

## Why is the N170 enhanced for inverted faces? An ERP competition experiment

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### ABSTRACT

The amplitude of the ERP component N170 is larger in response to inverted than to upright faces. The current study tested two main hypotheses that have been suggested to explain this effect: according to the first hypothesis inverted faces lead to augmentation of activity of the same neural populations used for the processing of upright faces due to the increased processing difficulty that these stimuli impose; according to the second hypothesis the processing of inverted faces involves recruitment of additional neural mechanisms to those used for upright face processing. We employed an ERP competition paradigm in which the effect of a context stimulus on the ERP to a simultaneously presented target stimulus is measured. In Experiment 1, an upright target face was paired with an upright face, inverted face or a non-face context stimulus. ERPs time-locked to the presentation of the target showed reduced N170 amplitude when the context was an upright face more than in non-face context trials, replicating the ERP competition effect for faces. Interestingly, in contrast to the hypothesis that inverted faces recruit mechanisms used for upright faces to a greater extent, competition effects were similar in the context of inverted and upright faces. In Experiment 2, the target stimuli were inverted faces. This time, competition effect was larger in inverted than in upright face context. Taken together, these findings correspond with the hypothesis that inversion of the face leads to recruitment of additional mechanisms as early as at the N170 time-window.

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### Introduction

One of the most well-established phenomena in face perception is that picture-plane inversion of a face stimulus dramatically impairs subjects' ability to recognize it (Yin, 1969; see Valentine, 1988 for review). Though inversion may increase processing difficulty for non-face pictures as well, the much larger inversion effect observed with faces as compared to other objects is often taken as evidence for the specificity of face processing in the human higher visual system (Kanwisher, 2000; Yin, 1969; Yovel and Kanwisher, 2004).

Event related potential (ERP) studies have shown an early negative component that peaks around 170 ms after stimulus onset (N170) that is much larger for faces than non-face stimuli (Bentin et al., 1996). This N170 component is found to be of higher amplitude and often of later latency for inverted than for upright faces (Anaki et al., 2007; Bentin et al., 1996; Caharel et al., 2006; de Haan et al., 2002; Eimer, 2000; Itier et al., 2006, 2007; Itier and Taylor, 2004; Jacques et al., 2007; Jacques and Rossion, 2007a; Marzi and Viggiano, 2007; Righart and de Gelder, 2006; Rossion et al., 1999, 2000). Similar to the behavioral phenomenon, in most studies this N170 face inversion effect (N170-FIE) has not been observed for non-face

stimuli (Bentin et al., 1996; Itier et al., 2007; Rossion et al., 2000, but see Eimer, 2000). Delineating the neural basis of the enhancement in electrical scalp recorded potentials for inverted faces is a challenging task since the spatial resolution of the EEG is particularly low. Different studies have suggested diverse cortical sources for the N170 component and various models to account for the N170-FIE. According to one view, the signal enhancement reflects greater effort of face-selective mechanisms, due to the increased difficulty to recognize inverted faces and extract relevant information such as configural and/or featural cues (Marzi and Viggiano, 2007; Rossion et al., 1999; Watanabe et al., 2003). This hypothesis is consistent with the suggestion that the difference in recognition abilities of upright and inverted faces as measured behaviorally is due to quantitative rather than qualitative processing differences (Sekuler et al., 2004) and we will therefore refer to this idea as the "quantitative hypothesis". An alternative account for the N170-FIE, which we will refer to as the "qualitative hypothesis" proposes that processing of inverted faces involves an early recruitment of additional mechanisms in addition to those used for the processing of upright faces (e.g. object-general encoding systems, eye-specific processing mechanisms) and therefore involves a qualitative change in the type of processing. This view is consistent with fMRI studies that have consistently shown signal enhancement for inverted relative to upright faces in object-related regions (Aguirre et al., 1999; Epstein et al., 2006; Haxby et al., 1999; Yovel and Kanwisher, 2005) as well as with ERP studies suggesting the involvement of eye-specific neural

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mechanisms in the processing of inverted faces that are silent when faces are viewed upright (Itier et al., 2007). Such recruitment of additional neural mechanisms can result in increased electrical potentials recorded distally on the scalp (see Rossion and Gauthier, 2002).

