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Effects of contrast inversion on face perception depend on gaze location: Evidence from the N170 component

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Face recognition is known to be impaired when the contrast polarity of the eyes is inverted. We studied how contrast affects early perceptual face processing by measuring the face-sensitive N170 component to face images when the contrast of the eyes and of the rest of the face was independently manipulated. Fixation was either located on the eye region or on the lower part of a face. Contrast-reversal of the eyes triggered delayed and enhanced N170 components independently of the contrast of other face parts, and regardless of gaze location. Similar N170 modulations were observed when the rest of a face was contrast-inverted, but only when gaze was directed away from the eyes. Results demonstrate that the contrast of the eyes and of other face parts can both affect face perception, but that the contrast polarity of the eye region has a privileged role during early stages of face processing.

Keywords: Face perception; contrast inversion; N170 component; event-related brain potentials.

Reversing the contrast polarity of familiar faces dramatically impairs their recognizability (e.g., Galper, 1970; Johnston, Hill, & Carman, 1992). This effect appears to be specific to face perception, as the recognition of non-face objects is much less sensitive to contrast reversal (Nederhouser, Yue, Mangini, & Biederman, 2007; Vuong, Peissig, Harrison, & Tarr, 2005). Changing contrast polarity may disproportionately affect face recognition because it removes shading and pigmentation information that is critical for the discrimination of facial identity (e.g., Kemp, Pike, White, & Musselman, 1996; Liu, Collin, Burton, & Chaudhuri, 1999; Liu, Collin, & Chaudhuri, 2000; Russell, Sinha, Biederman, & Nederhouser, 2006). The eye region in particular contains contrast-related signals that are relevant for face recognition. For this reason, the eyes may be prioritized during the structural encoding of faces, and serve as an "anchor" for holistic face processing (Nemrodov, Anderson, Preston, & Itier, 2014; Rossion, 2009; see also Orban de Xivry, Ramon, Lefèvre, & Rossion, 2008). In line with this hypothesis, it has been shown that fixating gaze on the nasion region (between and just below the eyes) is beneficial for many face processing tasks (Peterson & Eckstein, 2012). The first fixation on a face image is typically directed to this region (Hsiao & Cottrell, 2008). Inverting the contrast of the eyes should therefore have a greater effect on face processing than contrast inversions of other parts of a face, in particular when eye gaze is directed toward its preferred position near the eye region.

Gilad, Meng, and Sinha (2009) explored this hypothesis with "contrast chimera" faces, which include both contrast-inverted and contrast-normal regions, and demonstrated that restoring only the

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eye region of a contrast-inverted face to positive contrast improved recognition performance to approximately 90% of the level observed with contrast-normal faces (see also Sormaz, Andrews, & Young, 2013). They also showed that fMRI activity in the fusiform face area elicited by these positive-eyes chimeras was indistinguishable from the response to contrast-normal faces. Such observations suggest that the effects of contrast inversion on face processing might be primarily or even exclusively driven by the contrast of the eye region. In the present experiment, we tested this hypothesis by measuring the face-sensitive N170 component of the event-related potential (ERP). The N170 is an enhanced negativity at lateral occipital-temporal electrodes that emerges 150–200 ms post-stimulus in response to faces as compared to non-face objects (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000; see, 2011; for review). Because the N170 is generally unaffected by face familiarity (Eimer, 2000), it is interpreted as a neural marker of the perceptual structural encoding of faces that precedes their recognition. The N170 is highly sensitive to face inversion and to manipulations of face contrast. Upside-down faces and contrast-inverted faces elicit delayed and enhanced N170 components relative to upright or contrast-positive faces (e.g., Itier, Latinus, & Taylor, 2006; Itier & Taylor, 2002). Such N170 modulations have been attributed to disruptive effects on perceptual face processing caused by changing the typical orientation or the contrast polarity of faces (Itier et al., 2006; Rossion et al., 1999).

Several ERP studies have shown that early face processing might be particularly sensitive to the contrast polarity of the eye region. Itier, Alain, Sedore, and McIntosh (2007) found that N170 modulations elicited by contrast-inverted as compared to contrast-positive faces were eliminated for faces without eyes. Along similar lines, a recent ERP study with contrast chimera faces (Gandhi, Suresh, & Sinha, 2012) showed the usual N170 delay and enhancement for fully contrast-inverted faces, but found that the N170 to positive-eyes chimeras (where the eye region appeared in normal contrast) was statistically indistinguishable from the N170 component to contrast-normal faces. These observations suggest that early perceptual face processing stages that are reflected by the N170 are exclusively sensitive to the contrast polarity of the eye region, and remain unaffected by the contrast of other parts of the face. However, because Itier et al. (2007) and Gandhi et al. (2012) did not manipulate gaze location, these studies could not determine whether this differential effect depends critically on a fixation position near the eye region. A recent study (Nemrodov et al., 2014) has demonstrated that N170 face-inversion effects are strongly modulated by the current location of fixation (see also De Lissa et al., 2014, for similar findings), and this might also be the case for N170 modulations that are triggered by changing the contrast polarity of faces or face parts.

