Face identity matching is selectively impaired in developmental prosopagnosia

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Abstract

Individuals with developmental prosopagnosia (DP) have severe face recognition deficits, but the mechanisms that are responsible for these deficits have not yet been fully identified. We assessed whether the activation of visual working memory for individual faces is selectively impaired in DP. Twelve DPs and twelve age-matched control participants were tested in a task where they reported whether successively presented faces showed the same or two different individuals, and another task where they judged whether the faces showed the same or different facial expressions. Repetitions versus changes of the other currently irrelevant attribute were varied independently. DPs showed impaired performance in the identity task, but performed at the same level as controls in the expression task. An electrophysiological marker for the activation of visual face memory by identity matches (N250r component) was strongly attenuated in the DP group, and the size of this attenuation was correlated with poor performance in a standardized face recognition test. Results demonstrate an identity-specific deficit of visual face memory in DPs. Their reduced sensitivity to identity matches in the presence of other image changes could result from earlier deficits in the perceptual extraction of image-invariant visual identity cues from face images.

Keywords: Face perception, face recognition, developmental prosopagnosia, event-related potentials, N250r component

1. Introduction

Developmental prosopagnosia (DP) is a lifelong impairment in the ability to recognise faces in the apparent absence of brain damage or other cognitive impairments (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 evidence from family and twin studies suggests that there may be a genetic component to this disorder (Duchaine, Germine, & Nakayama, 2007; Lee, Duchaine, Wilson, & Nakayama, 2010). The exact nature of the face processing deficits in DP is still largely unknown. Successful face recognition is based on a number of successive processing stages. These stages include the part-based and holistic perceptual processing of face images, constructing representations of identity-related visual information and retaining them in memory, and matching this information with the visual properties of a currently seen face (for a cognitive model of the stages involved in face recognition, see Bruce & Young, 1986). Impairments of any of these processes can result in impairments of face recognition, as experienced by individuals with DP.

Neuroimaging studies of DP have shown that in contrast to face recognition disorders caused by brain injury (acquired prosopagnosia; Bodamer, 1947), the occipito-temporal "core" face processing network (e.g., Haxby, Hoffman, & Gobbini, 2000; 2002; Kanwisher, McDermott, & Chun, 1997) appears to be largely intact in DP (Avidan & Behrmann, 2009; Avidan, Hasson, Malach, & Behrmann, 2005; Avidan et al., 2014; Furl, Garrido, Dolan, Driver, & Duchaine, 2011; Hasson, Avidan, Deouell, Bentin, & Malach, 2003; but see also Berhmann, Avidan, Gao, & Block, 2007; Garrido et al., 2009). However, investigations of face-specific event-related potential (ERPs) in DP are now beginning to reveal systematic differences between DPs and control participants, both at early visual-perceptual stages of face processing, and at later memory-related stages associated with the recognition of facial identity (see Towler, Fisher, & Eimer, in press, for review). Most ERP studies of DP have focused on the N170 component, which is the earliest face-sensitive ERP component that emerges at occipital-temporal electrode

sites approximately 170 ms after stimulus onset. The N170 reflects an enhanced negativity for faces as compared to non-face objects, and is assumed to be generated during the structural encoding of faces and face parts in face-selective occipitotemporal visual areas (e.g., Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000). Most individuals with DP show normal N170 components to faces versus non-face objects (Towler, Gosling, Duchaine, & Eimer, 2012), suggesting that the ability to perceptually discriminate between faces and non-faces is largely intact. However, changes to the prototypical spatial configuration and contrast properties of face images (such as presenting face images upside-down, spatially scrambling internal facial features, or contrast-inverting the eye region) produce atypical N170 amplitude modulations in individuals with DP (Towler et al., 2012; Towler, Parketny, & Eimer, 2016; Fisher, Towler, & Eimer, 2016b). This suggests that perceptual face processing mechanisms in DP may be less well tuned to the spatial configuration and contrast properties that are the defining features of a typical upright face, and are therefore less sensitive to deviations from a prototypical visual face template.

The face perception deficits reflected by such atypical N170 responses in DPs are likely to adversely affect subsequent identity-related face processing stages, resulting in the severe face recognition problems experienced by individuals with DP. The processing of facial identity is associated with ERP components that emerge at post-stimulus latencies beyond 200 ms (N250 and N250r components). During the successful recognition of familiar faces and of learned target faces, an enhanced negativity at lateral posterior electrodes emerges at around 250 ms after stimulus onset (Gosling & Eimer, 2011; Tanaka, Curran, Porterfield, & Collins, 2006). This N250 component, which is assumed to reflect the activation of a stored representation of a particular individual face in longer-term visual memory, has also been observed for individuals with DP (Eimer, Gosling, & Duchaine, 2012; Parketny, Towler, & Eimer, 2015). However, the N250 in response to a learned target face was delayed in DPs as compared to age-matched control participants (Parketny et al., 2015), suggesting that such identity matching processes are