The purpose of the present study was to test these two hypotheses for the neural basis of the N170 FIE. To that effect we used the ERP competition paradigm developed by Jacques and Rossion (2004, 2006, 2007b) and Rossion et al. (2004). In their experiments, Jacques and Rossion concurrently presented on a screen two stimuli in the following way: The first stimulus (context stimulus) was either an upright face or a scrambled face. After a few hundreds of milliseconds a target stimulus, which was an upright face in all experimental conditions, was presented next to the context image (either peripherally (Jacques and Rossion, 2004) or centrally (Jacques and Rossion, 2006)) such that both context and target remained on the screen simultaneously. ERPs were time-locked to the onset of the second (target) face stimulus. In all experiments, lower amplitude (i.e. larger amplitude reduction) was observed for target faces preceded by a face (face context) than by a non-face (non-face context). Reduction of ERP amplitude due to concurrent presentation of the same stimulus-category was assumed to reflect a competition on representation in the visual system. Given that face stimuli are processed by largely overlapping populations of neurons, a face presented while another face is being processed will result in a reduced response recorded on the scalp as compared to the signal for a face presented concurrently with a non-face stimulus. Importantly, this effect was strongest at the N170 time-window where the most prominent face-sensitive potential is observed, and absent at early non-category specific stages like the P1 component (see Jacques and Rossion, 2007b for discussion). This finding reinforces the view that the signal reduction reflects competition on neural representation between same category stimuli sharing common neural resources for their encoding.

The ERP competition paradigm can therefore serve as an effective technique to evaluate the overlap in neural mechanisms that are involved in visual encoding of different stimulus categories with great temporal resolution. For example, Rossion et al. (2004) used the paradigm to investigate whether expertise with novel stimuli increases the overlap in neural representations used by faces and stimuli of expertise during early visual processing. This was done by competing faces with either face or non-face context before and after training with the non-face category. Evaluation of the N170 reduction to faces in a non-face context revealed enhancement in the competition effect after training, suggesting that non-face stimuli use more face-related encoding resources after training than before training.

In the present study, we sought to use the competition paradigm in order to investigate whether inverted faces engage the same neural encoding mechanisms used for upright faces to a greater extent (quantitative hypothesis) or whether they recruit additional neural mechanisms (qualitative hypothesis) at the N170 time-window. To that end we conducted two experiments. In the first experiment ERPs were time-locked to a target upright face that was concurrently presented with either an upright face, a non-face or an inverted face context stimulus that preceded the target upright face. We reasoned that if inverted faces involve the same mechanisms used for upright faces but with additional processing effort (quantitative hypothesis), signal reduction to the target upright face should be greater when preceded by inverted than by upright faces. Note that Experiment 1, in which targets are upright faces, can only provide information about the extent to which the different context stimuli recruit upright face-related processes and not if they can recruit other mechanisms. To further examine whether inverted faces recruit additional neural mechanisms not used for upright faces, we conducted a second experiment in which target stimuli were inverted faces presented in the context of either upright faces, inverted faces or non-faces.

As mentioned above, previous ERP competition studies examined the competition effect of scrambled images of faces on upright target faces. A secondary goal of the current study was to assess whether meaningful objects (e.g. chairs) produce the same or a different amount of competition effect with target face images as compared to the previously described competition with scrambled images. In order to do this we introduced to Experiment 1 two classes of non-face stimuli as context stimuli—scrambled images, to replicate previous findings, and photographs of chairs.

## Experiment 1

### Method

#### Subjects

Twenty-four subjects participated in the experiment (15 females, mean age 24.6, SD: 4.1) with normal or corrected to normal vision. Subjects were paid (\$10 an hour) or given course credit for their participation. Two of the subjects were excluded from analysis due to bad signal quality and no recognizable P1–N1 complex.

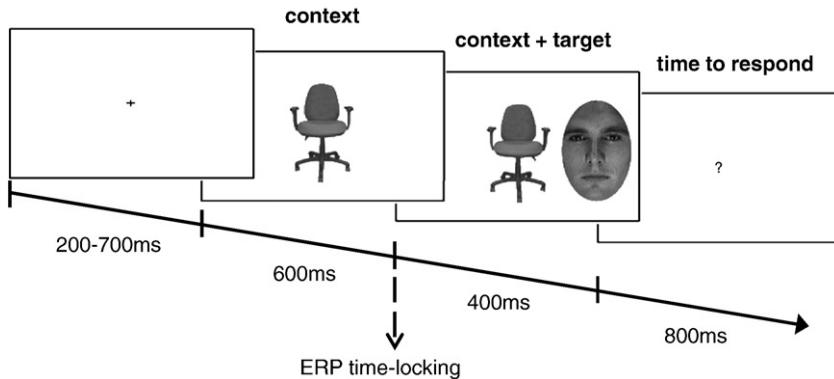
#### Stimuli

Eight pictures of faces, eight chairs and eight scrambled images of objects were used. The contour of each face image was cut in an ellipse form to remove hair and other external features. Then, using graphic software, images were gray scaled and matched for mean luminosity on a 255 point scale (faces = 193.7; chairs = 196.3; scrambled images = 189, n.s.). Inverted faces were the same images used for the upright face condition rotated by 180°.

