



Research report

Electrophysiological evidence for parts and wholes in visual face memory



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ABSTRACT

It is often assumed that upright faces are represented in a holistic fashion, while representations of inverted faces are essentially part-based. To assess this hypothesis, we recorded event-related potentials (ERPs) during a sequential face identity matching task where successively presented pairs of upright or inverted faces were either identical or differed with respect to their internal features, their external features, or both. Participants' task was to report on each trial whether the face pair was identical or different. To track the activation of visual face memory representations, we measured N250r components that emerge over posterior face-selective regions during the activation of visual face memory representations by a successful identity match. N250r components to full identity repetitions were smaller and emerged later for inverted as compared to upright faces, demonstrating that image inversion impairs face identity matching processes. For upright faces, N250r components were also elicited by partial repetitions of external or internal features, which suggest that the underlying identity matching processes are not exclusively based on non-decomposable holistic representations. However, the N250r to full identity repetitions was super-additive (i.e., larger than the sum of the two N250r components to partial repetitions of external or internal features) for upright faces, demonstrating that holistic representations were involved in identity matching processes. For inverted faces, N250r components to full and partial identity repetitions were strictly additive, indicating that the identity matching of external and internal features operated in an entirely part-based fashion. These results provide new electrophysiological evidence for qualitative differences between representations of upright and inverted faces in the occipital-temporal face processing system.

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Human faces are thought to be perceived and recognised by specialised cognitive and neural mechanisms that are distinct from those used to process other classes of objects. The face inversion effect (e.g., Yin, 1969) is often interpreted as evidence for this special status of face processing. Upside-down

faces are more difficult to identify and remember than faces that are seen in their canonical upright orientation, while the perception and recognition of non-face objects is typically much less affected by stimulus inversion (Valentine, 1988). Importantly, the detrimental effects of face inversion may

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reflect not merely a quantitative reduction in processing efficiency, but a fundamental qualitative difference in the visual processing of upright and inverted face. This qualitative difference in processing style stems from the assumption that upright faces are encoded and represented holistically, whereas the processing of inverted faces operates in a part-based fashion (Tanaka & Farah, 1993; see also Van Belle, De Graef, Verfaillie, Rossion, & Lefevre, 2010; Young, Hellawell, & Hay, 1987).

Perhaps the most compelling demonstration of holistic face processing is the composite face illusion (for a recent review, see Rossion, 2013). When participants are instructed to encode the identity of top halves of two faces while ignoring their bottom halves, they will often report that two physically identical top face halves look different when they are paired with the task-irrelevant bottom half of different face identities (Hole, 1994; Young et al., 1987). Even when the top halves are correctly classified as being the same, response times are slower than on trials where the bottom halves are identical, suggesting that faces are initially perceived holistically even when participants can eventually match their top halves. These composite face effects only occur when the top and bottom face halves are spatially aligned to create a canonical upright face configuration. They are abolished when face shape is disrupted by spatial misalignment, are entirely absent for non-face objects, and importantly are also absent when faces are inverted, indicating that they may be unique to upright faces (e.g., McKone, Kanwisher, & Duchaine, 2007). Together with other demonstrations of holistic face processing (e.g., Tanaka & Farah, 1993) for upright but not for inverted faces, the composite face illusion suggests that upright but not inverted faces are encoded and represented as non-decomposable wholes. The key characteristic of holistic face processing is that individual facial features are not represented independently, but that the context of other features of the same face is always taken into account when encoding and maintaining representations of upright faces (e.g., Rossion, 2013). However, the extent to which upright face representations are entirely holistic or whether part-based face representations might also exist for upright faces is currently debated (e.g., Behrmann, Richler, Avidan, & Kimchi, 2014). In this study, we used a novel experimental procedure where repetitions versus changes of internal and external facial features were manipulated independently to measure the contributions of holistic and part-based visual representations during a face matching task.

Specific brain regions and neural events have also been linked to holistic face processing. Functional neuroimaging and direct neuronal recordings in human and non-human primates have uncovered a network of face-selective clusters in the occipital and temporal lobes (e.g., Moeller, Freiwald, & Tsao, 2008; Tsao & Livingstone, 2008). Within this network, the middle fusiform gyrus (or “fusiform face area” – FFA; Kanwisher, McDermott, & Chun, 1997) has most consistently emerged as the key brain region involved in the holistic perception of face identity (Andrews, Davies-Thompson, Kingstone, & Young, 2010; Schiltz & Rossion, 2006; Schiltz, Dricot, Goebel, & Rossion, 2010). The precise timing of face-selective brain activity can be measured using event-related brain potentials (ERPs). The face-sensitive N170 component

is an important marker of perceptual encoding processes within the first 200 msec after encountering a face. The N170 is a negative-going ERP component at lateral posterior electrodes that is consistently larger for faces as compared to other non-face objects (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2011; Rossion & Jacques, 2011). This component is larger and delayed for inverted as compared to upright faces (Bentin et al., 1996; Eimer, 2000a; Rossion et al., 1999). Inversion-induced N170 amplitude enhancements have been interpreted as reflecting the additional contribution of object-selective neurons that are recruited simultaneously with face-selective neurons during the perceptual analysis of inverted faces but not by upright faces (e.g., Pitcher, Duchaine, Walsh, Yovel, & Kanwisher, 2011; Rosburg et al., 2010; for a similar suggestion, see; Towler, Gosling, Duchaine, & Eimer, 2012), in line with the hypothesis that upright and inverted faces are processed in a qualitatively different fashion. Although the N170 component is not generally sensitive to the identity of faces (e.g., Bentin & Deouell, 2000; Eimer, 2000b), under specific experimental conditions it has been shown to be sensitive to face identity and affected by the composite face illusion (Jacques & Rossion, 2009), suggesting that holistic face representations may already be generated during the early perceptual processing of individual faces.

