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Rapid Communication

Face, eye and object early processing: What is the face specificity?

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We investigated the human face specificity by comparing the effects of inversion and contrast reversal, two manipulations known to disrupt configural face processing, on human and ape faces, isolated eyes and objects, using event-related potentials. The face sensitive marker, N170, was shortest to human faces and delayed by inversion and contrast reversal for all categories and not only for human faces. Most importantly, N170 to inverted or contrast-reversed faces was not different from N170 to eyes that did not differ across manipulations. This suggests the disruption of facial configuration by these manipulations isolates the eye region from the face context, to which eye neurons respond. Our data suggest that (i) the inversion and contrast reversal effects on N170 latency are not specific to human faces and (ii) the similar increase of N170 amplitude by inversion and contrast reversal is unique to human faces and is driven by the eye region. Thus, while inversion and contrast reversal effects on N170 latency are not category-specific, their effects on amplitude are face-specific and reflect mainly the contribution of the eye region.
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Introduction

The processing specificity of faces compared to other objects has been a major debate in visual cognitive neurosciences over the past years. One aspect of this specificity is the configural processing of faces, the unique relationships among facial features that define individual identity, not seen in objects that are processed analytically (Bartlett and Searcy, 1993; Rhodes et al., 1993). The impairment in recognition of upside-down faces is disproportionate compared to that of inverted objects (Yin, 1969), and converging behavioral data suggest that this "face inversion effect" is due to the disruption of configural processing during face encoding and is unique to the face category (Rossion and Gauthier, 2002). Scalp electrophysiological studies of face processing, providing excellent temporal resolution of neural events, have focused mainly on a negative event-related potential (ERP) component occurring between 140 and 200 ms after stimulus onset at occipito-temporal electrodes. This N170 (Bentin et al., 1996) component is reliably larger to faces than to any object category tested (Bentin et al., 1996; Carmel and Bentin, 2002; Eimer, 2000b; Itier and Taylor, 2004d) and has become a marker for early face processing. Although its exact neural generators are still debated (Bentin et al., 1996; Itier and Taylor, 2004e; Rossion et al., 2003a; Watanabe et al., 2003), this component is thought to reflect structural encoding (Eimer, 2000b; Rossion et al., 1999), i.e. the extraction of a perceptual representation of the face, in occipito-temporal areas. It is delayed and enhanced by face inversion (Bentin et al., 1996; de Haan et al., 2002; Eimer, 2000a; Itier and Taylor, 2002, 2004b,d; Rossion et al., 1999, 2000; Sagiv and Bentin, 2001; Taylor et al., 2001c), an effect not reported with objects (Bentin et al., 1996; Rebai et al., 2001; Rossion et al., 2000). This neurophysiological face inversion effect, particularly on N170 latency, is considered by some researchers as the earliest consistent electrophysiological difference between face and object processing (Rossion and Gauthier, 2002; Rossion et al., 1999) and could reflect the early processing specificity for faces. In this paper, we show that inversion actually delays the N170 for all categories, and not only human faces.

Another manipulation that impairs face recognition is contrast reversal or photo-negative (Galper, 1970; Kemp et al., 1990) that also disrupts configural processing (Kemp et al., 1990; Lewis and Johnston, 1997) but, unlike inversion, preserves the general face organization (eyes above nose above mouth). We have shown that contrast reversal alters N170 in a similar way as does inversion (Itier and Taylor, 2002, 2004a,b,c), suggesting configural disruption by both manipulations at the structural encoding stage of face processing. However, this effect of photo-negative on the N170 to objects has not been tested, preventing any conclusion as to whether it is particular to the face category or general to visual stimuli.

In this electrophysiological experiment, we further characterized what makes the human face specific by comparing inversion and contrast reversal effects on early visual processing between

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object and face categories. We used a simple orientation detection task used previously (Rossion et al., 2000), in which 19 subjects discriminated upright from inverted stimuli (regardless of their contrast). By focusing attention on each stimulus, this task minimizes attentional bias to human faces (Vuilleumier, 2000) or level of categorization effects (Tanaka and Curran, 2001) that could impact on face–object differences. Its simplicity also minimizes category differences that could result from short-term memory difficulties. Finally, using the same task as previously used in the literature, and some of the same object categories, precluded task-related effects to be a reason for possible different results. We compared the effects of orientation (upright or inverted) and contrast (positive or negative) on the face marker N170 component recorded to objects (cars, chairs, houses) and faces. Ape faces were included to test the species specificity of N170. It has been shown that, although N170 to ape faces can be as large as that to human faces (Carmel and Bentin, 2002; de Haan et al., 2002), inverting ape faces does not affect N170 (de Haan et al., 2002), suggesting that these faces are processed like objects and N170 is sensitive to the human aspect of face stimuli (de Haan et al., 2002). We wished to extend this finding by comparing the effects of contrast reversal on N170 to both species. If N170 reflected processes of a broad-based face category and not processes particular to the human face, then inversion and contrast reversal should have the same effects for both ape and human faces. Finally, we explored the relations between face and eye processing by including isolated eyes as it has been suggested that N170, which is delayed and usually larger to isolated eye stimuli than to full faces (Bentin et al., 1996; Jemel et al., 1999; Taylor et al., 2001a,c), could reflect the activity of an eye detector (Bentin et al., 1996; Eimer, 1998). Our results show that N170 for upright faces does not reflect the activity of an eye detector, as suggested by some previous studies (Eimer, 1998), but that inversion and contrast reversal effects on that component are driven, to a large extent, by the eye region.

