, as observed on topographical maps (P1: PO7/PO8, PPO9h/PPO10h, PO9/PO10, O1/O2, POO9h/POO10h, I1/I2; N170: P9/P10, PPO9h/PPO10h, TPP9h/TPP10h, PO9/PO10, P7/P8, positions of the right hemisphere electrodes are indicated in Fig. 3. Also, a map of all electrode positions can be accessed here: http://www.ant-neuro.com/products/caps/waveguard/layouts/128/). Topographical distribution of the P1 and N170 can be seen clearly in Fig. 3, at 100 and 150 ms respectively. Amplitudes were quantified for each condition as the maximum voltage in individual subject averages, measured within a 30 ms window centered on the peak latency of each component as determined in the grand averaged waveform. These amplitude values were then submitted to repeated measures analyses of variance (ANOVAs) with the factors *condition* (change trials, same pre-change trials), *hemisphere* (left, right) and *electrode* (6 or 5 levels for the P1 and N170 respectively). Separate ANOVAs were conducted to compare the top change and the same pre-top-change conditions, the bottom change and the same pre-bottom change conditions, and the top change and the bottom change conditions.

Besides analyses on specific visual components of interest, well identified in all participants, we aimed at characterizing more precisely the time-course of holistic face processing in this experiment. Specifically, we analyzed EEG data at each electrode as a function of time in a series of pair-wise comparisons between the conditions of interest. These comparisons were performed between the top change and the same pre-top condition as well as between the bottom change and same pre-bottom condition. To statistically identify the latency of the onset of differential ERP responses between the compared conditions, we performed permutation tests (see Blair & Karniski, 1993; Nichols & Holmes, 2002) on each scalp electrode for each time sample in the ERP averages. This method has previously been used to assess the time-course of ERP face identity adaptation effects (Caharel, d'Arripe, Ramon, Jacques, & Rossion, 2009; Jacques et al., 2007; Jacques & Rossion, 2009; see also Rousselet, Pernet, Bennett, & Sekuler, 2005). In a given permutation sample, the ERP data (consisting of the whole electrode ∗ time-point matrix) for the two compared conditions 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 10,000 permutations to generate a distribution of ERP differences under the null hypothesis. Comparing the observed ERP difference between the two conditions compared with the permutation distribution allowed for the estimation of the probability that this observed ERP difference was due to chance (i.e. a *p*-value). The results of this analysis are displayed in both time-by-electrode statistical plots as well as topographical maps at discrete time points, where significant differences between the ERPs of the compared conditions are color-coded as a function of the amplitude of the difference. To minimize the probability of type I errors (false positives), resulting from the large number of comparisons performed, only differences at $p < 0.01$ (two-tailed), persisting for at least 20 consecutive time samples (Rugg, Doyle, & Wells, 1995) and including a cluster of at least two neighboring electrodes were considered significant.

Finally, we measured the lateralized readiness potential (LRP) for the top change and bottom change trials. The LRP was calculated via a two-step, data point subtraction procedure (Gratton,
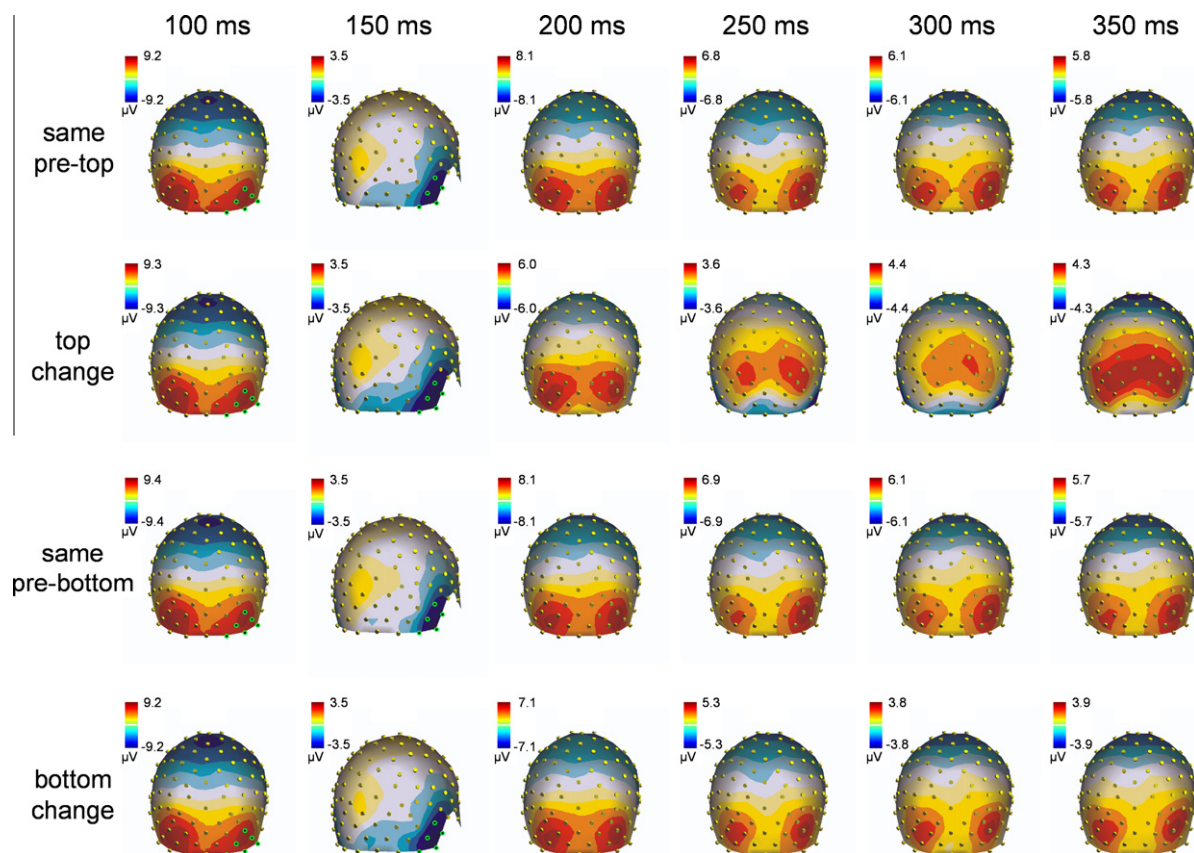

Fig. 3. Topographical plots of EEG activity for each of the 4 conditions at 50 ms intervals starting at 100 ms, the time of the P1. All plots are viewed from the back of the head, with the exception of the 150 ms plot, which has been tilted to reveal the right-dominant activity of the N170. The electrodes from the right hemisphere included in the P1 and N170 analyses are indicated in green on the 100 ms and 170 ms plot, respectively. Note that the topographies are highly similar for all conditions until the 250 ms window, at which point the activity for the top-change condition begins to differ from that of the other 4 conditions. Note also the difference in scale across the different maps.

