Reduced sensitivity to contrast signals from the eye region in developmental prosopagnosia

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Abstract

Contrast-related signals from the eye region are known to be important for the processing of facial identity. Individuals with developmental prosopagnosia (DP) have severe face recognition problems, which may be linked to deficits in the perceptual processing of identity-related information from the eyes. We tested this hypothesis by measuring N170 components in DP participants and age-matched controls in response to face images where the contrast polarity of the eyes and of other face parts was independently manipulated. In different trials, participants fixated either the eye region or the lower part of a face. In the Control group, contrast-reversal of the eyes resulted in enhanced and delayed N170 components, irrespective of the contrast of other face parts and of gaze location. In the DP group, these effects of eye contrast on N170 amplitudes were strongly and significantly reduced, demonstrating that perceptual face processing in DP is less well tuned to contrast information from the eye region. Inverting the contrast of other parts of the face affected N170 amplitudes only when fixation was outside the eye region. This effect did not differ between the two groups, indicating that DPs are not generally insensitive to the contrast polarity of face images. These results provide new evidence that a selective deficit in detecting and analysing identity-related information provided by contrast signals from the eye region may contribute to the face recognition impairment in DP.

Keywords: Face perception, face recognition, developmental prosopagnosia, contrast inversion, N170 component

1. Introduction

The neural face processing network is specialised for efficiently recognising and discriminating between the many individual faces we will see in our lifetimes. Damage to the component parts of this network through head trauma or stroke can result in the inability to recognise faces (Acquired Prosopagnosia; AP; Bodamer, 1947). A more common face recognition deficit is Developmental Prosopagnosia (DP), a lifelong impairment in the ability to recognise faces which cannot be attributed to brain damage (for recent reviews see Susilo & Duchaine, 2013; Towler & Eimer, 2012). DP affects approximately ~2% of the population (Kennerknecht et al., 2006; Kennerknecht, Pluempe, & Welling, 2008), and there is evidence from both family and twin studies to suggest that there is a genetic component to the disorder (Duchaine, Germine, & Nakayama, 2007; Lee, Duchaine, Wilson, & Nakayama, 2010; Wilmer et al., 2010; Zhu et al., 2010). While the core feature in DP is a face recognition deficit that is linked to impaired memory for familiar or newly learned faces, behavioural tests often also reveal severe face perception deficits in many individuals with DP (e.g. Duchaine et al., 2007), suggesting that relatively early stages in the perceptual processing of faces may already operate atypically in DP.

Event-related brain potential (ERP) measures can be used to assess such deficits in the perceptual structural encoding of faces within the posterior visual-perceptual regions of the face processing network in developmental prosopagnosia. The N170 component is a well-known electrophysiological marker of visual face processing that emerges within approximately 140-200 ms post-stimulus at lateral occipital-temporal electrodes as an enhanced negativity in response to faces as compared to non-face objects (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000b; Rossion & Jacques, 2008; see also Eimer, 2011 and Rossion & Jacques, 2011, for reviews). Source localization studies of the N170 suggest that this component is generated within regions of the core face processing network (Haxby, Hoffman, & Gobbini, 2000), such

as the inferior occipital gyrus, fusiform gyrus, and superior temporal sulcus (Bötzel, Schulze, & Stodieck, 1995; Itier & Taylor, 2004b; Rossion, Joyce, Cottrell, & Tarr, 2003; Watanabe, Kakigi, & Puce, 2003). Inter-cranial recordings from epileptic patients with intact facial recognition abilities have confirmed the role of lateral occipital and fusiform regions in the generation of the N170 (Jonas et al., 2012; Parvizi et al., 2012). Furthermore, when these posterior face processing regions are damaged in patients with AP, the face-sensitivity of the N170 component is often abolished (Dalrymple et al., 2011; Prieto, Caharel, Henson, & Rossion, 2011).

Individuals with DP generally show face-sensitive N170 components, and N170 amplitude differences between faces and non-face objects in DPs are often indistinguishable to those seen in control participants (Towler, Gosling, Duchaine, & Eimer, 2012; Towler, Gosling, Duchaine, & Eimer, 2014). This is consistent with fMRI findings which show that DPs have relatively normal levels of activation within the face-selective regions of the core face processing network that are assumed to generate the N170 (Avidan & Behrmann, 2009; Avidan, Hasson, Malach & Behrmann, 2005; Furl, Garrido, Dolan, Driver, & Duchaine, 2011), and also with the fact that DPs do not have problems distinguishing faces from non-face objects. However, the presence of face-sensitive N170 components in DP does not necessarily imply that perceptual face processing mechanisms operate in exactly the same way in DPs and in control participants with unimpaired face recognition abilities. Two studies from our lab have demonstrated that DPs show atypical patterns of N170 responses when the prototypical upright configuration of face images is altered by stimulus inversion (Towler et al., 2012) or by spatially scrambling the locations of internal facial features (Towler, Parketny, & Eimer, 2016). In participants with intact face recognition, presenting faces upside-down or scrambling face parts results in delayed and enhanced N170 components relative to intact upright face images (e.g., Bentin et al., 1996; Eimer, 2000a; Rossion et al., 1999; Zion-Golumbic, & Bentin, 2007). N170 enhancements in response to inverted and scrambled faces have been interpreted as reflecting the increased effort required to processes face images that do not fit the canonical spatial template for prototypical

upright faces (Rossion et al., 1999). Alternatively, such N170 amplitude enhancements may also reflect the additional recruitment of neuronal populations that are involved in the processing of non-face objects (Rosburg et al., 2010; Rossion et al., 2000; see also Sadeh & Yovel, 2010, for further discussion). In contrast to control participants, DPs do not show enhanced N170 amplitudes to inverted or scrambled faces relative to standard upright faces (Towler et al., 2012, 2016). The absence of these typical N170 amplitude modulations to face inversion and the scrambling of facial features suggests that perceptual face processing mechanisms in DP are less precisely tuned to the canonical upright orientation of faces and the prototypical spatial configuration of face parts in upright faces. As a result, these mechanisms may be less sensitive to spatial-configural deviations from a prototypical upright visual face template. In line with this interpretation, DPs appear to be less affected by face inversion than control participants in tasks that measure face recognition (Behrmann, Avidan, Marotta, & Kimchi, 2005; Duchaine, 2011; Duchaine, Yovel, & Nakayama, 2007) or holistic face processing (Avidan, Tanzer, & Behrmann, 2011; Palermo et al., 2011; DeGutis, Cohan, Mercado, Wilmer, & Nakayama, 2012).

Most research investigating perceptual impairments in DP has focused on configural or holistic aspects of face perception. However, it is an open question whether the extraction of cues to face identity that are based on holistic face processing is the only perceptual process that operates atypically in DP. To fully understand the nature of perceptual deficits in prosopagnosia, it is important to know whether the perceptual processing of other face properties that are known to be diagnostic for face recognition is also impaired in DP. In addition to the orientation of faces and the spatial arrangement of their component parts, the contrast polarity of face images is another important factor that affects the perception and recognition of faces in participants without face processing impairments. Contrast-inverted images of familiar faces are much more difficult to recognise than images in normal contrast, even though shape information and spatial relationships between facial features remain unchanged (Galper, 1970; Johnston, Hill, & Carmen, 1992). Importantly, contrast inversion appears to leave holistic face

processing intact (e.g. Hole, George, & Dunsmore, 1999), suggesting that it impairs aspects of face perception related to surface texture and pigmentation rather than global face shape. Analogous to face inversion and face scrambling, inverting the contrast polarity of face images also results in delayed and enhanced N170 components (Itier, Latinus, & Taylor, 2006; Itier & Taylor, 2002). This similarity suggests that face contrast may be part of a prototypical face template that contains both shape and surface pigmentation information, and that deviations from normal face contrast will therefore affect early visual-perceptual stages of face processing in a similar fashion as changes of canonical spatial-configural attributes. In line with this hypothesis, intracranial recordings have shown that the strongest and earliest responses of face-selective neurons in macaque visual cortex were elicited only when face features were shown both in their canonical locations and in their correct contrast (Ohayon, Freiwald, & Tsao, 2012). If perceptual face processing in DP is generally less precisely tuned to canonical visual templates of prototypical upright faces, and if these canonical perceptual face templates include contrast-related signals, DPs should be less sensitive than control participants to deviations from normal face contrast. Analogous to previous observations that N170 amplitudes are unaffected by face inversion and face scrambling in DP (Towler et al., 2012, 2016), such a reduced sensitivity to contrast inversion should be reflected by an atypical pattern of N170 responses to contrast-inverted as compared to contrast-normal face images in participants with DP.