In the present experiment, we varied the contrast of the eye region and the contrast of the rest of a face orthogonally and also manipulated fixation location, to test whether N170 components are exclusively sensitive to eye contrast, and whether this depends on eye gaze being directed toward the eye region. Participants performed a one-back repetition detection task with contrast-normal faces, fully contrast-inverted faces, and two types of contrast chimeras where either the contrast of the eye region or the rest of the face was inverted (negative-eyes and positive-eyes chimeras; see Figure 1A). This independent manipulation of the contrast of the eye region and of the rest of the face allowed us to determine the relative effects of contrast-inverting either of these regions on N170 amplitudes and latencies. One face image was presented at a time, and appeared unpredictably either in the upper or lower visual field, so that eye gaze was either centered between both eyes (Upper fixation condition) or between the nose and mouth (Lower fixation condition; see Figure 1B). N170 contrast inversion effects were measured separately for both fixation conditions to find out whether these effects are modulated by gaze location, that is, by the relative distance between fixation and the contrast-inverted part of a face.

METHODS

Participants

Fourteen participants (10 female) aged 20–39 years (mean age 28 years) took part in the study. Their face recognition abilities were tested with the Cambridge Face Memory Test (Duchaine & Nakayama, 2006). All scores were within ±1 standard deviation of the mean. This study was approved by the ethics committee of the Department of Psychological Sciences, Birkbeck College, University of London.

Stimuli and procedure

Photographs of 25 male and 25 female faces (front view; neutral expression; external features removed) were employed, with permission from Bruno Rossion's lab, where these face images were created

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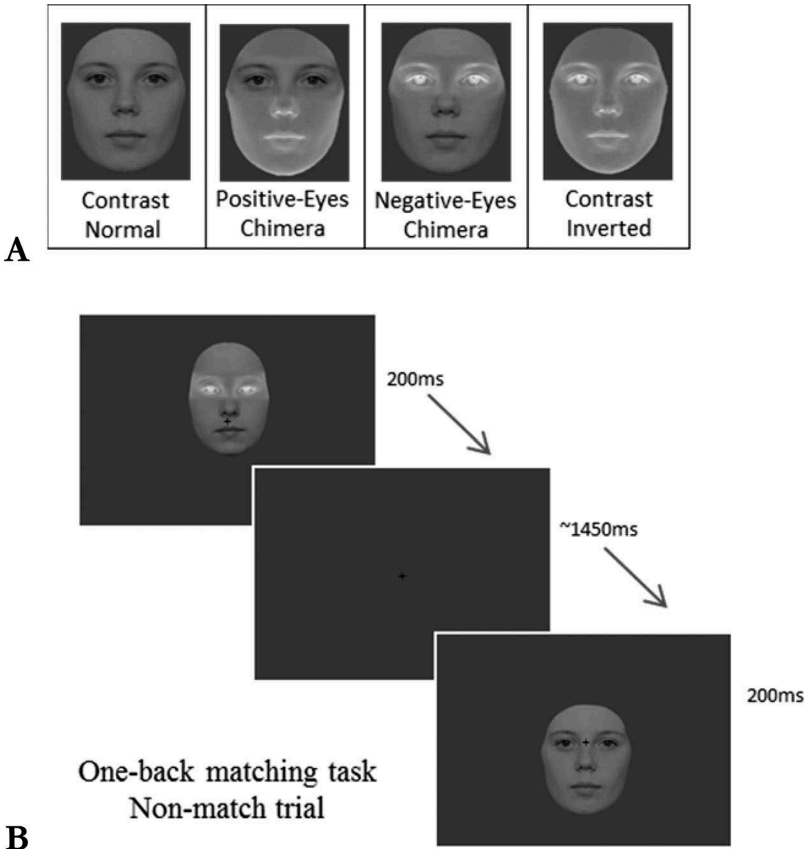

Figure 1. (A) Example of four different face contrast types tested (contrast-normal faces, contrast-inverted faces, positive-eye chimeras, negative-eye chimeras). For the positive-eyes chimeras, the face outside the eye region appeared in negative contrast. For the negative-eyes chimeras, the eye region was contrast-inverted and the rest of the face was contrast-normal. (B) Illustration of the stimulation procedure. Each face was presented for 200 ms, and there was an interval of approximately 1450 ms between two successive face presentations. Faces appeared randomly and unpredictably in a lower or upper position, so that participants' gaze was either on the upper part of the nose (Upper fixation condition), or on the area between the nose and the mouth (Lower fixation condition). In the example shown, a lower-fixation face is followed by a (non-matching) upper-fixation face.

