The face-sensitive N170 component in developmental prosopagnosia

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ABSTRACT

Individuals with developmental prosopagnosia (DP) show severe face recognition deficits in the absence of any history of neurological damage. To examine the time-course of face processing in DP, we measured the face-sensitive N170 component of the event-related brain potential (ERP) in a group of 16 participants with DP and 16 age-matched control participants. Reliable enhancements of N170 amplitudes in response to upright faces relative to houses were found for the DP group. This effect was equivalent in size to the effect observed for controls, demonstrating normal face-sensitivity of the N170 component in DP. Face inversion enhanced N170 amplitudes in the control group, but not for DPs, suggesting that many DPs do not differentiate between upright and inverted faces in the typical manner. These N170 face inversion effects were present for younger but not older controls, while they were absent for both younger and older DPs. Results suggest that the early face-sensitivity of visual processing is preserved in most individuals with DP, but that the face processing system in many DPs is not selectively tuned to the canonical upright orientation of faces.

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1. Introduction

People with prosopagnosia are unable to recognize and identify the faces of familiar individuals, despite normal low-level vision and intellect (Bodamer, 1947). Until recently, prosopagnosia was thought to result solely from acquired lesions to face-sensitive regions in occipito-temporal visual cortex, such as the middle and posterior fusiform gyri (e.g., Barton, 2008). However, the existence of a different form of prosopagnosia that occurs without history of neurological damage has now been established (e.g., Behrmann & Avidan, 2005; Duchaine & Nakayama, 2006b). In contrast to acquired prosopagnosia (AP), individuals with developmental prosopagnosia (DP) typically show severe impairments of face recognition that emerge in early childhood and are assumed to result from a failure to develop normally functioning face processing mechanisms (see Duchaine (2011), for a review).

The perception and recognition of faces is a complex achievement that is based on a number of functionally and anatomically distinct processing stages (Bruce & Young, 1986; Haxby & Gobbini, 2011). Problems at any of these stages could be responsible for the face recognition deficits in individuals with AP or DP. The question which face processing mechanisms are impaired in prosopagnosia has not yet been answered conclusively. In AP, two general sources of face recognition deficits have been distinguished—selective

impairments of early perceptual stages of face processing (apperceptive prosopagnosia; De Renzi, Faglioni, Grossi, & Nichelli, 1991), and face-selective deficits at later post-perceptual stages, which could include impairments of long-term face memory, or disconnections of face perception and face memory (associative prosopagnosia; De Renzi et al., 1991). An analogous distinction might also apply to individuals with DP.

To identify which stages in the face processing hierarchy are impaired in prosopagnosia, event-related brain potential (ERP) measures are particularly useful tools. ERPs provide online measures of neural activity and thus are able to track neural correlates of face perception and face recognition on a millisecond-by-millisecond basis. The earliest ERP markers of face recognition have been found at post-stimulus latencies of 200 ms and beyond (e.g., Schweinberger, Pfütze, and Sommer (1995), Begleiter, Porjesz, and Wang (1995), Bentin and Deouell (2000), Eimer (2000a), Schweinberger, Pickering, Jentzsch, Burton, and Kaufmann (2002)). For example, an occipito-temporal N250 component is triggered when famous faces are explicitly recognized, but not when these faces merely seem familiar (Gosling & Eimer, 2011). The N250 has been linked to an early stage of face recognition where incoming visual–perceptual information about a seen face is matched with stored representations of familiar faces in visual memory. We have recently employed this N250 component to trace the locus of face recognition deficits in DP (Eimer, Gosling, & Duchaine, 2012). Six of the twelve DPs tested showed an N250 component in response to famous faces on trials where they did not explicitly recognize these faces. This covert recognition effect

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indicates that visual memory for famous faces was intact in these DPs, and suggests that their face recognition deficits may be the result of disconnections between a visual store of familiar faces and semantic memory. Interestingly, the other six DPs tested in this study did not show such covert recognition effects for the N250 component, which indicates that the locus of face processing deficits differs across individuals with DP.

While the N250 component is linked to visual face memory and face recognition, the well-known face-sensitive N170 component reflects an earlier stage of face processing. The N170 is an enlarged negativity in response to faces as compared to non-face stimuli that is elicited between 150 and 200 ms after stimulus onset over lateral occipito-temporal areas, (e.g., Bentin, Allison, Puce, Perez, and McCarthy (1996), Eimer, Kiss, and Nicholas (2010), Eimer (2011), Rossion and Jacques (2011)). N170 components are typically accompanied by an enhanced positivity to faces at vertex electrode Cz (Bötzel & Grüsser, 1989; Jeffreys, 1989). Because the vertex positive potential (VPP) and the N170 component are usually closely associated, they are assumed to reflect the same underlying face-sensitive brain processes (e.g., Joyce and Rossion (2005)). Importantly, the N170 component is not affected by emotional facial expression (Eimer & Holmes, 2002, 2007) or by face familiarity (e.g., Bentin and Deouell (2000), Eimer (2000a)). This insensitivity to familiarity and emotional expression suggests that the N170 is linked to the perceptual structural encoding of facial features and configurations that occurs independently and in parallel with the analysis of emotional expression, and precedes the recognition and identification of individual faces (Bruce & Young, 1986).

Because the N170 component is a well-studied electrophysiological marker of face perception, finding out whether this component is preserved or abolished in AP or DP is important for our understanding of the nature of prosopagnosia. Given the firm links between the N170 and the perceptual structural encoding of faces, its absence in individuals with prosopagnosia would point to an early "apperceptive" locus of their face processing deficits. In contrast, if the N170 component was uniformly preserved in prosopagnosia, this would provide strong evidence of a post-perceptual "associative" locus of face recognition impairments.

The existing evidence with respect to the properties of the N170 component in prosopagnosia is inconclusive. Only very few studies have measured ERP markers of face processing in brain-damaged patients with AP. One study found no differential ERP modulations to faces versus houses in the N170 time range for patient PHD who has diffuse cortical damage including a focal left temporo-parietal lesion (Eimer & McCarthy, 1999), suggesting that AP can be due to a disruption of early face-selective perceptual processing stages. Longer-latency ERP markers of identity-sensitive face processing were also absent for the same patient (Eimer, 2000a). This was expected, as severe impairments in structural encoding should have knock-on effects on later face recognition processes. In contrast, another single-case study found a preserved face-selective N170 in prosopagnosic patient FD who had extensive lesions to ventral occipito-temporal cortex (Bobes et al., 2004). More recently, Dalrymple et al. (2011) recorded ERPs from five patients with AP, and found that the presence of a face-sensitive N170 depended upon the integrity of at least two of the three core face-sensitive regions (fusiform and occipital face areas, posterior superior temporal sulcus). Alonso-Prieto, Caharel, Henson, and Rossion (2011) reported a face-selective N170 component over the right but not left hemisphere for prosopagnosic patient PS, whose lesions include the left fusiform and right occipital face areas. In summary, these studies demonstrate that the face-sensitive N170 component is often absent in patients with AP, and that the presence of this component appears to be linked to the structural and functional integrity of posterior face processing areas, in particular the middle fusiform and inferior occipital face areas.

The question whether the face-sensitive N170 component is present or absent in individuals with developmental prosopagnosia has been investigated in several studies, but no clear pattern has emerged so far. There is some evidence that the N170 can be strongly attenuated or entirely abolished in DP. Bentin, Deouell, and Soroker (1999) tested one participant with DP and found that N170 amplitude differences in response to faces versus non-face objects were reduced relative to 12 control participants. Along similar lines, Kress and Daum (2003) found no statistically reliable N170 amplitude differences between faces and houses for two participants with DP, whereas such differences were consistently present in eight control subjects. Bentin, De Gutis, D'Esposito, and Robertson (2007) reported the absence of a differential N170 response to faces as compared to non-face control objects (watches) in one DP, whereas this effect was reliably present in a group of 24 control subjects. However, results from other studies demonstrate that the N170 is not always abolished in DP. Harris, Duchaine, and Nakayama (2005) measured MEPs or ERPs in response to faces and houses in a group of DPs. Of the five DPs tested with MEG, three showed a face-sensitive M170 component, while two did not. Two DPs were tested with EEG, and one of them showed a face-sensitive N170. Righart and De Gelder (2007) observed enhanced N170 amplitudes for faces relative to non-face control objects (shoes) for two DPs, whereas no such effect was present for two other DPs. Minnebusch, Suchan, Ramon, and Daum (2007) tested four DPs and found reliable N170 amplitude differences between faces and houses for three of them. In a recent MEG study, Rivolta, Palermo, Schmalzl, and Williams (2012) reported enhanced M170 components to images of faces versus places for a group of six DPs, and this enhancement was similar in magnitude to the effect observed for a group of 11 control participants. Finally, in an experiment designed to study the impact of perceptual training on face recognition (De Gutis, Bentin, Robertson, & D'Esposito, 2007), an individual with DP who had no differential N170 response to faces versus watches prior to training showed an enhanced N170 to faces after training. Overall, the main conclusion to be drawn from existing studies of the N170 component in DP is that results are highly variable across individuals. One main aim of this study was to investigate the presence or absence of the N170 across a much larger sample of sixteen participants with DP.