Coles, Sirevaag, Eriksen, & Donchin 1988; Miller & Hackley, 1992). First, amplitude values of the electrode reflecting activity of motor cortex (C3 or C4) of the ipsilateral side to the hand used for the response were subtracted from activity at the contralateral electrode, yielding a difference waveform equivalent to a bipolar derivation. Next, an average waveform was calculated from the difference waveform for trials on which the right hand was used and the waveform for trials in which the left hand was used. This averaging procedure eliminates any lateralized potentials not specific to the response (e.g., sensory evoked potentials), leaving a pure measure of movement-related lateralization. Waveforms of the LRPs were digitally smoothed using an 8 Hz low-pass filter to eliminate high-frequency noise in the waveform (e.g., Miller, 1998; Prime & Ward, 2004). Because the readiness potential is negative at central scalp sites, lateralization that is consistent with the cued response appears as increased negativity. The onset of the LRP was determined as the time point at which the waveforms began to differ significantly from zero for at least 25 consecutive time bins using a simple one tailed *t*-test with a threshold of $p < 0.01$.

3. Results

3.1. Behavioral stimuli validation task

Analyses of the behavioral stimulus validation task revealed a significant interaction between alignment and identity ($F(1, 16) = 6.78$, $p < 0.02$) with a highly significant difference in accuracy between the *same* and *bottom change* conditions for aligned faces ($p < 0.001$) but a smaller difference for misaligned stimuli ($p > 0.05$).

Response time data also showed a highly significant difference between *same* and *bottom change* trials for aligned faces ($p < 0.001$) but a smaller, non significant difference for misaligned stimuli ($p > 0.05$) even though the interaction was only marginally significant (($F(1, 16) = 3.85$, $p = 0.067$).

Overall, we determined that stimuli created in this manner do elicit a traditional behavioral CFE.

3.2. Behavioral data from ERP task

Participants' performance was at ceiling on the go/no-go task. They correctly responded to the *top change* trials ($M = 98.4\%$) with the same frequency with which they correctly inhibited a response on the *bottom change* trials ($M = 98.3\%$). Accuracy rates did not differ based on the hand used to make the response (left hand $M = 98.17\%$, right hand $M = 98.45\%$). The few trials with incorrect responses where removed from further analyses so that the electrophysiological correlate of the CFE could be analyzed without being contaminated by trials in which a behavioral response indicated a decision based on the changed bottom half of the face. This resulted in an approximately equal number of trials for top change and bottom change conditions.

The overall mean response time (RT) to *top change* trials with correct responses was 522 ms. RTs did not differ based on the hand used to provide the response (left, 521.9 ms; right, 522.3 ms).

3.3. Electrophysiological data

3.3.1. Peak component analyses
3.3.1.1. P1. In line with previous studies showing that sensitivity to differences between individual faces is not present as early as the P1 (Jacques et al., 2007), we found no effect of face identity change at this time point, either when the top or the bottom of the face changed. The absence of modulation by condition at the P1 is clearly visible in the topographic plots (Fig. 3, 100 ms) as well as

the time voltage plots (Fig. 4). A report of the significant findings for the P1 can be found in Supplemental material.

3.3.1.2. N170. With regards to the occipito-temporal N170, *top change* trials elicited a response of greater amplitude than the *same pre-top* trials (main effect of *condition:* ($F(1, 15) = 35.61$, $p = 0.001$; Fig. 4). Additionally, the main effect of *hemisphere* was significant due to greater amplitude in the right than the left hemisphere ($F(1, 15) = 310.24$, $p = 0.006$).

The ANOVA comparing the *bottom change* to the *same pre-bottom change* trials also revealed a main effect of condition, due to *bottom change* trials evoking a larger N170 than *same* trials ($F(1, 15) = 21.06$, $p < 0.001$), and a main effect of hemisphere, due to greater overall amplitude in the right, compared to the left, hemisphere ($F(1, 15) = 8.69$, $p = 0.010$; Fig. 4).

The ANOVA comparing the N170 modulations on the *top change* and *bottom change* trials revealed a main effect of condition, due to *top change* trials evoking a larger N170 than *bottom change* trials ($F(1, 15) = 8.78$, $p = 0.01$), and a main effect of hemisphere, due to greater overall amplitude in the right, compared to the left, hemisphere ($F(1, 15) = 9.27$, $p = 0.008$). The condition by hemisphere interaction was also significant ($F(1, 15) = 5.19$, $p = 0.038$) due to the fact that the difference between top and bottom change trials was slightly stronger in the right than left hemisphere.

In summary, traditional electrophysiological components analyses revealed no differentiation between the change of facial identity and same trials at the level of the P1. However, for the N170, both *top change* and *bottom change* trials elicited greater amplitude compared to *same* trials (see Fig. 4). There was also a larger response for *top change* (fixated) as compared to *bottom change* trials.

The fact that even *bottom change* trials elicited an enhanced N170 while participants fixated the top part of the face strengthens previous finding (Jacques & Rossion, 2009), being observed here with a different paradigm, task and stimuli, and with only one half of the face changing for both the top and bottom conditions. This effect is consistent with the perceptual illusion created by the alignment of the two different face parts.

3.3.2. The time-course of the composite face effect
Point-by-point permutation tests were performed to compare the *top change* and *same pre-top* conditions as well as the *bottom change* and *same pre-bottom* conditions over the entire time-course. Time-by-electrode plots displaying the magnitude of the condition difference at each time point at which the difference was significant are shown for each comparison in columns 1 and 2 of Fig. 5. Column 3 shows topographical maps reflecting these significant amplitude differences at 150 ms and 250 ms post-stimulus onset. As evident from the figure, consistent differences ($p < 0.01$) were found between the *change* and *same* conditions beginning at approximately 150 ms, the time of the N170 peak, in both comparisons (*top* vs. *same pre-top*; *bottom* vs. *same pre-bottom*).

Importantly, the difference between *bottom change* and *same* trials started to be significant at the same latency ($\sim$150 ms) as the difference between *top change* and *same* trials over right occipito-temporal electrode sites, even though the differences were of greater magnitude between the *top change* and *same* trials during the entire time-window of this first difference, which remained substantial for both comparisons until about 330 ms (Fig. 5). It can be seen from the topographical maps that the significant differences are stronger in the right hemisphere than the left for both *top* and *bottom-change* stimuli.