and first used (Laguesse, Dormal, Biervoye, Kuefner, & Rossion, 2012). Four different contrast versions (Figure 1A) were generated for each face, using Adobe Photoshop. Contrast-normal images were created by converting the original color images into grayscale, and adjusting their luminance to a constant level. Image contrast was inverted to produce fully contrast-inverted faces. Negative-eyes chimeras were constructed by contrast-inverting a horizontal section across the eye region of contrast-normal faces which included the eyes, lower eye socket, nasion, and eyebrows. The transition between the contrast-normal and inverted regions was smoothed in Photoshop to avoid abrupt contrast polarity changes. Negative-eyes chimeras were contrast-inverted to produce positive-eyes chimeras.

Luminance values for the four different face contrast types were recorded from a viewing distance of 100 cm with a Konica Minolta CS-100A color/luminance meter, which has a spatially restricted circular measurement window of approximately 1°. Because the experiment included two fixation conditions (fixation centered between both eyes or between nose and mouth), two luminance values within two spatially corresponding measurement windows were obtained for each face contrast type. Measurement windows were centered either on the nasion or the philtrum (the central ridge between the nose and the mouth) of the faces, respectively. For nasion-centered measurements, average luminance values were 12.30 cd/m^2 (contrast-normal faces), 18.12 cd/m^2 (fully contrast-inverted faces), 17.85 cd/m^2 (negative-eyes chimeras), and 12.28 cd/m^2 (positive-eyes chimeras). For philtrum-centered measurements, average luminance values were 10.47 cd/m^2 (contrast-normal faces), 21.22 cd/m^2 (fully contrast-inverted faces), 10.47 cd/m^2 (negative-eyes chimeras), and 21.17 cd/m^2 (positive-eyes chimeras). Faces were presented against a gray

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background (4.92 cd/m^2). The visual angle of all face images was 3.55° × 2.76°.

All face stimuli were shown on a CRT monitor for 200 ms at a viewing distance of 100 cm. The intertrial interval varied randomly between 1400–1500 ms. A black fixation cross (size: 0.60° × 0.60°) remained on the screen throughout each experimental block. Faces appeared either in the upper or lower visual field, randomly intermixed across trials, with a vertical displacement relative to central fixation of ±1.35° (Figure 1B). For faces in the upper visual field, the fixation cross was located on the philtrum (Lower fixation condition). For faces in the lower visual field, fixation was centered on the nasion (Upper fixation condition). Participants were instructed to maintain gaze on the central fixation cross throughout each block. The experiment included 10 blocks of 80 trials, resulting in a total of 800 trials. Each of the eight combinations of stimulus type (contrast-normal, contrast-inverted, positive-eyes chimera, negative-eyes chimera face type; Figure 1A) and stimulus location (upper versus lower; Figure 1B) appeared on 90 randomly distributed trials throughout the experiment. Repetitions of the same face image across successive trials were not allowed on these trials. On the remaining 80 randomly interspersed trials, the image that was presented on the preceding trial was immediately repeated at the same location. Participants performed a one-back matching task, and responded with a right- or left-hand button press (counterbalanced across participants) to immediate stimulus repetitions. Following the main experiment, participants completed the Cambridge Face Memory Task, where the faces of six target individuals shown from different viewpoints have to be memorized and then distinguished from distractor faces (see Duchaine & Nakayama, 2006, for a detailed description).

EEG recording

EEG was recorded using a BrainAmps DC amplifier with a 40 Hz low-pass filter and a sampling rate of 500 Hz from 27 Ag-AgCl scalp electrodes. Electrodes at the outer canthi of both eyes were used to record the horizontal electroculogram (HEOG). During recording, EEG was referenced to an electrode on the left earlobe, and was re-referenced offline relative to the common average of all scalp electrodes. Electrode impedances were kept below 5 kΩ. The EEG was epoched from 100 ms before to 250 ms after face stimulus onset. Epochs with HEOG activity exceeding ±30 µV (horizontal eye movements), activity at Fpz exceeding ±60 µV (blinks and vertical eye movements), and voltages at any electrode exceeding ±80 µV (movement artifacts) were removed from analysis. EEG was averaged relative to a 100-ms pre-stimulus baseline for each combination of stimulus type (contrast-normal, contrast-inverted, positive-eyes chimera, negative-eyes chimera) and fixation position (upper, lower). Only non-target trials (i.e., trials where the immediately preceding image was not repeated) were included in the ERP analyses. N170 peak latencies were computed at lateral posterior electrodes P9 and P10 (where this component is maximal) within a 150–200-ms post-stimulus time window. N170 mean amplitudes were calculated for the same electrode pair and time window. Additional analyses were conducted for P1 peak latencies (measured within an 80–130-ms post-stimulus time window). All *t*-tests comparing N170 latency or amplitude differences between stimulus types were Bonferroni-corrected, and corrected *p*-values are reported.