In addition to its generic face-sensitivity, the N170 component is also highly sensitive to face inversion. Numerous behavioural studies have indicated that upright faces are processed in a more configural or holistic manner than inverted faces or objects (e.g., Tanaka and Sengco (1997), Young, Hellawell, and Hay (1987), Van Belle, de Graef, Verfaillie, Rossion, and Lefèvre (2010)), and that stimulus inversion has much stronger effects on the recognition of faces than on object recognition (Yin, 1969). These observations suggest that inversion-induced impairments of face recognition may be linked to disruptions of configural face processing, which may be tailored for specifically upright faces. In line with this view, a recent study that employed single-unit recording in the macaque middle face patch provided strong evidence that faces are represented by an upright template, regardless of the orientation of an observed face (Freiwald, Tsao, & Livingstone, 2009).

Many ERP experiments have demonstrated that the N170 in response to inverted faces is enhanced and delayed relative to the N170 that is triggered by upright faces (e.g., Bentin et al., 1996; Eimer, 2000b; Rossion et al., 2000; Itier, Alain, Sedore, & McIntosh, 2007). Two types of explanation have been proposed for the presence of inversion-induced enhancements of N170 amplitudes (Sadeh & Yovel, 2010). Quantitative accounts assume

that upright and inverted faces activate the same face-specific mechanisms, and that the enhancement of the N170 component to inverted faces reflects the increased effort required to process these faces (Rossion et al., 1999; Marzi & Viggiano, 2007), possibly due to inversion-induced disruptions of configural processing (e.g., Sagiv & Bentin, 2001; see also Eimer, Gosling, Nicholas, & Kiss, 2011, for further evidence for links between the N170 and configural face processing from rapid neural adaptation). Alternative qualitative accounts explain inversion-induced N170 enhancements by proposing that inverted faces activate additional neural populations (such as neurons sensitive to non-face objects) which are not activated by upright faces (e.g., Rossion et al., 2000). Consistent with this possibility, object-selective brain areas respond more strongly to inverted faces than upright faces (Haxby et al., 1999; Yovel & Kanwisher, 2005), and TMS to the object-sensitive lateral occipital area disrupts the processing of inverted, but not upright faces (Pitcher, Duchaine, Walsh, Yovel, and Kanwisher 2011). Along similar lines, it has also been suggested that inverted but not upright faces may selectively activate eye-specific neurons (Itier et al., 2007). Quantitative and qualitative accounts of N170 face inversion effects are not mutually exclusive. For example, Rosburg et al. (2010) measured ERPs to upright and inverted faces both from the scalp and intracranially, and found inversion-induced activity modulations during the N170 time range in both face-selective and house-selective cortical areas, consistent with a hybrid account of N170 face inversion effects.

While reliable face inversion effects on N170 amplitudes have been repeatedly observed in studies with young adult participants, there is now evidence that this effect may not be found in older individuals. Gao et al. (2009) reported that inversion-induced N170 amplitude enhancements which were reliably observed for a group of young participants (aged 23–35 years) were absent for a group of older participants whose age ranged between 61 and 85 years. This dissociation suggests that there may be important changes in the operation of perceptual face processing stages in older individuals (see also Daniel & Bentin, 2012, for similar results). Given the prominence of N170 face inversion effects in current discussions about face perception and its neural basis, it is clearly important to find out whether such effects are also present in individuals with DP. If they are, this would indicate that DPs differentiate between upright and inverted faces in the typical manner during the structural encoding of faces. In contrast, atypical N170 face inversion effects would point to differences between DPs and control participants at early stages of face perception. To date, few studies have investigated N170 face inversion effects in DP, and results have been inconclusive. In an MEG study, Dobel, Putsche, Zwitserlood, and Junghöfer (2008) found normal effects of face inversion on M170 amplitude across a group of seven DPs. In contrast, De Gelder and Stekelenburg (2005) tested a single participant with DP and found no inversion-induced N170 amplitude enhancement. Righart and De Gelder (2007) tested four participants with DP and found that typical N170 face inversion effects were absent for three of them. The second main aim of the present study was to systematically evaluate the sensitivity of the N170 component to face inversion in DP, for a large group of sixteen participants.

In addition to demonstrating the presence or absence of a face-sensitive N170 component or of N170 face inversion effects at the group level, these ERP modulations may also be effective neural markers of prosopagnosia in individual DPs. Even though group fMRI studies have found weaker face-selectivity and smaller face-selective areas in DP (Furl, Garrido, Dolan, Driver, & Duchaine, 2011), individual DPs often fall within the normal range on these measures (Behrmann, Avidan, Marotta, & Kimchi, 2005; Furl et al., 2011; but see also Bentin et al. (2007), Von Kriegstein, Kleinschmidt, &

Giraud (2006)). For example, only three of 15 DPs tested in a recent fMRI study did not show face-selectivity in the fusiform gyrus (Furl et al., 2011). Because all or nearly all individuals with normal face processing exhibit a face-sensitive N170 and an N170 face inversion effect, a failure to exhibit either of these effects may be indicative of impaired early face processing in individual DPs. The observation that N170 face inversion effects appear to be age-dependent even in individuals without face recognition impairments (Gao et al., 2009) further underlines the importance of assessing ERP markers of face processing in DP not just at the group level, but also for each individual participant.

We measured N170 components to upright and inverted faces and to non-face stimuli for 16 individuals with DP. All of them reported severe and consistent difficulties in recognizing familiar faces since childhood. These reports were verified with standardized tests of face processing (see Table 1). Stimuli and procedures were identical to those used in a previous study (Eimer & Holmes, 2002). Photographic images from five categories (upright neutral faces, inverted neutral faces, upright fearful faces, inverted fearful faces, or upright houses) were sequentially presented at fixation. Participants had to detect and respond to the immediate repetition of an image that was shown on the preceding trial (one-back task). For the participants with intact face processing abilities tested previously (Eimer & Holmes, 2002), upright faces triggered enhanced N170 amplitudes relative to upright houses, in line with the face-sensitivity of this component. In addition, the N170 was enhanced and delayed for inverted as compared to upright faces, thus confirming the presence of typical N170 face inversion effects. Emotional expression had no effect on N170 amplitude or latency, in line with the assumption that the face-sensitive brain processes that give rise to this component are not involved in the analysis of emotional facial expression. To confirm these findings, and contrast them with the effects observed for the group of DPs, a new group of sixteen age-matched control participants with intact face processing capabilities was included in the present study.

Two main analyses were conducted to investigate the presence and the properties of the face-sensitive N170 component in individuals with DP. The first set of analyses compared ERPs to upright neutral faces and non-face control stimuli (upright

Table 1
Details of the 16 DPs who participated in this experiment and their performance on different behavioural tests of face processing. For the Famous Face Test (FFT), the percentage of correctly recognized faces is listed (recognition rate for unimpaired participants is above 90%; Garrido et al., 2008). For the Cambridge Face Memory Test (CMFT), the Cambridge Face Perception Test (CFPT) with upright and inverted faces (upr/inv), and for the Old–New Test (ONT), z-scores of each individual's performance are listed (see text for details).