Methods

Subjects

Nineteen healthy adults (9 females, mean age 26.6 years, 3 left-handed) participated in the experiment which was approved by the French Comité Opérationnel pour l'Ethique dans les Sciences de la vie du CNRS. All subjects had normal or corrected-to-normal vision and signed informed written consent.

Stimuli and experimental design

Fifty grayscale pictures of six object categories including human faces (Fig. 2) were used. Ape faces, chairs, cars and eyes stimuli are taken from Carmel and Bentin (2002), but ape faces were restricted to great apes for which clear human-like facial features were visible. The Victorian houses were from a Corel Draw CD-ROM. All pictures (5 × 5° visual angle) were centered on a black screen and presented in upright, inverted, negative (contrast-reversed) and inverted–negative formats (total = 50 × 6 × 4 = 1200 trials). Inverted stimuli were obtained by rotating upright pictures by 180° and photo-negatives by inverting contrasts (Photoshop 5.0). Ten blocks of 120 stimuli (5 per category per format) were presented for 250 ms with a randomized ISI (1000–1300 ms) during which a centered white fixation cross appeared. Stimuli were randomly intermixed, and the block order was counterbalanced across subjects. In this orientation judgment task, subjects had to press the left control key for all upright stimuli and the right control key for all inverted stimuli, regardless of category or contrast, as rapidly and accurately as possible. Buttons were reversed for half of the subjects. Accuracy and reaction times were recorded.

Electrophysiological recordings and measures

ERPs were recorded (NeuroScan 4.2) via 31 electrodes mounted on a cap (Easycap) according to the 10/10 system. Three additional ocular electrodes monitored vertical and horizontal eye movements from the outer canthi and the left supraorbital ridge. Electrode impedances were kept under 5 KΩ. The sampling acquisition rate was 500 Hz. EEG was amplified using a SynAmps system. Cz was the reference lead during acquisition; an average reference was calculated off-line. EEG was epoched in 1-s sweeps with a 100 ms pre-stimulus baseline. Trials contaminated with eye movements and other artifacts (≥±100 μV) were rejected. Accepted trials were averaged according to categories and format and digitally filtered (0.1–30 Hz). The N170 ERP component was measured at four posterior sites on each hemisphere (TP9/TP10, P7/P8, PO9/PO10, O1/O2) within a ±30-ms window around the maximum of the grand-average means. For each subject, the latency of each component was taken at the electrode where the amplitude was maximal over each hemisphere, and the amplitude was measured at the other electrodes over that hemisphere at that latency (Picton et al., 2000). As most studies measured the N170 only at P7/P8 (or T5/T6) sites and this measurement difference could be the cause of discrepant results, we also analyzed the data from only these two electrodes.

Data analyses

Repeated measures analyses of variance (ANOVA) were conducted using Greenhouse–Geisser adjusted degrees of freedom; post-hoc *t* tests used Bonferroni corrections for multiple comparisons. Within-subject factors included contrast (2), orientation (2) and category (6) for hits and RTs. Additional factors (hemisphere (2) and electrode (4)) were used for peak latencies and amplitudes. Analyses were also performed for each format (Table 1) and each category separately, using all four electrodes pairs and P7/8 only (Table 2).

Results

Behavioral performances

Performances on this orientation discrimination task were very good (~95% on average across categories and formats). As seen in Fig. 1, inversion decreased accuracy and increased reaction times only for human faces [orientation × category, $F(2.8,50.9) = 4.71$, $P < 0.006$ and $F(3,54.7) = 4.85$, $P < 0.004$ respectively]. Contrast reversal, however, decreased accuracy for houses, chairs and eyes [$F(4.1,73.2) = 4.67$, $P < 0.002$] and increased RTs for all categories except human faces and chairs [$F(3,53.6) = 16.8$, $P < 0.0001$]. Thus, the human face category was the only one affected by inversion and was not affected by contrast reversal. Human

Table 1
Effects of category on the N170 component

		F	P	Comparisons
Upright	N170 latency	29.52	0.0001	human faces < eyes ~ cars ~ houses ~ chairs ~ apes (*****, *)
	N170 amplitude	65.66	0.0001	chairs ~ houses ~ cars < human faces ~ apes ~ eyes (*, **, ****)
Inverted	N170 latency	11.03	0.0001	human faces < cars ~ eyes ~ chairs ~ houses ~ apes (***)
	N170 amplitude	92.54	0.0001	chairs ~ houses ~ cars < apes < eyes ~ human faces (*****, *****)
Negative	N170 latency	18.01	0.0001	human faces ~ cars ~ chairs ~ houses ~ eyes < apes (****)
	N170 amplitude	54.16	0.0001	houses < cars ~ chairs ~ apes < eyes ~ human faces (*****, *****)
Inverted-Negative	N170 latency	12.59	0.0001	human faces ~ cars ~ chairs ~ eyes ~ houses < apes (***)
	N170 amplitude	57.19	0.0001	houses ~ cars ~ chairs ~ apes < eyes < human faces (*****, ***)

Categories are in ascending order of latency and amplitude. Significant pair-wise comparisons are reported at the various possible P values (~means the difference between two adjacent categories is not significantly different).