RESULTS

Behavioral performance

Participants detected 81% of all immediate face stimulus repetitions in the one-back task. Mean response time (RT) on these target trials was 618 ms. There were no significant differences between the four face types (normal, inverted, positive-eyes or negative-eyes chimera) for RTs, $F(3, 39) = 2.6$, or error rates, $F(3, 39) = 1.7$, on these infrequent target trials.

ERP components

Upper fixation

Figure 2 shows ERP waveforms measured at lateral posterior electrodes P9/P10 in response to faces that appeared in the lower visual field (Upper fixation condition). The contrast polarity of the eye region affected N170 latencies and amplitudes, with delayed and enhanced N170 components to faces with contrast-inverted eyes, and this was the case regardless of whether the contrast of the rest of the face was normal or inverted (Figure 2, top panels). Changing the contrast polarity of the rest of the face did not affect N170 amplitudes or latencies when the contrast of the eye region was held constant (Figure 2, bottom panels). In other words, with fixation on the nasion, N170 modulations were driven entirely by the

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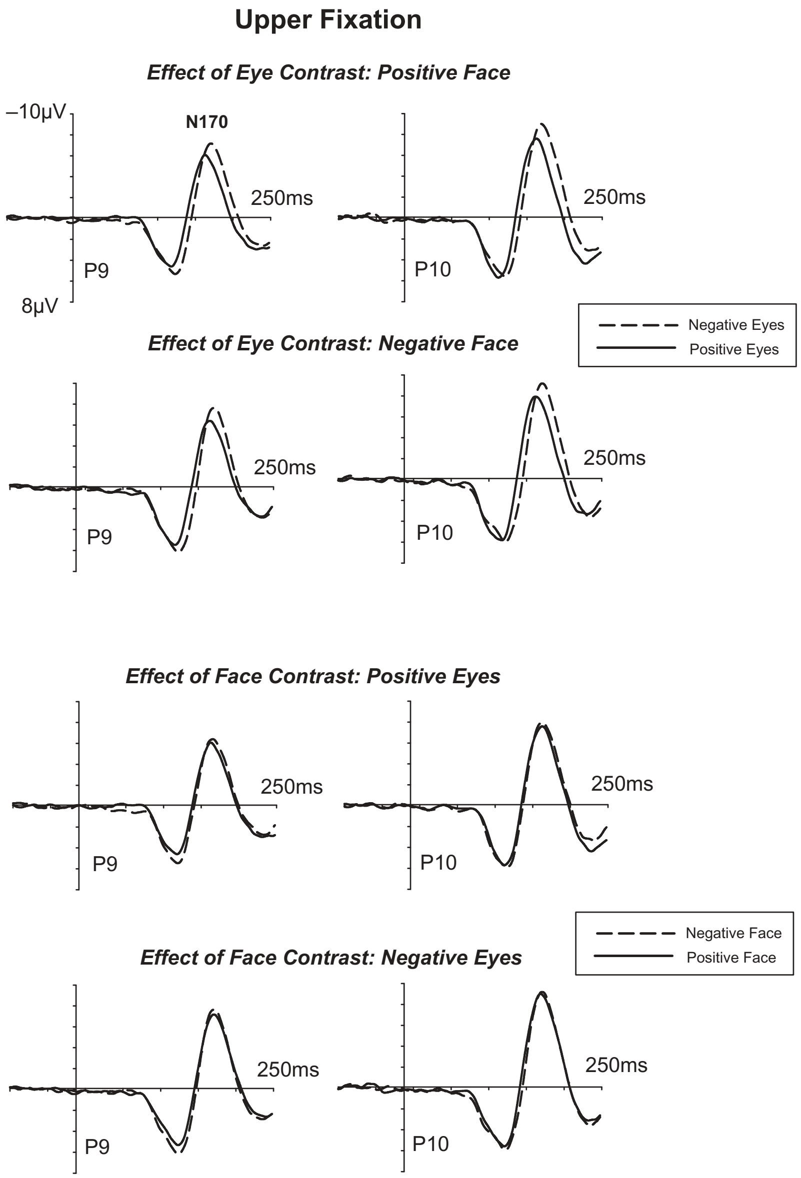