#### Procedure

We used the same stimulus presentation parameters used by Rossion et al. (2004). Each trial began with a context stimulus, presented in the center of the screen for one second. Six hundred milliseconds after the onset of this context stimulus a target face appeared to the right or left of it for 400 ms. Therefore both stimuli were present simultaneously on the screen for 400 ms and then had a common offset. Immediately after the offset of both stimuli a question mark appeared in the center of the screen for 800 ms, indicating that a response should be given, followed by a 200–700 ms fixation cross (Fig. 1). The context stimulus could be one of four stimulus categories: Upright Face, Inverted Face, Chair or Scrambled Object presented in a pseudo-randomized order. The second (target) stimulus was an upright face in all trials, presented either to the right or the left of the context stimulus, resulting in eight experimental conditions (Context stimulus × Visual Field). In the Upright and Inverted conditions the face identity of the context stimulus and the target stimulus within a given trial were never the same.

Stimuli were presented using the psychtoolbox for Matlab (psychtoolbox, Brainard, 1997). The size of the images was 8.5 × 6.5 cm (~5° × 3.7°) on average, and the center of the second stimulus was presented 9.5 cm (5.5°) from the center of the screen. We used 75 repetitions per condition, divided into 6 runs equal in length. Subjects were seated in a dimly lit room at a distance of approximately 100 cm from a 17" CRT screen, and were instructed to fixate on the center of the screen throughout the whole run. Participants were asked to press a response key according to the side at which the second stimulus appeared. This task assured that attention allocation was even throughout the whole experiment. Subjects were asked to provide their response only during the time when the question mark was present on the screen, and not to move their eyes from the center at any stage of the task. All subjects used their right hand for the task execution. A 1-min practice trial was given to the subjects at the beginning of the experiment and repeated as many times as needed for them in order to feel that they can maintain central fixation. None of the subjects manifested



**Fig. 1.** Experimental design and parameters. ERPs were time-locked to the onset of the target. Note that the target always appeared next to a context stimulus that had a prior onset.

difficulties to follow these instructions, and no one needed more than 3 practice trials.

#### EEG recording and ERP analysis

EEG was recorded from 64 Ag/AgCl active electrodes (BioSemi Active Two system, the Netherlands: <http://www.biosemi.com>) mounted on a flexible cap according to the extended international 10/20 system, reference free. Three additional electrodes were used: one electrode on the tip of the nose as a common reference channel for offline data treatment, and two EOG channels placed at the outer canthus of each eye for horizontal eye movement monitoring. EEG was digitized at a sampling rate of 256 Hz. Data were analyzed offline using the eeglab tool for Matlab (Delorme and Makeig, 2004). After uploading data to Matlab as referenced to the nose channel, a common average reference was computed using the 64 data channels. The data of each subject underwent a filtering procedure with a bandwidth of 1.5–30 Hz, and averaged to produce one epoched data file per condition, with –100 to 600 ms epochs where the 0 ms point is locked to the stimulus onset and the 100 ms prior to the onset serve as baseline. These epoch files were manually inspected for epochs containing eye movements and blinks, which were discarded from further analysis. We analyzed the ERP at the P1 and the N170 time windows at three electrode sites in each hemisphere where the face-selective effects are usually the largest (P8, PO8 and P10 in right hemisphere; P7, PO7 and P9 in left hemisphere). Peak amplitude for P1 was defined as the signal peak between 80 and 140 ms, and the N170 peak amplitude was defined as the lowest peak between 150 and 230 ms.

#### Data analysis

Statistical analysis was carried out on Statistica 7.0 (StatSoft Inc). First, 3-way ANOVA with Context stimulus, Hemisphere and Visual Field (VF) as repeated measures was performed. A Greenhouse-Geisser correction was applied when sphericity was violated. Post-hoc *t*-tests (Bonferroni corrected for multiple comparisons) were then performed when necessary.

#### Results and discussion

**Fig. 2** shows ERPs time-locked to the presentation of the lateralized target stimulus (upright face), as a function of the central context stimulus and visual field. The N170 peak amplitudes in microvolts for each condition are reported in **Table 1** (see Supp Fig. 1 for scalp topographies).

#### The N170 component

A 3-way ANOVA with the factors Context Stimulus (Upright, Inverted, Chair, Scrambled), Hemisphere (Right, Left) and VF (Right, Left) as repeated measures revealed a main effect of Context

Stimulus ( $F(3,63) = 23.48, p < 0.0001$ ) and a significant 3-way interaction ( $F(3,63) = 3.4, p < 0.05$ ).