The goal of the present study was to obtain more direct electrophysiological evidence for the existence of non-decomposable holistic representations of upright faces, and to investigate the hypothesis that in contrast to upright faces, inverted faces are represented in an exclusively part-based fashion. To address these issues, we employed a sequential face identity matching task, and measured the N250r component as an electrophysiological marker of the activation of representations of facial identity in visual face memory (Schweinberger, Huddy, & Burton, 2004; Schweinberger, Pickering, Jentzsch, Burton, & Kaufmann, 2002). The N250r component is an enhanced posterior negativity that is elicited when face images of the same individual are presented in succession, relative to trials where faces of two different individuals are shown. This component emerges approximately 220 msec after stimulus onset, is maximal at inferior lateral posterior electrodes, and is accompanied by a positivity at frontocentral electrode sites (see Schweinberger, 2011; for a review). This topography suggests that the N250r originates from face-selective inferior occipito-temporal regions, and source localisation studies using EEG and MEG have indicated that this component is primarily generated in the fusiform gyrus in a region located anterior to the neural generator of the face-sensitive N170 component (Schweinberger, Kaufmann, Moratti, Keil, & Burton, 2007; Schweinberger et al., 2002). The N250r component has been shown to increase in amplitude (i.e., become more negative) as the perceived similarity between sample and test faces increases (e.g., Wirth, Fisher, Towler, & Eimer, 2015). This observation is in line with the idea that the N250r marks the successful identity match between a perceptual face representation and a representation that is stored in visual face memory (Schweinberger & Burton, 2003; see also; Towler, Kelly, & Eimer, 2015). The fact that N250r components have been shown to be larger for familiar than for unfamiliar face repetitions (e.g., Herzmann, Schweinberger, Sommer, & Jentzsch,

2004; Herzmann, & Sommer, 2007) and are not only elicited by repetitions of physically identical unfamiliar face stimuli, but also when different images of the same individual are presented in succession (e.g., Bindemann, Burton, Leuthold, & Schweinberger, 2008; Fisher, Towler, & Eimer, 2016; Wirth et al., 2015; Zimmermann & Eimer, 2013), demonstrates that the N250r does not simply reflect the detection of matching low-level perceptual features, but is associated with the processing of facial identity. The link between the N250r component and the ability to process face identity is further strengthened by the observation that N250r amplitudes triggered by image-invariant identity matches are correlated with an independent measure of face recognition ability (Wirth, et al., 2015). Given these strong links between the N250r component and face identity processing, the N250r can be used as a tool to investigate the holistic versus part-based nature of the representations that are involved in visual face identity matching processes.

Previous studies have shown that N250r components are attenuated and delayed for repetitions of inverted as compared to upright faces (e.g., Itier & Taylor, 2004; Jacques, d'Arripe, & Rossion, 2007; Schweinberger et al., 2004), suggesting that face identity matching processes operate less efficiently with upside-down face images. This difference may primarily be due to quantitative differences in the speed and efficiency of identity matching processes between upright and inverted faces, but could also reflect fundamental qualitative differences in the nature of the underlying face representations. Identity repetitions of upright faces may be detected more rapidly because the matching process can be based on holistic representations of facial identity in visual face memory, whereas it has to rely on part-based representations for inverted faces. The question whether N250r components reflect the activation of holistic or part-based representations of individual faces, and whether this may differ for upright and inverted faces, has not yet been systematically investigated. To investigate these issues, a sequential face identity matching task is required where trials with face identity repetitions or changes are accompanied by partial repetition trials where some face parts are repeated and others change. We designed such a novel face identity matching task with unfamiliar faces. A set of 100 different faces was generated on the basis of ten front-facing male face images which controlled for various attributes such as age, race, the presence of facial hair, facial expression, and the direction of eye gaze. The internal features (eyes, nose, mouth, and internal face shape) and external features (hair and head contour) of these ten faces were separated and recombined into every possible combination of all individual internal and external features, producing 100 unique face images in total (see Fig. 1 for examples). Two of these faces were presented in rapid succession on each trial. There were four different trial types that appeared with equal probability in each block. On full repetition trials, two identical face images were shown. On full change trials, the two faces differed in their external and internal features. On external feature repetition trials, the faces had different internal but the same external features. On internal feature repetition trials, the external features changed and the internal features remained the same. Participants' task was to decide whether the two images on each

trial showed an identical face or whether there was a change in the internal features, external features, or both, between the first and second face. As previous studies have suggested that the identity-related processing of unfamiliar faces may be biased towards external features (e.g., Bonner, Burton, & Bruce, 2003; Want, Pascalis, Coleman, & Blades, 2003), these specific task instructions were chosen to encourage participants to place equal emphasis on internal and external facial features. Because task-relevant changes in either or both of these features were unpredictable and equally likely, discriminating between change and no-change trials should be most straightforward if it can be based on holistic face representations rather than on representations where internal and external features are coded separately and independently. In separate blocks, the identity matching task was performed with upright or with inverted faces.

ERPs were computed for all four trial types, separately for blocks with upright and inverted faces, in order to obtain N250r components as markers of identity matching processes on trials with full face identity repetitions and critically, also on trials where external facial features were repeated while internal features changed, or vice versa. Because the N250r reflects an enhanced negativity that is triggered by repetitions versus changes of faces or face parts, matching processes that are based exclusively on internal features can be assessed by comparing ERPs on internal feature repetition trials and full change trials. Because there is an external feature change on both types of trials, any N250r component for internal feature repetition as compared to full change trials will therefore reflect identity matching processes that are based on internal features. Analogously, an N250r obtained on external feature repetition versus full change trials will be linked to matching processes that operate on external features. We employed this logic to test whether the face identity matching processes that are reflected by the N250r are based on part-based or on holistic non-decomposable representations of facial identity. If these processes operate in a strictly part-based fashion, repetitions of internal or external facial features should be registered separately and independently. In this case, reliable N250r components should be elicited not only when full repetition trials and full change trials are compared, but also for internal and on external feature repetition trials relative to full change trials. Furthermore, if these part-based identity matching processes operate in parallel and completely independently of each other, the N250r component on full repetition trials should equal the sum of the two N250r components on internal and external feature repetition trials, reflecting the separate contributions of the two matching processes that are based on internal and external features. In contrast, an identity matching process that is exclusively based on non-decomposable holistic face representations should be reflected by an entirely different pattern of N250r components. Within a holistic representation, specific face parts should not be accessible independently of all other facial features. Therefore, a repetition of internal or external features should not be detected by face identity matching mechanisms on partial repetition trials where there is a change in the other set of features. In this case, an N250r component should only be present on full repetition trials, but should be entirely absent on internal and external feature



Fig. 1 – Examples of individual face stimuli from the present experiment. The face pairs in the top and bottom rows share the same internal features but have different external features. The pairs in the left and right columns have the same external and different internal features.

repetition trials. If upright faces are encoded and maintained in a holistic fashion, while representations of inverted faces are essentially part-based, this should be reflected by a corresponding difference in the pattern of N250r components in blocks with upright and inverted faces. For inverted faces, N250r components should be present on internal and external feature repetition trials, with their sum equalling the N250r on full repetition trials. For upright faces, N250r components should be exclusively confined to full repetition trials.