Participant	Age	Sex	FFT	CFMT	CFPTupr	CFPTinv	ONT
			(%)	z	z	z	z
MC	41	M	24.6	−1.38	−1.54	−1.62	−2.46
EW	32	F	13.3	−2.64	.92	.2	−3.43
CM	29	M	20.7	−4.29	−3.1	−2.89	−14.34
NE	31	F	33.3	−2.77	−1.06	−1.62	−4.17
JA	46	F	43.6	−2.64	−.92	−.49	−3.35
AH	48	F	60.0	−1.76	−1.06	−.63	−2.04
AM	28	F	46.4	−2.64	−1.74	−.49	−2.88
SW	28	F	22.0	−2.64	−1.74	−1.05	−2.95
KS	29	F	15.1	−2.9	−.92	−1.05	−9.03
SC	22	F	44.7	−2.64	−.51	.08	−4.15
JL	67	F	40.0	−1.76	−2.29	−.49	−6.27
SN	54	F	52.5	−2.26	−2.15	.36	.42
MZ	48	F	53.6	−2.52	−1.33	.22	−6.47
CP	39	F	34.7	−2.64	−.92	1.21	−1.11
RL	49	M	19.6	−3.65	−1.88	−.77	−5.87
MP	49	M	36.8	−2.9	−1.33	.64	−4.42

houses), in order to test the generic face-sensitivity of the N170 in DP. At the group level, the question was whether upright faces would trigger reliably enhanced N170 amplitudes relative to houses across all 16 DPs tested, and whether any such effect would be similar in size or smaller than the effect observed for the group of 16 age-matched control participants. At the level of individual DPs, the presence or absence of a face-sensitive N170 component was assessed with a non-parametric bootstrap procedure (Di Nocera & Ferlazzo, 2000). In a second set of analyses, inversion-induced effects on N170 amplitudes and latencies were investigated, both at the group level and at the level of individual DPs. At the group level, the question was whether typical inversion-induced N170 modulations (enhanced and/or delayed N170 components for inverted relative to upright faces) would be observed across all DPs tested, and whether these face inversion effects would be equal or reliably different from the effects observed for participants with normal face processing abilities. Again, bootstrap procedures were used to establish the presence of face inversion effects on N170 amplitudes and latencies for individual DPs. To assess the possible impact of participants' age on the N170 and its sensitivity to face inversion in DPs and controls, additional analyses were conducted for sub-groups of younger and older participants.

2. Methods

2.1. Participants

Sixteen participants with DP (12 females) were tested. Their age ranged between 22 and 67 years (mean age: 40 years). All reported severe difficulties with face recognition since childhood. They were recruited after contacting us on our research website 〈http://www.faceblind.org〉. To assess and verify their reported face recognition problems, behavioural tests were conducted in two sessions on separate days, prior to the EEG recording session. Impairments in the recognition of famous faces were measured in the Famous Face Test (FFT) for images of 60 celebrities from entertainment, politics, or sports (see Duchaine & Nakayama (2005), for details). Table 1 shows recognition percentage for famous faces in the FFT, separately for each of the sixteen DPs tested. As expected, DPs generally performed poorly in this test, with an average face recognition rate of 33.5% (ranging between 13.3% and 60% for individual DPs). For participants with unimpaired face recognition abilities, the average recognition rate is 84.6% ($SD = 11.2$%) for the same set of famous faces (Garrido, Duchaine, & Nakayama, 2008). To rule out deficits in basic visual functioning as cause of their face recognition deficits, the DPs also completed the low-level visual–perceptual tests of the Birmingham Object Recognition Battery (Riddoch & Humphreys, 1993). Test performance was within the normal range for all DPs tested.

Table 1 shows z-scores of the performance of all 16 DPs in other behavioural face processing tests. In the Cambridge Face Memory Test (CFMT), faces of six target individuals shown in different views are memorized, and then have to be distinguished from two simultaneously presented distractor faces (see Duchaine and Nakayama (2006a), for a full description). In the Old–New Face Recognition test (ONT; Duchaine & Nakayama, 2005), ten target faces (young women photographed under similar conditions and from the same angle) are memorized. In the test phase, target faces and 30 new faces are presented in random order, and an old/new discrimination is required for each face. In the Cambridge Face Perception Test (CFPT; Duchaine, Yovel, & Nakayama, 2007), one target face in three-quarter view is shown above six frontal-view morphed test faces that contain a different proportion of the target face and have to be sorted according to their similarity to the target face. Faces are presented either upright or inverted (shown separately in Table 1). As can be seen from the z-scores in Table 1, all DPs were impaired in the CFMT, and all except one in the ONT. There was also some evidence for face perception deficits in the CFPT, and these appeared more pronounced for upright faces than for inverted faces.

Sixteen participants without DP (seven females) were also tested with EEG, using identical procedures to those used for the DP group. Each control participant was individually age-matched (within a range of ± 4 years) with a participant with DP. The age of control participants ranged between 22 and 65 years. The mean age of this control group (40 years) was identical to the mean age of the DP group. To assess the age-dependence of N170 effects, the DP group and the control group were each subdivided into a younger and an older sub-group, with eight participants in these sub-groups. Younger DPs were aged 22–39 years (mean age: 29.7 years), and younger controls were aged 22–37 years (mean age: 29.2 years). The age range of the eight older DPs was 41–67 years (mean age: 50.2 years), and the age range of the eight older controls was 38–65 years (mean age: 50.2 years).

2.2. Stimuli and procedure

Participants sat in a dimly lit sound attenuated cabin. Photographs of faces or houses were presented on a CRT monitor at a viewing distance of 100 cm, using E-Prime software (Psychology Software Tools, Pittsburgh, PA). Stimuli were identical to those employed in a previous study (Eimer & Holmes, 2002). They included faces of 10 different individuals and 10 different houses. Faces were either fearful or neutral, and were presented either upright or upside-down, resulting in a total of 40 different face images. Houses were always presented upright. All stimuli were presented at fixation, with eye gaze straight ahead, against a grey background (17.6 cd/m²). They subtended a visual angle of $5.5° \times 7.5°$, and their average luminance was 21.9 cd/m².

The experiment consisted of four experimental blocks with 115 trials per block. Participants performed a one-back task where they had to respond with a right-hand button press to the immediate repetition of an image that was presented on the preceding trial. Each block included 15 target trials where such immediate repetitions of an identical image occurred. In the remaining 100 trials per block, non-repeated upright or inverted neutral or fearful faces, or upright houses were presented in random order and with equal probability. Stimuli were presented for 300 ms, and were separated by an intertrial interval of 1000 ms.

2.3. EEG recording and data analysis

EEG was DC-recorded with a BrainAmps DC amplifier (upper cut-off frequency 40 Hz, 500 Hz sampling rate) and Ag-AgCl electrodes mounted on an elastic cap from 23 scalp sites (Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO8, and Oz, according to the extended international 10–20 system). Horizontal electrooculogram (HEOG) was recorded bipolarly from the outer canthi of both eyes. During online recording, EEG was referenced to an electrode placed on the left earlobe, and was re-referenced off-line to the average of the left and right earlobe. Impedances of all electrodes were kept below 5 kΩ. No off-line filters were applied. EEG was epoched off-line from 100 ms before to 300 ms after stimulus onset. Epochs with activity exceeding ± 30 μV in the HEOG channel (reflecting horizontal eye movements) or ± 60 μV at Fpz (indicating eye blinks or vertical eye movements) were excluded from analysis, as were epochs with voltages exceeding ± 80 μV at any other electrode.

Following artefact rejection, averages were computed for non-target trials (i.e., trials where no immediate stimulus repetition occurred and no manual response was recorded), separately for upright neutral faces, inverted neutral faces, upright fearful faces, inverted fearful faces, and upright houses. All ERPs were computed relative to a 100 ms pre-stimulus baseline. N170 mean amplitudes were computed at lateral posterior electrodes P7 and P8 for the 150–190 ms interval after stimulus onset. N170 latencies were quantified as the latency of the most negative peak voltage measured during the 130–190 ms post-stimulus interval.

To investigate the face-sensitivity of the N170 component in the DP group and compare it to the control group, N170 mean amplitudes in response to upright neutral faces and upright houses were compared. To measure and contrast N170 face inversion effects in both groups N170 mean amplitudes and peak latencies were compared for upright and inverted faces. Preliminary analyses demonstrated that N170 amplitudes and face inversion effects on N170 amplitude and latency were unaffected by the emotional expression of faces. This was the case for the DP group and for participants without DP, confirming previous observations (Eimer & Holmes, 2002). Therefore, analyses of N170 face inversion effects were based on ERPs to upright and inverted faces that were averaged across neutral and fearful faces. To identify differences in the face-sensitivity of the N170 and in inversion-induced modulations of N170 amplitudes or latencies between participants with and without DP, further analyses were conducted across DPs and control participants, with group as between-subject factor. In additional analyses of the impact of participants' age, the between-subject factor age (younger versus older) was also included.