Figure 2. Grand-averaged ERPs elicited at lateral temporo-occipital electrodes P9 (left hemisphere) and P10 (right hemisphere) in the 250-ms interval after stimulus onset in the Upper fixation condition. Ticks on the time axes represent 50 ms intervals. Top panels: Effects of the contrast of the eye region (negative eyes vs. positive eyes) on N170 components, shown separately for face images where the area outside the eye region was contrast-normal (positive face) or contrast-inverted (negative face). Bottom panels: Effects of the contrast of the rest of the face (negative face vs. positive face) on N170 components, shown separately for face images where the eye region was contrast-normal (positive eyes) or contrast-inverted (negative eyes).

contrast of the eye region, but remained unaffected by the contrast polarity of the rest of the face. In addition to these N170 differences, eye contrast also affected the peak latency of the earlier P1 component, which appeared to be delayed specifically for face images with contrast-inverted eyes (Figure 2, top panels).

These observations were confirmed by analyses of N170 peak latencies and mean amplitudes with repeated-measures ANOVAs with the factors Eye contrast (positive, negative), Face contrast (positive, negative), and Hemisphere (left, right). There were significant effects of Eye contrast on N170 latencies, $F(1, 13) = 108.72$, $p < .001$, $\eta_p^2 = .89$, and N170 amplitudes, $F(1, 13) = 21.31$, $p < .001$, $\eta_p^2 = .62$, reflecting delayed and enhanced N170 components for faces with contrast-inverted eyes. These effects did not interact with Hemisphere, both $F < 2.2$. Analyses of N170 peak latencies (collapsed across

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electrodes P9 and P10) confirmed N170 delays for face images with negative versus positive eyes both when the rest of the face was positive (170.4 ms vs. 163.4 ms; $t(13) = 7.7$, $p < .001$) or negative (170.4 ms vs. 162.6 ms; $t(13) = 9.7$, $p < .001$). Likewise, N170 amplitude enhancements for faces with negative versus positive eyes were reliable both when the rest of the face was positive (1.55 µV; $t(13) = 4.23$, $p < .002$) or negative (1.07µV; $t(13) = 3.97$, $p < .004$). The absence of interactions between eye and face contrast, both $F < 1.2$, showed that the contrast polarity of the rest of the face did not affect the delay and enhancement of N170 components to negative eyes. There were also no main effects of Face contrast on N170 latency, $F < 1.2$, or amplitude, $F < 3.2$, confirming that the contrast polarity of the rest of the face had no impact on N170 components in the Upper fixation condition.

An analysis of P1 peak latencies with the factors Eye contrast, Face contrast, and Hemisphere revealed a significant effect of Eye contrast, $F(1, 13) = 11.53$, $p < .005$, $\eta_p^2 = .47$, confirming that the P1 component was delayed for faces with contrast-inverted eyes. There was no main effect of face contrast, and no interactions between eye or face contrast and hemisphere, all Fs < 1.9. To test whether the N170 delay for faces with contrast-inverted as compared to contrast-normal eyes can be completely accounted for by the delay of the preceding P1 component to contrast-inverted eyes, we performed an additional analysis of P1-N170 peak-to-peak differences (obtained by subtracting P1 peak latencies from N170 peak latencies) for the factors Eye contrast, Face contrast, and Hemisphere. A main effect of Eye contrast, $F(1, 13) = 8.21$, $p < .013$, $\eta_p^2 = .39$, confirmed that the N170 delay in response to contrast-inverted eyes remained reliably present even when the corresponding earlier P1 delay is taken into account.