* $0.01 < P < 0.05$.
** $0.005 < P < 0.01$.
*** $0.001 < P < 0.005$.
**** $0.0001 < P < 0.001$.
***** $P < 0.0001$.

faces elicited overall faster reaction times than the other categories [$F(2.6,46.6) = 46.13$, $P < 0.0001$], especially in upright positive [$F(2.8,51) = 8.62$, $P < 0.0001$] and negative [$F(2.7,48.8) = 52.15$, $P < 0.0001$] formats. This suggests a faster processing of human faces compared to other objects when presented in the usual canonical orientation.

Table 2
Summary of the effects of inversion and contrast reversal on the N170 component for each category analyzed separately

		Cars	Houses	Human faces	Ape faces	Chairs	Eyes
Effect of orientation (inversion)	Latency	$F = 16.1^{****}$ inv > up	$F = 21.12^{*****}$ inv > up	$F = 102.89^{*****}$ inv > up	$F = 19.55^{*****}$ inv > up	$F = 13.22^{***}$ inv > up	$F = 43.43^{*****}$ inv > up
	(at P7/8 only)	($F = 24.4^{*****}$)	($F = 33.4^{*****}$)	($F = 102.8^{*****}$)	($F = 7.1^{*}$)	($F = 7.8^{*}$)	($F = 29.4^{*****}$)
	Amplitude	_	_[1]	$F = 7.06^{*}$ inv > up	$F = 8.08^{*}$ inv < up	_	$F = 6.93^{*}$ inv < up
	(at P7/8 only)	(–)	($F = 10.32^{**}$)	($F = 15.23^{***}$)	(–)	(–)	($F = 7.56^{*}$)
Effect of contrast reversal (photo-negative)	Latency	$F = 10.89^{***}$ neg > pos	$F = 6.28^{*}$ neg > pos	$F = 138.86^{*****}$ neg > pos	$F = 50.34^{*****}$ neg > pos	_	$F = 22.8^{*****}$ neg > pos
	(at P7/8 only)	($F = 8.6^{**}$)	(–)	($F = 143.6^{*****}$)	($F = 19.2^{*****}$)	(–)	($F = 26.5^{*****}$)
	Amplitude	_	$F = 11.29^{***}$ neg < pos	$F = 16.21^{****}$ neg > pos	$F = 43.02^{*****}$ neg < pos	$F = 55.83^{****}$ neg > pos	_
	(at P7/8 only)	(–)	($F = 13.76^{*}$)	($F = 6.94^{*}$)	($F = 83.84^{*****}$)	($F = 47.45^{*****}$)	(–)

inv = inverted; up = upright; neg = negative; pos = positive. [1]Larger N1 amplitude for inverted than upright houses at parietal sites only (orientation × electrode, $F(2.1, 38.4) = 8.26$, $P < 0.001$) in agreement with the orientation effect at P7/8 sites.

* $0.01 < P < 0.05$.
** $0.005 < P < 0.01$.
*** $0.001 < P < 0.005$.
**** $0.0001 < P < 0.001$.
***** $P < 0.0001$.

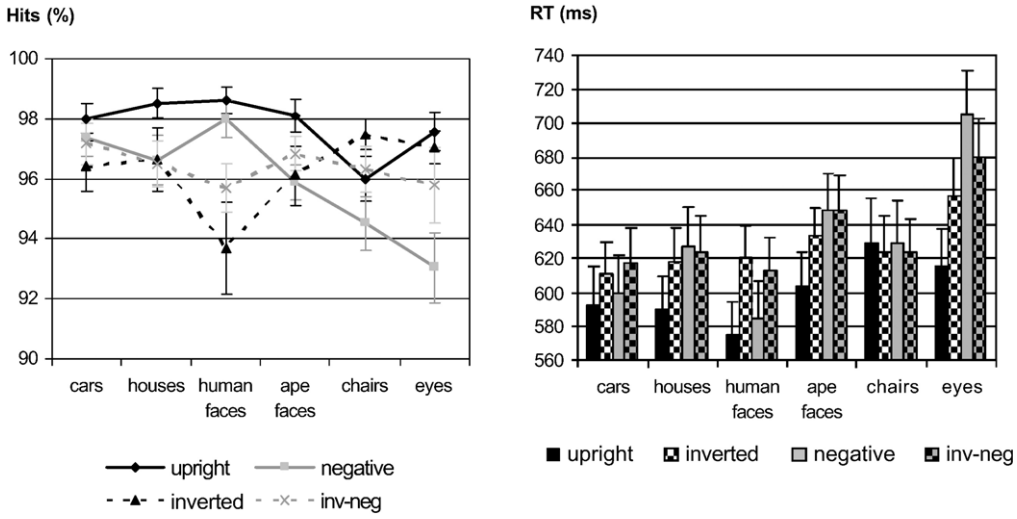


Fig. 1. Percentage hits and mean reaction times displayed for all categories in each format.

Neurophysiological measures—the N170 component

Effects of category

Compared to all categories, human faces elicited the shortest N170s (Figs. 2, 3A) in positive contrasts (upright and inverted) and in upright negative formats (Table 1). Ape faces, in contrast, elicited the longest N170 latencies, especially in negative formats. Along with the faster reaction time measures, this earlier N170 shows that human faces are processed faster than objects.