We observed a second ERP difference, but only for the *top change* vs. *same* comparison, starting between 350 and 400 ms at central and centro-parietal electrode sites (Fig. 5), which was identified as a P3b. Amplitude of the P3b has been described as having
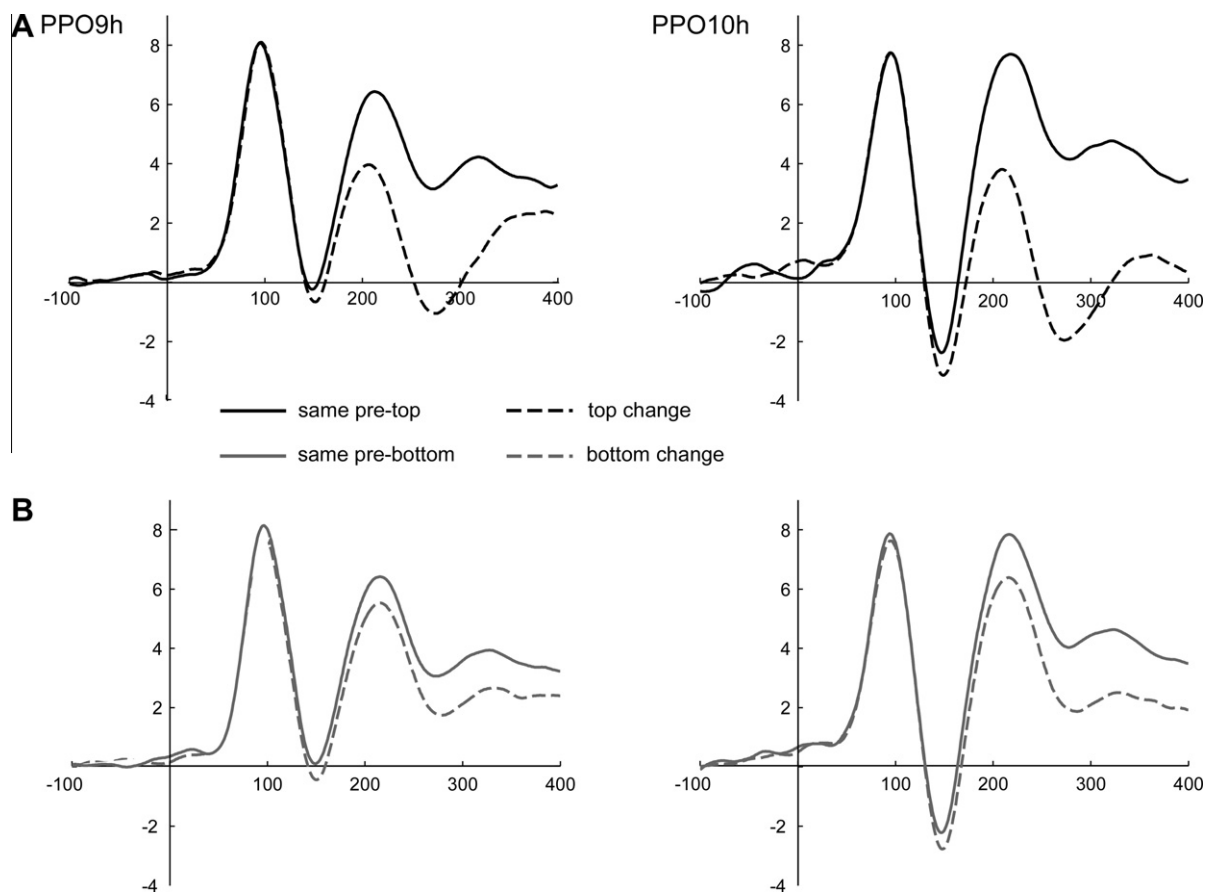
Fig. 4. Grand average ERP waveforms elicited by the top change and same pre-top trials (A) and bottom change and same pre-bottom trials (B) at occipito-temporal electrodes PPO9 h and PPO10 h of the left and right hemisphere, respectively.

an inverse relationship with the probability of the target stimulus (Duncan-Johnson & Donchin, 1977). Therefore, it is not surprising that we observed a quite large P3b in the present study, in which the probability of a *top change* stimulus was quite low throughout the experiment. Interestingly, the topography of the P3b to *top change* stimuli, beginning at approximately 230 ms, differed from the activity observed for *bottom change* stimuli and *same* stimuli at the same latency (Fig. 3). The topographical patterns of activation to *bottom change* stimuli were highly correlated with those of *same* stimuli at this latency. This is evident both from Fig. 3, as well as Fig. 6 which depicts the correlation values between scalp topographies measured for *top change* stimuli and for *same* stimuli, as well as between *bottom change* stimuli and *same* stimuli. Note that while topographies to both *top change* and *bottom change* stimuli differ slightly from the topography for the *same* stimuli around the time point of the N170, only *top change* stimuli yield a different topography at later time points, beginning around 230 ms.

3.3.3. Lateralized readiness potential

Mean lateralization waveforms calculated from C3/C4 are illustrated in Fig. 7. On *top change* trials, lateralization at central sites began at approximately 300–320 ms following stimulus onset, peaking at around 470–480 ms post onset. The onset time of the LRP was identified as 352 ms, from which time the LRP differed significantly ($p < 0.01$) from the baseline of zero for the remaining duration of the ERP epoch. For *bottom change* trials, rather, the mean lateralization waveform did not produce a visible LRP and did not produce a significant deflection from baseline at any point

within the 800 ms post-stimulus-onset epoch. Fig. 8 depicts the resulting topographies when trials in which subjects responded with the left hand are subtracted from trials in which subjects responded with the right hand. For top change trials, the lateralized potential evoked by response preparation is evident in polarized activity over motor cortex at electrode sites C3 and C4. No similar lateralized response preparation activity is present for the bottom change trials.