Lower fixation

Figure 3 shows ERP waveforms measured at P9/P10 to faces in the upper visual field (Lower fixation condition). In contrast to the Upper fixation condition, N170 latencies and amplitudes were systematically affected not only by eye contrast (upper panel), but also by the contrast polarity of the rest of the face (lower panel). There were main effects of Eye contrast, $F(1, 13) = 13.4$, $p < .001$, $\eta_p^2 = .51$, and Face contrast, $F(1, 13) = 20.5$, $p < .001$, $\eta_p^2 = .61$, on N170 latency, and no interaction between these factors, $F < 1.32$, suggesting that the effects of eye and face contrast on the latency of the N170 were independent and additive. N170 peak latencies (collapsed across P9 and P10) were reliably delayed for negative versus positive face contrast images (Figure 3, bottom panel) both when the eyes were positive (164.4 ms vs. 161.9 ms; $t(13) = 3.61$, $p < .006$) or negative (168.6 ms vs. 165.6 ms; $t(13) = 3.97$, $p < .004$). A significant interaction between Eye contrast and Hemisphere on N170 latency, $F(1, 13) = 5.26$, $p < .05$, $\eta_p^2 = .29$, was due to the fact that the N170 delay caused by negative eyes was largely confined to the right hemisphere (see Figure 3, top panel). At right-hemisphere electrode P10, this delay for negative versus positive eyes was present when the rest of the face was positive (165.4 ms vs. 161.3 ms; $t(13) = 4.08$, $p < .003$) or negative (170.3 ms vs. 164.0 ms; $t(13) = 4.75$, $p < .002$). There were no corresponding N170 delays over the left hemisphere (both $t < 1.6$). For N170 mean amplitudes, there were significant effects of both Eye contrast, $F(1, 13) = 19.4$, $p < .001$, $\eta_p^2 = .60$, and Face contrast, $F(1, 13) = 15.9$, $p < .001$, $\eta_p^2 = .55$, and an interaction between these two factors, $F(1, 13) = 8.4$, $p < .05$, $\eta_p^2 = .39$. N170 amplitude enhancements to negative versus positive eyes (Figure 3, top panel) were present both when the rest of the face was positive (1.81 µV; $t(13) = 4.83$, $p < .001$) and negative (0.91 µV; $t(13) = 2.90$, $p < .04$). However, the contrast of the rest of the face affected N170 amplitude only when the eyes were positive (1.27 µV; $t(13) = 4.33$, $p < .002$), but had no significant differential effect for faces with negative eyes (0.37 µV; $t < 1.8$).

P1 peak latencies were not systematically affected by the contrast polarity of the eyes or the rest of the face (see Figure 3). There were no significant effects of Eye contrast, Face contrast, or interactions between these two factors and Hemisphere in the Lower fixation condition, all $F < 2.9$.

Comparison between fixation conditions

The comparison of Figures 2 and 3 shows that gaze location strongly affects how N170 components are modulated by inverting the contrast polarity of the eye region and the rest of the face. This was confirmed by additional analyses that included Fixation (nasion vs. philtrum) as an additional factor. An interaction between Eye contrast and Fixation for N170 latency, $F(1, 13) = 22.53$, $p = .001$, $\eta_p^2 = .63$, was due to the fact that the N170 delay caused by inverting the eye region was twice as large with upper fixation (7.3 ms) than lower fixation (3.7 ms). There

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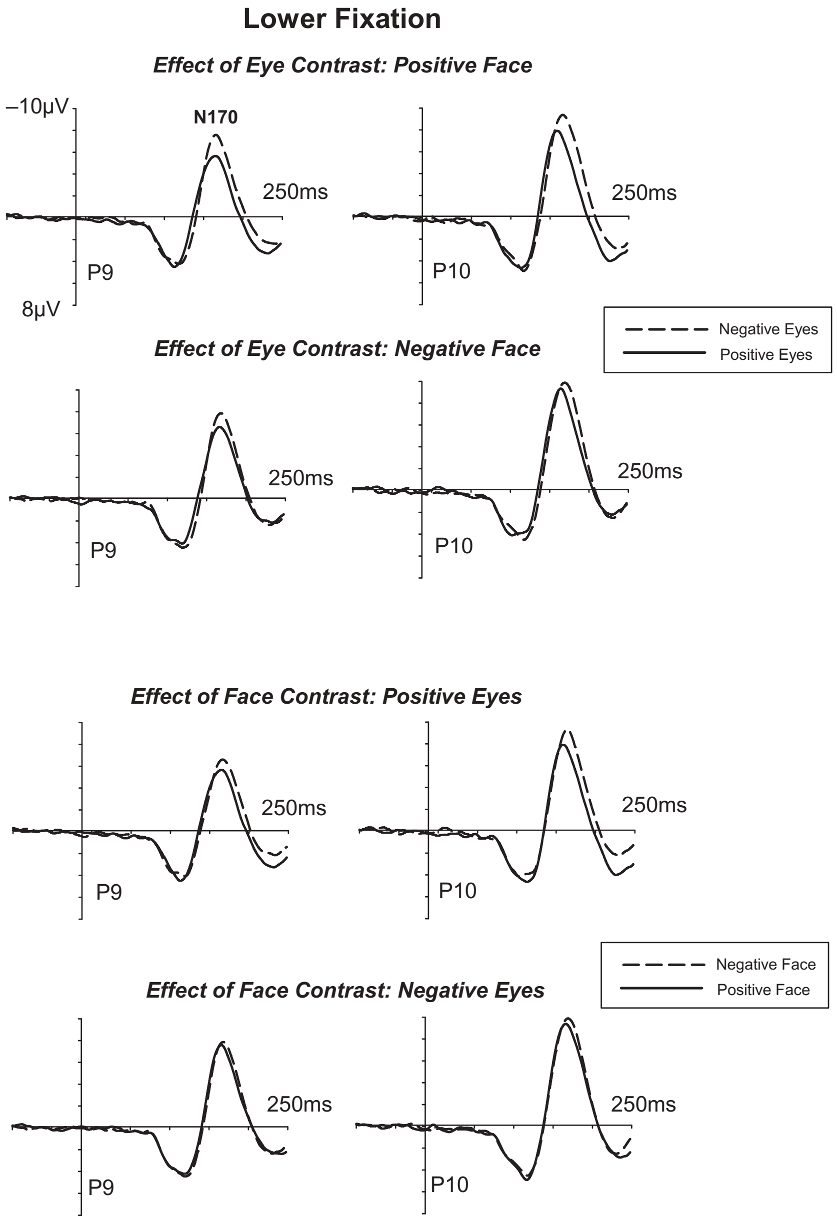