To explore the source for the 3-way interaction we performed post-hoc comparisons (Bonferroni corrected) for the Context Stimulus effect in each of the hemispheres by visual field conditions. To assess whether our data replicate previous competition effects between faces and non-faces, we first examined the difference between the response to a target upright face in the context of faces and non-faces. For contralateral stimuli over both hemispheres, ERPs to target upright faces were smaller in the context of upright and inverted faces than in the context of scrambled images and chairs (all simple comparisons were significant). For ipsilateral stimuli over the RH, ERPs were significantly smaller in the context of upright relative to scrambled images and chairs, and significantly smaller in the context of inverted faces relative to scramble faces. For ipsilateral stimuli over the LH, ERPs to target upright faces were smaller for upright faces relative to scrambled images.

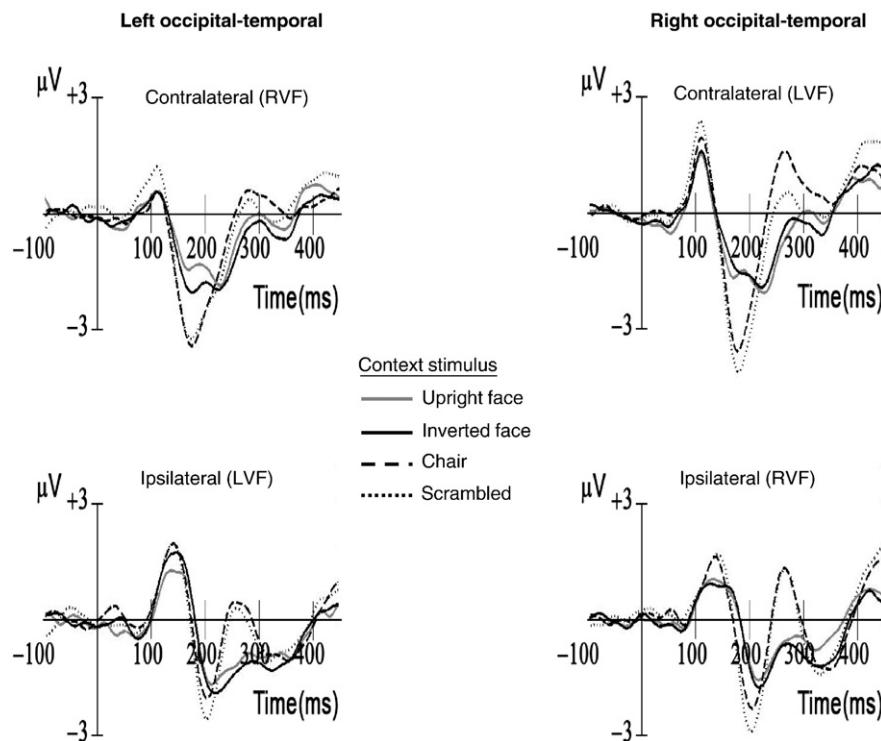
These findings replicate previous ERP competition effects between faces and scrambled images and also extend the face competition effect to meaningful objects (i.e. chairs).

The main goal of the current experiment was to test whether inverted faces engage upright face mechanisms to a greater extent than upright faces (quantitative hypothesis). To that effect we compared the competition effect for upright and inverted context stimuli. As can be seen in **Fig. 2**, there is no difference in ERP to upright target faces in the context of upright as compared to inverted faces in both hemispheres and visual fields (all  $p > 0.2$ ). Thus, upright and inverted faces did not differ in the magnitude of their competition effects with the upright target face, providing no evidence to the idea that inverted faces recruit to a greater extent mechanisms that are engaged by upright target faces.

Lastly, we asked whether meaningful objects compete to the same extent with upright faces as scrambled stimuli do. Paired comparisons between chairs and scrambled stimuli as contexts did not show any significant difference in competition effects with target upright faces (all  $p > 0.05$ ).

#### The P1 component

Repeated measure ANOVA with Context stimulus, Hemisphere and VF as repeated measure factors revealed a main effect of Context stimulus ( $F(3,63) = 5.59, p < 0.001$ ). Post-hoc *t*-tests (Bonferroni corrected) revealed that the P1 peak for target faces was larger in scrambled context relative to both face contexts, and to chair context relative to upright face context. No further significant competition effects were observed on the P1 component. These P1 effects may suggest that differences at the P1 level underlie the effect measured at the N170 peak that follows it. To examine whether the N170 effects that we revealed are independent of the P1 effects, we conducted a similar ANOVA on a measure of the N170 component that is based on



**Fig. 2.** ERPs recorded to upright target faces as a function of the simultaneously presented context stimulus (Experiment 1). ERPs over the occipito-temporal right hemisphere represent the average signal across channels P8, PO8 and P10. ERPs over the occipito-temporal left hemisphere represent the average signal across channels P7, PO7 and P9.

the difference between the P1 and the N170 peaks (see for example Goffaux et al., 2003).. This ANOVA resulted in a main effect of Context Stimulus ( $F(3,63) = 38.92$ ,  $p < 0.0001$ ) and a Context Stimulus by Hemisphere interaction ( $F(3,63) = 4.23$ ,  $p < 0.05$ ). Bonferroni corrected post-hoc *t*-tests showed similar findings to those we reported for the N170 amplitude above. Additional effects that were found in this analysis were that for ipsilateral stimuli the N170 is of lower amplitude in the context of upright faces relative to chairs over the LH, and lower amplitude in the context of chairs relative to inverted faces over the RH. Most importantly, similar to the N170 peak amplitude analysis, this analysis revealed no difference in the competition effect of upright and inverted context stimuli with upright target stimuli.