Across formats, the largest N170 amplitudes were seen for human faces and eyes (Figs. 2 and 3B). For upright stimuli (positive contrast), the largest amplitudes were found for eyes (Table 1, Fig. 3B) followed by human and ape faces that did not differ but were significantly larger than the other categories. Upright houses, cars and chairs all elicited smaller N170s. In inverted–positive and upright negative formats, N170 amplitudes to human faces and eyes no longer differed (Fig. 4) and were larger than all other categories followed by ape faces, also larger than all the rest. The same pattern was also found in the inverted–negative format, except that N170 was slightly larger to human faces than to eyes. Thus, we reproduced a larger and delayed N170 for eye stimuli compared to whole faces seen upright (Bentin et al., 1996; Jemel et al., 1999; Taylor et al., 2001c). However, the N170 amplitude for inverted and negative human faces was no longer different from that to eyes (Fig. 4). Although N170 latency was still faster for faces than for eyes in these inverted and negative formats, this result suggests that what drives the face N170 increase in amplitude with inversion and contrast reversal is the eye region. This conclusion was confirmed by the absence of a category effect when we ran a separate ANOVA on the N170 amplitude including only human faces and eyes [$F(1,18) = 0.25$, $P = 0.625$], the differences being found in category by orientation and category by contrast interactions only. The category effect was not significant in a post-hoc ANOVA including only inverted faces and eyes [$F(1,18) = 3.77$, $P < 0.07$] and was borderline significant for negative faces and eyes tested separately [$F(1,18) = 4.59$, $P = 0.046$]. When we only included electrodes P7/8 in the analyses, where N170 is maximal, the category effect was again not significant for either inverted face and eye ($P = 0.239$) or negative face and eye ($P = 0.773$) analyses.

Effects of inversion and contrast reversal

Inversion increased N170 latencies [$F(1,18) = 104.2$, $P < 0.0001$] for all categories (Table 2, Fig. 3A), with the largest impact on human faces [$F(3.5, 62.6) = 6.23$, $P < 0.001$]. As this result is in contrast to previous studies, analyses were redone using only P7/P8 sites. Again, an inversion effect was found for each category (Table 2), albeit of smaller size for ape faces and chairs. At these lateral parietal electrodes, the difference between positive upright and positive inverted items was ~10 ms for human faces and houses, ~8 ms for cars and ~5 ms for the other categories. For amplitudes, inversion had an effect only for human faces, ape faces and eyes [$F(3.5,62.5) = 5.27$, $P < 0.002$]. When only P7/8 sites were used, a small inversion effect was found for houses. Eyes also presented an inversion effect that was due to contrast-reversed categories: when only positive upright eyes were compared to positive inverted eyes, no inversion effect was found ($P = 0.61$) (Fig. 5). While N170 was increased for inverted human faces, it was slightly decreased for inverted eyes and ape faces (Fig. 3B). For eyes, this amplitude decrease occurred only at occipital sites for positive contrast pictures [contrast × inversion × electrode interaction, $F(1.8,33.2) = 14.4$, $P < 0.0001$]. For apes, the inversion effect was seen at parieto-occipital and temporo-parietal sites only [$F(1.8,31.8) = 3.88$, $P < 0.05$].

Contrast reversal also increased latencies for all categories [$F(1,18) = 96.6$, $P < 0.0001$] except chairs, with a larger impact on human and ape faces [$F(3.2,57.4) = 9.57$, $P < 0.0001$]. When only P7/8 electrodes were used, the effect disappeared for houses but remained for all the other categories (Table 2). Contrast reversal increased amplitudes for human faces and chairs, while it decreased N170 for houses and ape faces [$F(2.9,51.5) = 32.54$, $P < 0.0001$]. The same effects were found at P7/8 sites. The fact that inversion and contrast reversal had different effects on human and ape faces demonstrates that the N170 is sensitive to the species of the face.

Except for faces, N170 latencies were shorter for upright positive pictures but not significantly different among the other three formats [$F(1,18) = 68.4$, $P < 0.0001$] (Fig. 3A). For ape faces, however, N170s were significantly longer to negative ($P < 0.007$) and inverted–negative ($P < 0.001$) than to inverted–positive pictures, reflecting a greater disruption of contrast reversal than inversion for apes. For human faces, N170 latencies to inverted and to negative images did not differ significantly, but