The goal of the present study was to test this hypothesis by measuring N170 components to normal and contrast-inverted upright faces in a group of 11 participants with DP and 11 age- and gender-matched control participants. In addition to normal-contrast and fully contrast-inverted faces, we also employed two types of partially contrast-inverted face images ("contrast chimeras"; see Gilad, Meng, & Sinha, 2009). These images were generated by selectively inverting the contrast of the eye region within an otherwise normal-contrast face (negative-eyes chimeras) or by leaving the eye region unchanged and contrast-inverting the rest of the face (positive-eyes chimeras; see Figure 1A). Previous studies have shown that restoring

the normal contrast of the eye region in an otherwise contrast-inverted face improved face recognition to approximately 90% of the level observed for normal-contrast faces (Gilad et al., 2009; Sormaz, Andrews, & Young, 2013), and also strongly reduced the effects of contrast inversion on the N170 component (Fisher, Towler, & Eimer, 2015; Gandhi, Suresh, & Sinha, 2012). Such observations demonstrate that contrast signals from the eye region are particularly important during early perceptual stages of face processing. These stages appear to be specifically sensitive to deviations from the typical contrast within this region, presumably because contrast-related signals from this region are particularly important for face detection and face recognition processes (e.g., Gilad et al., 2009; Peterson & Eckstein, 2012; Sormaz et al., 2013). Participants with intact face processing abilities tend to fixate the area between both eyes during face perception and recognition tasks (Hsiao & Cottrell, 2008). In contrast, there is some evidence that individuals with DP tend to avoid the eye region during the visual exploration of face images (Schmalzl et al., 2008; Schwarzer et al., 2007). This may contribute to their face recognition difficulties, either due to a general preference to attend to non-diagnostic facial features, or because avoidance of the eyes in the course of development could result in a reduced perceptual sensitivity that is specific to contrast signals from the eye region.

The procedures used in the present experiment were identical to those used in a previous study from our lab where participants without face recognition impairments were tested (Fisher et al., 2015). Contrast-normal faces, fully contrast-inverted faces, positive-eyes chimeras, and negative-eyes chimeras appeared in a random order in each block. Participants performed a one-back task where they had to respond to infrequent immediate repetitions of the same face image. This task was employed to ensure that participants' attention would remain focused on the face images throughout the experimental blocks. The orthogonal manipulation of the contrast polarity of the eye region and of the rest of the face made it possible to independently assess the effects of contrast signals from these two regions on the N170 component in DPs and control participants. To investigate whether these effects may be modulated by gaze location, the main

part of these face images appeared unpredictably either in the upper or lower visual field on each trial (see Figure 1A). As a result, no preparatory eye movements to particular parts of a face were possible prior to stimulus presentation, so that eye gaze was either centred between both eyes (upper fixation condition) or between the nose and mouth (lower fixation condition).

In our earlier study with participants without face recognition impairments (Fisher et al., 2015), contrast-reversal of the eye region elicited enhanced and delayed N170 components, irrespective of the rest of the face, and independently of gaze location. Contrast-reversal of the rest of the face had no effect on the N170 when fixation was close to the eye region, but produced a delay and enhancement of the N170 when participants fixated between the nose and mouth. The same N170 results should be observed in the present study for control participants, and the critical new question was whether DPs would show a qualitatively different pattern of N170 modulations to contrast-inverted faces. If face perception in DP was generally less well tuned to canonical face templates (e.g., Towler et al., 2012, 2016), and also to the typical face contrast that is represented in such templates, face processing in DP may be overall less sensitive to contrast inversion relative to the control group. In this case, inversion-induced N170 modulations should be smaller or perhaps entirely absent in the DP group, regardless of whether the eye region, the rest of the face, or the whole face is contrast-inverted. Alternatively, DPs may be especially insensitive to contrast-related signals from the eye region. This should be reflected by reduced or absent N170 modulations in response to contrast-inverted eyes in the DP group, while contrast signals from other parts of the face may have similar effects on the N170 in both groups. Furthermore, gaze location may also affect N170 modulations induced by contrast inversion differently in the two groups. As the eye region is the default fixation location for control participants, while DPs tend to avoid this region, atypical effects of contrast inversion on N170 components might be particularly pronounced in the upper fixation condition where gaze is focused on the eye region. Finally, it is also possible that perceptual face processing deficits in DP are confined to the configural or holistic analysis of face shape and

that there are no differences in the perceptual processing of contrast-related signals from faces between DPs and control participants. In this case, the pattern of contrast-induced N170 modulations should be very similar across both groups.

2. Methods

2.1 Participants

Eleven participants with developmental prosopagnosia (5 females; aged 21-59 years; mean age 36.5) and eleven control participants that were gender-matched and aged-matched within +/- 4 years (5 females; aged 24-59 years; mean age 36.8) were tested. All participants gave written informed consent prior to the experiment, and all had normal or corrected-to-normal vision. DP participants were recruited through two research websites (http://www.faceblind.org; http://www.prosopagnosia.bbk.ac.uk). All reported difficulties with face recognition since childhood, and their impairment was assessed with a battery of behavioural tests. In order to test long-term face memory, the Famous Faces Test (FFT) required participants to identify 60 people who are famous in popular culture, e.g. actors, musicians, politicians. The ability of the DP participants to learn new faces was assessed with the Cambridge Face Memory Test (CFMT). Participants were required to memorize faces of six target individuals shown from different viewpoints which they then had to identify among other similar distractor faces in a test array (see Duchaine & Nakayama, 2006, for a detailed description). The Old-New Face Recognition Test (ONT, Duchaine & Nakayama, 2005) tested face learning by asking DP participants to memorize 10 faces, and then to distinguish these learned faces from 30 novel faces by making an old/new judgement for each item. The Cambridge Face Perception Test (CFPT, Duchaine et al., 2007) assessed the ability of DPs to perceptually process faces in the absence of memory

demands. Participants were shown a target face presented together with six-front view morphed test faces that resembled the target face to varying degrees. These test faces had to be rearranged in order of their degree of similarity to a target face. DPs completed this task when the target and test faces were upright, and when they were inverted.

The DP participants' individual z-scores for these four behavioural tests are shown in Table 1. All DPs scored below -1 z-score of the mean on both the FFT and CFMT, with 10 DPs on the FFT and 9 DPs on the CFMT, scoring below -2 z-scores. Out of the 11 DPs, 10 were impaired on the ONT scoring below -2 z-scores, and one was unimpaired. For the upright CFPT 4 DPs performed at more than -2 z-scores below the mean and 3 DPs performed at more than -1 z-score, whilst the remaining 4 were unimpaired. Because impaired face recognition is the defining feature of DP, the criterion employed to classify a particular individual as DP was that they should be impaired (below -2 z-scores of the mean) in at least two of the three face recognition tests (FFT, CFMT, ONT). Ten of the eleven individuals who were included in the DP group met this criterion. Another participant (CS) was included in the DP group because their scores in all three face recognition tests were close to the criterion (see Table 1), and they also showed poor performance in the CFPT with upright faces, indicative of clear face perception difficulties. All control participants reported that they were confident in their face recognition abilities, and were all within ±1 standard deviation of the mean on the CFMT.