In summary, results of Experiment 1 a) show similar competition effects for upright and inverted faces and therefore do not support the hypothesis that the N170-FIE reflects processing enhancement for inverted faces by upright face mechanisms; b) replicate the previously reported competition effect between scrambled stimuli and upright faces, and c) extend the face-scrambled competition effect to a face-object competition, by showing that upright faces compete with real objects such as chairs to the same extent as with scrambled stimuli.

In Experiment 1 we asked whether inverted faces recruit to a greater extent the same mechanisms used for the processing of upright faces. Results show no evidence for a quantitative difference

in the involvement of the neural populations that are in use for upright faces when faces are inverted. However, this experiment cannot assess whether inverted faces recruit additional resources not used for upright face processing at the N170 latency (qualitative hypothesis). In order to test this hypothesis, we conducted Experiment 2, in which we used inverted faces as targets, and examined whether they compete more with inverted face context than with upright face context. Given that inverted and upright faces compete similarly with upright faces (Experiment 1), if in Experiment 2 inverted faces presented as context lead to stronger signal reduction for the inverted target faces than upright face context, it suggests that mechanisms used for the processing of inverted faces do not fully overlap with mechanisms used for the processing of upright faces.

## Experiment 2

### Method

#### Subjects

Nineteen subjects participated in Experiment 2 (11 females, mean age 25, SD: 3.3), with normal or corrected to normal vision. Subjects were paid or given course credit for their participation. One subject was excluded from analysis due to bad signal quality and no recognizable P1–N1 complex.

#### Stimuli

Stimuli in the present experiment consisted of the same face and chair images that were used in the previous experiment. We used only the chairs as non-face condition, given that the specific goal of replicating the results by Jacques and Rossion with scrambled images was no longer needed.

#### Procedure

Task and presentation mode were identical to the first experiment. The context could be an Upright Face, an Inverted Face or a Chair, the second stimulus being an inverted face presented on either side of the

**Table 1**

N170 peak amplitudes in Experiment 1. Values are in microvolts, representing the N170 for upright faces as a function of the context stimulus next to which they were presented (upright face, inverted face, chair and scrambled image). RH: right hemisphere; LH: left hemisphere; RVF: right visual field; LVF: left visual field.

	RH		LH	
	RVF	LVF	RVF	LVF
Upright face	$-2.21 \pm 0.18$	$-3.62 \pm 0.29$	$-3.09 \pm 0.16$	$-2.32 \pm 0.14$
Inverted face	$-2.48 \pm 0.18$	$-3.40 \pm 0.27$	$-3.40 \pm 0.18$	$-2.53 \pm 0.14$
Chair	$-3.4 \pm 0.25$	$-5.08 \pm 0.26$	$-4.54 \pm 0.22$	$-3.02 \pm 0.18$
Scrambled	$-3.94 \pm 0.23$	$-5.51 \pm 0.25$	$-4.66 \pm 0.26$	$-3.35 \pm 0.20$

screen. As a result, this experiment included 6 experimental conditions (Context stimulus  $\times$  VF).

#### EEG recording and ERP analysis

As described in Experiment 1.

#### Results and discussion

**Fig. 3** shows ERPs time-locked to the presentation of the target inverted face as a function of the preceding context stimulus. Right hemisphere ERPs are averaged across electrodes P8, P10 and PO8, left hemisphere ERPs are averaged across electrodes P7, P9 and PO7. **Table 2** shows the N170 peak amplitude for each of the conditions (see supp **Fig. 2** for scalp topographies).

#### The N170 component

In order to test whether the N170 peak amplitude to the target inverted face was modulated by the context stimulus, we conducted a 3-way ANOVA with Context Stimulus (Upright, Inverted, Chair), Hemisphere and VF as repeated measures which yielded a main effect of Context Stimulus ( $F(2,34) = 16.8$ ,  $p < 0.0001$ ), as well as a significant 3-way interaction of Context Stimulus by VF by Hemisphere ( $F(2,34) = 4.27$ ,  $p < 0.05$ ). We therefore examined the effect of Context Stimulus for each of the visual fields by Hemisphere conditions using post-hoc comparisons of the 3 category types, Bonferroni corrected for multiple comparisons.