We also assessed the presence of statistically reliable N170 effects at the level of individual DPs. For that purpose, a non-parametric bootstrap procedure (Efron & Tibshirani, 1993; Di Nocera & Ferlazzo, 2000) was employed. This method establishes the reliability of ERP amplitude or peak latency differences between two experimental conditions by resampling two sets of trials that are drawn randomly (with replacement) from the combined dataset, and then computing amplitude or latency differences between the two resulting ERPs for a pre-defined time window and electrode. This procedure is 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 observed ERP difference between conditions can be assessed for individual participants. If the probability of obtaining the observed difference by chance is below 5%, it can be accepted as statistically significant (see also Dalrymple et al. (2011), Eimer et al. (2012), Oruç et al. (2011)). This bootstrap method was used to test the reliability of N170 differences between faces and houses, and of inversion-induced N170 amplitude and latency modulations for individual participants.

3. Results

3.1. Behaviour

Participants with DP were less accurate than control participants in detecting immediate stimulus repetitions (78.7% versus 91.4%), and this difference was significant ($t(30)=2.77$; $p<.01$). There was also a trend for DPs to be slower than controls in correctly detecting image repetitions (625 ms for DPs, 568 ms for control participants), although this difference failed to reach significance ($t(30)=1.7$; $p=.085$). Both DPs and control participants were more accurate in detecting immediate repetitions of upright faces than repetitions of inverted faces (control participants: 95% versus 87%; $t(15)=3.21$; $p=.006$; DPs: 78% versus 72%; $t(15)=2.4$; $p=.03$). The size of this face inversion effect on target detection accuracy did not differ between the two groups ($F<1$). False alarms to non-repeated images occurred on 1.9% and 1.6% of all non-target trials in the DP and control groups, respectively.

3.2. The face-sensitivity of the N170: upright neutral faces versus upright houses

Fig. 1 shows grand-averaged ERP waveforms obtained at vertex electrode Cz and at lateral posterior electrodes P7 and P8 in response to upright neutral faces and upright houses. ERPs are shown separately for the DP group (top panel) and the group of

control participants (bottom panel). Fig. 1 also includes topographic maps of N170 difference amplitudes for both groups. These maps were generated by subtracting ERP mean amplitudes measured in the 150–190 ms post-stimulus time window in response to houses from mean amplitudes to upright neutral faces. Enhanced N170 components to faces as compared to houses were observed at P7/8 in both groups. Importantly, this amplitude difference was similar in size for participants with and without DP. These observations were substantiated by statistical analyses of N170 mean amplitudes obtained at P7/8. For control participants, there was a main effect of stimulus category (faces versus houses: $F(1,15)=7.66$; $p<.02$), reflecting larger N170 components to faces as compared to houses. Although this effect tended to be larger over the right hemisphere, the stimulus category × recording hemisphere interaction was not significant. Very similar results were obtained for the group of DPs. There was also an effect of stimulus category, $F(1,15)=25.3$; $p<.001$, demonstrating the face-sensitivity of the N170 component in this group. This effect also tended to be more pronounced at P8, but there was no reliable interaction with recording hemisphere. The similarity of the face-sensitive N170 for participants with and without DP was further assessed in an analysis of N170 mean amplitudes across both groups, with group (DPs versus Controls) as additional factor. There was a main effect of stimulus category ($F(2,30)=30.1$; $p<.001$) again confirming the presence of larger N170 amplitudes to faces versus houses. But critically, there was
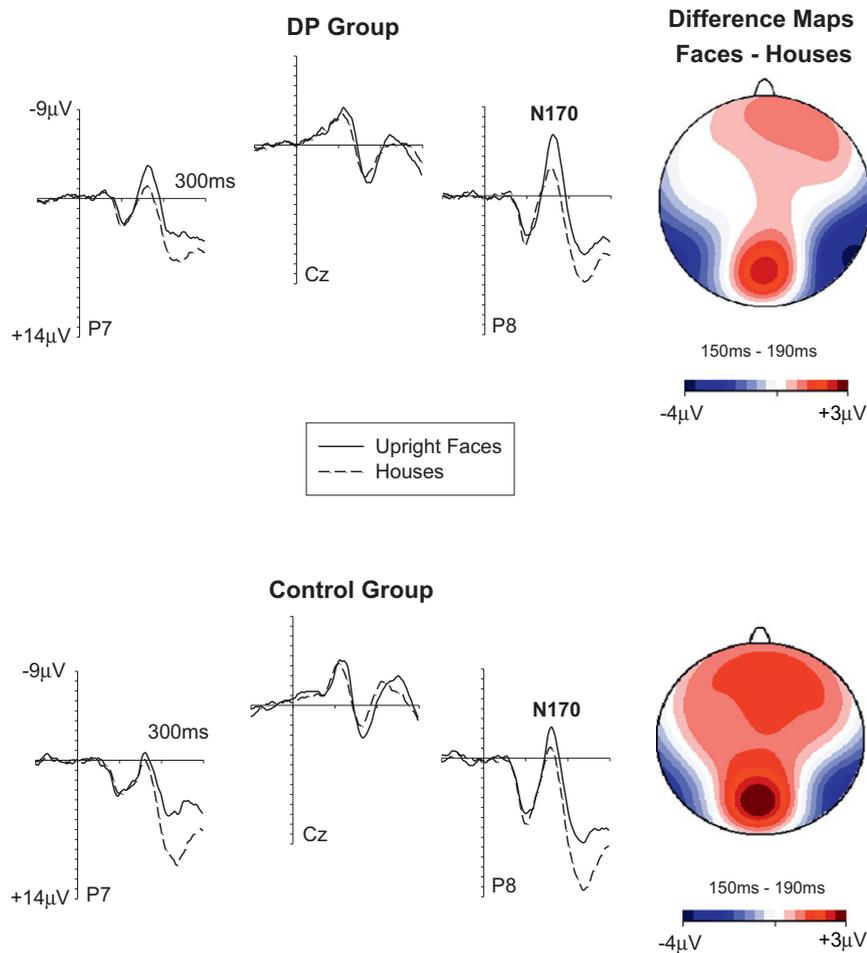

Fig. 1. Grand-averaged ERPs elicited by upright neutral faces and upright houses at vertex electrode Cz, and at lateral temporo-occipital electrodes P7 and P8 in the 300 ms interval after stimulus onset, for the group of sixteen DPs (top panel), and for the group of sixteen age-matched control participants without DP (bottom panel). Topographic maps on the right shows the scalp distribution of ERP difference amplitudes (upright neutral faces versus upright houses) in the N170 time window (150–190 ms post-stimulus), for the DPs (top) and control participants (bottom).

no indication of any interaction between stimulus category and group, or between stimulus category, recording hemisphere, and group (both $F(2,30) < 1$), which further underlines that the face-sensitivity of the N170 component was very similar for the DP group and for participants without DP. Participants' age had no effect on this face-sensitivity of the N170 in the control group (stimulus category × age: $F < 1$). In the DP group, N170 enhancements to faces versus houses were larger for younger than for older participants (stimulus × category × age: $(2,15)=12.7$; $p < .01$), but follow-up analyses confirmed that N170 face-sensitivity was reliable in both age groups.