triggered less rapidly in DP. A similar N250 component has also been found in tasks where two face images are shown in quick succession. When the second face shows the same individual as the first face, an enhanced negativity is elicited bilaterally at occipitotemporal electrodes, relative to trials where faces of two different individuals are shown. This N250r ("r" for repetition) component is assumed to reflect the selective activation of a working memory representation of the first face that is triggered by an identity match with an on-line perceptual representation of the second face (Schweinberger & Burton, 2003; see also Begleiter, Porjesz, & Wang, 1995; Schweinberger, Pfütze, & Sommer, 1995; Schweinberger, Pickering, Burton, & Kaufmann, 2002; Schweinberger, Huddy, & Burton, 2004; Towler, Kelly, & Eimer, 2015). In the face processing model proposed by Bruce & Young (1986), this process would correspond to the activation of a particular face recognition unit (FRU) in visual memory (see also Burton, Bruce, & Johnston, 1990). The fact that N250r components remain present when two different images of the same individual are shown (e.g., Bindemann, Burton, Leuthold, & Schweinberger, 2008; Kaufmann, Schweinberger, & Burton, 2009; Zimmermann & Eimer, 2013; Wirth, Fisher, Towler, & Eimer, 2015) shows that these components do not simply reflect a match between low-level visual image features, but are sensitive to higher-level visual aspects of facial identity. N250r components to identity repetitions are not only elicited when face identity is task-relevant, but also when another face property has to be matched and identity can be ignored (Zimmermann & Eimer, 2014), indicating that the encoding of facial identity into working memory operates in an obligatory fashion for attended faces.

The goal of the present study was to use the N250r component to investigate the encoding and temporary working memory storage of identity-related face information in DP. Some behavioural studies have found that DPs are impaired in matching the identity of two successive unfamiliar face images (DeGutis, Cohan & Nakayama, 2014; Shah, Gaule, Gaigg, Bird & Cook, 2015), whereas other studies have shown no or little deficit (Ulrich et al., 2016). It is currently unknown whether individuals with DP have a particular deficit in detecting that

dissimilar images of the same face belong to the same individual, or whether visual dissimilarity more generally impairs their ability to perceptually match other facial attributes, such as emotional expression. If there are any perceptual or working memory impairments in DP, these may be specific to representations of facial identity, and leave the representation of emotional expression unaffected. This has been suggested by studies showing that DPs are relatively normal in their ability to recognise categorically distinct basic emotions (Duchaine, Parker, & Nakayama, 2003; Humphreys, Avidan, & Behrmann, 2007; Palermo et al., 2011), more subtle and complex expressions (Duchaine et al., 2003; Duchaine, et al., 2007; Palermo et al., 2011) and are also able to successfully complete expression matching tasks (Bentin, DeGutis, D'Esposito, & Robertson, 2007; Garrido et al., 2009; Lee et al., 2010). DPs also show typical neural responses to emotional versus neutral faces (Avidan et al., 2014; Dinkelacker et al., 2011, Furl et al., 2011; Van den Stock et al., 2008; Towler et al., 2016). However, some DPs do report having difficulty reading expression in their daily lives (e.g. Lee et al., 2010), and some of them show impairments in standardised expression recognition tests (e.g. De Haan & Campbell, 1991; Duchaine, Yovel, Butterworth & Nakayama 2006; see also Biotti & Cook, 2016).

To test whether face identity matching but not expression matching is selectively impaired in DP, we employed two sequential matching tasks that were identical to the procedures used in a previous ERP study (Fisher, Towler, & Eimer, 2016a) with young participants without face processing impairments. On each trial, two different face stimuli (S1 and S2) were presented successively at fixation, and these images were separated by a short interval (200 – 300 ms). Repetitions versus changes of identity and of expression between S1 and S2 were varied orthogonally across trials, resulting in four different trial conditions (repetition of both identity and expression; change of identity and expression; identity repetition/expression change; identity change/expression repetition; see Figure 1). There were two blocked task conditions. In the identity task, participants had to report the presence of an identity repetition versus change, and to ignore repetition or changes of facial expression. In the expression task,

they reported expression repetitions versus changes, while ignoring face identity. Twelve participants with DP and twelve age-matched control participants were tested. Their performance in the two tasks was assessed separately for trials where the task-relevant and irrelevant attributes were congruent (both repeated or both changed), and trials where they were incongruent (identity repetition/expression change, or vice versa). If DPs are selectively impaired in matching face identity but not in matching facial expression, they should perform poorly in the identity task but at the same level as control participants in the expression task. In our previous study with young unimpaired volunteers (Fisher et al., 2016a), symmetrical behavioural congruency effects were found. The detection of identity repetitions or changes was impaired on trials with incongruent changes/repetitions of facial expression, and analogous interference effects were found for task-irrelevant face identity in the expression task. Such congruency effects are often found in tasks where observers have to judge one particular stimulus attribute and disregard another task-irrelevant attribute of the same stimulus, and show that the task-irrelevant feature cannot be selectively ignored (Garner interference; Garner, 1976). If representations of face identity in working memory are selectively impaired in DP, this could be reflected by asymmetrical behavioural congruency effects for the DP group in the present study, with stronger interference effects of task-irrelevant expression in the identity task than for task-irrelevant identity in the expression task.