In contrast to the N170 to target upright faces that was similar in the context of upright and inverted faces (Experiment 1), the N170 amplitude to target inverted faces tested here was smaller (i.e. larger competition effect) in the context of inverted faces than in the context of upright faces over the right hemisphere for both VFs (**Fig. 3**). This effect was not significant over the left hemisphere.

Furthermore, the N170 to inverted target faces was larger in the context of chairs than inverted faces in the RH for both visual fields and contralaterally in the LH. The ERPs to inverted target faces in the

**Table 2**

N170 peak amplitudes in Experiment 2. Values are in microvolts, representing the N170 for upright faces as a function of the context stimulus next to which they were presented. RH: right hemisphere; LH: left hemisphere; RVF: right visual field; LVF: left visual field.

	RH		LH	
	RVF	LVF	RVF	LVF
Upright face	$-4.01 \pm 0.21$	$-3.07 \pm 0.22$	$-4.21 \pm 0.19$	$-3.13 \pm 0.20$
Inverted face	$-3.04 \pm 0.20$	$-2.48 \pm 0.20$	$-3.70 \pm 0.19$	$-2.9 \pm 0.22$
Chair	$-4.83 \pm 0.30$	$-5.16 \pm 0.26$	$-4.96 \pm 0.27$	$-3.86 \pm 0.30$

context of upright faces was significantly smaller than in the context of chair stimuli only in the RH/LVF.

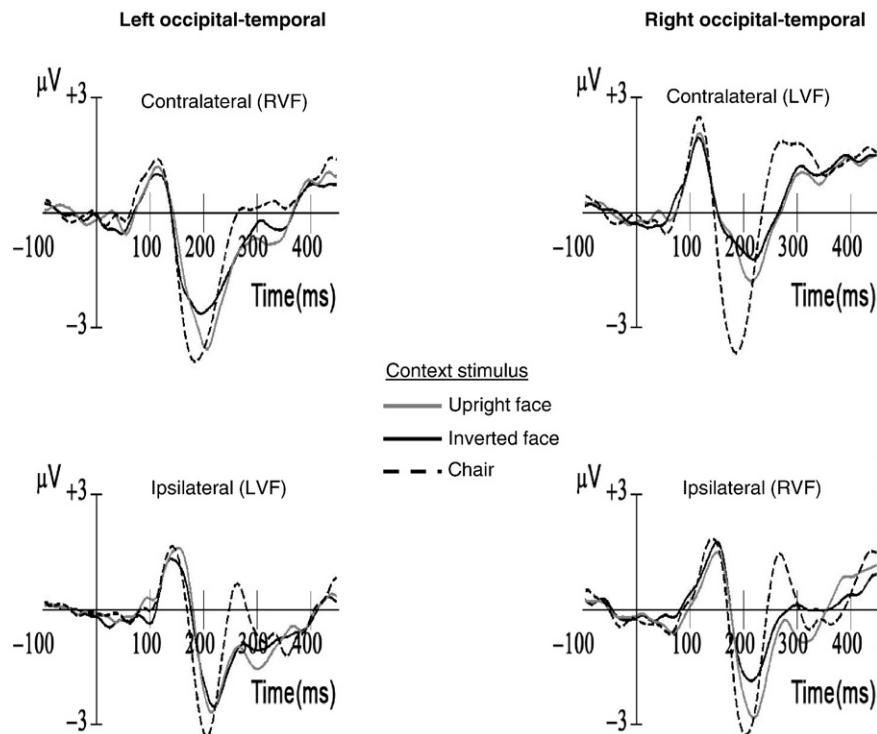
#### The P1 component

Repeated measure ANOVA with all three factors—Category, VF and Hemisphere—did not reveal any significant main effect or interaction in the P1 peak amplitude measure.

In summary, taken together with the results of Experiment 1, the competition effect at the N170 time-window in Experiment 2 suggests that inverted faces involve early recruitment of supplementary mechanisms in addition to those used for the processing of upright faces, in the right hemisphere. Thus, a mere quantitative change in the processing of inverted relative to upright faces would not be a satisfactory explanation of the N170 FIE. Instead, our data suggest a qualitative difference in the way upright and inverted faces are processed as early as at the N170 level.

#### General discussion

The goal of the present study was to reveal whether inverted faces recruit at the N170 time latency the same mechanisms used for upright faces but with increased activation level or whether they recruit additional neural processes. To that end we used an ERP competition paradigm in which upright and inverted faces are



**Fig. 3.** ERPs recorded to inverted target faces as a function of the simultaneously presented context stimulus (Experiment 2). ERPs over the occipito-temporal right hemisphere represent the average signal across channels P8, PO8 and P10. ERPs over the occipito-temporal left hemisphere represent the average signal across channels P7, PO7 and P9.

presented simultaneously. The main premise of this paradigm is that faces share processing mechanisms to a greater extent than they do with any other type of visual stimulus. Hence, a face presented while another face is already being processed should produce a decreased response of the N170 compared to a face presented concurrently with a non-face, as was previously demonstrated (Jacques and Rossion, 2004, 2006, 2007b; Rossion et al., 2004) and replicated in this study. By comparing the magnitude of competition between upright and inverted faces, we can assess the extent to which these two stimuli share neural mechanisms at specific time-points (e.g. N170).