As can be seen from the topographic map in Fig. 1 (bottom panel), control participants showed the typical N170 scalp distribution: An occipito-temporal N170 component was accompanied by a component of opposite polarity (Vertex Positive Potential; VPP) at midline frontocentral electrodes. The activation pattern observed for the group of DPs in the same time window was qualitatively similar, although the frontocentral VPP component was less pronounced. The reliability of the VPP in both groups was evaluated in analyses of mean amplitudes measured

in the N170 time window (150–190 ms post-stimulus) at midline electrodes Cz and Fz, for the factors stimulus category (face versus house) and electrode (Fz versus Cz). The VPP was present in the control group ($F(1,15)=5.64$; $p < .05$), but not in the DP group ($F(1,15) < 1$). However, there was no reliable stimulus category × group interaction ($F < 1$). Fig. 2 shows ERPs recorded at right occipito-temporal electrode P8 in response to upright neutral faces and houses, separately for each of the 16 DPs tested. Face-sensitive N170 components (i.e., enhanced N170 amplitudes to faces relative to houses) were present for most but not all DPs. To study the presence and reliability of the N170 for individual DPs, non-parametric bootstrap analyses were conducted separately for each DP on N170 mean amplitude differences between upright faces and houses at P8. Reliably enhanced N170 components in response to faces were confirmed for twelve of the 16 DPs tested (as indicated by the symbol ⌢ in Fig. 2). For two others (AH and MP), N170 amplitude differences were in the expected direction, but did not reach significance in the bootstrap analyses. Only two participants with DP (MZ and RL) showed no evidence for an N170 amplitude enhancement to face stimuli, but if anything
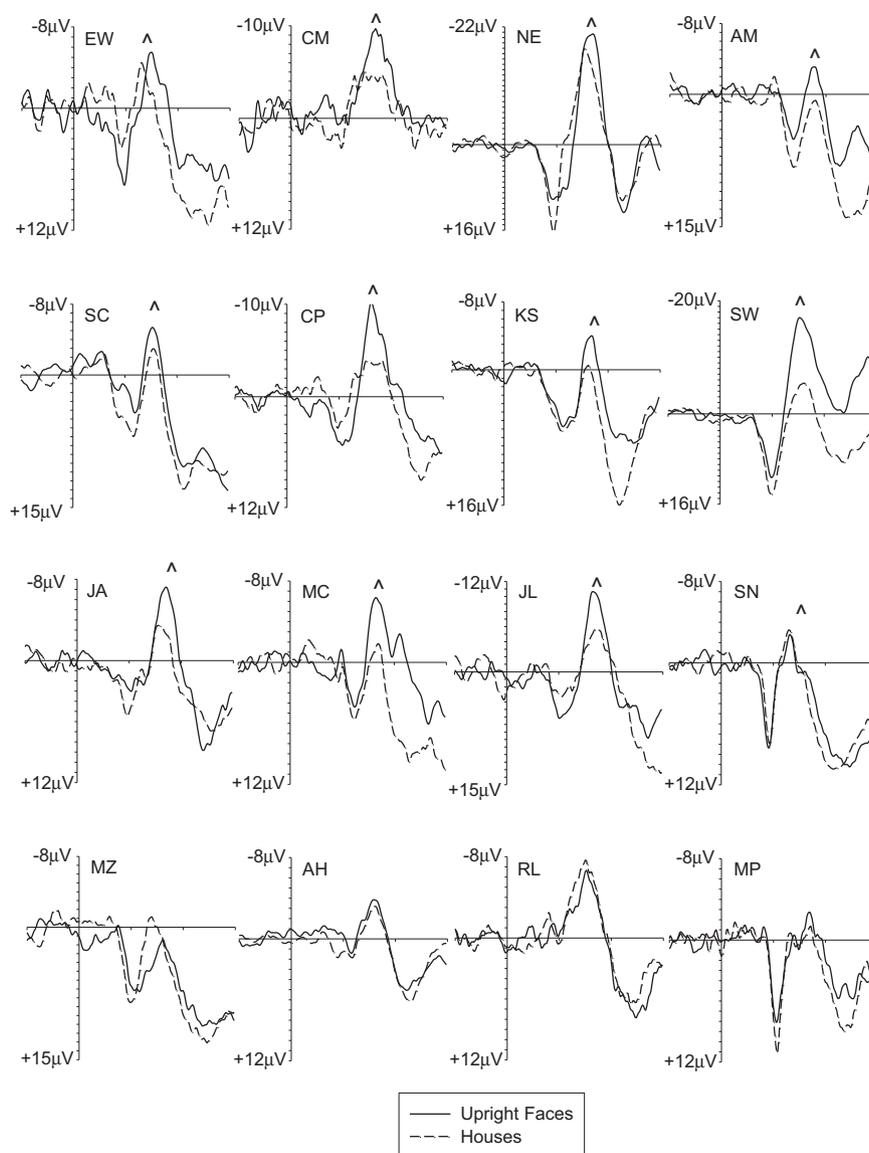

Fig. 2. ERPs elicited for each of the sixteen DPs tested at right occipito-temporal electrode P8 to upright neutral faces (solid lines) and upright houses (dashed lines). Bootstrap analyses confirmed that twelve of the sixteen DPs showed reliably enhanced N170 amplitudes to faces versus houses, as indicated by the symbol ⌢. Note that different voltage scales were used for individual DPs.

a tendency in the opposite direction. Analogous bootstrap analyses were conducted for each of the 16 control participants. Nine of them showed reliably larger N170 amplitudes to faces versus houses. For the other seven, N170 components were numerically larger to faces than to houses, but this difference remained below the significance threshold in the bootstrap analyses.

3.3. Effects of face inversion on the N170 component

Fig. 3 shows grand-averaged ERP waveforms obtained at lateral posterior electrodes P7 and P8 in response to upright and inverted faces (collapsed across neutral and fearful faces), for the DP group (top) and the group of control participants (bottom). For the control group, the typical effects of face inversion on the N170 were observed: Relative to upright faces, inverted faces elicited enhanced and delayed N170 components. Remarkably, no inversion-induced N170 amplitude enhancements were observed for the DP group. If anything, the N170 to upright faces tended to be larger than the N170 to inverted faces for participants with DP.

These observations were confirmed by statistical analyses of N170 mean amplitudes. For the control group, there was a main effect of face orientation (upright versus inverted: $F(1,15)=6.73$; $p < .05$) on N170 mean amplitudes, reflecting larger N170 components to inverted as compared to upright faces. This effect tended to be larger over the right hemisphere, although the interaction between face orientation and recording hemisphere

was not significant ($F(1,15)=2.84$; $p=.11$). In marked contrast, face orientation had no effect on N170 mean amplitudes in the DP group ($F(1,15) < 1$). This difference between the two groups was further confirmed in an additional analysis of N170 mean amplitudes across groups. There was a significant interaction between face orientation and group ($F(2,30)=6.29$; $p < .02$), demonstrating that inversion-induced N170 amplitude enhancements differed reliably between participants with and without DP.

To assess the impact of participants' age on face inversion effects on N170 amplitudes, separate analyses were conducted for younger and older participants. Fig. 3 (bottom panel) shows ERPs obtained at right posterior electrode P8 for younger and older DPs and control participants, and demonstrates that age had a strong effect in the control group, but not for participants with DP. N170 amplitude enhancements to inverted faces were absent not just for older DPs, but also in the younger sub-group. For younger control participants, the typical pattern of larger N170 components to inverted faces was observed. In contrast, this effect was absent in older controls. This pattern was confirmed by analyses of N170 mean amplitudes at P8 for both groups with age (younger versus older sub-group) as additional factor. For DPs, there was no main effect of face orientation and no interaction between face orientation and age (both $F(1,15) < 1.6$). For control participants, a significant face orientation × age interaction was present ($F(1,15)=9.81$; $p < .01$), and this was due to the fact that a significant face inversion effect was present in the younger sub-group ($F(1,7)=24.26$; $p < .005$), but not in the older sub-group ($F < 1$). When analyses were conducted separately for younger
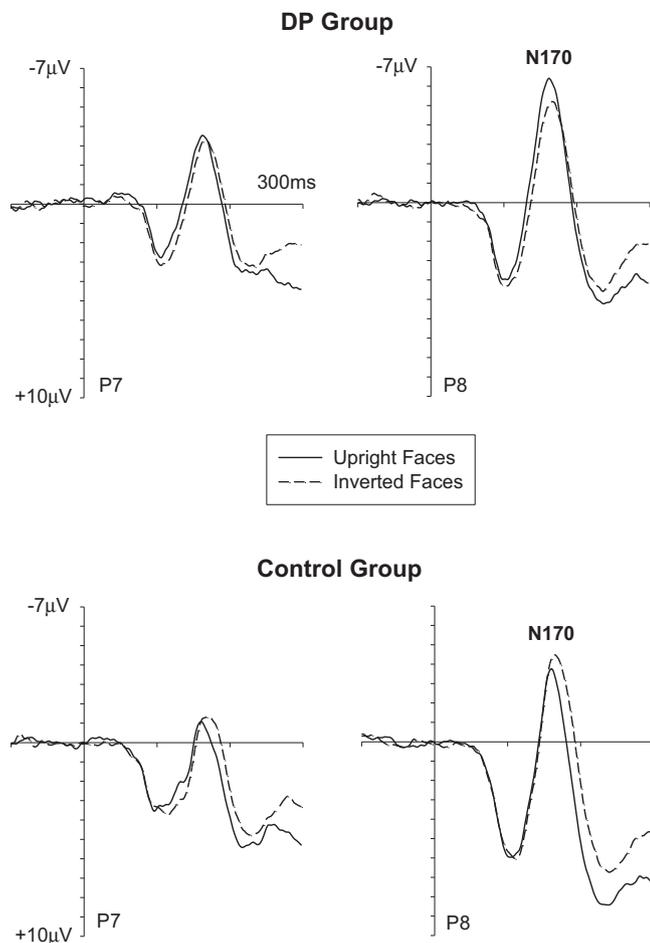