Instead of being exclusively based on holistic or on part-based representations, an alternative possibility is that both types of representations can be involved in visual face identity matching processes (e.g., [Behrmann et al., 2014](#)). In this case, reliable N250r components may be present on internal and external feature repetition trials in blocks with upright faces, reflecting the contribution of part-based face representations. However, if matching the identity of upright faces also involves holistic processes that are only elicited when both internal and external features are repeated, the N250r on full repetition trials should be larger than the sum of the two N250r components measured on internal and external feature repetition trials. If only upright but not inverted faces can be processed and represented in a holistic fashion, such a super-

additive N250r component to full face repetitions should only be observed in blocks with upright faces, whereas N250r components in inverted face blocks should be strictly additive.

1. Materials and methods

1.1. Participants

Twelve paid volunteers (six female, mean age 31 years, one left-handed) were tested. All had normal or corrected-to-normal vision, and gave written and verbal informed consent prior to testing.

1.2. Stimuli and procedure

Participants were seated in a dimly lit, sound-attenuated and electrically shielded chamber. Face stimuli were presented on a CRT monitor at a viewing distance of 100 cm, using E-Prime software (Psychology Software Tools, Pittsburgh, PA). The face stimuli were created using 10 images of male Caucasian faces obtained from the PUT Face Database ([Kasinski, Florek, & Schmidt, 2008](#)) and the University of Stirling Online

Database. All images were converted to greyscale, and were edited using Adobe Photoshop to homogenise large differences in overall luminance, and skin tone and hair. Distinguishing characteristics (e.g., piercings or blemishes) were removed from the images. The internal features of each of the ten faces were paired with the external features of each of the other ten faces to create a total of 100 face stimuli (ten original faces, 90 newly created composite faces; see Fig. 1 for examples). All stimuli were presented on a CRT monitor against a dark background (4 cd/m^2) at a viewing distance of 100 cm. Stimulus presentation, timing and response recording were controlled by E-Prime (Psychology Software Tools, Pittsburgh, PA). On each trial, two faces were presented in rapid succession. The first face (S1) was presented for 400 msec and the second face (S2) was presented for 200 msec. These two face images were separated by a 200 msec interstimulus interval. The intertrial interval was 1500 msec. S1 stimuli occupied a visual angle of $5.8^\circ \times 8^\circ$. S2 stimuli were 10% larger in order to avoid pixel-wise matching. The average luminance of all face stimuli was 21 cd/m^2 .

There were four types of S1–S2 sequences that occurred in random order in each block. On full repetition trials, the S1 and S2 face images were identical. On full change trials, the S1 and S2 faces differed both in terms of their external and internal features. On external feature repetition trials, the internal features of the two faces differed but their external features were identical. On internal feature repetition trials, the external features of the S1 and S2 faces differed, but their internal features were identical. Participants were instructed to encode both the internal and external features of the S1 face and to decide whether both were repeated in the S2 face, or whether there was a change between the two faces. They signalled the presence of a full repetition by pressing one response key and the presence of any change (a change of internal features, external features, or both) by pressing another response key. These two alternative responses were executed with the index or middle finger of one hand, and response hand was counterbalanced across participants.

The experiment contained 24 blocks, with 50 trials per block, resulting in 1200 trials in total. There were 300 trials for each of the four different types of S1–S2 sequences. Faces were presented in a pseudorandom order in which each face (of the 100 faces) was presented as the S1 face within a two block period (100 trials). In half of all blocks, the faces were presented in their standard upright position. In the other half, all face images were inverted. Half of all participants completed 12 blocks with upright faces before performing the same face matching task in 12 blocks with inverted faces. This order was reversed for the other half of participants. All participants were given a training block of 50 trials before starting the first experimental block with upright faces and inverted faces, respectively. After each block, they received on-screen feedback about their average accuracy and response times (RTs) in this block.

1.3. EEG recording and data analysis

EEG was DC-recorded with a BrainAmps DC amplifier (upper cut-off frequency 40 Hz, 500 Hz sampling rate) and Ag–AgCl

electrodes mounted on an elastic cap from 27 scalp sites Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P9, P3, Pz, P4, P8, P10, PO9, PO7, PO8, PO10 and Oz, according to the extended international 10–20 system. Bipolar horizontal electrooculogram (HEOG) was recorded from the outer canthi of both eyes. An electrode placed on the left earlobe served as reference for online recording, and EEG was re-referenced off-line to the common average of all scalp electrodes. Electrode impedances were kept below 5 k Ω . No additional off-line filters were applied. ERPs in response to the S2 face on each trial were computed on the basis of EEG epochs obtained between 50 msec before and 500 msec after S2 onset, relative to a 100 msec baseline from 50 msec before to 50 msec after S2 onset. Epochs with activity exceeding $\pm 30 \mu\text{V}$ in the HEOG channel (reflecting horizontal eye movements) or $\pm 60 \mu\text{V}$ at Fpz (indicating eye blinks or vertical eye movements) were excluded from all analyses, as were epochs with voltages exceeding $\pm 80 \mu\text{V}$ at any other electrode. Trials with incorrect responses were excluded from the EEG analysis.