In the first experiment we found that inverted faces do not compete with upright faces to a greater extent than upright faces do. This finding is inconsistent with the claim that inverted faces utilize to a greater degree the same mechanisms used for the processing of upright faces (quantitative hypothesis). In the second experiment we found larger competition between two inverted faces than between upright and inverted faces. In other words, a difference in N170 amplitude to the target face as a function of the orientation of the face context was found only when the target was inverted but not when it was upright, although the context stimuli were precisely the same in both experiments. Taken together, these findings suggest that in addition to the shared mechanisms for the processing of upright and inverted faces, inverted faces also recruit additional neural encoding mechanisms that are not used for upright faces (qualitative hypothesis), as early as the N170 time-window. This effect was found in the right hemisphere, in accordance with the well-established superiority of the right hemisphere in face processing in general (e.g. Le Grand et al., 2003; Rhodes, 1985; Rossion et al., 2003; Sergent et al., 1992; Yovel et al., 2008), and in electrophysiological measures to face stimuli in particular (e.g. Bentin et al., 1996; George et al., 1996; Sadeh et al., 2008; Sadeh et al., in press). Finally, the present study also extended results of previous reports by including a category of non-face objects, in addition to the scrambled stimuli. We found an effect of competition on visual representation at the N170 time-window between upright faces and real objects such as chairs, mainly in stimulus presentation sites that are contralateral to the recording site.

What may be the additional mechanisms involved in the processing of inverted faces? Several fMRI studies have shown that inverted faces generate a larger response than upright faces in object-general areas of the extrastriate cortex, meaning that once inverted, faces become closer to objects in terms of resources engaged by our perceptual system (Aguirre et al., 1999; Epstein et al., 2006; Haxby et al., 1999; Yovel and Kanwisher, 2005). In addition to the enhanced response to inverted faces in regions that show preference to non-face objects, some studies also reported a slight decrease in responsiveness of face-selective regions when faces are inverted (Gauthier et al., 1999; Haxby et al., 1999; Kanwisher et al., 1998; Mazard et al., 2006; Yovel and Kanwisher, 2005). Although any direct inference from the functional MRI studies of face inversion discussed hereby to ERP studies is speculative, it is plausible that the relatively wide spread object-related activations observed for inverted faces are reflected in the enhanced scalp recorded potentials at the N170 time-window (see Rossion and Gauthier, 2002). The shift in activity pattern toward object-related processes is also in line with the prevalent view according to which inversion of a face breaks down holistic processing, which is a specific attribute of face processing (Farah et al., 1995a,b; Freire et al., 2000) and leads to its perception at the individual feature level similarly to the way objects are perceived. Further evidence for the role of general object mechanisms in the processing of inverted faces comes from a patient with visual agnosia but normal face recognition who had a particularly large inversion effect (Moscovitch and Moscovitch, 2000; Moscovitch et al., 1997).

Our findings, however, do not provide direct evidence that the qualitative change in neural activity to inverted faces represents involvement of object-sensitive mechanisms rather than other types

of mechanisms, and may also be compatible with models such as the one conceived by Itier and colleagues (2006, 2007). Itier hypothesized that the inversion of a face triggers a neural system specifically responsible for eye processing, which is normally inhibited when a full face is being processed. According to Itier's suggestion the N170 originates mostly from the superior temporal sulcus region, where face-selective and eye-selective neurons coexist. When the eyes are presented in their normal facial context, the eye selective neurons are not (or less) activated. However, when eyes are presented alone or within an inverted face, these neurons come into action probably due to interruption of the face configuration which breaks the inhibition to the eye-specific neurons. Quite similarly, Sagiv and Bentin (2001) speculated that the N170 FIE stems from a stronger activation of a face component analyzer. These suggestions are compatible with the view that the N170 FIE represents a certain change in neural population encoding rather than a mere augmentation of activity of the same neural populations involved in face processing.