4. Discussion

4.1. Identity adaptation effects during face encoding

We observed that when the identity of the top half of a face changes in a stimulation train of identical faces, the face-sensitive N170 is larger in amplitude over occipito-temporal electrodes compared to the N170 elicited by identical faces. This is in line with previous observations of a larger N170 to different compared to immediately repeated whole faces (e.g., Heisz, Watter, & Shedden, 2006; Itier & Taylor, 2002; Jemel, Pisani, Calabria, Crommelinck, & Bruyer, 2003) as observed most prominently in face identity adaptation paradigms using a long adaptation duration and a short ISI between adapter and target (Caharel et al., 2009; Jacques et al., 2007), or in the comparison of ERPs obtained in blocks of different faces and those obtained from blocks of identical faces (Ewbank, Smith, Hancock, & Andrews, 2008). Here we observed this same effect using a new oddball paradigm, when only the top half of the face changes identity on a small number of trials.
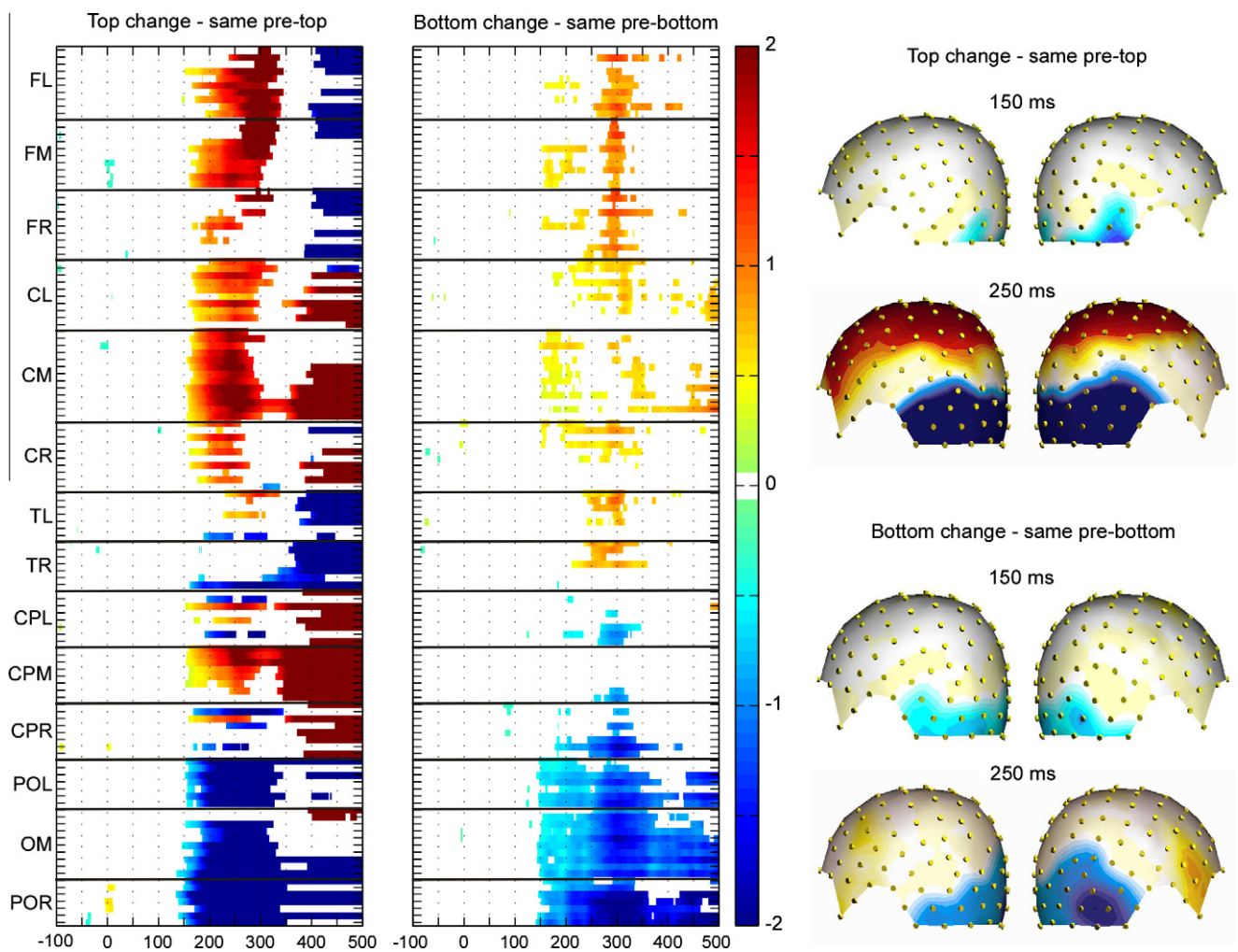
Fig. 5. Time-by-electrode statistical plots of the significant ERP differences between conditions. Left column: statistical plots of the significant differences ($p < 0.01$, two-tailed; 10,000 permutations) between the *same pre-top* and *top-change* conditions. Middle column: significant differences between the *same pre-bottom* and *bottom change* conditions. Only significant differences are color-coded and displayed as a function of the amplitude difference between the compared ERP waveforms. The 128 electrodes displayed on the *y*-axis are grouped as a function of their location in frontal (F), central (C), temporal (T), central parietal (CP), occipito-temporal (PO) and occipital (O) scalp regions, as well as left hemisphere (L), midline (M) and right hemisphere (R). The right column depicts topographic maps with views of the left and right parietal-occipital regions of the scalp and shows the significant differences at two different time points for both the *top – same pre-top* conditions (above) an the *bottom – same pre-bottom* conditions (below).

Interestingly, the effect observed here on the N170 appears to be as large as the effect observed in previous studies when both halves of the face change between an adapter and a target face (see Jacques & Rossion 2009; Jacques et al., 2007). However, substantial differences in terms of the paradigms used prevent us from making firm claims on this issue.

Importantly, the sensitivity to a change of facial identity started at the latency of the N170 peak, with no evidence of earlier effects, for instance on the P1 component or in the time-window in between these two clear visual components. P1 face repetition effects have been previously observed, albeit inconsistently. However, they were likely to be due to low-level effects of stimulus repetition, which were minimized here by changing the size and position of the faces on each consecutive trial.

The effect of facial identity repetition, beginning at the N170, was prolonged until about 300 ms at occipito-temporal sites (with a polarity reversal at central sites). This later effect of face identity repetition has been previously found (Jacques et al., 2007) and characterized as the N250 repetition effect ("N250r", e.g., Schweinberger, Huddy, & Burton, 2004).

4.2. The early (N170) composite face effect takes place during encoding of face representations

When the non-fixated (bottom) half of the face changed in rare trials, eliciting a visual composite illusion (i.e. perception of a slightly different top half of the face, see Fig. 1), there was also a significant N170 increase at occipito-temporal electrode sites. This effect not only replicates the recent observation of Jacques and Rossion (2009) using a new paradigm, but is observed here for the first time despite two facts: (1) that participants did not provide any overt behavioral response to the change of the bottom half of the face (i.e. increase of errors or RTs), and (2) that there was no electrophysiological evidence of a response-related bias in the *bottom change* condition, as indicated by the absence of an LRP component.