Following artifact rejection, EEG epochs were averaged to compute ERP waveforms for the four trial types (full repetition, full change, internal feature repetition, external feature repetition), separately for blocks with upright and inverted faces. ERP mean amplitudes in the N250r time window (230–300 msec after S2 onset) were measured at four lateral posterior electrode sites over the left hemisphere (P7, PO7, P9, and PO9), and at the corresponding electrodes over the right hemisphere (P8, PO8, P10, and PO10), and were averaged across these four electrode locations on either side. Statistical analyses of N250r amplitudes were conducted with repeated-measures ANOVAs for the factors external feature repetition (repetition vs change), internal feature repetition (repetition vs change), face orientation (upright vs inverted), and hemisphere (left vs right). Additional analyses were conducted separately for blocks with upright and inverted faces. Apart from the factor hemisphere, the same factors were employed for the analyses of behavioural performance. To compare N250r onset latencies between blocks with upright and inverted faces, a jackknife-based method was employed. Difference waveforms were computed by subtracting ERPs on full repetition trials where both internal and external features were repeated from full change trials where both internal and external features changed. The jackknife-based procedure described by Miller, Patterson, and Ulrich (1998) was employed to determine and compare the onset of the N250r components to upright and inverted face repetitions. With this method, onset latencies were measured on the basis of grand-averaged difference waveforms (full repetition – full change) computed for subsamples of participants, where one participant is subsequently excluded from the original sample. N250r onset was defined as the point in time where N250r difference waveforms exceeded an absolute threshold value of $-1 \mu\text{V}$. N250r onset latency differences between upright and inverted faces were evaluated in analyses with the factor orientation, with F -values (F_c) corrected according to the formula described by Miller et al. (1998).

2. Results

2.1. Behaviour

Fig. 2 shows RTs on trials with correct responses and error rates for the four trial types, separately for upright and inverted faces. As expected, RTs were generally slower in blocks with inverted faces relative to blocks with upright faces (512 msec vs 472 msec), as confirmed by a main effect of face orientation [$F(1,11) = 7.04$, $p < .025$, $\eta_p^2 = .39$]. There were also main effects of external feature repetition [$F(1,11) = 13.28$, $p < .005$, $\eta_p^2 = .55$] and internal feature repetition [$F(1,11) = 12.03$, $p < .005$, $\eta_p^2 = .56$], as well as a trend towards an interaction between these two factors [$F(1,11) = 3.4$, $p = .09$, $\eta_p^2 = .24$]. This was due to the fact that RTs were faster on full change trials than on the other three types of trials (see Fig. 2, line graphs), presumably because “change” responses were more frequent than repetition responses (75% vs 25%), and the presence of a change could be detected most rapidly on full change trials. Follow-up analyses with paired *t*-tests confirmed that RTs were faster on full change trials than on full repetition trials, trials with an external feature change, and trials with an internal feature change, for both upright or inverted faces [all $t(11) > 3.7$, all $p < .003$]. There were no significant RT differences between the other three types of trials (all $t < 1.1$, all $p > .27$), and no interactions involving the factor face orientation (all $F < 1.9$).

Errors were generally more frequent in blocks with inverted faces as compared to blocks with upright faces (9% vs 2%), as reflected by a main effect of face orientation [$F(1,11) = 18.11$, $p < .001$, $\eta_p^2 = .62$]. There were main effects of external feature repetition [$F(1,11) = 14.68$, $p < .001$, $\eta_p^2 = .57$] and a trend for internal feature repetition [$F(1,11) = 3.45$, $p < .09$, $\eta_p^2 = .24$] on

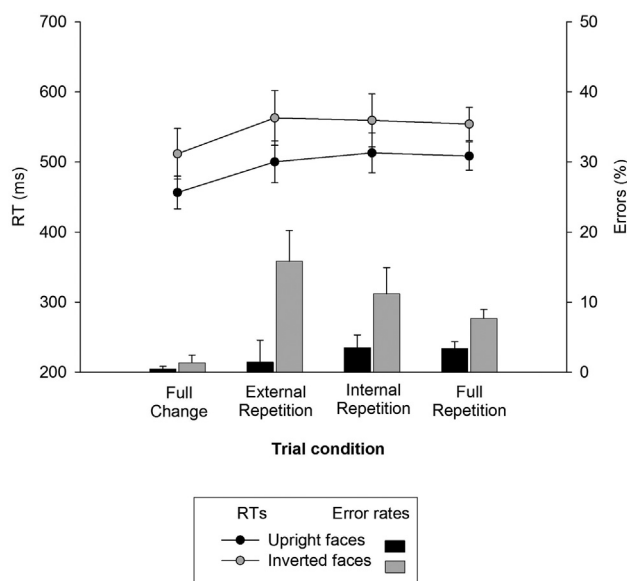


Fig. 2 – Response times (RTs, line graphs) and error rates (bar graph) for the four different trial types (full change, external repetition, internal repetition, full repetition), shown separately for blocks with upright or inverted faces. Error bars represent one standard error of the mean.

error rates, and an interaction between these two factors [$F(1,11) = 5.19$, $p < .05$, $\eta_p^2 = .32$]. A significant interaction between orientation and external feature repetition [$F(1,11) = 17.56$, $p < .001$, $\eta_p^2 = .62$] was accompanied by a three-way interaction between face orientation, external feature repetition, and internal feature repetition [$F(1,11) = 6.72$, $p < .05$, $\eta_p^2 = .38$]. As can be seen in Fig. 2 (black bars), error rates for upright faces were generally very low across conditions (full change trials: .4%; external repetition trials: 1.4%; internal repetition trials: 3.5%; full repetition trials: 3.3%). For inverted faces (grey bars), error rates were lowest on full change trials (1.3%), intermediate on full repetition trials (7.7%), and largest on trials with external or internal feature repetitions (15.8% and 11.2%, respectively). This shows that on trials with a partial repetition of either internal or external facial features, the probability of participants' incorrectly reporting a full face repetition was much higher with inverted faces than with upright faces, while the effects of face inversion on error rates were less pronounced on full repetition and full change trials. To assess this pattern statistically, an additional ANOVA of error rates was conducted with the factors face orientation and trial type (full repetition/change vs partial repetition). There was a significant interaction between orientation and trial type, $F(1,11) = 8.46$, $p < .015$, $\eta_p^2 = .44$, confirming that error rates were more strongly affected by face inversion on partial repetition trials.

2.2. N250r components

Fig. 3 (top panels) shows ERPs elicited at lateral posterior electrodes over the left and right hemisphere in response to S2 faces on full repetition trials, full change trials, and trials with external or internal feature repetitions, separately for blocks with upright faces (top panel) and blocks with inverted faces (bottom panel). For upright faces, clear N250r components were triggered on full repetition trials relative to full change trials. On trials with external or internal feature repetitions, N250r components also appeared to be present, but were much smaller in size relative to full repetition trials. In blocks with inverted faces, N250r components were generally attenuated and delayed, but were also larger in response to full face repetitions relative to trials where only external or internal features were repeated. The scalp topography of N250r components on full repetition trials is shown in Fig. 3 (bottom panel), separately for blocks with upright and inverted faces. The N250r shows its typical distribution with a lateralized posterior negativity accompanied by a frontal positivity (e.g., Schweinberger, 2011). N250r amplitudes are clearly attenuated in blocks with inverted face images.