2.2 Stimuli and procedure

The stimulus set consisted of 25 male and 25 female faces (front view; neutral expression; external features removed) and was taken with permission from Laguesse, Dormal, Biervoye, Kuefner, and Rossion (2012). Each face was image processed to create four contrast versions (Figure 1A), using Adobe Photoshop. The original colour images were converted to greyscale and luminance-balanced to produce the contrast-normal images. For each image, greyscale colour values were reversed in polarity 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. These negative-eyes chimeras were contrast-inverted to produce positive-eyes chimeras.

Luminance values for the four different face contrast types were measured from a viewing distance of 100 cm with a Konica Minolta CS-100A colour/luminance meter, which has a spatially restricted circular measurement window of approximately 1°. Because the experiment included two fixation conditions (upper and lower fixation), two luminance values were obtained for each of the four contrast types, centred either on the nasion (as in the upper fixation condition) or the philtrum (as in the lower fixation condition). For nasion-centred 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-centred 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 grey 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 inter-trial interval varied randomly between 1400–1500 ms. A black fixation cross (size: 0.60° × 0.60°) remained on the screen throughout each experimental block in a fixed position at the centre of the screen. Fixation location was manipulated by presenting individual faces unpredictably at two different vertical positions relative to the central fixation cross. In the upper fixation condition, the main part of a face image appeared in the lower visual field, and fixation was centred between the two eyes on the nasion. In the lower fixation condition, the main part of a face appeared in the upper visual field, and fixation was centred between the nose and mouth on the

philtrum (see Figure 1B). These two fixation conditions were randomly intermixed across trials. The vertical displacement of face images in these two fixation conditions was ±1.35°.

Participants were instructed to maintain their gaze on the central fixation cross throughout each block. The experiment included 10 blocks of 80 trials, resulting in a total of 800 trials. There were eight combinations of face contrast type (contrast-normal, contrast-inverted, positive-eyes chimera, and negative eyes chimera) and fixation condition (upper versus lower fixation). Each of the eight trial types appeared on 90 randomly distributed trials throughout the experiment. Repetitions of the same face image across successive trials never occurred 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, by responding to these immediate stimulus repetitions with a right- or left-hand button press (counterbalanced across participants). Prior to the start of the main experiment, participants completed one training block of 27 randomly selected nontarget trials and 3 randomly interspersed immediate repetition (target) trials. DP and control participants performed identical tasks.

2.3 EEG recording and analyses

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 electrooculogram (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 contrast 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 mean amplitudes were computed at lateral posterior electrodes P9 and P10 (where this component is maximal) within a 150 – 200 ms post-stimulus time window. N170 peak latencies 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).

To evaluate the effects of face contrast on the N170 component at the level of individual participants, additional analyses of individual ERP waveforms were conducted, using a non-parametric bootstrap procedure (Di Nocera & Ferlazzo, 2000). In this analysis, the reliability of ERP amplitude differences between two experimental conditions is assessed by resampling and averaging two sets of trials that are drawn randomly (with replacement) from the combined dataset, and computing differences between the two resulting ERPs. This procedure is then repeated a large number of times (10,000 iterations in the current study). The resulting distribution of difference values has a mean value of zero, because both sample pairs are drawn from the same dataset. Based on this distribution, the reliability of an empirically observed ERP difference between conditions can be determined for individual participants. If the probability of obtaining the observed difference by chance is below 5%, it can be accepted as statistically significant (see Dalrymple et al., 2011; Eimer, Gosling, & Duchaine, 2012; Oruc et al., 2011; Towler et al., 2012; Towler et al. 2016, for previous applications of this procedure in ERP studies of DP). In the present experiment, this bootstrap procedure was based on EEG mean amplitudes obtained on individual trials between 150 and 200 ms after stimulus onset (collapsed across P9 and P10). Separate bootstrap analyses assessed how the contrast polarity of the eye

region affected N170 amplitudes in the upper and lower fixation conditions, for each of the 11 participants with DP and the 11 control participants.

3. Results

3.1 Behavioural Performance

Accuracy in the one-back task and mean reaction times (RTs) to infrequent targets in this task were analysed with two ANOVAs with the factors eye contrast (positive versus negative), face contrast (positive versus negative), fixation condition (upper versus lower) and group (DPs versus Controls). Participants with DP were less accurate than Controls in detecting immediate face repetitions (62% versus 79%), as reflected by a main effect of group on error rates, $F(1,20) = 5.47$, $p = .03$, $\eta_p^2 = .22$. False Alarms on trials where a non-repeated face image was shown occurred on less than 3% of these trials for both groups, with no significant difference between groups for False Alarm rates, $F(1,20) = 2.2$, $p < .15$. RTs to targets were also slower in the DP group (648 ms as compared to 607 ms in the Control group), but this difference between the two groups was not significant, $F(1,20) = 1.71$, $p = .21$. There were no significant main effects or interactions for any of the other factors, and no additional interactions involving the factor group for either accuracy or RTs, all $F < 1.4$.

3.2. N170 components

Figures 2 and 3 show ERP waveforms measured for the DP group (top panels) and Control group (bottom panels) in the upper and lower fixation conditions, respectively. Separate ERP wavefoms are shown for the four different face contrast types (contrast-normal, contrast-inverted, positive-eyes chimera, negative-eyes chimera). For the Control group, the pattern of N170 modulations was similar to the effects previously observed with a different and younger

group of participants without face recognition impairments (Fisher et al., 2015). Inverting the contrast of the eye region resulted in enhanced and delayed N170 components in both fixation conditions, irrespective of the contrast of the rest of the face. Inverting face contrast outside the eye region appeared to modulate N170 amplitude and latency only in the lower fixation condition. Participants with DP also showed clearly defined N170 components. However, the N170 amplitude enhancement produced by inverting the contrast of the eye region appeared strongly attenuated for DPs relative to the Control group both in the upper and lower fixation conditions.

3.2.1. N170 Amplitude – Group-level Analyses

N170 mean amplitudes were analysed in ANOVAs for the factors group, eye contrast, face contrast, and hemisphere (left: P9; right: P10) that were conducted separately for the upper and lower fixation conditions. In the upper fixation condition (Figure 2), there was no significant effect of face contrast, $F(1,20)=3.1$, $p=.09$, and no interaction between face contrast and group, $F<1$, indicating that the contrast polarity of face parts outside the eye region did not affect N170 amplitudes when fixation was near the eyes. There was however a highly significant main effect of eye contrast, $F(1,20)=16.76$, $p<.001$, $\eta_p^2=.46$, demonstrating that contrast inversion of the eye region increased N170 amplitudes. Crucially, an interaction between eye contrast and group, $F(1,20)=7.85$, $p<.02$, $\eta_p^2=.28$, showed that this effect differed between the DP and Control groups. To assess this difference, follow-up ANOVAs were conducted separately for both groups. In the Control group, N170 amplitudes were larger to faces with contrast-inverted eyes than for faces with normal eye contrast (-5.91 μV versus -3.91 μV; $F(1,10)=21.56$, $p<.001$, $\eta_p^2=.68$), regardless of whether the rest of the face was contrast-positive or contrast negative (see Figure 2, bottom panels) There were no significant interactions involving the factors eye

contrast, face contrast, or hemisphere in the Control group, all F<4.6. For the DP group, there was no overall significant difference in N170 amplitudes between faces with negative versus positive eyes (-7.25 μV versus -6.88 μV; F<1; Figure 2, top panels).