The presence of an N170 effect in *bottom change* trials, despite the fact that the fixated top half undergoes no physical change, indicates that individual faces are not only "processed" holistically, in a general sense, but that they are *perceived* holistically: as early as ~150–160 ms, the human brain has accumulated sufficient
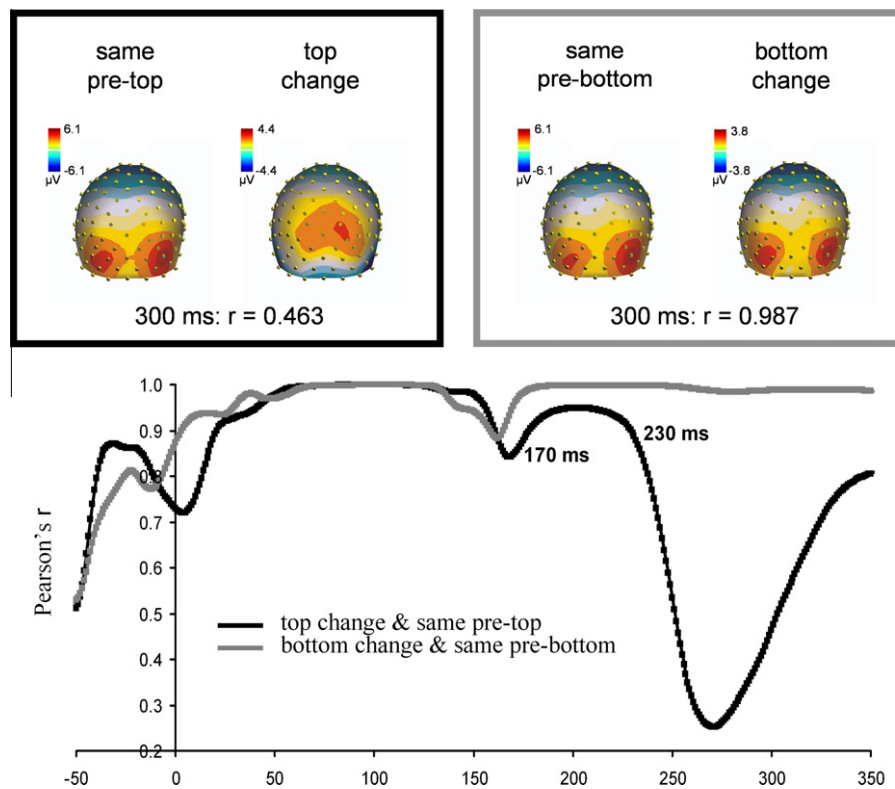
Fig. 6. Pearson correlation values computed between the scalp topographies obtained in the *same pre-top* and in the *top-change condition* (black) and between the topographies obtained in the *same pre-bottom* and in the *bottom change* condition (grey) are plotted as a function of time. Note that the correlation coefficients are close to 1 around the P1 time-window ($\sim$100 ms), indicating identical scalp distribution of EEG activity (irrespective of absolute amplitude variations) at that latency. There is a first slight reduction in correlation at the latency of the N170 peak because of a local change in topography: the N170 is significantly larger in the change conditions than in the no-change conditions. Then, the topographies in the *bottom change* and *same pre-bottom* conditions remain highly correlated while the *top change* and *same pre-top* conditions show a second large difference in topography starting around 230 ms. This second deviation can be attributed to the parietal P3b, which was only present for the top-change condition (see the top left inset).
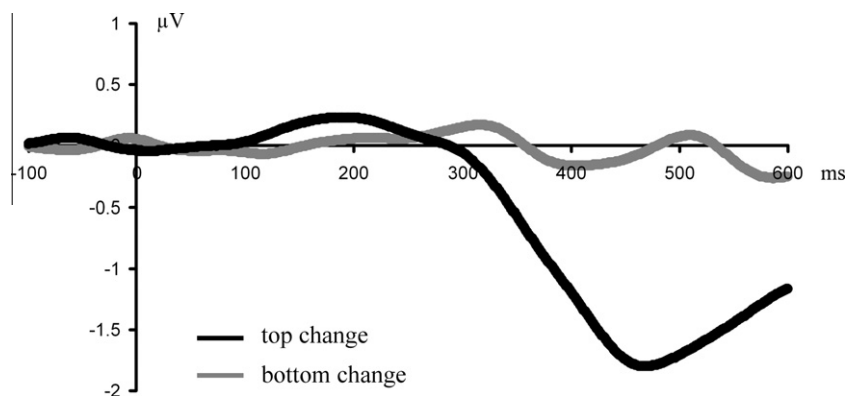

Fig. 7. Grand average lateralized readiness potentials on *top change* (go) and *bottom change* (no-go) trials. Note that significant lateralization of motor preparation occurred only for the *top change* (go) trials with an approximate onset of 310–330 ms. No LRP was observed for the *bottom change* trials.

evidence to distinguish individual faces, based on a holistic representation.

As in the previous study, (Jacques & Rossion, 2009), we attribute the N170 effect observed for the *bottom change* trials to the (illusory) perception of a new top part of the face at fixation rather than to the perception of the bottom half as an independent entity. This interpretation is based on two observations. First, this early effect in the *bottom change* condition disappears entirely when the bottom half is slightly misaligned spatially ($\sim$0.6°) (Jacques & Rossion, 2009). In the misaligned condition in that study, the identity change of the bottom half remains conspicuous, but the top part

of the face does not appear different (i.e. the illusion vanishes).[2] Second, the modulation of N170 amplitude in the *bottom change* condition, relative to the *same* face condition, took place *as early as* the modulation of the N170 for the *top-change* condition. This suggests that the N170 modulation when the bottom changed identity was

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[2] In the present study, we did not use an additional misaligned condition, as it would have doubled the duration of the already long experiment, in which we sought to replicate the main effect found in our previous study (Jacques & Rossion, 2009) while adding a number of manipulations related to the participants' response mode (go/nogo and different response hands across blocks).
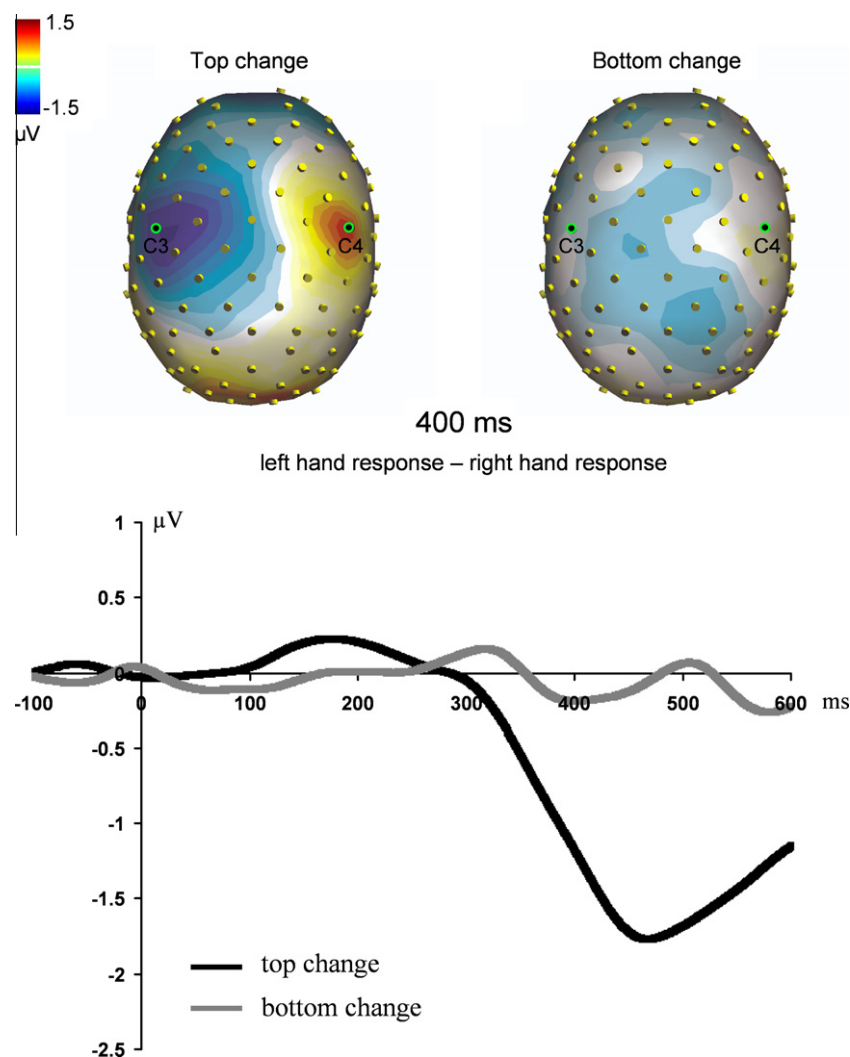
Fig. 8. Scalp topographies of a subtraction wave (activity generated by trials in which subjects responded with their left hand minus activity generated by trials in which subjects responded with their right) depicting the lateralization of EEG activity as subjects prepare to respond to the stimuli on the *top change* trials (left) and the absence of such activity on the *bottom change* trials (right).

due to the global perception of a new face, including the illusory perception of a top change. The fact that the effect was not as strong when the bottom changed as compared to the top change can be attributed in part to the fact that participants were fixated on the top half of the face throughout the task. Moreover, the top part of a face is more salient than the bottom part of the face, and thus it may be that an effect of greater magnitude is evoked when the more salient part of the face changes.