In the overall analysis of N250r amplitudes across both face orientations, there were main effects of external feature repetition [$F(1,11) = 22.36$, $p < .001$, $\eta_p^2 = .67$] and internal feature repetition [$F(1,11) = 26.19$, $p < .001$, $\eta_p^2 = .70$] that both interacted with face orientation [both $F(1,11) > 29.86$, $p < .001$, $\eta_p^2 = .73$], demonstrating that N250r components elicited by repetitions of internal or external facial features were attenuated in blocks with inverted faces (see below). There was also an interaction between external feature repetition and internal feature repetition [$F(1,11) = 11.89$, $p < .005$, $\eta_p^2 = .52$]. This interaction reflects the fact that N250r components on full

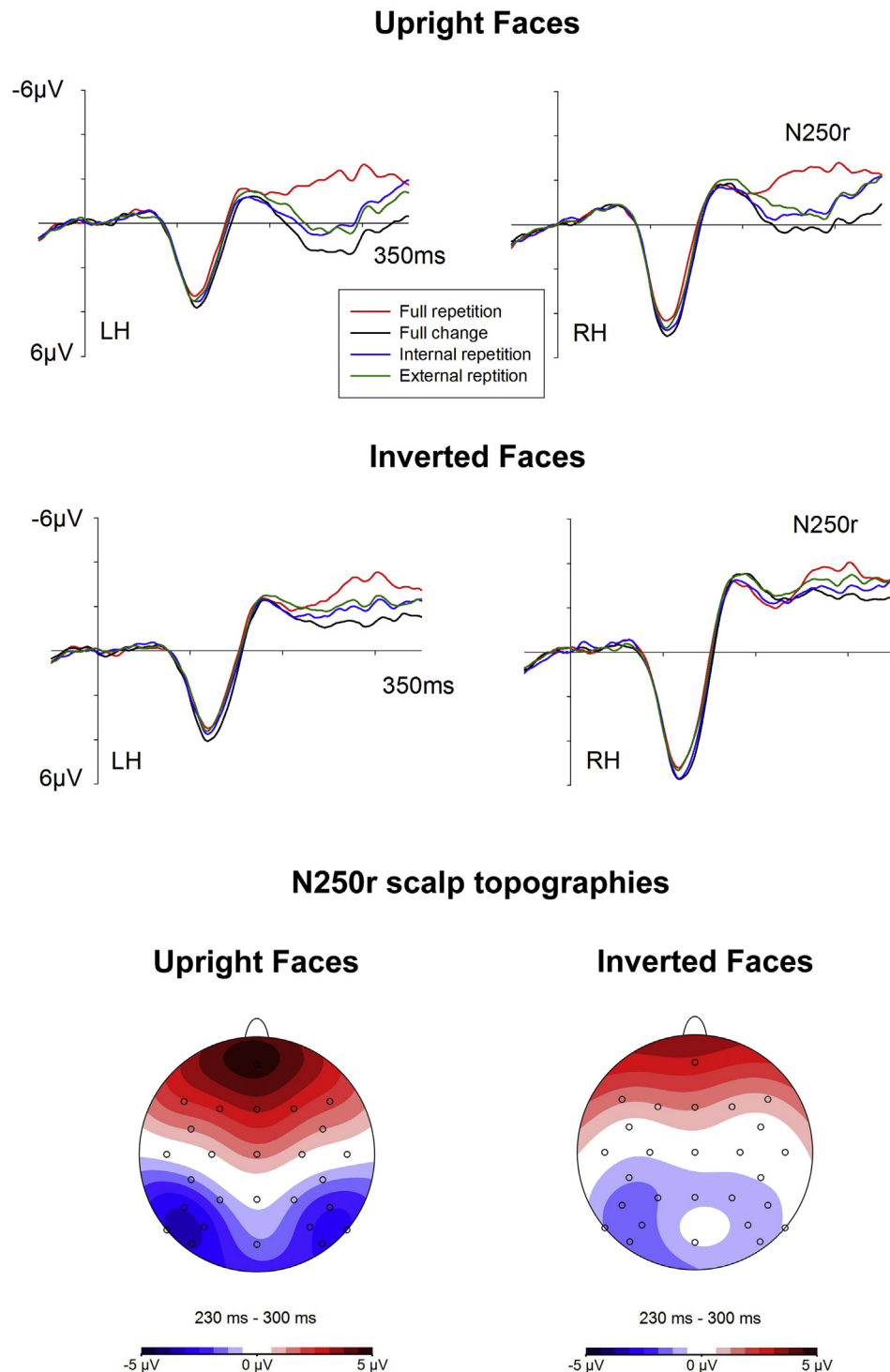


Fig. 3 – Top panels: grand-averaged event-related brain potentials (ERPs) measured in the 350 msec interval after the onset of the S2 face at lateral posterior electrodes over the left hemisphere (LH) and right hemisphere (RH). ERPs are shown separately for the four different trial types. Bottom panel: Topographical maps showing the scalp distribution of N250r components to full face repetitions in blocks with upright faces (left) and inverted faces (right). These maps were generated by subtracting ERP mean amplitudes measured in the 230–300 msec post-stimulus time window on full change trials from ERPs on full repetition trials.

repetition trials were generally larger than the sum of the two N250r components elicited on external and internal feature repetition trials, (i.e., a super-additive N250r component to full face repetitions). However, and critically, there was also a

highly significant three-way interaction between external feature repetition, internal feature repetition, and face orientation [$F(1,11) = 28.47$, $p < .001$, $\eta_p^2 = .72$], which suggests that the additivity versus super-additivity of the N250r component

to full face repetitions was determined by whether faces were presented upright or upside-down.