N170 amplitudes in the lower fixation condition (Figure 3) were modulated by face contrast, $F(1,20)=25.66$, $p<.001$, $\eta_p^2=.56$, with larger N170 components to images with negative face contrast (-6.68 μV versus -5.84 μV). There was no interaction between face contrast and group, $F(1,20)=2.63$, $p=.12$, indicating that contrast-inverting face parts outside the eye region increased N170 amplitudes in both groups. There was also a two-way interaction between eye contrast and face contrast, $F(1,20)=10.92$, $p<.004$, $\eta_p^2=.35$, that was further modulated by hemisphere, $F(1,20)=11.04$, $p<.003$, $\eta_p^2=.35$. As can be seen in Figure 3, the N170 amplitude enhancement produced by inverting the contrast of the rest of the face was larger when the eye region was contrast-positive (as was already observed in our previous study; Fisher et al., 2015), and this modulation was more pronounced over the right hemisphere. Importantly, neither of these differential effects interacted with group, both F<1. As in the upper fixation condition, there was a main effect of eye contrast for N170 amplitude, $F(1,20)=23.53$, $p<.001$, $\eta_p^2=.54$, with larger N170 components to faces with contrast-negative eyes. Importantly, this effect of eye contrast again differed between the DP and Control groups, $F(1,20)=5.06$, $p<.04$, $\eta_p^2=.20$. Separate ANOVAs conducted for both groups confirmed that control participants showed increased N170 amplitudes for faces with negative as compared to positive eyes (-6.42 μV versus -4.47 μV; $F(1,10)=18.85$, $p<.001$, $\eta_p^2=.65$). For the DP group, this differential effect was smaller (-7.43 μV versus -6.72 μV) but still statistically reliable, $F(1,10)=5.10$, $p<.05$, $\eta_p^2=.34$.

In sum, control participants showed similar effects of eye contrast on N170 amplitudes in the upper and lower fixation conditions. For the DP group, the effect of eye contrast was absent in the upper fixation condition and strongly reduced in the lower fixation condition.

Contrast-inversion of face parts outside the eye region only affected N170 amplitudes when the lower part of faces outside the eye region was fixated, and this was the case for both groups. This was confirmed in an overall ANOVA conducted across both fixation conditions, with the additional factor fixation (upper, lower). There was an interaction between eye contrast and group, $F(1,20)=7.06$, $p<.02$, $\eta_p^2=.26$, reflecting the fact that contrast-inverting the eye region produced larger N170 amplitude enhancements in the Control group relative to the DP group. The absence of an interaction between eye contrast, fixation and group, $F<1.1$, showed that this group difference was not affected by whether the eye region or the lower part of the face was fixated. The enhancement of N170 amplitudes by contrast-inverting face parts outside the eye region was strongly modulated by fixation, $F(1,20)=11.91$, $p<.003$, $\eta_p^2=.25$, and the fixation-dependence of this effect did not differ between DPs and Controls, $F<1.4$.

3.2.2 Effects of eye contrast on N170 Amplitude in Individual Participants

The group-level analyses reported above suggest that N170 amplitudes were much less sensitive to the contrast polarity of the eye region in DPs as compared to control participants, both when fixation was near the eyes and when the lower part of a face outside the eye region was fixated. To find out whether N170 amplitudes were reliably modulated by eye contrast for at least some of the DPs tested, additional analyses were conducted at the level of individual participants in both groups. The effect of eye contrast was computed for each participant as the difference between N170 mean amplitudes to face images with contrast-positive and contrast-negative eye regions, collapsed across face contrast (positive, negative) and hemisphere (P9, P10). The significance of this difference for each individual participant was then assessed with non-parametric bootstrap analyses (Di Nocera & Ferlazzo, 2000), separately for the upper and lower fixation conditions. Figure 4 shows N170 mean amplitude differences between faces with normal

and contrast-inverted eye regions for each individual DP (grey bars) and control participant (black bars), with asterisks indicating statistically reliable differences. In the upper fixation condition, ten out of eleven control participants showed significantly increased N170 components to faces with contrast-inverted eyes. This differential effect was reliable for only four of the eleven DPs tested, and one DP participant showed a significant N170 amplitude modulation in the opposite direction. In the lower fixation condition, nine out of the eleven control participants showed a significant N170 enhancement to contrast-negative eyes. A reliable effect in the same direction was also present for seven of the eleven DPs, although these effects were generally smaller than for most control participants. The same DP (PR) who showed an opposite N170 amplitude effect in the upper fixation condition also had a reliable inverted effect in the lower fixation condition.

To find out whether the size of N170 amplitude modulations caused by inverting the contrast polarity of the eye region in individual participants with DP was associated with their ability to perceptually discriminate between different face identities, raw error scores in the Cambridge Face Perception Test (upright trials) were correlated with the effect of eye contrast on N170 amplitudes (collapsed across the upper and lower fixation conditions and hemispheres). In the CFPT, an error score of 94 reflects chance performance. Visual inspection of the individual N170 effects of eye contrast (see Figure 4) suggested that DP participant PR was an outlier, with more negative N170 components for contrast-normal than for contrast-inverted eyes (the opposite pattern to the control group and other DPs). Grubb's Test (Grubb, 1969) confirmed the outlier status of PR (z=2.65, p<.05), who was therefore excluded from the correlation analysis. For the remaining 10 participants with DP, there was a strong correlation between the effect of inverting eye contrast on N170 amplitudes and performance on the CFPT with upright faces, which was statistically reliable (r=.72, p<.02). As shown in Figure 5, large error scores in the CFPT were associated with small effects of contrast-inverted eyes on N170

amplitudes, and better CFPT performance was linked to larger (i.e., more typical) N170 amplitude modulations.

3.2.3 N170 Latency

Figures 2 and 3 suggest that inverting the contrast of the eye region resulted in a delay of N170 peak amplitudes in both groups and both fixation conditions. This was assessed in an ANOVA of N170 peak latencies with the factors fixation, eye contrast, face contrast, hemisphere, and group. Contrast inversion of the eye region delayed N170 peak latencies by 6 ms relative to faces with contrast-positive eyes (171 ms versus 165 ms; $F(1,20)=43.47$, $p<.001$, $\eta_p^2=.69$). This effect did not interact with group, $F<1$. Contrast-inverting face parts outside the eye region also produced a small but reliable N170 peak amplitude delay relative to when they were presented in normal contrast (170 ms versus 167 ms; $F(1,20)=23.08$, $p<.001$, $\eta_p^2=.54$). Again, this contrast-induced N170 latency modulation did not differ between the two groups, $F<1$. There was no interaction between eye contrast and face contrast, $F<1$, and no other significant interaction involving any of the experimental factors (including fixation), all $F<3.7$.

3.2.4 P1 latency

As can be seen from Figure 2 (bottom panels), eye contrast did not only modulate the N170 component in the Control group, but also affected the latency of the earlier P1 component in the upper fixation condition, with a delayed P1 in response to faces with contrast-negative eyes (as was also observed by Fisher et al., 2015). This P1 latency modulation appeared to be smaller or absent for the DP group (Figure 2, top panels). To confirm these observations, P1 peak latencies in the upper fixation condition were analysed with the factors eye contrast, face

contrast, hemisphere, and group. There was main effect of eye contrast, $F(1,20)=6.67$, $p<.02$, $\eta_p^2=.25$, and critically, an interaction between eye contrast and group, $F(1,20)=4.85$, $p<.04$, $\eta_p^2=.20$, as well as an interaction between eye contrast, group, and hemisphere, $F(1,20)=8.39$, $p<.01$, $\eta_p^2=.30$. To explore these interactions, follow-up analyses were conducted separately for DPs and control participants. In the Control group, the P1 was reliably delayed in response to face images with negative as compared to positive eyes over the right hemisphere (119 ms versus 111 ms; $F(1,10)=15.90$, $\eta_p^2=.61$), while no such P1 latency modulation was present in the DP group. There was no reliable effect of eye contrast on P1 latency over the left hemisphere in either group, both $F<1$. Face contrast did not affect P1 latencies in the upper fixation condition, $F<1$. In the lower fixation condition, no significant effects or interactions involving the factors eye contrast, face contrast, and group were present for P1 latencies, all $F<4.2$.