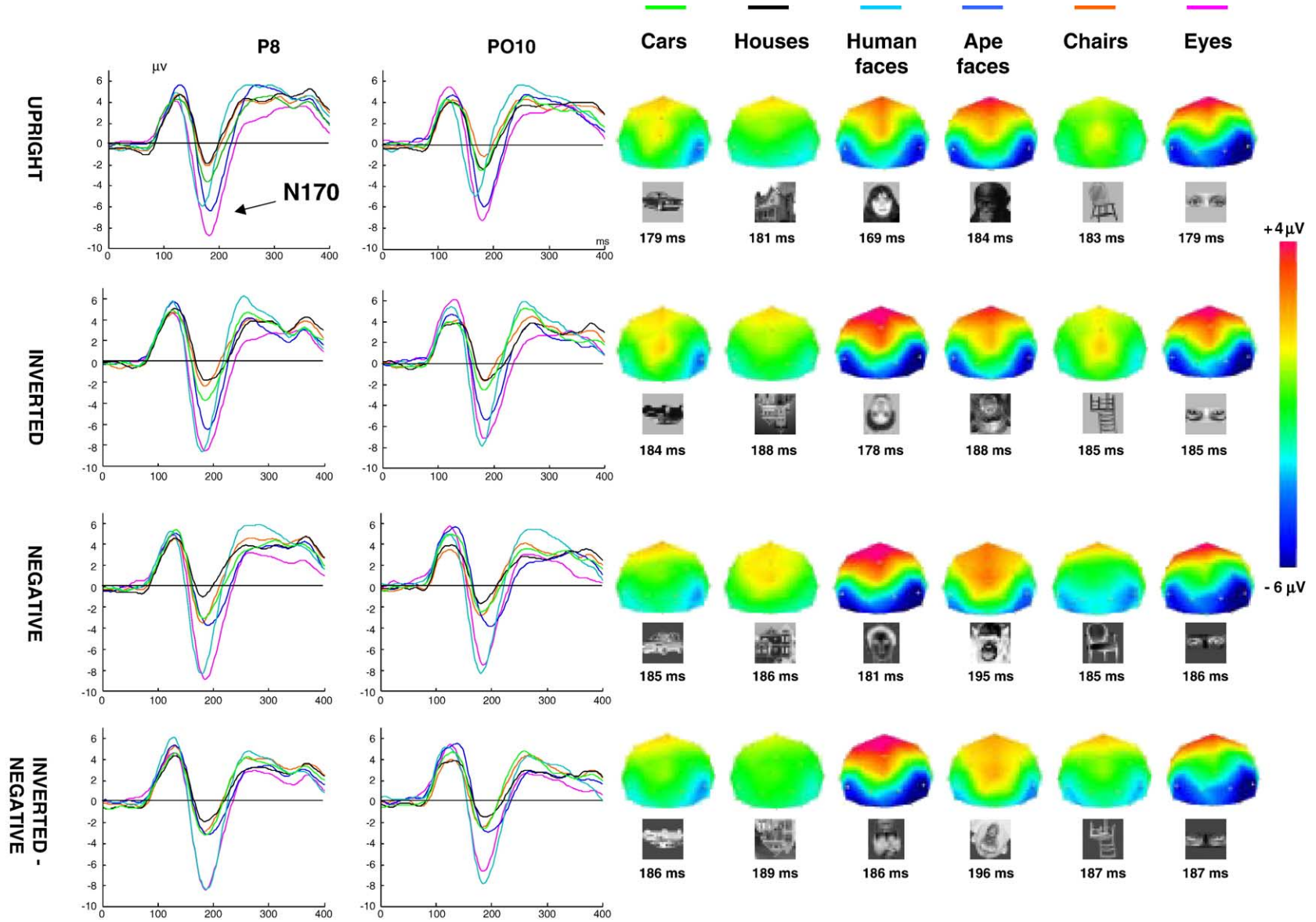


Fig. 2. For each of the upright, inverted, negative and inverted–negative formats, the N1/N170 is displayed at P8 and PO10 electrodes for all categories. Topographies of each category were taken at the latency of maximum N170 amplitude. Human faces, ape faces and eyes showed the same topographies that were not seen for the objects. The N170s to human faces and eyes are different in upright format but become very similar in the other formats. Note the large reduction in amplitude for negative ape faces.

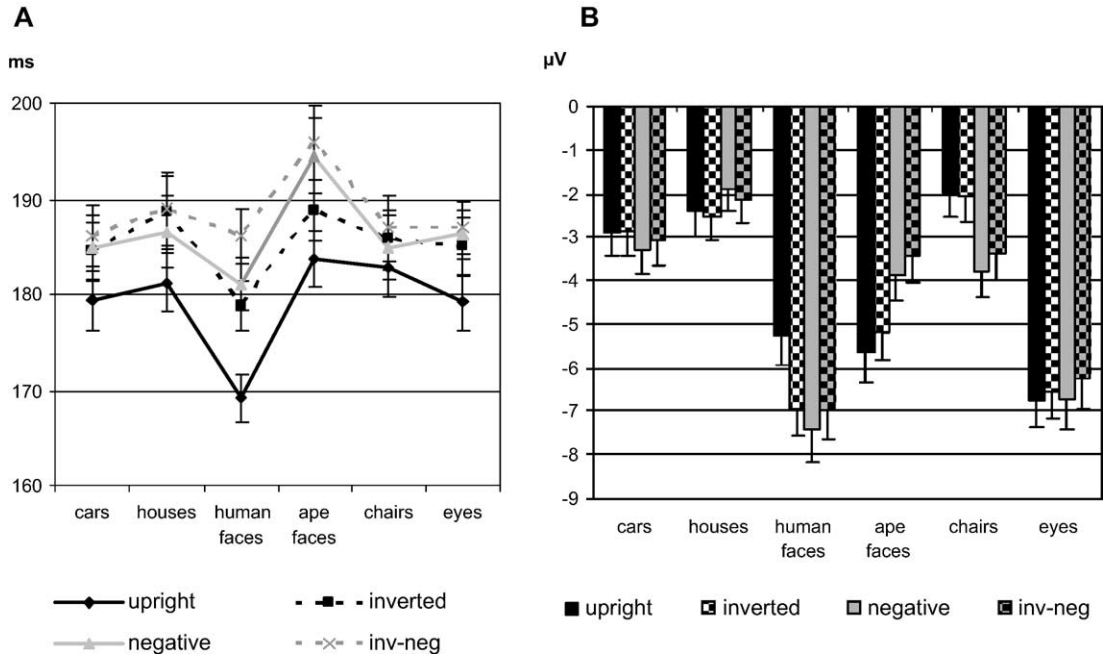


Fig. 3. The N170 component (A) latency and (B) amplitude, displayed for all categories and formats, measured across TP9/10, P7/8, PO9/10 and O1/2 electrodes. The amplitude represents the mean across all electrodes measured. Human faces elicited the fastest N170 in upright and inverted formats. The additive effect of inversion and contrast reversal on latency is seen only for human faces. The N170 amplitude to transformed human faces is very similar to that for isolated eyes, while no such effect is seen for ape faces. Note the differential impact of inversion and contrast reversal on N170 amplitude for human and ape faces, suggesting species sensitivity early in the visual processing stream.

both were shorter than to inverted–negative faces ($P < 0.0001$). This reflected an additive effect of orientation and contrast that was unique to the human face category.