Fig. 3. Grand-averaged ERPs elicited by upright and inverted faces (collapsed across neutral and fearful faces) at lateral temporo-occipital electrodes P7 and P8 in the 300 ms interval after stimulus onset, for the group of sixteen DPs (top panel), and for the group of sixteen age-matched control participants without DP (bottom panel).
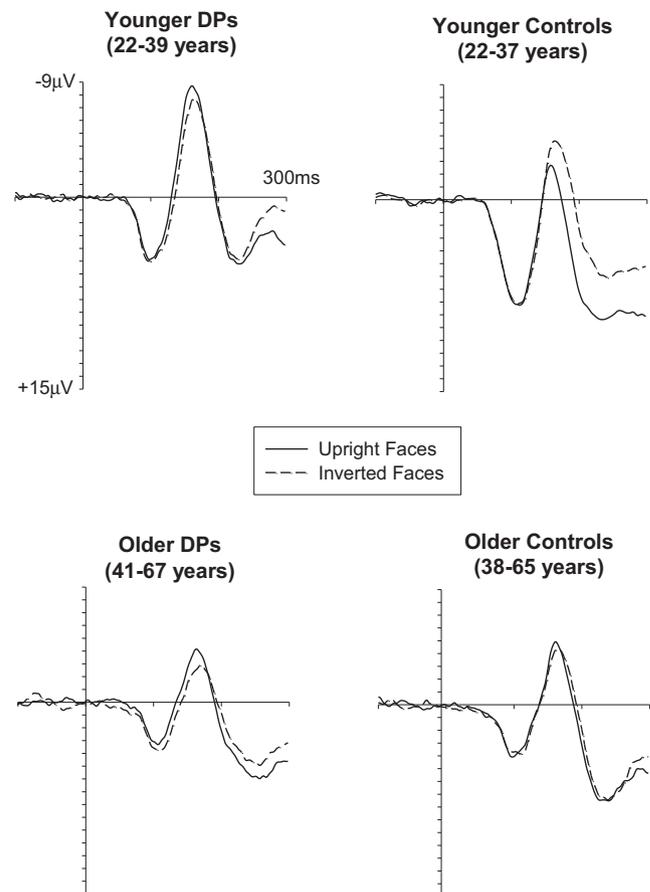

Fig. 4. Grand-averaged ERPs elicited by upright and inverted faces (collapsed across neutral and fearful faces) at right temporo-occipital electrode P8 in the 300 ms interval after stimulus onset, for the sub-groups of younger DPs and controls (top panel), and for the sub-groups of older DPs and controls (bottom panel).
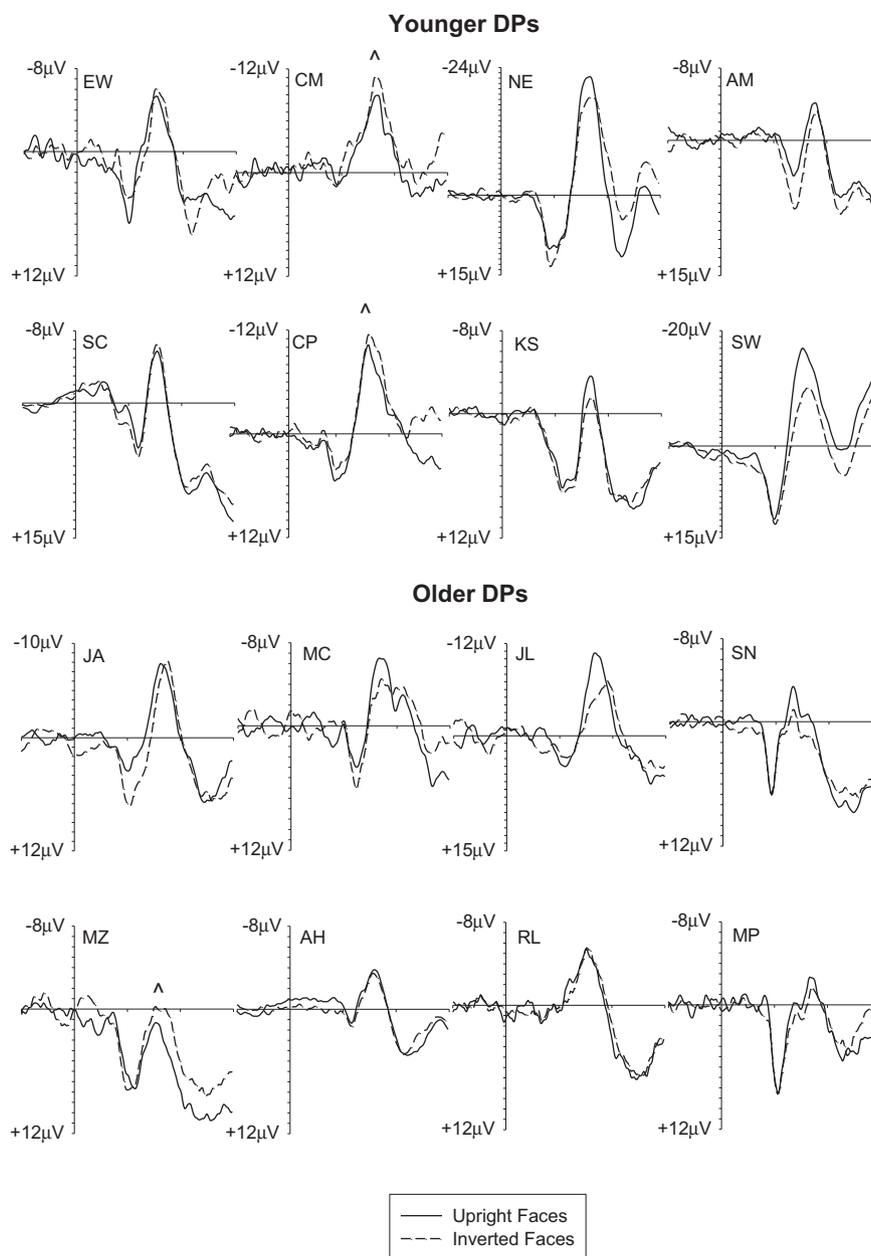
Fig. 5. ERPs elicited for each of the sixteen DPs tested at right occipito-temporal electrode P8 in response to upright and inverted faces (collapsed across neutral and fearful faces). Bootstrap analyses showed that only three of the sixteen DPs showed reliably enhanced N170 amplitudes to inverted faces, as indicated by the symbol ⌃. Note that different voltage scales were used for individual DPs.

and older participants, with group now included as between-subject factor, a significant face orientation × group interaction for younger participants ($F(2,15)=12.43$; $p < .005$) reflected the presence of N170 face inversion effects for controls and the absence of such effects for DPs. In contrast, no face orientation × group interaction was present for older participants ($F(2,15) < 1$).

Analyses of N170 peak latencies in the control group revealed the typical effect of face orientation ($F(1,15)=6.36$ $p < .03$), as the N170 component was delayed for inverted as compared to upright faces (168 ms versus 163 ms; see Fig. 2). There was an interaction between orientation and recording hemisphere ($F(1,15)=5.98$ $p < .03$), as this effect was more pronounced over the right hemisphere. In the DP group, there was only a 2 ms latency difference for the N170 to inverted and upright faces (163 ms versus 161 ms), which was not significant ($F < 1$). However, there was no significant face orientation × group interaction

($F < 1$). Participants' age had no effect on inversion-induced N170 latencies in either group (both $F < 1$).