To further investigate the role of face orientation on N250r components to full and partial repetitions of facial features, separate N250r analyses were conducted for blocks with upright and inverted faces. For upright faces, there were main effects of internal feature repetition [$F(1,11) = 82.82, p < .001, \eta_p^2 = .88$] and external feature repetition [$F(1,11) = 36.13, p < .001, \eta_p^2 = .77$], and critically, an interaction between these two factors [$F(1,11) = 40.33, p < .001, \eta_p^2 = .79$], due to the fact that the N250r to fully matching faces was larger than the sum of the N250r components to repetitions of external and internal features only. This is illustrated in Fig. 4 (top panel), which shows N250r difference waveforms obtained by subtracting ERPs measured on full change trials from ERPs on trials with a full or partial repetition of facial features. Because there was no overall difference between N250r amplitudes measured over the left and right hemispheres, and no three-way interaction between internal and external feature repetitions and hemisphere, both $F < 1.5$, ERPs were collapsed across hemisphere for these analyses. The N250r to full face repetitions (solid line) was larger than the sum of the two N250r components obtained on trials with a repetition of external or internal features (dashed line), demonstrating that a super-additive N250r was elicited on full repetition trials in blocks with upright faces. A qualitatively different pattern of results was observed for inverted faces. There was a main effect of external feature repetition [$F(1,11) = 9.82, p < .01, \eta_p^2 = .47$] and an almost significant effect of internal feature repetition [$F(1,11) = 4.94, p < .09, \eta_p^2 = .24$]. An interaction between internal face repetition and hemisphere [$F(1,11) = 8.13, p < .05, \eta_p^2 = .43$] was due to the fact that the N250r to internal feature repetitions was significant over the left hemisphere [$t(11) = 2.47, p < .03$], but not over the right hemisphere ($t < 1$). Critically, and in marked contrast to the pattern of N250r results observed for upright faces, there was no interaction between internal and external feature repetitions for inverted faces ($F < 1$), indicating that the N250r component to full repetitions of inverted faces was equal to the sum of the N250r components elicited in response to repetitions of external and internal features. This is illustrated in Fig. 4 (middle panel), where the N250r to full repetitions of inverted faces (solid line) is compared to the sum of the N250r components in response to repetitions of external or internal features only (dashed line). The absence of any amplitude differences between the N250r to full face repetitions and the summed N250r components to partial repetitions shows that for inverted faces, the N250r component reflected the additive contributions of internal and external facial feature repetitions.

As can be seen in Fig. 4 (top panel), the N250r component for full repetitions of upright faces did not differ from the sum of the two N250r components to partial feature repetitions during its initial phase between 190 and 220 msec after S2 onset. This is due to the fact that for upright faces, the N250r to repetitions of external features emerged earlier than the N250r to repetitions of internal features (see also Fig. 3, top panel). This was confirmed in an analysis of ERP mean amplitudes measured during the 190–220 msec post-stimulus interval for blocks with upright faces. There was a main

effect of external feature repetition [$F(1,11) = 11.04, p < .01, \eta_p^2 = .50$], but no effect of internal feature repetition ($F < 1$), and no interaction between these two factors ($F < 1$), confirming that during this early time window, identity matching processes between upright faces were based on their external features only.

To confirm the generic effects of face inversion on the N250r component, ERPs on full repetition and full change trials were directly compared between blocks with upright and inverted faces. Fig. 4 (bottom panel) shows N250r difference waveforms obtained by subtracting ERPs on full change trials from ERPs on full repetition trials, separately for upright and inverted faces. N250r components were clearly attenuated and delayed for inverted faces. An analysis of ERP mean amplitudes measured in the N250r time window with the factors trial type (full repetition vs full change) and face orientation (upright vs inverted) revealed a significant interaction between both factors [$F(1,11) = 41.96, p < .001, \eta_p^2 = .79$], confirming the attenuation of N250r amplitudes for inverted faces. To determine whether the onset latency of N250r components differed between upright and inverted faces, a jackknife-based analysis was performed on N250r difference waveforms for full repetition minus full change trials (collapsed across the left and right hemisphere) using a fixed onset criterion of $-1 \mu\text{V}$. The N250r emerged earlier for upright faces than for inverted faces (218 msec vs 270 msec), and this onset latency difference was significant, $t_c(11) = 2.6, p = .025$.

2.3. Early face repetition effect

As can be seen from the difference waveforms in Fig. 4, N250r components were preceded by an earlier negative deflection that started over lateral posterior electrodes approximately 100–170 msec after stimulus onset, and returned to baseline before the N250r component emerged. This early negativity reflects a reduction of P1 amplitudes for trials with internal and/or external repetitions of facial features as compared to full change trials (see Fig. 3). In order to explore whether this early repetition effect reflects high-level face identity processing or lower-level differences in image similarity between change and repetition trials, we analysed ERP mean amplitudes obtained in the 110–160 msec post-stimulus time window at lateral posterior electrodes over the left and right hemispheres in the same way as the N250r component. An ANOVA was conducted with the factors external feature repetition, internal feature repetition, face orientation and hemisphere. This analysis revealed main effects of internal feature repetition [$F(1,11) = 14.81, p = .003, \eta_p^2 = .57$], and external feature repetition [$F(1,11) = 58.33, p < .001, \eta_p^2 = .84$], reflecting reduced P1 amplitudes on feature repetition as compared to feature change trials. There was no interaction between these two factors ($F < 1$), and no three-way interaction between internal feature repetition, external feature repetition, and face orientation ($F < 2.6$), demonstrating that the P1 amplitude reductions elicited by internal and external feature repetitions were entirely additive, both for upright and inverted faces. Importantly, there were no interactions between face orientation and internal or external feature repetitions (both $F < 1$), which shows that these early repetition effects were equal in size for upright and inverted faces.