Discussion

In this paper, we addressed the issue of early face specificity by comparing the effects of inversion and contrast reversal on the early-face-sensitive ERP component N170 recorded to human and ape faces, isolated eyes and various object categories. Firstly, we found that human faces were processed faster than all the other visual categories, including other face types like ape faces (Carmel and Bentin, 2002). This was evident in the systematically earlier N170 latency in all pair-wise comparisons and shorter reaction times. This faster processing for human faces was even found in the inverted format for N170 measures, despite inversion causing the greatest N170 delay for faces. Although reported previously (Carmel and Bentin, 2002; Itier and Taylor, 2004d), this faster processing has been controversial (Rossion and Gauthier, 2002; Rossion et al., 2000). We believe it is an important characteristic of human face processing.

Secondly, we found that the N170, reflecting structural encoding of faces, was delayed by inversion for all categories tested, and not only for human faces. This result contrasts with previous studies finding no inversion effects for the objects tested (e.g. cars, mugs, shoes, houses or chairs; Bentin et al., 1996; Eimer, 2000a; Rebai et al., 2001; Rossion et al., 2000; Stekelenburg and de Gelder, 2004). Only two recent studies reported a delay of N170 with inversion of cars (Rossion et al., 2003b) and animal faces

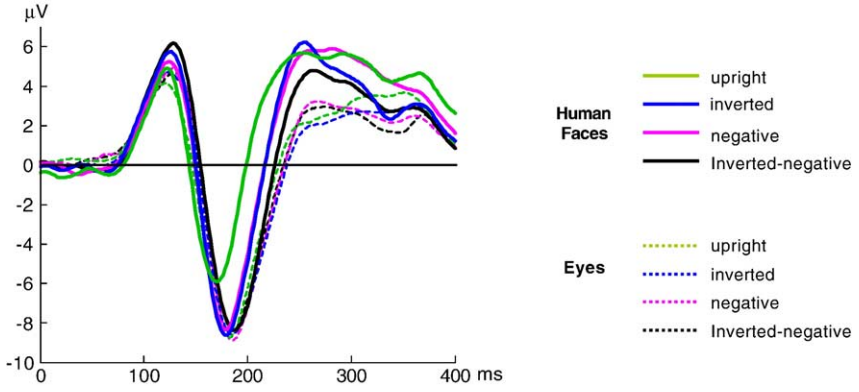


Fig. 4. The N170 at P8 electrode for face and eye stimuli seen in all formats. While N170 to upright human faces is faster and smaller than to upright eyes, the signal is no longer significantly different between the two categories when faces are inverted or in photo-negative, suggesting that what drives the increase in the face N170 to inversion and contrast reversal is the eye region as a pair of eyes is still processed as a pair of eyes regardless of inversion or contrast.

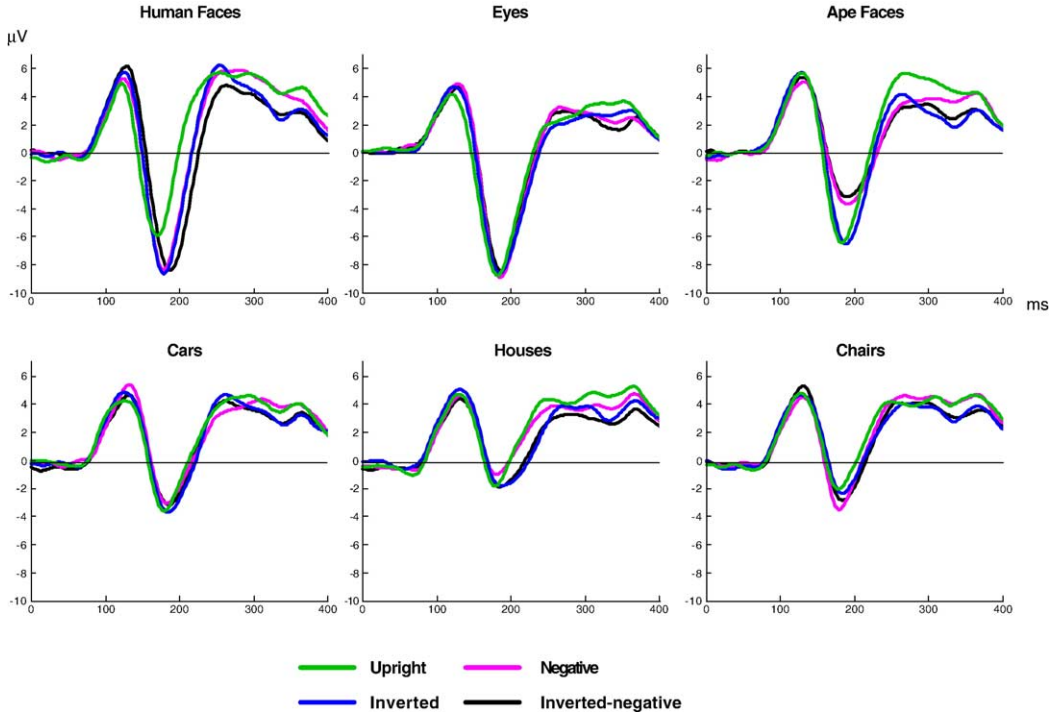


Fig. 5. For each category, the N170 is displayed at electrode P8 in the four formats. Note the unique pattern of increased latency and amplitude of N170 for human faces with inversion, contrast reversal and their conjunction. The fact that the same manipulations produced different results on N170 to faces and objects demonstrates, along with the topographies seen in Fig. 2, the involvement of different neuronal generators for these categories. This is true for ape faces as well, as shown by a very different effect of contrast reversal on N170 for that category compared to human face.