The absence of consistent face inversion effects on N170 amplitude across participants with DP is illustrated in Fig. 5, which shows ERPs recorded at right occipito-temporal electrode P8 in response to upright and inverted faces (collapsed across neutral and fearful faces), separately for the eight younger DPs (top) and the eight older DPs (bottom). Typical face inversion effects on N170 amplitudes (i.e., reliably enhanced N170 components for inverted relative to upright faces, as revealed by bootstrap analyses) were only found for three DPs, but were absent for the remaining 13 DPs tested. Fig. 6 shows individual face inversion effects on N170 mean amplitudes, obtained by subtracting ERPs to inverted faces from ERPs to upright faces. Results are plotted separately for younger and older participants, both for DPs (dark bars) and controls (light bars), and sorted by the absolute size and polarity of these effects. Larger N170 components
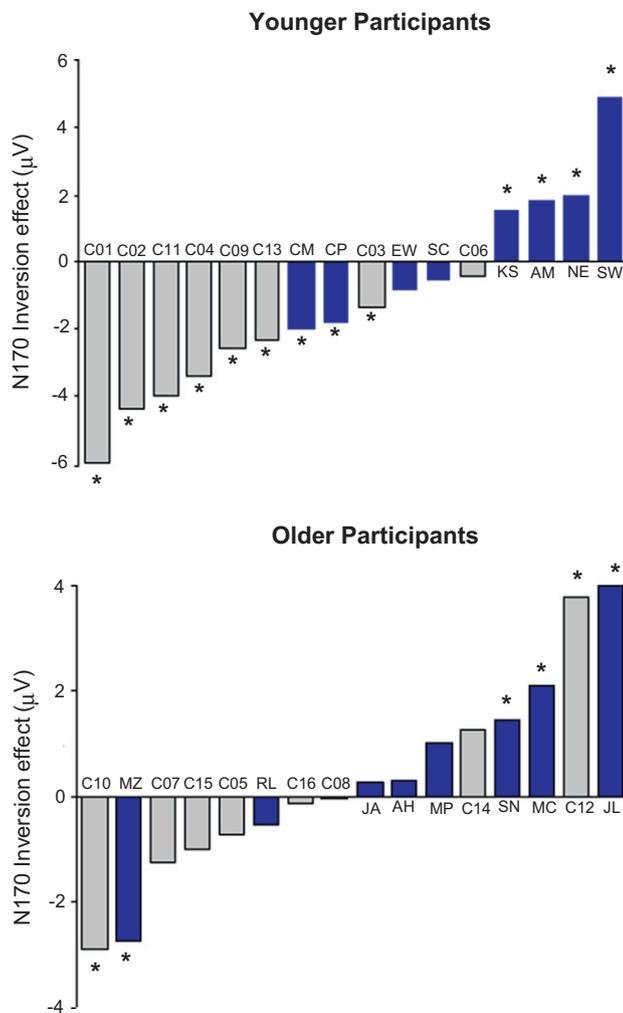
Younger Participants

Older Participants

Fig. 6. Face inversion effects on N170 amplitudes for individual DPs (dark bars) and control participants (light bars), sorted according to the size and polarity of this effect. Amplitude values were obtained by subtracting N170 mean amplitudes to inverted faces from N170 mean amplitudes to upright faces, with negative values (on the left) reflecting typical N170 face inversion effects, and positive values larger N170 amplitudes to upright faces. Significant differences, as revealed by bootstrap analyses, are indicated by asterisks. Results are shown separately for younger and older participants.

to inverted faces are reflected by negative values and are plotted on the left, and larger N170 amplitudes to upright faces (reflected by positive values) are plotted on the right. Significant amplitude differences, as demonstrated by single-subject bootstrap analyses, are indicated by asterisks. A clear dissociation between controls and DPs is apparent for younger participants (Fig. 6, top panel): seven of the eight younger controls tested showed reliably enhanced N170 amplitudes to inverted as compared to upright faces. In contrast, this typical N170 face inversion was observed for only two of the younger DPs, whereas as four others even showed a reversal of this effect, with significantly enhanced N170 amplitudes to *upright* faces. As expected on the basis of the group level analyses, no such clear dissociation between controls and DPs was evident for older participants. At the individual level, bootstrap analysis revealed that only one older DP and one older control participant showed a significantly enlarged N170 to inverted faces. Three other older controls showed N170 amplitude differences in the same direction, which did not pass the conservative significance threshold of the single-case bootstrap analysis. Only one older control participant showed reliably enhanced N170 amplitudes to

upright as compared to inverted faces, whereas this unusual pattern was observed for three of the older DPs (see Fig. 6).

3.4. Correlations between behavioural performance and N170 face inversion effects

There were no statistically significant correlations between the performance of individual participants with DP in behavioural face processing tests (FFT, CFMT, CFPT, ONT) and individual N170 face inversion effects (i.e., mean amplitude differences between upright and inverted faces in the N170 time window). However, a reliable correlation was found for the DP group between the effect of face inversion on target detection accuracy in the main experimental task (the percentage of correctly detected immediate repetitions of upright versus inverted faces) and the N170 face inversion effects observed in this task ($r(15)=.601$, $p=.014$): DPs who tended to show the typical pattern of larger N170 components to inverted versus upright faces showed a larger advantage in detecting repetitions of upright versus inverted faces, while atypical N170 face inversion effects in the DP group were linked to smaller performance differences in response to upright versus inverted target faces. Across the 16 control participants, there was no such link between N170 face inversion effects and the effects of face inversion on target detection in the one-back task.

4. Discussion

We measured the face-sensitive N170 component in a group of 16 individuals with developmental prosopagnosia and in 16 age-matched control participants to find out whether the N170 is present or absent in DP, and to investigate how face inversion affects this component in participants with DP. Results demonstrated that the face-sensitivity of the N170 component in DPs and in control participants is very similar. N170 amplitude enhancements in response to inverted faces are largely absent in individuals with DP, regardless of their age. A different pattern was observed for controls, where this effect was present but was strongly age-dependent. As discussed below, these observations are important for understanding which face processing mechanisms are disrupted in DP.

4.1. N170 shows normal face-sensitivity in most DPs

The comparison of ERPs to upright neutral faces and upright houses demonstrated that the face-sensitivity of the N170 component is largely preserved in DP. Fig. 1 shows grand-averaged ERP waveforms across all sixteen DPs (top panel), and across all 16 age-matched control participants (bottom panel), and demonstrates that enhanced N170 amplitudes to upright faces as compared to houses were triggered in a similar fashion in both groups. The absence of any interaction between stimulus category and group provides strong evidence that the face-sensitive N170 component is triggered in a very similar fashion in participants with and without DP. This conclusion is further supported by Fig. 2, which shows ERPs triggered in response to upright faces and houses at right temporo-occipital electrode P8 for individual DPs. Twelve of the 16 DPs tested had reliably larger N170 amplitudes to faces relative to houses, and two others showed the same, albeit non-significant, N170 difference.

These observations are based on a large sample of participants with DP, and therefore allow more general conclusions than previous studies where single cases or a much smaller number of participants were tested. In these earlier studies, the face-sensitivity of the N170 was found to be preserved in some individuals with DP, and abolished in others (Bentin et al., 1999,

2007; Harris et al., 2005; Kress & Daum, 2003; Righart & De Gelder, 2007; Minnebusch et al., 2007; Rivolta et al., 2012). The results from the present study strongly suggest that the presence of a normal face-sensitive N170 component is the rule rather than the exception in developmental prosopagnosia. In this respect, DPs might differ from patients with AP, where a disruption of N170 face-sensitivity is more common (e.g., Alonso-Prieto et al. (2011), Dalrymple et al. (2011), Eimer and McCarthy (1999)). The finding that most DPs have a face-sensitive N170 component is consistent with observations from fMRI studies that many DPs show enhanced activation to faces versus non-face objects in face-selective posterior brain areas (Furl et al., 2011), and extends these results by demonstrating face-sensitivity at relatively early perceptual stages of visual processing. These observations indicate that at least some aspects of the structural encoding of facial features and configurations remain intact in most individuals with DP. It is also important to note that even though N170 enhancements for faces versus houses were larger for younger than for older DPs, these effects remained reliably present for older DPs and also for older controls (see also Daniel and Bentin (2012), for additional evidence that the face-sensitivity of the N170 is not age-dependent, for a group of much older participants with a mean age of 77 years).