Figure 3. Grand-averaged ERPs elicited at lateral temporo-occipital electrodes P9/10 in the 250-ms post-stimulus interval in the Lower fixation condition. Ticks on the time axes represent 50 ms intervals. Top panels: Effects of eye contrast (negative eyes vs. positive eyes) on N170 components, for face images where the area outside the eye region was contrast-normal (positive face) or contrast-inverted (negative face). Bottom panels: Effects of the contrast of the rest of the face (negative face vs. positive face) on N170 components, for face images where the eye region was contrast-normal (positive eyes) or contrast-inverted (negative eyes).

was also an interaction between Face contrast and Fixation $F(1, 13) = 22.58$, $p < .001$, $\eta_p^2 = .63$, as inverting the contrast of the rest of the face delayed the N170 in the Lower fixation condition, but had no impact on N170 latency with upper fixation. For N170 amplitude, Eye contrast did not interact with Fixation, $F < 1$, demonstrating that inverting the contrast of the eye region enhanced N170 amplitudes regardless of gaze location. However, the effect of Face contrast on N170 amplitude was modulated by Fixation $F(1, 13) = 6.26$, $p < .05$, $\eta_p^2 = 0.32$, as inverting the contrast of the rest of the face enhanced N170 amplitude with lower fixation, but had no effect in the Upper fixation condition.

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DISCUSSION

Inverting the contrast polarity of face images impaired early stages of perceptual face processing, and this was reflected by delayed and enhanced face-sensitive N170 components for contrast-inverted as compared to contrast-normal faces. Recent studies have shown that restoring the normal contrast polarity of the eye region while the rest of the face remains contrast-inverted improves recognition performance (Gilad et al., 2009; Sormaz et al., 2013) and can eliminate inversion-related N170 modulations (Gandhi et al., 2012). The present experiment demonstrated that contrast-inversion of the eyes or of the rest of the face can both affect N170 components, depending on which part of a face is fixated.

Inverting the contrast polarity of the eye region delayed and enhanced the N170. These effects were not modulated by the contrast polarity of the rest of the face, regardless of whether fixation was centered between the eyes or on the lower part of the face. This observation that N170 latency and amplitude modulations triggered by negative eyes are independent of the contrast polarity of other face parts confirms and extends earlier observations (Gandhi et al., 2012), and demonstrates that changing the polarity of the eye region affects perceptual face processing regardless of the polarity of the rest of the face. Although negative eyes elicited delayed N170 components in both fixation conditions, this delay was larger when gaze was centered near the eyes (Upper fixation) than when gaze was centered below the nose (Lower fixation condition). In addition, the N170 delay for negative eyes was present bilaterally in the Upper fixation condition, but was restricted to the right hemisphere with lower fixation. This shows that the proximity of the eye region to current fixation modulates the degree to which contrast inversion of this region affects perceptual face processing.

It should be noted that the larger N170 delay for negative versus positive eyes in the Upper fixation condition may at least in part be due to the fact that the earlier P1 component was also reliably delayed for faces with negative eyes in this condition, although the N170 delay remained significant even when the P1 latency difference was taken into account. A P1 delay in response to contrast-inverted as compared to contrast-normal stimuli has been observed before (Itier & Taylor, 2002). The fact that this P1 delay was only found in the Upper fixation condition when the eye region was contrast-inverted shows that it is not simply a result of the luminance differences between the four face contrast types used in this study (see Liu et al., 1999, for a study where the luminance of normal and contrast-inverted faces was controlled), but appears to be specific to the contrast polarity of the eyes when gaze is focused nearby.