In addition to performance, N250r components to identity repetitions versus changes were measured in both tasks, separately for trials where facial expression was repeated or changed between S1 and S2. If working memory representations of face identity are impaired in DP, N250r components to face identity repetitions should be reduced or absent in individuals with DP relative to age-matched control participants. In our previous study with young unimpaired volunteers (Fisher et al., 2016a), N250r components were larger in the identity task but remained reliably present in the expression task, demonstrating that the identity of the first face was encoded into working memory and matched with the identity of the second face even

when identity had to be ignored. In both tasks, N250r components were smaller and delayed on expression change relative to expression repetition trials. This suggests that facial identity and expression are not represented independently in visual working memory, and that neither of these two attributes can therefore be entirely ignored when it is task-irrelevant. If participants with DP have a deficit in matching face identity information in visual working memory with a currently seen face, N250r components should generally be smaller (or perhaps be even entirely absent) in DPs relative to control participants. Attenuated N250r amplitudes in the DP group would show that the activation of stored visual representations of individual faces that is triggered by an identity match is generally reduced in DP. Because DPs are particularly impaired when perceptually matching the identity of visually dissimilar faces (White, Rivolta, Burton, Al-Janabi, & Palermo, 2016), performance in the identity task and N250r components in this task for the DP group should be particularly affected on trials where an identity repetition is accompanied by a task-irrelevant change of facial expression. Although face identity repetitions versus changes had to be ignored in the expression task, an N250r was still expected to remain present for control participants (as in Fisher et al., 2016a). An absence of N250r components in this task for the DP group would suggest that in contrast to individuals with unimpaired face processing, DPs do not store and match facial identity in an obligatory fashion.

2. Methods

2.1. Participants

Twelve participants with DP (8 female), aged 21-49 years (mean age 33 years), and twelve control participants (9 female; age range 21-46 years, mean age 32 years) took part in this study. Each DP participant was individually age-matched to one control participant, within an age range of +/- 4 years. 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 DPs reported difficulties with face recognition since childhood, and their impairment was assessed with a battery of behavioural tests. Impairments of long-term face memory were investigated with the Famous Faces Test (FFT; Duchaine & Nakayama, 2005), which required participants to identify 60 individuals who are famous in popular culture (e.g. actors, musicians, politicians) from face photographs. The ability of 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) also 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. To investigate their ability to recognize emotional expression, DP participants also completed the Reading the Mind in the Eyes Test (RMET; Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001). In the RMET, participants have to match a photograph showing only the eye region of a face with one of four possible written specifications of nuanced emotional expressions. To confirm that their face recognition abilities were within the normal range, all Control participants completed the CFMT prior to the start of the EEG testing session.

Table 1.

Z-values for 12 DP participants in the Famous Faces Test (FFT), Cambridge Face Memory Test (CFMT), the Cambridge Face Perception Test (CFPT) for upright and inverted faces, the Reading the Mind in the Eyes Test (RMET) and the Old-New Test (ONT). Scores on the ONT are also shown as *d'* values.

	CFMT	CFPT Upright	CFPT Inverted	FFT	ONT	ONT *d'*	RMET
EB	-2.52	-0.92	1.35	-5.6	-6.54	1.25	1.94
DM	-3.78	-0.92	-0.06	-4.25	-7.13	1.12	-0.28
CM	-4.29	-3.1	-2.89	-7.72	-14.34	0.38	-1.11
TW	-2.52	-1.74	0.79	-9.46	-3.61	2.08	1.39
SK	-1.25	-0.78	-0.2	-5.21	-3.36	1.78	1.67
KT	-2.52	-0.92	-0.2	-5.98	-1.54	2.51	0.28
KS	-2.9	-0.92	-1.05	-8.49	-9.03	0.87	-0.28
DD	-2.77	0.17	-0.77	-5.21	-3.36	1.78	1.67
LR	-2.39	-0.38	-0.63	-6.56	-4.9	1.54	-0.28
MF	-2.14	-2.29	0.5	-5.96	-10.35	0.76	0.83
ZS	-2.14	-0.92	-0.35	-6.95	-2.04	2.26	1.94
PH	-3.02	-3.24	-1.48	-8.49	-5.52	1.41	-0.83