4.2. N170 face inversion effects are absent in most DPs

In contrast to the face-sensitivity of the N170, there were reliable differences between the DP and control groups in the effects of face inversion on N170 amplitudes. In the control group, N170 components were delayed and enhanced for inverted as compared to upright faces (Fig. 3, bottom panel), in line with many previous reports (e.g., Bentin et al. (1996), Eimer (2000b), Itier et al. (2007); Rossion et al. (2000)). In contrast, face inversion effects on N170 amplitudes were absent for the DP group (Fig. 3, top panel), and this difference was substantiated by a reliable interaction between face orientation and group. However, these observations at the group level do not provide a full account of the pattern of N170 face inversion effects, which turned out to be strongly age-dependent in the control group, but not in the group of DPs. As shown in Fig. 4, large inversion-induced N170 amplitude modulations were found for the eight younger control participants, but not for the older controls. This difference is reminiscent of previous observations by Gao et al. (2009) and Daniel and Bentin (2012), who found that N170 amplitude enhancements to inverted as compared to upright faces were present in young but absent in elderly participants. A notable difference is that the mean age of the older participants in these two earlier studies was above 70 years, while the older controls in the current experiments were considerably younger (38–65 years). This age range is rarely studied in N170 research, where claims about "typical" N170 effects are usually based on samples of participants in their twenties (but see Wolff, Wiese, and Schweinberger (in press), for a recent exception). The fact that atypical N170 face inversion effects were obtained in the current study for middle-aged control participants suggests that such generalizations of findings from young adult participants to older age groups may not always be warranted. They also suggest that important qualitative differences in the way that face perception operates may not only emerge in the elderly, but already in middle age.

These observations for control participants are also important to qualify the absence of N170 face inversion effects for DPs. As is evident in Fig. 4, these effects differed markedly between younger DPs and younger controls. Young controls showed larger N170 amplitudes for inverted versus upright faces, whereas age-matched young DPs did not. In contrast, there were no significant

group differences for older participants. In other words, the interaction between face orientation and group that was found across all participants was primarily driven by the younger sub-group. The ERP waveforms for individual participants with DP shown in Fig. 5 underline the fact that face inversion effects on N170 were largely absent for DPs, irrespective of their age.

4.3. Conclusions

The generic face-sensitivity of the N170 component is very similar in DPs and control participants, whereas N170 face inversion effects are reliably different between these two groups. What do these similarities and differences imply with respect to the locus of face processing deficits in DP? The absence of face inversion effects on N170 amplitudes in most DPs suggest that they tend to process upright and inverted faces in a similar fashion, perhaps because they are less efficient than controls in utilizing the prototypical spatial-configural information provided by upright faces. In fact, the performance observed for the DP group in the Cambridge Face Perception Test (CFPT) suggests that they were relatively less affected by the disruption of this information through face inversion. Their CFPT performance was less impaired for inverted faces than for upright faces (Inverted $z = -.52$; Upright: $z = -1.35$), and this difference was statistically reliable ($t(15) = 3.36$; $p < .004$).

It is interesting to note that the presence of atypical N170 face inversion effects has also been observed for other types of developmental disorders, such as in individuals with autism spectrum disorder (ASD; Webb et al., 2012) or Williams Syndrome (WS; Grice et al., 2001). The similarity of these findings and the current observations for individuals with DP suggest common underlying deficits in global aspects of face perception that may be specifically tuned to the processing of upright faces. Age is clearly another important factor for the presence versus absence of N170 face inversion effects. Taylor, Batty, and Itier (2004) found that inversion-induced N170 amplitude enhancements typically found with younger adults only emerged around the age of 11–12 years. For younger children, this effect was inversed, with larger N170 components for upright relative to inverted faces. Elderly participants also show no enhancement of the N170 for inverted faces (Daniel & Bentin, 2012; Gao et al., 2009), and the current results suggest that this deviation from the pattern commonly observed with young adult participants may already emerge in middle age.

Is there a common factor that might link the different populations that show atypical N170 face inversion effects (young children, older adults, individuals with DP or with other developmental disorders)? One candidate factor is the degree of selective functional specialization within ventral visual areas for upright faces. The observation that upright faces trigger equally large or even larger N170 components than inverted faces could reflect a tendency for upright faces to activate object-sensitive areas that would otherwise only be activated by non-face objects or inverted faces due to a general reduction in cortical face-specificity. The level of face-selectivity in visual processing does indeed change considerably in the course of development: Activation in face-selective regions becomes progressively more specialized through childhood into adulthood (Golarai et al. 2007; Joseph et al., 2011), and the same face-selective regions appear to become less differentiated and specialized with age (Park et al., 2004). Individuals with ASD show reduced or atypical neural specialization for faces (e.g. Pierce, Muller, Ambrose, Allen, and Courchesne (2001)), and a reduction in the face-selectivity of the FFA has been demonstrated for DPs (Furl et al., 2011). Individuals with WS were found to have much larger FFAs than

matched controls, again demonstrating an atypical neural specialization for faces (Golarai et al., 2010).

Some authors have recently challenged the claim that cortical regions increase in their face-selectivity during development, and have argued that face perceptual expertise is mature during early childhood (McKone, Crookes, Jeffery, & Dilks, 2012). Although this claim is in line with developmental ERP studies which have found no systematic changes in the face-sensitivity of the N170 from 4 years onwards (Kuefner, de Heering, Jacques, Palmero-Soler, & Rossion, 2010), it is inconsistent with ERP and fMRI studies of face inversion, which demonstrate that the neural systems involved in expert adult face perception have a protracted developmental trajectory, and only become fully tuned to upright faces in early adulthood (Taylor et al., 2004; Passarotti, Smith, DeLano, & Huang, 2007).

The suggestion that the absence of reliable N170 face inversion effects observed for DPs in the current study is linked to a general reduction in the upright face-selectivity of visual processing that is not exclusive to DP, but is also found in younger children, older adults, and individuals with other developmental disorders raises the obvious question how this reduction is linked to the face recognition impairments that are the defining feature of DP. In our study, older control participants and older DPs did not differ with respect to their N170 face inversion effects (Fig. 4), yet the older controls (and older individuals in general) are clearly not prosopagnosic. Robust differences in the effects of face inversion on N170 amplitudes were found between younger controls and younger DPs, and it is possible that these differences mark a critical distinction between DPs and individuals with intact face processing abilities: DPs have poor face recognition because they never achieve the degree of upright face-specific functional specialization in visual processing that is characteristic for typically developing adults, who may use compensatory strategies to cope with the age-related general decline in functional specialization when processing faces. Such strategies may not be available to individuals with DP who have never developed a typically specialized face processing system.

How can the hypothesis that DPs show a reduced level of functional specialization for faces be reconciled with the observation that the generic face-sensitivity of the N170 component in response to upright faces as compared to houses was essentially normal for the DP group? It is important to note that the N170 is not a monolithic component that is tightly linked to one specific face processing mechanism, but instead reflects multiple neural sources that are associated with different sub-processes involved in face perception (e.g., Eimer et al. (2010), Rossion and Jacques (2008, 2011), Sadeh, Podlipsky, Zadanov, and Yovel (2010)). While there is clear evidence that the N170 component is associated with configural/holistic face processing (Eimer et al., 2011; Sagiv & Bentin, 2001), it has also been demonstrated that N170 amplitudes are sensitive to isolated face parts, such as the eyes (Bentin et al., 1996; Itier et al., 2007). The preserved face-sensitivity of the N170 in most DPs tested in this study may reflect the normal operation of one aspect of face processing (e.g., the detection and encoding of face parts), whereas the absence of N170 face inversion effects in DP could indicate an impairment of another aspect (e.g., configural face processing), which may be associated with a reduced or atypical degree of functional specialization of the face processing system.

In summary, the present study has provided new insights into the properties of the N170 component in developmental prosopagnosia, and into the nature of face processing deficits in DP. The generic face-sensitivity of the N170 tends to be present in individuals with DP, indicating that some basic aspects of face perception are operational. The fact that inversion-induced N170 modulations are abolished or even reversed in most DPs points to a general reduction in the early selectivity of visual processes tuned specifically to upright faces as one source for the face recognition deficits in developmental prosopagnosia.

Acknowledgements

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