4. Discussion

The goal of the current study was to find out whether face perception in DP is less sensitive to the prototypical contrast relationships of face images than in control participants, and whether this specifically affects the processing of contrast polarity signals from the eye region. To test this hypothesis, we measured N170 components to contrast-normal and fully contrast-inverted faces, as well as to positive-eyes and negative-eyes chimeras, in a group of 11 participants with DP and 11 age-matched control participants. N170 components were obtained separately for trials where the eye region or the lower part of a face was fixated. The pattern of N170 results observed for the Control group confirms the finding of our previous study (Fisher et al., 2015) that the contrast polarity of the eye region is particularly important during the perceptual encoding of faces. Inverting the contrast of the eye region resulted in an enhancement and delay of N170 components. These effects were independent of the contrast polarity of the

rest of the face and were present both when fixation was close to the eye region and when the lower part of the face was fixated. Inverting the contrast polarity of face parts outside of the eye region affected N170 amplitudes only in the lower fixation condition. This pattern of contrast-related N170 modulations in the Control group shows that contrast signals from the eye region play a special role during the structural encoding of faces. Inverting the contrast of face images generally impairs the processing of information that can be extracted from three-dimensional shape-from-shading cues (Johnston et al., 1992; Lui, Collins, & Chaudhuri, 2000) and from the surface reflectance properties of face texture and pigmentation (Russell, Sinha, Biedermann, & Nederhouser, 2006; Vuong, Peissig, Harrison, & Tarr, 2005). Because the eye region contains several important contrast-related signals (e.g. the boundaries between the sclera, iris and pupil of the eye, and contrast differences between the eyes and surrounding regions including eyebrows), inverting the contrast polarity of this region is particularly detrimental for face recognition, and restoring this region to normal contrast eyes in an otherwise contrast-inverted face leads to dramatic improvements in recognition performance (Gilad et al., 2009; Gandhi et al., 2012; Sormaz et al., 2013).

The critical new finding of the present study was that in the DP group, early face-sensitive stages of visual processing, as reflected by N170 components, were generally much less sensitive to changes in the contrast polarity of the eye region relative to control participants. Both when fixation was focused near the eye region and when it was directed to the lower part of a face, N170 amplitude enhancements elicited in response to face images with contrast-inverted eyes were reliably reduced in the DP group relative to the Control group. In the upper fixation condition, the effect of eye contrast on N170 amplitude was not significant across all DPs. In the lower fixation condition, this effect was reliable at the group level but significantly smaller than the corresponding N170 amplitude modulation in the Control group. Additional analyses at the level of individual participants revealed that DPs generally showed reduced effects of eye contrast on N170 amplitudes in both fixation conditions (see Figure 4). In the upper

fixation condition, this effect was reliably present for ten out of eleven control participants but only for four DPs. In the lower fixation condition, seven DPs showed a significant sensitivity of the N170 to eye contrast, but these effects were smaller than the effects observed for control participants. The observation that a higher proportion of DPs showed N170 modulations to contrast inversion of the eye region while fixating on the lower part of the face than when fixation was located near the eye region is consistent with experience-based accounts of visual face templates. If there is a general tendency for DPs not to fixate on the eye region but on the lower part of faces (e.g. Bobak, Parris, Gregory, Bennetts, & Bate, 2016; Schwarzer et al., 2007), this might result in the development of an increased perceptual sensitivity to contrast signals from the upper visual field region that contains the eyes. In this context it is worth noting that typical N170 amplitude enhancements to deviations in contrast polarity from canonical face templates progressively emerge throughout childhood and into early adulthood (e.g., Itier & Taylor, 2004a). The current findings show that in addition to impairments in the holistic processing of the global shape of upright faces that were revealed in previous DP studies (e.g., Behrmann et al., 2005; Avidan et al., 2011; Towler et al., 2012, 2016), perceptual face processing in DP is also characterised by an atypical processing of contrast relationships that are present in natural face images. This suggests that DP may be linked to an atypical experience-dependent developmental trajectory of spatially selective contrast-sensitive biases in the posterior occipito-temporal face processing network (for a more general discussion of the role of developmental factors in DP, see Towler & Eimer, 2012).

The current results also showed that DPs do not appear to have a more general problem in extracting other types of contrast-related signals from face images. Contrast-inverting parts of the face outside the eye region resulted in very similar N170 modulations in both groups. Larger N170 components to images where the rest of the face was contrast-inverted versus contrast-normal were present in both groups, but only in the lower fixation condition. When fixation was near the eyes, the contrast of the rest of the face did not affect N170 amplitudes in either group

(analogous to our previous results for a group of younger participants with unimpaired face processing; Fisher et al., 2015). The absence of any interactions between face contrast and group confirmed that the effects of contrast inversion of areas outside the eye region were essentially identical for DPs and control participants, suggesting that the local contrast relationships within these areas were being encoded similarly in both groups. The fact that DPs showed normal sensitivity to the contrast polarity of the nose and mouth regions of face images suggests that perceptual encoding mechanisms in DP may be more finely tuned to the typical contrast relationships in the lower face regions than to the contrast of the eye region. This finding is consistent with a previous study from our lab which showed that DPs have normal face-sensitive N170 components to Mooney faces as compared to Mooney houses (Towler et al., 2014). Mooney faces are two-tone black and white images, where the cues used to detect the presence of a face are provided by the typical contrast relationships present in face images. If DPs are better able to extract contrast signals from face parts outside of the eye region, they may also be able to use these signals more efficiently than signals from the eyes as a source of identity-related information. Further evidence that DPs may have normal processing of the mouth region comes from a part-to-whole matching task (DeGutis et al., 2012), where DPs showed a whole-face advantage only when matching the mouth region, but not when matching the eyes, whereas control participants showed whole-face advantages for the eyes and the mouth.

Additional evidence that a reduced sensitivity to contrast signals from the eye region is linked to impairments in the perceptual processing of individual faces was provided by the correlation between N170 amplitude modulations elicited by contrast-inverted eyes and performance on the CFPT in the DP group. Individuals with DP who performed better in the CFPT also showed more typical N170 amplitude enhancements in response to face images where the eye region was contrast-inverted, while poor individual CFPT scores were associated with smaller N170 amplitude differences between contrast-normal and contrast-inverted eyes (see Figure 5). These results suggest that specific impairments in the processing of contrast

information from the eyes can produce more general deficits in tasks that require identity-related perceptual discriminations between different faces. The findings from this correlation analysis also highlight the importance of exploring data from DP experiments at the level of individual participants. Although a deficit in everyday face recognition ability is common to all DPs, this deficit can be linked to underlying perceptual and memory impairments which may vary considerably across individuals (as illustrated by the test scores for individual DPs in Table 1). To achieve a better understanding of the causes of DP, it is therefore important to explore this individual variability in neural and cognitive measures of different aspects of face processing. In the present study, group-level analyses suggested that the perceptual processing of eye contrast is generally atypical in DP, whereas analyses at the individual level showed that for a minority of DPs, the effects of inverted eye contrast on N170 amplitudes were well within the normal range (see Figure 4). Furthermore, the significant correlation between CFPT performance and N170 modulations in response to contrast inversion of the eye region in the DP group (Figure 5) suggests that face perception deficits in DP may be linked to a quantitative reduction in the sensitivity to contrast signals from the eye region rather than to qualitative differences in processing face contrast information between DPs and Controls.

Overall, the differential pattern of N170 amplitude modulations to contrast-inverting the eye region or of the rest of the face between the DP and Control groups suggests that the structural encoding of faces in DP is less well tuned to contrast-related signals specifically when these signals originate from the eye region. The strong reduction of N170 amplitude enhancements for faces with contrast-inverted eyes in participants with DP relative to control participants is strikingly similar to previous observations that N170 amplitudes in DPs are less sensitive to deviations from the prototypical upright face template produced by stimulus inversion (Towler et al., 2012) and scrambling the spatial configuration of face parts (Towler et al., 2016). These differences have been interpreted as evidence that perceptual face processing in DP is less precisely tuned to the canonical orientation and spatial arrangement of upright faces,

which may reflect the fact that prototypical upright face templates are less well developed in DP. The current finding that the effects of contrast polarity signals from the eye region on N170 amplitudes are also strongly attenuated in individuals with DP suggests that this information is also an important part of such canonical face templates. If these contrast signals are less perceptually salient in DP, this can result in a selective impairment in the extraction of identity-related signals from the eye region, which may contribute to the face recognition deficits experienced by individuals with DP. A reduced sensitivity to the contrast information provided by the eye region may result in an inability to utilize subtle texture and pigmentation signals which are important for the recognition of facial identity. In observers with unimpaired face recognition, contrast inversion selectively affects the ability to extract identity information from faces, but does not impair inanimate object recognition (Nederhouser, Yue, Mangini, & Biedermann, 2007), and has little effect on emotional expression recognition (Harris, Andrews, & Young, 2014). A similar pattern is observed for the cognitive and perceptual deficits in DP, which are generally specific to the processing of facial identity, with object recognition or the recognition of emotional facial expression typically unimpaired or much less affected (see Duchaine, 2011; Towler & Eimer, 2012; Susilo & Duchaine, 2013, for reviews). This suggests that selective impairments in the detection and analysis of contrast signals from faces may be an important visual-perceptual factor in DP (see also Russell, Chatterjee, & Nakayama, 2012, for evidence that DPs show deficits in the use of pigmentation information from faces during face matching tasks).