(Rousselet et al., 2004), but they tested only one category at a time. Here, inversion delayed N170 for all six categories, including ape faces and isolated eyes. Although the magnitude of this effect was largest for human faces, this result demonstrates that the latency delay by inversion is not specific to the human face category as previously thought (Rossion and Gauthier, 2002; Rossion et al., 2000) but rather reflects a disruption of the processing for non-canonical views of objects. This orientation effect cannot be due to task-related attention as Rossion et al. (2000) did not find any such delays for five categories using exactly the same task. The discrepancy cannot either be due to the measurement difference between studies (restricted to T5/6 or P7/8 sites in most cases while analyzed across eight occipito-temporal sites here) as a clear inversion effect was found for all categories when only P7 and P8 electrodes were used in the analyses. The absence of inversion effects for object categories in previous studies remains unclear, but the finding is an important argument against the view that the inversion effect on N170 latency is the only one that systematically differentiates between faces and other objects (Rossion and Gauthier, 2002; Rossion et al., 2000). Similarly, a delay in the N170 response with contrast reversal was observed for most categories and not just human faces. These manipulations thus seem to delay early processing of any visual category, which suggests the visual system is trained by experience to respond optimally to positive contrast and to canonical upright orientation. However, the inversion effect was far larger for human faces than any other category, and inversion and contrast reversal had additive effects only for human faces, shown by a larger delay of N170 for inverted–negative faces compared to inverted or negative faces alone (Fig. 3A). This parallels the additive effects found behaviorally in some studies (Bruce and Langton, 1994; Kemp et al., 1990; Lewis and Johnston, 1997) and suggests that these manipulations affect different processes operating in normal face perception. Exactly what is disrupted by inversion and contrast reversal is still debated. Inversion disrupts the general prototypical spatial layout of the face (i.e. eyes above nose above mouth) that is preserved in photo-negatives. Both manipulations seem to change the specific featural relationships that are specific to an individual face. Contrast reversal does so in a more subtle way compared to inversion as the spatial relationships among features are preserved but appear different because of the light and shading variations and the pigmentation/texture cues that are dramatically changed (Kemp et al., 1990, 1996; Lewis and Johnston, 1997). The fact that the N170 latency is even more delayed when the face is both upside-down and in photo-negative suggests that both the prototypical layout of the face and the pigmentation/texture cues are processed at the structural encoding stage for human faces.

Inversion and contrast reversal both increased N170 amplitude for human faces as shown previously (Bentin et al., 1996; de Haan et al., 2002; Eimer, 2000a; Itier and Taylor, 2002, 2004a,b,c,d; Rossion et al., 1999, 2000; Sagiv and Bentin, 2001; Taylor et al., 2001c), a pattern that was not found for the other categories. Chairs presented an increase of amplitude with contrast reversal but no effect of inversion. No effect of inversion was seen for the other objects, except for houses when only P7/8 sites were used, confirming a previous report (Eimer, 2000a). Ape faces and eyes presented a very small inversion effect but in the opposite direction, i.e. a reduced N170, that was larger over occipital and parieto-occipital sites, while the face inversion effect was maximal at lateral parietal electrodes. Eyes presented an inversion effect at P7/8 sites, but this was due to negative contrast pictures as the effect disappeared when only positive upright and inverted eyes

were compared. Fig. 4 clearly shows no inversion effects at parietal sites for apes, in agreement with a previous report (de Haan et al., 2002), nor for eyes. Ape faces also presented a clear reduction of amplitude with contrast reversal, i.e. the opposite of human faces. Thus, ape faces presented very different effects of inversion and contrast reversal compared to human faces, suggesting the N170 does not merely reflect processes associated with any type of face but processes particular to the human face.