Inverting the contrast of face parts outside the eye region can also modulate perceptual face processing, as reflected by the N170 component, but this depends critically on gaze direction. With fixation located between the nose and mouth, N170 components were delayed and enhanced when the rest of the face was contrast-negative. The N170 delay was independent of the contrast polarity of the eye region, while the N170 amplitude enhancement was only reliable for faces with positive eyes (Figure 3, bottom panel). When gaze was focused on the upper part of a face between the two eyes, the contrast polarity of the rest of the face had no impact on N170 amplitudes and latencies (Figure 2, bottom panel). The fact that the contrast inversion of face parts outside the eye region affected N170 components only in the Lower fixation condition again shows that the perceptual analysis of faces is highly sensitive to image contrast near the currently fixated location. The contrast polarity of face parts outside the eye region is not always irrelevant for early stages of perceptual face processing, but will affect face perception when gaze is directed away from the eyes. The fact that restoring the normal polarity of the eye region in contrast chimera faces does not improve face recognition up to the level observed with normal faces (Gandhi et al., 2012; Sormaz et al., 2013) may be linked to the effects of inverting the contrast of the rest of the face on perceptual face processing, as demonstrated in this experiment during lower fixation.

Although the contrast of the rest of the face can affect perceptual face processing, our results also emphasize the central importance of contrast information from the eye region. The fact that N170 modulations triggered by contrast-inverted eyes were robustly present in both fixation conditions, and the observation that they were independent of the contrast of the rest of the face, both demonstrate a privileged status of the eye region that is already apparent during early face processing stages between 150 and 200 ms post-stimulus. In addition to comparing the effects of contrast-inverting the eye region with the effects of inverting the whole of the rest of the face, as was done in the present study, future research should also investigate how manipulating only the contrast of one specific face part outside the eye region (such as the

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mouth) affects the N170 component, whether there are systematic differences in N170 contrast-inversion effects between facial features, and how this is affected by gaze direction and current task demands. It should also be noted that no eye tracker was employed in the present study to continuously monitor the precise location of fixation on the nasion or philtrum, and that there may have been subtle differences in gaze direction between individual upper or lower fixation trials. However, the fact that the vertical position of each face stimulus was unpredictable rules out anticipatory gaze adjustments, and makes it highly likely that participants' gaze was close to the nasion or philtrum on the majority of all trials.

The current results show that structural encoding of faces is highly sensitive to contrast signals from the eye region, and that contrast information from other parts of the face may affect perceptual processing primarily when eye gaze is directed away from the eyes to lower parts of a face image. Reversing the contrast polarity of faces generally impairs face perception and recognition, and this has been attributed to the disruption of information that can be derived from skin pigmentation (e.g., Vuong et al., 2005), or of three-dimensional shape-from-shading information that is important for representing facial shape (e.g., Johnston et al., 1992). Reversing the contrast polarity of the eye region is particularly disruptive, because this region contains several contrast-related signals (the boundaries between the sclera, iris, and pupil of the eye, contrast differences between the eyes and surrounding regions, and the shape of the eyebrows) that appear to be critical for face-detection and recognition processes (e.g., Gilad et al., 2009; Peterson & Eckstein, 2012; Sormaz et al., 2013). The delay and enhancement of the face-sensitive N170 component to faces with contrast-inverted eyes may thus be interpreted as an electrophysiological marker for impaired perceptual structural encoding when these signals are disrupted. It has previously been shown that relative to intact faces, the N170 to faces without eyes is also delayed (Eimer, 1998; Itier et al., 2007), analogous to the N170 delay elicited by contrast-inverting the eye region in the present study. This effect may reflect a similar disruption of face-processing mechanisms that are selectively tuned to the eye region. Our additional finding that N170 modulations triggered by contrast-inverting the eyes or the rest of the face are strongly affected by fixation location may reflect systematic retinotopic biases that are linked to the special role of contrast-related signals from the eye region. Because fixation near the eyes is the default setting during face perception (Hsiao & Cottrell, 2008), the face-processing system may be particularly sensitive to contrast information that originates from a region that extends horizontally from fixation into the left and right visual field. Such a retinotopic bias would account for the fact that contrast-inverting the rest of the face affects N170 components only in the Lower fixation condition, where the inverted areas fall within the critical retinotopic region next to fixation (see also Chan, Kravitz, Truong, Arizpe, & Baker, 2010, for further evidence for retinotopic biases in face processing). It will also be important to determine whether any such biases toward particular retinotopic regions in face processing may be modulated by top-down factors such as selective spatial attention.

Overall, this study has demonstrated the importance of contrast signals for early stages of perceptual face processing. Because contrast differences between different face parts remain constant under a wide variety of lighting conditions, they are critical for the rapid detection of a generic face template in the visual field (Sinha, 2002). Contrast information from the eyes has a privileged role, and focusing gaze and selective attention on the eye region therefore provides the optimal reference point for the construction of contrast-sensitive representations during the perceptual structural encoding of faces.

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