In addition to the impact of eye contrast on N170 amplitudes, we also observed another even earlier difference in the effects of eye contrast between the DP and Control groups. For control participants, the peak latency of the P1 component was delayed in response to face images with contrast-inverted eyes, over the right hemisphere in the upper fixation condition only. A similar P1 delay was already observed in our previous study (Fisher et al., 2015) for negative versus positive eyes when fixation was near the eye region (see also Itier & Taylor, 2002,

for related observations). P1 components are generally thought to reflect relatively low-level visual processing stages in extrastriate cortex. However, the fact that this P1 latency delay appears to be confined to the right hemisphere, and to be specifically triggered by contrast inversion of the eye region but not by contrast-inverting the lower part of the face, suggest that it may reflect a rapid visual-perceptual detection mechanism that is selectively tuned to contrast signals from the eye region. If such signals are extracted within the first 100 ms after stimulus onset, they may then be relayed to subsequent higher-level structural encoding processes that are reflected by the N170 component. The fact that there was no such delay of the P1 to contrast-inverted eyes in the DP group could suggest that early perceptual mechanisms are less sensitive to eye contrast signals in individuals with DP, which may then result in impairments during the construction of structural representations of faces that are suitable for their recognition.

Finally, it should be noted that the present study found a dissociation between N170 amplitude and N170 latency measures. As discussed above, manipulating the contrast polarity of the eye region produced much smaller N170 amplitude enhancements in the DP group relative to the control group. However, there was no comparable difference between the two groups for N170 peak latencies. In control participants, N170 components were significantly delayed by contrast inversion of the eye region, and there was a smaller but still reliable N170 delay when the rest of the face was contrast-inverted, in line with previous observations that contrast inversion affects N170 latencies (e.g., Itier & Taylor, 2002). Importantly, there were no differences in these inversion-induced N170 delays between DPs and control participants. Very similar dissociations between atypical N170 amplitudes accompanied by typical N170 latencies have already been observed in previous studies with DPs where N170 components to upright versus inverted faces or to intact versus scrambled faces were compared (Towler et al., 2012; Towler et al., 2016), suggesting that N170 amplitude and latency measures are linked to different aspects of perceptual face processing. N170 latency delays to faces with non-canonical properties are assumed to reflect a delay in the activation of face-selective neural populations in response to

face images that deviate from the prototypical upright face template (e.g., Rossion et al., 1999). The fact that DPs and control participants show similar delays of N170 components to inverted, scrambled, or contrast-inverted faces suggests that there are no systematic differences between these two groups in timing of face-selective neural responses. In contrast, N170 amplitude increases observed in response to non-canonical faces for participants with unimpaired face processing abilities have been interpreted as the result of an additional recruitment of neurons that are usually activated by non-face objects (e.g., Rossion et al., 2000; Rosburg et al., 2010; Sadeh & Yovel, 2010). According to this interpretation, such N170 amplitude enhancements reflect a general reduction in the categorical tuning of neural responses to atypical face images, which are no longer exclusively face-selective but also include the activity of neurons that that are involved in the perception of other non-face object categories. In this context, the reduction or absence of differential N170 amplitude modulations to upside-down, scrambled, or contrast-inverted faces or face parts in DP suggests that canonical and non-canonical faces are not processed in a qualitatively different fashion. If the selective recruitment of face-selective neural populations during early perceptual stages of face processing depends on a match between the features of a currently seen face image and a stored template of a prototypical upright face, and if the precision or availability of such templates is selectively impaired in DP, even standard upright faces may recruit a mixture of face-selective and object-selective neuronal populations, resulting in similar N170 amplitudes to canonical and non-canonical face images.

In conclusion, the current study has shown that the perceptual processing of faces in DP shows a reduced sensitivity to deviations of the typical contrast relationships in the eye region. A deficit in the ability to detect and analyse such contrast signals is likely to impair the extraction of texture and pigmentation information from face images that is important for the recognition of facial identity. The profound face recognition problems experienced by individuals with DP may thus at least in part originate at early sensory-perceptual stages of face processing within the first 200 ms after a face is first encountered.

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Figure Legends

Figure 1. (a) Example of the four different face contrast types tested (contrast-normal faces, positive-eye chimeras, negative-eye chimeras, contrast-inverted faces). 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 one-back matching task. Each face was presented for 200 ms, and there was an interval of approximately 1450 ms between each successive face presentation. 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.

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. ERPs are shown for the four face contrast types, separately for the DP group (top panels) and the Control group (bottom panels). Ticks on the time axes represent 50 ms intervals.

Figure 3. 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 lower fixation condition. ERPs are shown for the four face contrast types, separately for the DP group (top panels) and the Control group (bottom panels). Ticks on the time axes represent 50 ms intervals.

Figure 4. Effect of eye contrast on N170 amplitudes for each individual participant, calculated as the difference between face images with negative and positive eyes (collapsed across face contrast and electrodes P9/P10), for the upper (left panel) and lower fixation (right panel) conditions, for individual DPs (black bars) and Controls (grey bars). The effects for individual DP participants are labelled with their initials, corresponding to Table 1.

Figure 5. Correlation between the performance of 10 individual participants with DP in the Cambridge Face Perception Test (CFPT) with upright faces and the effect of eye contrast on N170 amplitudes for these participants. Raw individual error scores in the CFPT and N170 mean amplitude differences between face images with negative and positive eyes (collapsed across the upper and lower fixation conditions and electrodes P9 and P10) are shown on the x- and y-axis, respectively.

Table 1

Z-values for 11 DP participants in the Famous Faces Test (FFT), Cambridge Face Memory Test (CFMT), the Cambridge Face Perception Test (CFPT) for upright and inverted faces, and the Old-New Test (ONT).

Participant	Age	Gender	FFT	CFMT	CFPT upright	CFPT inverted	ONT
CS	35	F	-1.74	-1.88	-2.15	0.36	-3.03
CM	31	M	-7.72	-4.29	-3.1	-2.89	-14.34
NW	25	F	-7.34	-2.01	0.24	-0.36	-6.68
KS	31	F	-8.49	-2.9	-0.92	-1.05	-9.03
JG	45	M	-8.88	-2.77	-2.56	-0.63	-8.16
DD	45	M	-5.21	-2.77	0.17	-0.77	-3.36
SM	53	F	-8.49	-1.25	-2.01	-1.05	-2.72
MW	59	M	-3.67	-2.14	-1.6	-0.2	-6.49
GW	21	M	-8.49	-2.52	-1.33	-1.05	-6.41
PR	29	M	-7.53	-3.27	-0.65	-0.91	1.04
MC	27	F	-4.83	-3.02	-1.19	1.07	-4.9