In intracranial recordings in epileptic patients, McCarthy et al. (1999) found a small amplitude decrease for inverted relative to upright faces in N200 face-specific sites. This may appear to be in contradiction with the scalp recorded N170 that is larger for inverted than upright faces. However, the lower N200 amplitude to inverted than upright faces is only reported for electrode sites that were predefined as face-specific. Assuming that electrodes implemented directly on the surface of the cortex capture more circumscribed activity than scalp electrodes, the results reported by McCarthy and colleagues may parallel the activation decrease for inverted faces found in fMRI for face-selective regions. The scalp recorded N170, however, being recorded from much more distal sites than the intracranial N200, may incorporate distributed generators including face-specific and non-face-specific ones. Thus, intracranial ERP data do not support a quantitative explanation of the N170 FIE that predicts an augmentation of activity to inverted faces in face-specific regions, but may rather be in agreement with the hypothesis that the neural basis of the N170 FIE is related to an integration of additional processes. Direct testing of this hypothesis requires measurement of the response to inverted faces in non-face selective cortex. Unfortunately, McCarthy and colleagues did not report signals to inverted faces in non-face-specific sites.

A few recent studies employed an adaptation procedure to investigate the properties of the face N170 (ERP) or M170 (MEG; Magnetoencephalogram) (Eimer et al., in press; Harris and Nakayama, 2007, 2008; Jeffreys, 1996; Kovacs et al., 2006, 2007). In these studies the two stimuli were presented sequentially, using short inter-stimulus interval (Kovacs et al., 2006, 2007) or rapid adaptation technique (double pulse adaptation) comprised of brief stimulus presentation and short inter-stimulus interval (Eimer et al., in press; Jeffreys, 1996; Harris and Nakayama, 2007, 2008). Similarly to findings of the competition paradigm, the N170 to faces adapted by a previously presented face were consistently smaller in amplitude than N170 to faces adapted by a non-face. When upright and inverted faces were used as adaptors for upright target faces, both face orientations equally adapted the subsequent upright face at the M170 component (Harris and Nakayama, 2008) or the N170 component (Eimer et al., in press), which is in line with our findings in Experiment 1. In their recent report, Eimer and colleagues (in press) further examined the adaptation effect on inverted face target stimuli. Similar to results from Experiment 2 here, Eimer and colleagues found that when the target stimulus is an inverted face, inverted face adaptors cause a stronger reduction to its N170 amplitude than upright face adaptors, in the right hemisphere. In addition to this observation, Eimer et al. found that inverted target faces show an equivalent reduction in N170 to inverted houses. This new interesting observation led the authors to propose the possibility that the N170 FIE might stem from activation of cells that are tuned to stimulus orientation Note that despite similarities in findings between rapid

adaptation and competition ERP studies of face perception, it remains an open question whether they reflect the same or different neural processes.

Effects of neural competition during simultaneous presentation of stimulus-pairs have been extensively studied with single cell recordings in monkeys (Desimone, 1998; Miller et al., 1993; Reynolds et al., 1999; Sato, 1989; Zoccolan et al., 2005) and in fMRI studies (Beck and Kastner, 2005, 2009; Kastner et al., 1998). Single cell recordings from ventral visual cortex of the monkey revealed systematic reduction of firing rates of neurons in response to a pair of preferred and non-preferred stimuli presented simultaneously as compared with the response to the preferred stimulus of the cell presented alone. Whereas response suppression at the single cell level may reflect local competitive interactions between neighboring neurons probably via local inhibitory networks (e.g. Miller et al., 1993), in ERP competition studies we record massive field potentials from large groups of neurons, reflecting input and information build-up of larger regions. In addition, the current ERP competition paradigm measures scalp response to the appearance of one stimulus only, presented simultaneously to another one but with a deferred onset. Therefore, response suppression in competitive interactions paradigms in ERP may reflect a different neuronal phenomenon than the one measured in single cells. One possibility is that ERP competition reflects the interruption to the onset of synchronous activity of neuron populations. Potentials recorded distally from the cells reflect synchronized activity onsets of large populations of neurons, which may be reduced for a second stimulus onset.

Finally, it may be proposed that the effect of the contextual stimulus on the N170 of the secondly presented stimulus is due to differences in attention allocation to the context. Given that faces are stimuli of particularly high and immediate importance for us as social beings, they may capture our spatial attention during early visual processing more than non-face stimuli (Bindemann et al., 2007; Ro et al., 2001, 2007; Theeuwes and Van der Stigchel, 2006). The question of attention as a possible account for the concurrent presentation paradigm was investigated and ruled out by Jacques and Rossion (2007b). Furthermore, if findings reflect effects of attention allocation to the context, our two experiments would produce the same pattern of response for upright and inverted context stimuli, which generated different competition effects across our two experiments. Therefore an effect of face orientation on concurrent inverted but not upright faces may be best explained in the framework of competition on encoding resources. According to this view the N170 for the second stimulus is influenced by the context stimulus to the degree of overlap in visual encoding processes.

To conclude, our findings suggest that the signal enhancement for inverted faces at the N170 time-window is not due to an augmentation of activity of the neural populations that code upright faces but rather seems to be related to early recruitment of additional mechanisms.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2010.06.029.

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