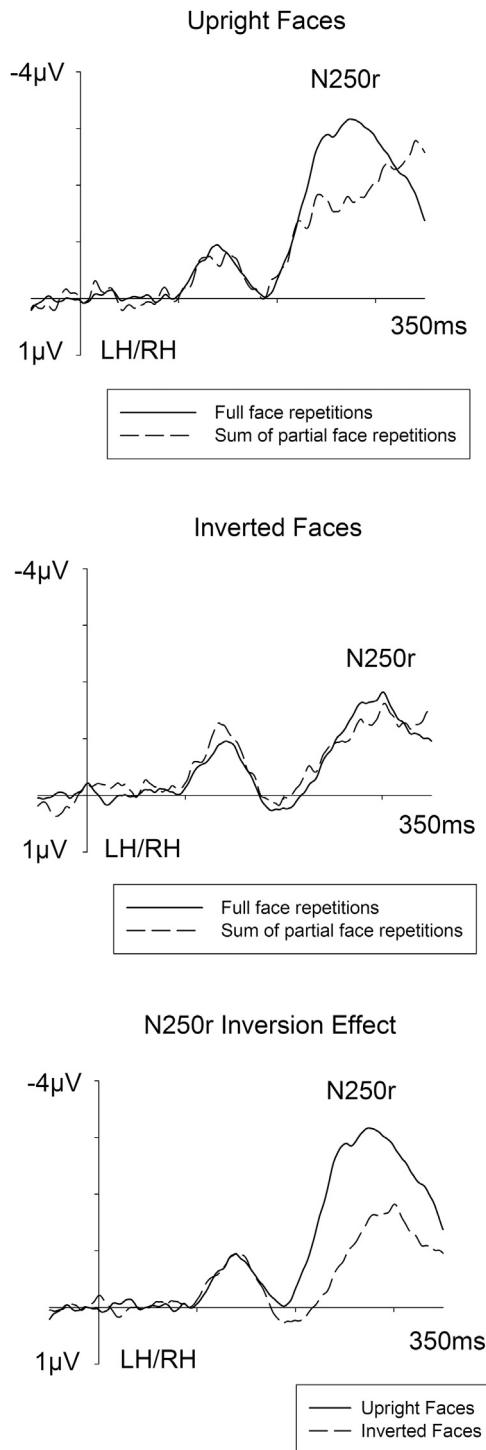


Fig. 4 – Grand average N250r difference waveforms shown for the 350 msec interval after S2 onset. All difference waves are collapsed across hemisphere and lateral posterior electrode sites. Top and middle panels: N250r components for full face repetitions (obtained by subtracting ERPs on full change from full repetition trials) and the sum of the two N250r components to partially matching faces (obtained by subtracting full change trials from internal repetition trials, and full change trials from external repetition trials, and summing the resulting two N250r difference waveforms), shown separately for blocks

3. Discussion

The goal of the present study was to investigate qualitative differences between upright and inverted faces in the nature of the representations involved in face identity matching processes. For upright faces, these processes may be based on non-decomposable holistic representations of individual faces, whereas they might be purely part-based for inverted faces. To test this hypothesis, we recorded N250r components as markers of identity matching processes in visual face memory in a task where participants had to judge whether two successively presented faces were the same or differed with respect to their internal features, external features, or both. The current findings strongly suggest that there are both quantitative and qualitative differences in the way in which upright and inverted faces are stored and matched in visual memory.

In line with previous observations (Itier & Taylor, 2004; Jacques et al., 2007; Schweinberger et al., 2004), N250r components elicited on full face repetition trials as compared to full change trials were attenuated and delayed in blocks with inverted faces relative to upright face blocks. The N250r onset delay for inverted versus upright faces was approximately 50 msec, which matches the 50 msec delay found for RTs in blocks with inverted faces, suggesting that these RT costs are primarily due to a delay in the onset of visual face identity matching processes, as reflected by the N250r component. The reduction of N250r amplitudes for inverted as compared to upright faces indicates that these matching processes may also have been more temporally variable and/or less precise in blocks with inverted faces. The lack of precision in matching inverted face images was also evident in error rates, which were reliably higher in blocks with upside-down faces.

These behavioural and electrophysiological differences could be due to quantitative differences in the time course or the precision with which representations of facial identity can be generated in response to upright and upside-down faces. However, they could also reflect fundamental qualitative differences between holistic identity matching processes for upright faces and part-based matching processes for inverted faces. These alternative possibilities can be assessed on the basis of the N250r results observed on partial repetition trials where internal facial features were repeated while external features changed, or vice versa. If upright faces are encoded and represented in a strictly holistic fashion as non-decomposable wholes (e.g., Rossion, 2013; Tanaka & Farah, 1993), N250r components indicative of successful face identity matching should only be elicited on full repetition trials. No N250r should be present on trials where only the internal or external features of an upright face was repeated, because face parts cannot be explicitly represented and matched outside of the context of other facial features. This prediction was not confirmed. In upright face blocks, repetitions of external or internal features triggered small but reliable N250r

with upright or inverted faces. Bottom panel: N250r components on full repetition trials (obtained by subtracting full change from full repetition trials) in blocks with upright or inverted faces.

components on trials where the other facial features changed, demonstrating that such partial feature repetitions were detected during visual face identity matching processes. While this observation rules out the hypothesis that upright faces are processed and represented in an entirely holistic fashion (Rossion, 2013), the comparison of N250r components elicited on trials with full versus partial feature repetitions demonstrated that holistic representations are involved in the identity matching of upright faces. The N250r triggered on full repetition trials was larger than the sum of the two N250r components elicited on internal and external feature repetition trials. This super-additivity of the N250r component in response to full repetitions of upright faces shows that the processes responsible for matching the identity of upright faces does not operate in an entirely part-based fashion independently for different facial features. It suggests instead that internal and external features of upright faces are represented in an integrated fashion in inferior occipito-temporal brain regions, and that face identity matching processes are at least in part based on such integrated holistic representations in visual face memory. However, the fact that residual N250r components to partial repetitions of internal or external features remained reliably present in upright face blocks, and the fact that repetitions of external facial features were matched prior to the emergence of internal feature or holistic face matching processes shows that holistic processing is not necessarily an exclusive strategy for the perceptual encoding and maintenance of upright faces. The presence of such feature-based matching responses for upright faces is incompatible with theoretical accounts that stress the notion that upright faces are exclusively represented as non-decomposable wholes. Our results suggest that for upright faces, holistic and part-based representations of facial identity can coexist. The role that these two types of representations play during face perception and recognition may differ as a function of task demands. Because target faces were defined as faces that fully matched a previously seen face in the current experiment, participants were required to attend to the whole face rather than face parts, and this may have encouraged a holistic mode of face processing. In other face matching tasks where only specific parts of face images are task-relevant (such as composite face tasks; e.g., Young et al., 1987), part-based representations may play a more prominent role, although holistic face representations are clearly still involved.