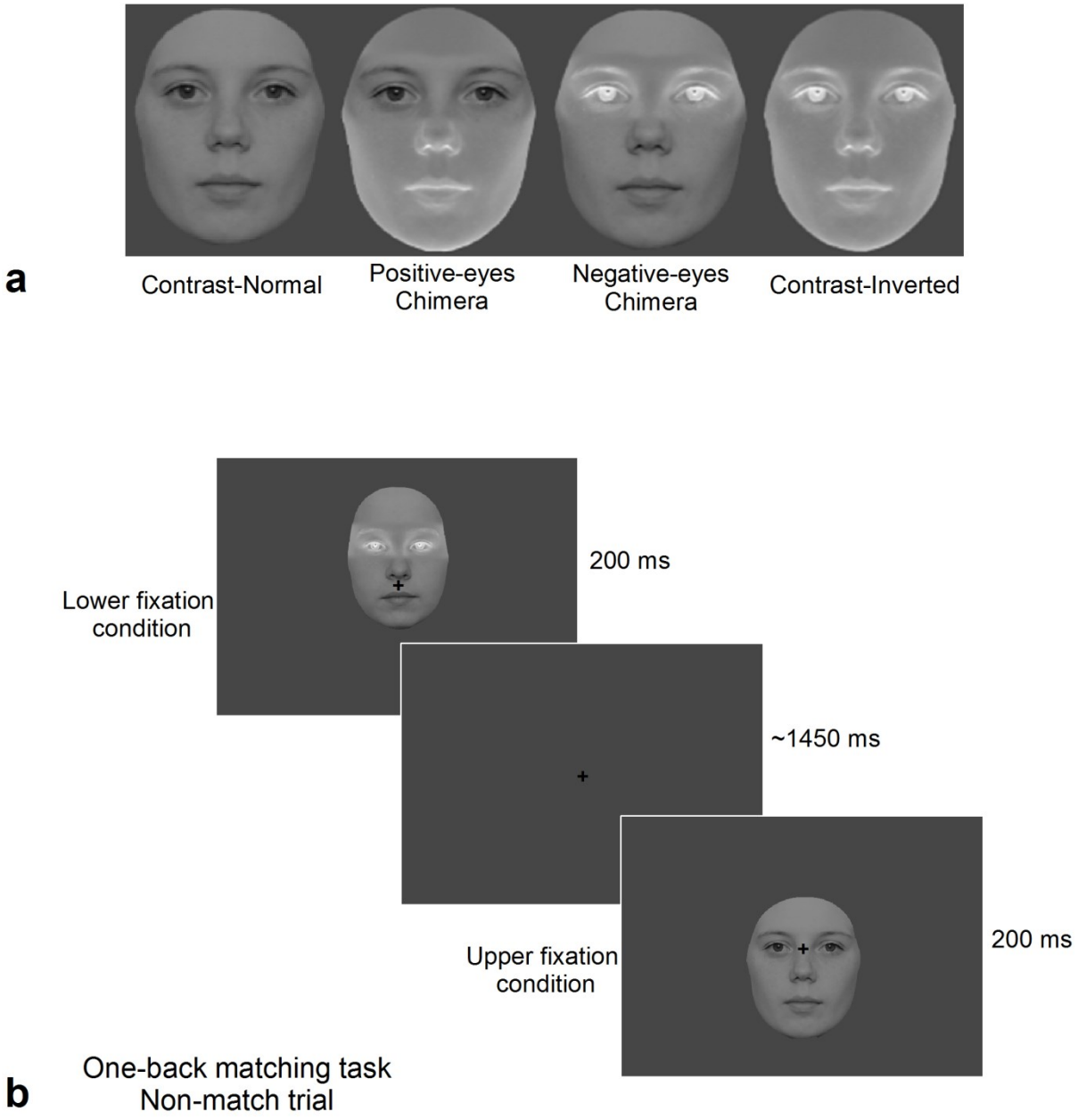
a
Contrast-Normal
Positive-eyes Chimera
Negative-eyes Chimera
Contrast-Inverted
Lower fixation condition
200 ms
~1450 ms
Upper fixation condition
200 ms
b
One-back matching task
Non-match trial

Figure 1

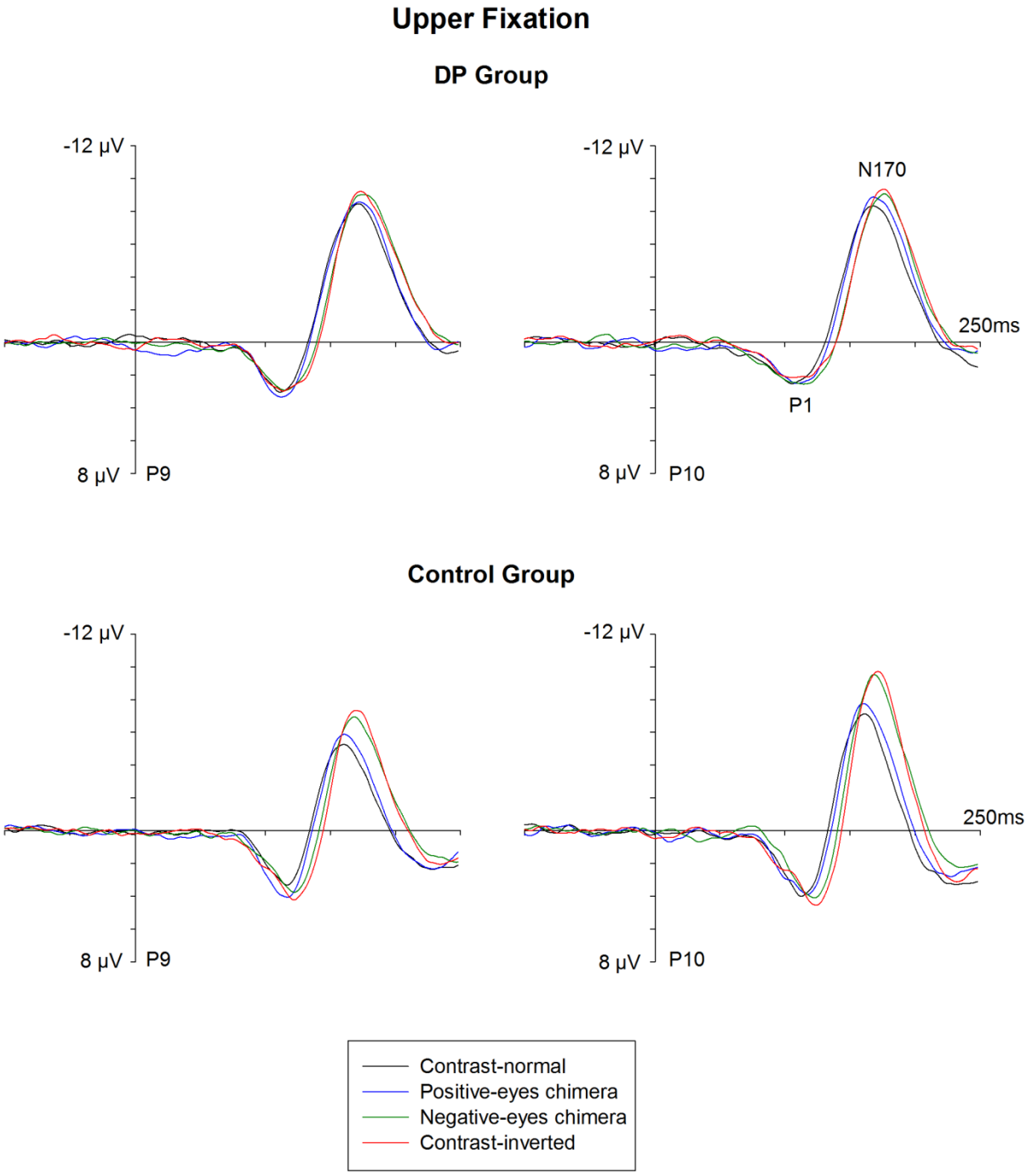
Upper Fixation
DP Group
-12 µV
8 µV
P9
-12 µV
N170
250ms
P1
8 µV
P10
Control Group
-12 µV
8 µV
P9
-12 µV
250ms
8 µV
P10
Contrast-normal
Positive-eyes chimera
Negative-eyes chimera
Contrast-inverted