The main goal of the present study was to more clearly disentangle the perceptual vs. decisional contributions to the CFE. We believe that we provide solid evidence for the perceptual nature of this effect. This belief is supported, first, by considering the present data in light of what is known about the nature of the N170 face-sensitive component, i.e. that it is primarily a perceptual response independent of decision processes. The N170, a component whose positive counterpart on the central electrode sites – the vertex positive potential (VPP) – was originally reported by Jeffreys (1989; see also Bötzel and Grüsser, 1989), is the first reliable marker of sensitivity to faces in the human brain (Bentin et al., 1996; Bötzel, Schulze, & Stodieck, 1995; Eimer, 2000a; Rossion et al., 2000), at least when low-level visual cue differences between faces and other complex visual forms are controlled (Rousselet, Husk, Bennett, & Sekuler, 2008; see Rossion & Jacques, 2008). Its larger amplitude to faces than other visual stimuli may start as early as

120–130 ms. Considering the difference in the fastest visual responses recorded in the monkey and human brain (e.g., Schroeder, Molholm, Lakatos, Ritter, & Foxe, 2004), this time-frame is compatible with the mean onset latency of neurons responding selectively to faces in the monkey infero-temporal cortex (IT), i.e. about 90–100 ms (e.g., Kiani, Esteky, & Tanaka, 2005). That is, the mean onset latency of the N170 face effect – the larger response to faces than other visual categories – appears to correspond to the earliest activation of face representations in the human brain (Rossion & Jacques, 2008). Supporting this view, a large and typical N170 response is elicited by very different kinds of stimuli as long as they are readily perceived (i.e. interpreted) as faces by the visual system (i.e. photographs, schematic faces, line drawings, faces made by object parts, inverted faces, half-faces, isolated eyes, etc... see Rossion & Jacques, 2010). Considering this, the present findings support the view that the locus of the composite face effect emerges from the stage of processing in which the perceptual encoding of the facial representation takes place.

4.3. Ruling out attentional confounds for the early N170 composite effect

Given that the N170 can be modulated to a certain extent by attentional processes (Crist, Wu, Karp & Woldorff, 2008; Eimer,

2000b; Jacques & Rossion, 2007; although see Eimer & Holmes, 2002), it could be argued that the N170 modulation that we observed to bottom change trials was simply elicited by covert shifts in attention to the changed part of the stimulus. However, we do not believe that this was the case for several reasons. First, there is no evidence that the N170 could be modulated by attention when the change is unpredictable and subjects do not consciously attend to the location where the change takes place. For instance, in Eimer's (2000b) attentional manipulation, participants were explicitly instructed to pay attention to a particular category (faces) or another (i.e. chairs). When attention was paid to faces, the N170 was (slightly) increased. Here, subjects were told to *ignore* the bottom part of the face. Moreover, Eimer's (2000b) findings hold only for stimuli presented at fixation, whereas the bottom halves here were out of fixation. Second, in our previous study (Jacques & Rossion, 2009), misaligned faces were also used. A change of the bottom half of the misaligned face could be just as likely to induce covert shifts in attention as a change in the bottom half of an aligned face. However, no N170 modulation to the *bottom change* stimuli was observed in the misaligned condition. Furthermore, when faces were upside-down, changes in the bottom half (presented in the upper visual field) of the face did not modulate the N170 (Jacques et al., 2007) in either the aligned or misaligned conditons, with effects of face identity repetition occurring only at a later latency.

Third, while it is true that spatial attention has been shown to modulate the N170 to lateralized face stimuli, it also induces a complementary modulation of the preceding P1 component (Jacques & Rossion, 2007). Here we found no P1 modulation to the bottom-change stimuli. Finally, although N170 modulation by attention is less well documented, the P3 is known to be modulated by attention (e.g., Mangun & Hillyard, 1995; Polich, 1996). In our study, unlike that of the *top-change* condition, P3 topography for the *bottom change* condition was highly similar to that of the *same* condition (Fig. 6). It seems unlikely to us that an attentional effect would be isolated to the N170 and not present in the P1 or P3, as was the case in the current experiment. Thus, we feel confident that the N170 modulation observed to the *bottom change* stimuli was elicited by the perceived illusion of a different face, rather than any attentional shifts towards the bottom half of the face.

4.4. Lack of evidence for behavioral and electrophysiological response bias

During an active discrimination face task, the differential amplitude of the N170 component can be predictive of response output. For instance, variations in amplitude related to multiple in-plane face orientations (0°, 30°, 60°, …) can correlate with the accuracy and response times in a face identity matching task (Jacques & Rossion, 2007). However, these early differences between the conditions of visual stimulation can also be observed in the absence of direct output (i.e. during passive stimulation, or when the task performance is not affected by stimulus manipulation). In fact, N170 amplitude differences between conditions can be completely independent of decision making (Philiastides & Sajda, 2006). Hence, finding a CFE as early as the N170, as in the study of Jacques and Rossion (2009), is, in itself, a strong argument against the claim that holistic effects have a decisional basis (Richler, Gauthier, et al., 2008).

This argument is strengthened by the fact that, in the present study, the N170 effect for the *bottom change* stimuli was not accompanied by any response-related decisional component. That is, we found a clear N170 effect, in the occipito-temporal cortex lasting a few hundred ms (Fig. 5) even when participants experienced no conflict or bias in their decision with respect to the stim-

ulus processed. A conflict in decision could have been evident in two ways. The first would be to have obtained a behavioral response on a significant number of *bottom change* trials. Lacking that, a decisional conflict could have been noted by the preparation to respond based on initial stimulus processing, but a subsequent abortion of the response after thorough processing. This would have been evident in the presence of an LRP to the *bottom-change* stimuli. The LRP, recorded over electrode sites contralateral to the hand used to respond, is sensitive to low levels of response activation that are not associated with the ultimate overt behavior. This means that the LRP can develop based on an indication that a response may be needed, even if the response is never actually executed (e.g., de Jong et al., 1988; Hackley & Miller, 1995; Miller, 1998). The presence of an LRP on *bottom change* trials would have indicated a discrepancy between an initial decision to provide a response based on the bias that all face parts change together (Richler, Gauthier, et al., 2008), and the ultimate correct decision to not respond. We found no hint of response activation for the composite illusion evoked by *bottom change* trials. Rather, we observed a large LRP only to *top change* trials; the stimuli for which a response was made. Additionally, when considering that fact that the P3b is also thought to be related to decisional aspects of stimulus processing (Nieuwenhuis, Aston-Jones, & Cohen, 2005; Verleger et al., 2006), it is important to note that we observed a P3b that differed in topography from the *same* stimuli only for *top change* stimuli, while the *bottom change* stimuli showed topographical patterns of activation that remained highly correlated with those evoked by the *same* stimuli at all time points following the N170 (Fig. 6).