The pattern of N250r components observed to full versus partial face repetitions in blocks with inverted faces was very different from the N250r results found in upright face blocks, which demonstrates that there are indeed qualitative differences in representations of facial identity for upright and inverted faces. N250r components elicited by full repetitions of inverted faces were identical in size to the sum of the two N250r components on internal and external feature repetition trials. The presence of such an additive N250r in inverted face blocks suggests that the processes responsible for the matching of external and internal features operated separately of each other in a part-based fashion, with each process contributing independently and additively to the N250r component. The contrast between the super-additivity of the N250r component with upright faces and the additivity of the

N250r in blocks with inverted faces was reflected by a highly significant interaction between face orientation, external feature repetition, and internal feature repetition. This dissociation is the central finding of the current experiment, because it provides new and direct electrophysiological evidence for fundamental qualitative differences in the identity-related processing of upright and inverted faces. For upright faces, representations of facial identity in visual memory are at least partially holistic, whereas inverted faces are exclusively represented in a part-based fashion. Although the presence of N250r components to partial face repetitions in the current experiment suggests the existence of part-based face representations for upright faces, an alternative interpretation of these results needs to be considered. The amplitude of N250r components generally reflects the degree of similarity between two visual face representations during face matching. It is possible that rather than being based on both holistic and part-based visual representations for upright faces (as previously suggested) the comparison process is entirely based on a non-decomposable holistic representation of the whole face. On this account, the reduced N250r amplitudes observed on partial repetition trials would reflect a reduced degree of perceived similarity. However, the fact remains that the N250r to external feature repetitions were elicited earlier than N250r components to internal feature repetitions, and prior to the emergence of a super-additive N250r component to full face repetitions. This temporal dissociation between part-based and holistic face comparison processes strongly suggests that some face features were represented on the basis of their constituent parts during upright face matching.

This qualitative difference in the nature of the representations involved in the identity matching of upright and inverted faces may also be responsible for the observed effects of face inversion on error rates. Even though errors were generally more frequent in blocks with inverted faces than in upright face blocks, this difference was most pronounced on partial repetition trials where participants had to report the presence of a change in spite of the fact that either the internal or external features were repeated (as shown in Fig. 2). If external and internal feature repetitions versus changes are registered in an independent part-based fashion for inverted faces, these two processes will result in separate match/mismatch decisions that can affect response decision processes independently. This may increase the probability that participants incorrectly report an identity match on partial repetition trials. Furthermore, given that the encoding capacity of visual face memory is severely limited (e.g., Towler et al., 2015), it is also possible that on a subset of trials, participants were able to encode only the external or internal features of inverted faces, but not both. This would result in incorrect responses on partial repetition trials where the change occurred in the non-encoded face part. Because both possible sources of incorrect responses on partial repetition trials are a direct result of the part-based nature of visual representations of inverted faces, they will have less impact on the identity-related processing of upright faces that is at least in part based on holistic representations that are integrated across internal and external features.

In addition to the N250r, the current study also examined an earlier face repetition effect that overlaps in time with the sensory-evoked P1 component, and has been observed in a number of previous N250r experiments (e.g., Fisher et al., 2016; Schweinberger et al., 2002; Wirth et al., 2015; Zimmermann & Eimer, 2013). The reduction of P1 amplitudes for face repetitions versus changes could in principle already reflect identity-sensitive face processing mechanisms related to visual face memory, or could be due to low-level differences in the amount of visual change between repetition and change trials. In the current experiment, internal and external feature repetitions contributed in a completely additive fashion to this early repetition effect, and this effect was also found to be entirely insensitive to the difference between upright and inverted faces. Both observations strongly suggest that P1 amplitude modulations observed on face repetition versus face change trials are not linked to holistic face identity matching mechanisms that are tuned to upright faces. Instead, they are likely to reflect low-level differences in the amount of visual change between a face pair on a particular trial, with changes of internal and external features both contributing independently to an increase in P1 amplitudes. The absence of any evidence for holistic face processing during early sensory visual processing stages that give rise to the P1 component strongly suggests that holistic representations of face identity are not immediately available to the visual system during the perceptual processing of face stimuli, but only emerge at subsequent stages beyond 200 msec after stimulus onset.

If the processes involved in the identity matching of upright faces involve both part-based and holistic aspects, it is important to determine whether these two aspects operate in a particular temporal sequence. Classic models of visual object recognition (e.g., Biederman, 1987) assume that objects are first represented on the basis of their local parts or features, and that holistic representations emerge later in time in the processing hierarchy. In contrast to such local-to-global accounts, an alternative view is that in the case of face processing, the initial representation of faces and of face identity is a coarse global-holistic representation which then becomes more local and finely detailed over time (global-to-local or reverse-hierarchical accounts of face perception; e.g., Hochstein & Ahissar, 2002; Rossion, Dricot, Goebel, & Busigny, 2011). In the present study, the N250r component in upright face blocks was initially exclusively elicited by repetitions of external facial features, and became sensitive to internal feature repetitions about 30 msec later. At this point in time, the N250r to full face repetitions became super-additive (see Fig. 4, top panel). This time course is not consistent with global-to-local accounts where a global-holistic face representation is available at an earlier point in time than information derived from a more fine-grained analysis of face parts, and is more in line with local-to-global models. A similar bias for external facial features has been observed in previous behavioural studies of identity-related face processing with unfamiliar faces (e.g., Bonner et al., 2003; Want et al., 2003). It should be noted that the apparent temporal precedence of external over internal facial feature repetitions at the level of the N250r component was not restricted to upright faces, but was also observed in blocks with inverted

faces (see Fig. 3, lower panels). Because N250r components are initially generated by a partial identity match between external facial features, the observation that N250r components are delayed by face inversion suggests that (in addition to face inversion abolishing holistic face processing) part-based face identity matching processes are also delayed by face inversion.

In summary, the current study has provided novel evidence for qualitative differences between the way in which upright and inverted faces are represented during face identity matching. For upright faces, holistic memory representations of facial identity in the occipito-temporal face processing system coexist with part-based representations. For these faces, we found that the matching of face parts (i.e., external facial features) in visual memory preceded the face matching of holistic representations for upright faces. In contrast, there was no evidence for the involvement of holistic representations during the identity matching of inverted faces. The identity of inverted faces appears to be determined exclusively in a part-based fashion.

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