Figure 2

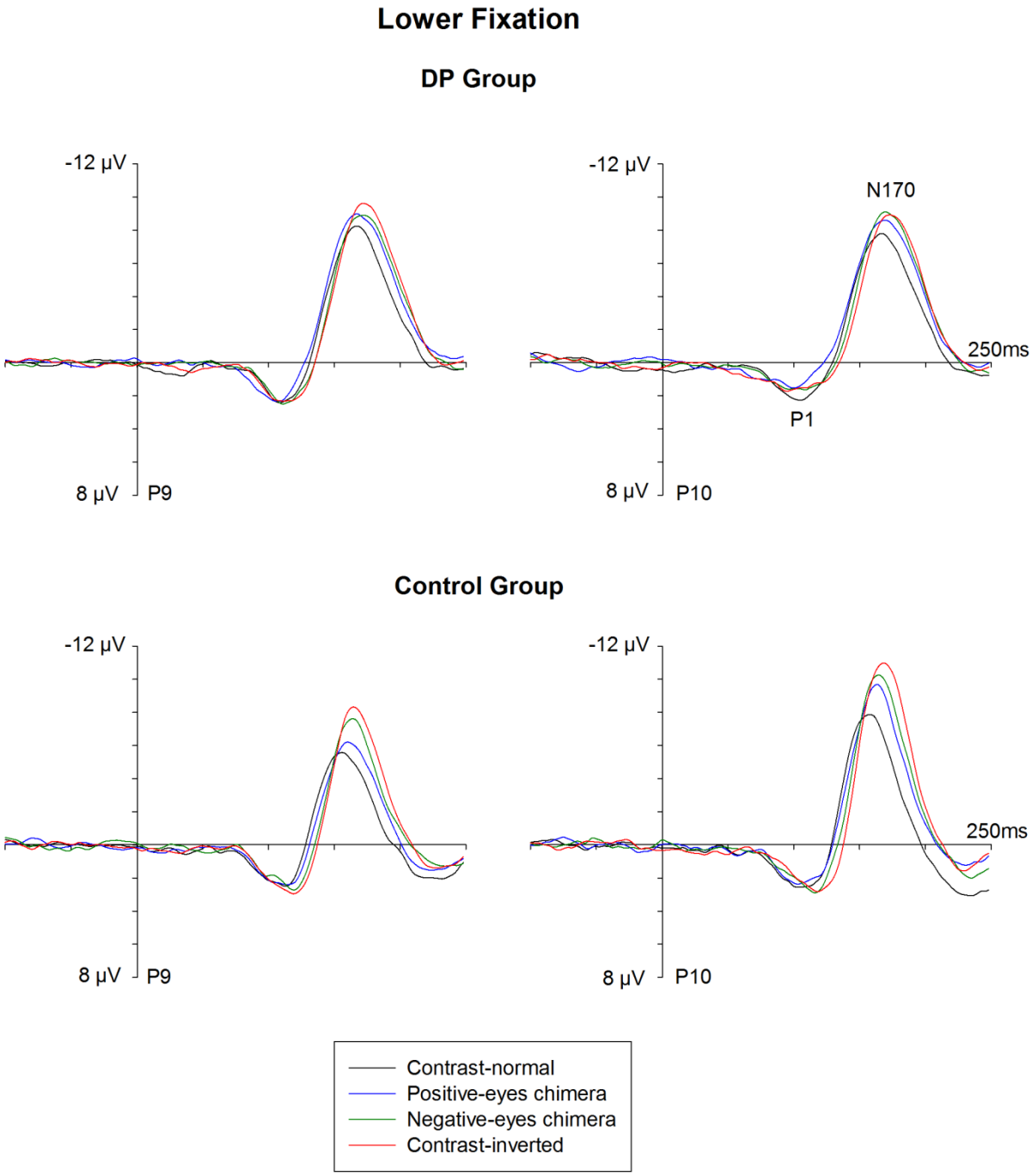
Lower Fixation
DP Group
-12 µV
8 µV
P9
-12 µV
N170
250ms
P1
8 µV
P10
Control Group
-12 µV
8 µV
P9
-12 µV
250ms
8 µV
P10
Contrast-normal
Positive-eyes chimera
Negative-eyes chimera
Contrast-inverted

Figure 3

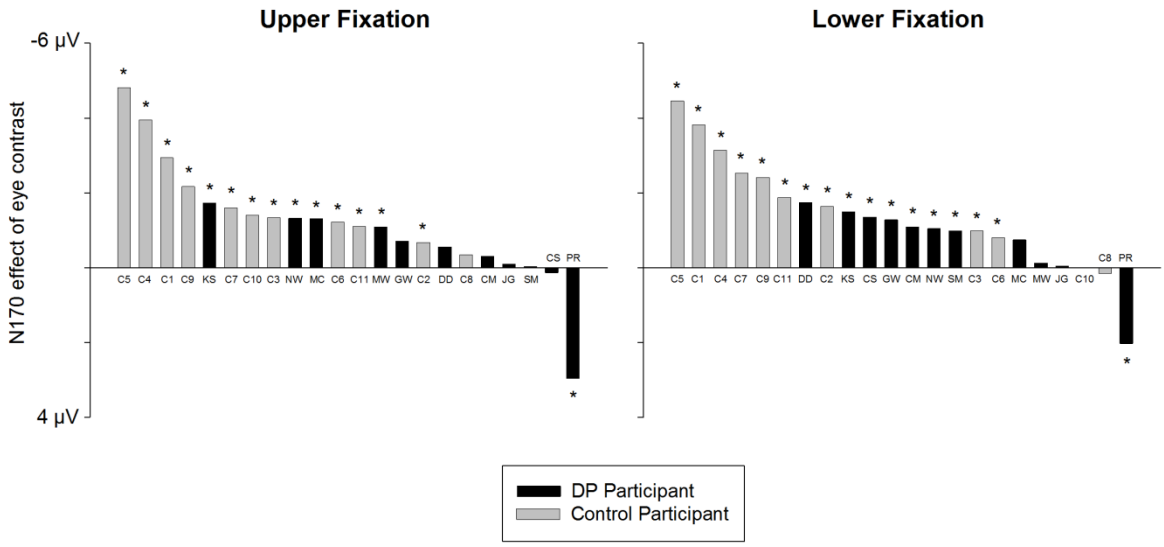
Upper Fixation
Lower Fixation
-6 µV
4 µV
N170 effect of eye contrast
C5 C4 C1 C9 KS C7 C10 C3 NW MC C6 C11 MW GW C2 DD C8 CM JG SM CS PR
C5 C1 C4 C7 C9 C11 DD C2 KS CS GW CM NW SM C3 C6 MC MW JG C10 C8 PR
DP Participant
Control Participant

Figure 4

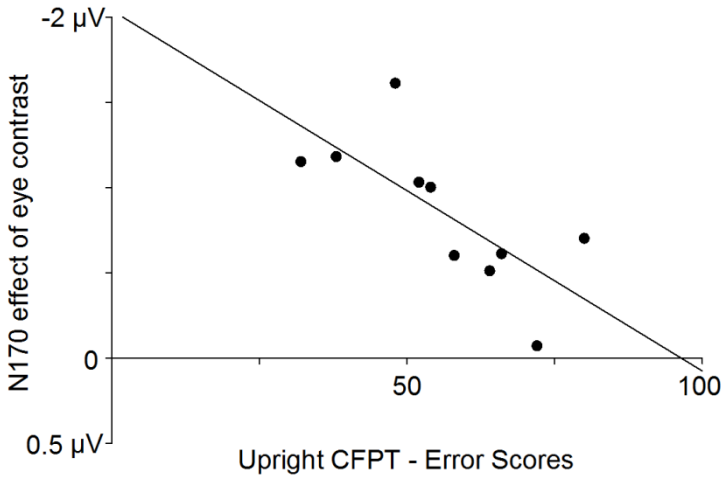
-2 µV
N170 effect of eye contrast
0
0.5 µV
50
100
Upright CFPT - Error Scores

Figure 5