Although systematically found in ERP studies, the increase in N170 amplitude with inversion and contrast reversal for human faces is at odds with other findings in the literature. Single cell recordings in monkeys have shown that, compared to upright faces, the response of face-selective cells to inverted faces is delayed (Perrett et al., 1988) and slightly decreased (Hasselmo et al., 1989; Perrett et al., 1988), like that to contrast-reversed faces (Ito et al., 1994; Perrett et al., 1984). Similarly, intracranial studies in humans have shown that the face-specific N200 component recorded directly from the cortical surface is delayed by inversion and of smaller amplitude for inverted than upright faces, especially in the right hemisphere (McCarthy et al., 1999). fMRI studies in humans have found an area of the fusiform gyrus implicated in face perception that responds more to faces than to objects (Kanwisher et al., 1997; McCarthy et al., 1997; Puce et al., 1995). That area has been reported to respond similarly for upright and inverted faces (Aguirre et al., 1999; Haxby et al., 1999), or less for inverted faces (Kanwisher et al., 1998; Yovel and Kanwisher, 2004), as seen with contrast-reversed faces (George et al., 1999). From this literature, we would expect a decrease of the human face N170 amplitude with inversion and contrast reversal rather than an increase. How can this increase be accounted for? One fMRI study reported an increase in activation for inverted faces in cortical areas adjacent to the fusiform gyrus and known to be activated by objects (Haxby et al., 1999). This was the basis for the hypothesis that object-selective neurons would be recruited in addition to face-selective neurons to produce the larger N170 amplitude for inverted human faces (Rossion et al., 2000). The recruitment of object-selective neurons would be due to the disruption of the face configuration by inversion and contrast reversal. In contrast, our data suggest that the larger N170 seen for human faces is due to a recruitment of neurons responding to the eye region of the face. Indeed, the N170 recorded for isolated eyes did not vary with the manipulations, suggesting that photo-negative or inverted eyes are processed like normal upright eyes. The N170 to human faces, however, which was very different from that to eyes in the upright positive format, increased in amplitude with inversion and contrast reversal and was no longer significantly different from N170 to eyes (Figs. 3 and 4). Given the distribution of the N170 recorded to objects, the contribution of neurons from object-selective areas should change the shape and distribution of the N170 which is not the case here. In contrast, inverted faces seem to activate the same areas as upright faces, as suggested by source modeling of the N170 (Itier and Taylor, 2004e; Watanabe et al., 2003), with no evidence of additional object cortical recruitment.

Our hypothesis that the eye region drives this increase in N170 with inversion and contrast reversal fits well with the monkey literature and human intracranial recordings. In the monkey cortex, some cells are selective to eyes and some to whole faces, with the response of eye-selective neurons being modulated by the face context (Perrett et al., 1988). In humans, the intracranial N200 was larger to faces than to isolated eyes at ventral sites (fusiform gyrus) but larger to eyes than to faces at lateral sites (middle temporal gyrus; McCarthy et al., 1999), suggesting eye-selective N200s over lateral temporal cortices. Neuromagnetic recordings have also shown separable localization for faces and eyes in the fusiform regions (Taylor et al., 2001b). Thus, several sources such as the fusiform and the inferior occipital gyri likely interact to generate the N170; their different contributions depending on the task could explain the various N170 modulations with experimental conditions. The N200 findings concord with recent source localizations of N170 to the superior temporal sulcus region (superior temporal and middle temporal gyri; Itier and Taylor, 2004e; Watanabe et al., 2003). This is further corroborated by neuropsychological cases of prosopagnosic patients showing clear N170s despite fusiform gyrus damage (Rossion et al., 2003a). It thus seems that, in the human lateral temporal cortex, face-selective and eye-selective neurons coexist, and their activity is a major contribution in generating the scalp N170. In the normal upright face, features are perceived in relation to each other to create a global face percept to which face-selective neurons respond. Eye-selective neurons would not be responding to the eyes of the upright face, possibly by an inhibition mechanism from face cells such as the one proposed by Allison et al. (2002). This hypothesis is supported by the finding that the N170 is of equivalent size for intact upright faces and upright faces without eyes (Eimer, 1998). Although in inverted and contrast-reversed faces, configuration is altered, albeit differently, the eyes are still clearly seen. At the neuronal level, disrupting the facial configuration would impair the inhibition mechanism from face cells, allowing eye-selective neurons to respond to the eye region, hence enhancing the N170 amplitude and latency. It is thus possible that the N170 for inverted and negative faces reflects eye-selective neurons rather than face-selective neurons or both cell types. The shorter latency of N170 to inverted and negative faces than to eyes could still be explained by the earlier firing of face-selective neurons, despite the latency delay of face neurons induced by inversion. Alternatively, it is possible that the presence of eyes within the face context actually speeds up face processing, shortening N170 latency even when the face is upside-down or in photo-negative. This could explain why, for intact upright faces, N170 is shorter than for faces without eyes, although the amplitude does not vary (Eimer, 1998). This hypothesis of the eye region driving the N170 increase in amplitude for inverted and negative human face photographs is also in agreement with the absence of such inversion effects for Mooney (Latinus and Taylor, 2005) and schematic (Henderson et al., 2003; Sagiv and Bentin, 2001) faces. In these faces, no clear eye features can be seen and the N170 actually decreases (Henderson et al., 2003; Latinus and Taylor, 2005; Sagiv and Bentin, 2001) due to the decrease in response magnitude of face-sensitive neurons with inversion (Hasselmo et al., 1989; McCarthy et al., 1999; Perrett et al., 1988). The fact that eyes can be seen in ape faces yet inverted (and negative) ape faces did not yield increased N170 amplitudes suggests that the selectivity of neurons to eyes is specific to the human species. This species selectivity agrees with an adaptive role of eye morphology for gaze processing through evolution, given that humans are the only primate species with white sclera and have the largest index of exposed sclera size (Kobayashi and Kohshima, 1997). This allows the use of eye direction as a cue of active communication, a fundamental aspect of human social cognition.

In conclusion, our data show that the specificity of the human face is reflected in its unique pattern of N170 latency and amplitude changes to both inversion and contrast reversal that

was not seen with the other categories. The amplitude increase of the N170 seen only for inverted and contrast-reversed human faces likely reflects the activation of neurons responding to the eye region of the face. The face inversion and contrast reversal effects on the face N170 thus seem mainly driven by the eye region.

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