Given these observations, it appears that we were able to measure the neural correlates of the CFE in the absence of any behavioral or electrophysiological decision-related biases. Indeed, we found no hint of a response-related bias at the P3b, the LRP, or in the behavioral response. Nevertheless, we observed a robust perceptual effect of the composite face illusion at the N170. This observation is difficult to reconcile with the proposal that the CFE reflects essentially decisional response components rather than perceptual processes, or even that the perceptual contributions to holistic effects are affected by preexisting decisional biases (Cheung et al., 2008; Richler, Gauthier, et al., 2008; Wenger & Ingvalson, 2002).

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.bandc.2010.08.001.

References

Ashby, F. G., & Townsend, J. T. (1986). Varieties of perceptual independence. *Psychological Review, 93*, 154–179.
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 potential. *Psychophysiology, 30*, 518–524.

Bötzel, K., & Grusser, O. J. (1989). Electric brain potentials evoked by pictures of faces and non-faces: A search for 'face-specific' EEG-potentials. *Experimental Brain Research, 77*, 349–360.

Bötzel, K., Schulze, S., & Stodieck, S. R. G. (1995). Scalp topography and analysis of intracranial sources of face-evoked potentials. *Experimental Brain Research, 104*, 135–143.

Caharel, S., d'Arripe, O., Ramon, M., Jacques, C., & Rossion, B. (2009). Early adaptation to unfamiliar faces across viewpoint changes in the right hemisphere: Evidence from the N170 ERP component. *Neuropsychologia, 47*, 639–643.

Cheung, O. S., Richler, J. J., Palmeri, T. J., & Gauthier, I. (2008). Revisiting the role of spatial frequencies in the holistic processing of faces. *Journal of Experimental Psychology – Human Perception and Performance, 34*, 1327–1336.

Coles, M. G. H. (1989). Modern mind–brain reading: Psychophysiology, physiology, and cognition. *Psychophysiology, 26*, 251–269.

Crist, R. E., Wu, C., Karp, C., & Woldorff, M. G. (2008). Face processing is gated by visual spatial attention. *Frontiers in Human Neuroscience, 1:10*. doi:10.3389/neuro.09.010.2007.

de Heering, A., Rossion, B., Turati, C., & Simion, F. (2008). Holistic face processing can be independent of gaze behavior: Evidence from the face composite effect. *Journal of Neuropsychology, 2*, 183–195.

de Jong, R., Wierda, M., Mulder, G., & Mulder, L. J. M. (1988). Use of partial information in responding. *Journal of Experimental Psychology: Human Perception and Performance, 14*, 682–692.

Duncan-Johnson, C. C., & Donchin, E. (1977). On quantifying surprise: The variation of event-related potentials with subjective probability. *Psychophysiology, 14*, 456–467.

Eimer, M. (2000a). Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology, 111*, 694–705.

Eimer, M. (2000b). Attentional modulation of event-related brain potentials sensitive to faces. *Cognitive Neuropsychology, 17*, 103–116.

Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing. *Neuroreport, 13*, 427–431.

Ewbank, M. P., Smith, W. A. P., Hancock, E. R., & Andrews, T. J. (2008). The M170 reflects a viewpoint-dependent representation for both familiar and unfamiliar faces. *Cerebral Cortex, 18*, 364–370.

Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. N. (1998). What is "special" about face perception? *Psychological Review, 105*, 482–498.

Galton, F. (1883). *Inquiries into human faculty and its development*. London: Macmillan.

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*(3), 495–504.

Goffaux, V., & Rossion, B. (2006). Faces are "spatial" – Holistic face perception is supported by low spatial frequencies. *Journal of Experimental Psychology: Human Perception and Performance, 32*, 1023–1039.

Gratton, G., Coles, M. G. H., & Donchin, E. (1992). Optimizing the use of information: Strategic control of activation of responses. *Journal of Experimental Psychology: General, 121*, 480–506.

Gratton, G., Coles, M. G. H., Sirevaag, E., Eriksen, C. W., & Donchin, E. (1988). Pre- and post-stimulus activation of response channels: A psychophysiological analysis. *Journal of Experimental Psychology: Human Perception and Performance, 14*, 331–344.

Hackley, S. A., & Miller, J. O. (1995). Response complexity and precue interval effects on the lateralized readiness potential. *Psychophysiology, 32*, 230–241.

Heisz, J. J., Watter, S., & Shedden, J. A. (2006). Automatic face identity encoding at the N170. *Vision Research, 46*, 4604–4614.

Hole, G. J. (1994). Configurational factors in the perception of unfamiliar faces. *Perception, 23*, 65–74.

Hole, G. J., George, P., & Dunsmore, V. (1999). Evidence for holistic processing of faces viewed as photographic negatives. *Perception, 28*, 341–359.

Ishizu, T., Ayabe, T., & Kojima, S. (2008). Configurational factors in the perception of faces and non-facial objects: An ERP study. *International Journal of Neuroscience, 118*(7), 955–966. doi:10.1080/00207450701769398.

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.

Jacques, C., d'Arripe, O., & Rossion, B. (2007). The time course of the inversion effect during individual face discrimination. *Journal of Vision, 7*(8:3), 1–9. doi:10.1167/7.8.3. http://journalofvision.org/7/8/3/.

Jacques, C., & Rossion, B. (2006). The speed of individual face categorization. *Psychological Science, 17*, 485–492.

Jacques, C., & Rossion, B. (2007). Early electrophysiological responses to multiple face orientations correlate with individual discrimination performance in humans. *NeuroImage, 36*, 863–876.

Jacques, C., & Rossion, B. (2009). The initial representation of individual faces in the right occipito-temporal cortex is holistic: electrophysiological evidence from the composite face illusion. *Journal of Vision, 9*(6):8, 1–16. doi:10.1167/9.6.8. http://journalofvision.org/9/6/8/.

Jacques, C., & Rossion, B. (2010). Misaligning face halves increases and delays the N170 specifically for upright faces: Implications for the nature of early face representations. *Brain Research, 1318*, 96–109.

Jeffreys, D. A. (1989). A face-responsive potential recorded from the human scalp. *Experimental Brain Research, 78*, 193–202.

Jemel, B., Pisani, M., Calabria, M., Crommelinck, M., & Bruyer, R. (2003). Is the N170 for faces cognitively penetrable? Evidence from repetition priming of Mooney faces of familiar and unfamiliar persons. *Cognitive Brain Research, 17*, 431–446.

Kadlec, H., & Townsend, J. T. (1992). Signal detection analysis of dimensional interactions. In F. G. Ashby (Ed.), *Multidimensional models of perception and cognition* (pp. 181–228). Hillsdale, NJ: Erlbaum.

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.

Kiani, R., Esteky, H., & Tanaka, K. (2005). Differences in onset latency of macaque inferotemporal neural responses to primate and non-primate faces. *Journal of Neurophysiology, 94*, 1587–1596.

Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2004). Impairment in holistic face processing following early visual deprivation. *Psychological Science, 15*, 762–768.

Letourneau, S. M., & Mitchell, T. V. (2008). Behavioral and ERP measures of holistic face processing in a composite task. *Brain and Cognition, 67*, 234–245.

Mangun, G. R., & Hillyard, S. A. (1995). Mechanisms and models of selective attention. In M. D. Rugg & M. G. H. Coles (Eds.), *Electrophysiology of mind: Event-related brain potentials and cognition* (pp. 40–85). New York: Oxford.

Martens, U., Leuthold, H., & Schweinberger, S. (2010). Parallel processing in face perception. *Journal of Experimental Psychology: Human Perception and Performance, 36*(1), 103–121.

Michel, C., Rossion, B., Han, J., Chung, C. H., & Caldara, R. (2006). Holistic processing is finely tuned for faces of one's own race. *Psychological Science, 17*, 608–615.

Miller, J. (1998). Effects of stimulus-response probability on choice reaction time: Evidence from the lateralized readiness potential. *Journal of Experimental Psychology: Human Perception and Performance, 24*, 1521–1534.

Miller, J., & Hackley, S. A. (1992). Electrophysiological evidence for temporal overlap among contingent mental processes. *Journal of Experimental Psychology: General, 121*, 195–209.

Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Human Brain Mapping, 15*, 1–25.

Nieuwenhuis, S., Aston-Jones, G., & Cohen, J. D. (2005). Decision making, the P3 and the locus coeruleus–norepinephrine system. *Psychological Bulletin, 131*, 510–532.

Philiastides, M. G., & Sajda, P. (2006). Temporal characterization of the neural correlates of perceptual decision making in the human brain. *Cerebral Cortex, 16*, 509–518.

Polich, J. (1996). Meta-analysis of P3 normative aging studies. *Psychophysiology, 33*, 334–353.

Prime, D., & Ward, L. M. (2004). Inhibition of return from stimulus to response. *Psychological Science, 15*, 272–276.

Puce, A., Allison, T., Gore, J. C., & McCarthy, G. (1995). Face-sensitive regions in human extrastriate cortex studied by functional MRI. *Journal of Neurophysiology, 74*, 1192–1199.

Richler, J. J., Gauthier, I., Wenger, M. J., & Palmeri, T. J. (2008). Holistic processing of faces: Perceptual and decisional components. *Journal of Experimental Psychology: Learning Memory and Cognition, 34*, 328–342.

Richler, J. J., Tanaka, J. W., Brown, D. D., & Gauthier, I. (2008). Why does selective attention to parts fail in face processing? *Journal of Experimental Psychology: Learning Memory and Cognition, 34*, 1356–1368.

Robbins, R., & McKone, E. (2007). No face-like processing for objects-of-expertise in three behavioural tasks. *Cognition, 103*, 34–79.

Rossion, B. (2008). Picture-plane inversion leads to qualitative changes of face perception. *Acta Psychologica, 128*, 274–289.

Rossion, B. (2009). Distinguishing the cause and consequence of face inversion: The perceptual field hypothesis. *Acta Psychologica, 128*, 274–289.

Rossion, B., & Boremanse, A. (2008). Nonlinear relationship between holistic processing of individual faces and picture-plane rotation: Evidence from the face composite illusion. *Journal of Vision, 8*(4):3, 1–13. doi:10.1167/8.4.3. http://journalofvision.org/8/4/3/.

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.

Rossion, B., & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. *NeuroImage, 39*, 1959–1979.

Rossion, B., & Jacques, C. (2010). The N170: Understanding the time-course of face perception in the human brain. In S. Luck & E. Kappenman (Eds.), *The Oxford handbook of ERP components*. Oxford University Press.

Rousselet, G.,A., Husk, J. S., Bennett, P. J., & Sekuler, A. B. (2008) Time course and robustness of ERP object and face differences. *Journal of Vision, 8*(12):3, 1–18. doi:10.1167/8.12.

Rousselet, G. A., Pernet, C., Bennett, P. J., & Sekuler, A. B. (2005). Spatial scaling factors explain eccentricity effects on face ERPs. *Journal of Vision, 5*, 755–763.

Rugg, M. D., Doyle, M. C., & Wells, T. (1995). Word and nonword repetition within- and across-modality: An event-related potential study. *Journal of Cognitive Neuroscience, 7*, 209–227.

Schiltz, C., Dricot, L., Goebel, R., & Rossion, B. (2010). Holistic perception of individual faces in the right middle fusiform gyrus as evidenced by the composite face illusion. *Journal of Vision, 10*(2):25, 1–16.

Schiltz, C., & Rossion, B. (2006). Faces are represented holistically in the human occipitotemporal cortex. *Neuroimage, 32*, 1385–1394.

Schroeder, C. E., Molholm, S., Lakatos, P., Ritter, W., & Foxe, J. J. (2004). Human–Simian correspondence in the early cortical processing of multisensory cues. *Cognitive Processing, 5*, 140–151.

Schweinberger, S. R., Huddy, V., & Burton, A. M. (2004). N250r: A face-selective brain response to stimulus repetitions. *Neuroreport, 15*, 1501–1505.

Sergent, J. (1984). An investigation into component and configural processes underlying face perception. *British Journal of Psychology, 75*, 221–242.

Sergent, J., Ohta, S., & Macdonald, B. (1992). Functional neuroanatomy of face and object processing – A Positron emission tomography study. *Brain, 115*, 15–36.

Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology, 46*, 225–245.

Tanaka, J. W., & Sengco, J. A. (1997). Features and their configuration in face recognition. *Memory and Cognition, 25*, 583–592.

Taubert, J., & Alais, D. (2009). The composite illusion requires composite face stimuli to be biologically plausible. *Vision Research, 49*, 1877–1885.

Thomas, R. D. (1995). Gaussian general recognition theory and perceptual independence. *Psychological Review, 102*, 192–200.

Verleger, R., Jaskowski, P., & Wascher, E. (2005). Evidence for an integrative role of P3b in linking reaction to perception. *Journal of Psychophysiology, 19*, 165–181.

Verleger, R., Paehge, T., Kolev, V., Yordanova, J., & Jaskowski, P. (2006). On the relation of movement-related potential to the go/no-go effect on P3. *Biological Psychology, 73*, 298–313.

Wenger, M. J., & Ingvalson, E. M. (2002). A decisional component of holistic encoding. *Journal of Experimental Psychology: Learning Memory and Cognition, 28*, 872–892.

Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception, 16*, 747–759.