Individual z-scores for these behavioural tests (as well as d' scores for the ONT) are shown in Table 1 for all twelve participants with DP. The z-scores shown in Table 1 were computed on the basis of control group scores, as reported in the original articles where these tests were first described. As expected, all DPs performed poorly in the three face recognition tests (CFMT, FFT, and ONT). Because impaired face recognition is the defining feature of DP, the criterion employed to classify a particular individual as DP and include them in the present study was that their performance in at least two of the three face recognition tests (FFT, CFMT, ONT) was below -2 z-scores of the mean. All DPs were strongly impaired (z-scores below -4) in the FFT, and eleven of the twelve DPs tested had z-scores below -2 in the CFMT and ONT. In contrast, only three DPs had a z-score of below -2 in the CFPT with upright faces, and only one in the CFPT with inverted faces. Importantly, all participants with DP performed within the

normal range in the RMET, suggesting that none of them were impaired in their ability to recognize emotional expression. All control participants reported that they were confident in their face recognition abilities. All scored above -1 standard deviation of the mean on the CFMT (mean raw score: 62, range 52-70; maximum possible score: 72). In the DP group, the mean CFMT score was 36 (range 28-48).

2.2. Stimuli and Procedure

Stimuli and experimental procedures were identical to our previous study (Fisher et al., 2016a). Stimuli were black-and-white photographs of six different male faces taken from the NimStim database (Tottenham et al., 2009). In each photograph, the actor showed a happy, fearful, or neutral facial expression. There were two different versions (mouth-open or mouth-closed) for each individual person and facial expression, resulting in a total of 36 different face images (see Figure 1 for examples). External facial features were removed from all face images, and the average luminance of all images was equated (22 cd/m^2), using Adobe Photoshop. All stimuli were presented at the centre of a CRT monitor at a viewing distance of approximately 100 cm against a grey background (15 cd/m^2). On each trial, two face images (S1 and S2) were presented in succession. To avoid repetitions of physically identical images and thus identical retinal stimulation on trials where S1 and S2 images showed the same identity and emotion, all S2 images were 10% larger than the S1 images (4.68º x 6.09º versus 4.25º x 5.67º). Furthermore, all S1-S2 stimulus pairs differed with respect to their features in the mouth region (mouth-open followed by mouth-closed, or vice versa; see Figure 1). Stimulus presentation and response collection was controlled with the Cogent 2000 toolbox (www.vislab.ucl.ac.uk/Cogent/) for MATLAB (Mathworks, Inc.).

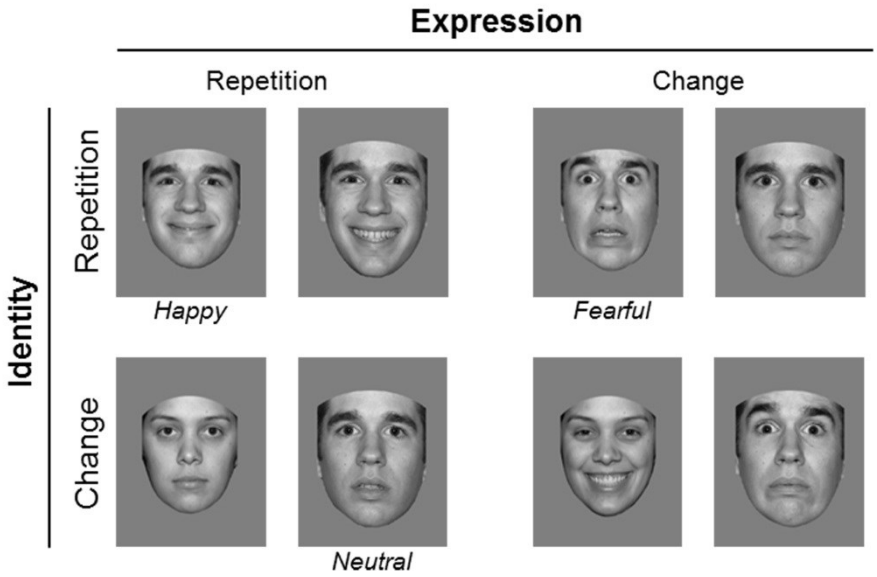


Figure 1. Examples of face stimuli pairs shown on different trials. In different blocks, participants had to match either the identity or the expression of two successively presented faces, and to ignore repetitions or changes in the other currently irrelevant dimension. On each trial, two different versions of face images (mouth-open or mouth-closed) were shown, and the second face was 10% larger than the first face. The top row shows identity repetition trials, and the bottom row identity change trials. Expression repetition and expression change trials are shown on the left and right, respectively.

On each trial, the S1 face was presented for 300ms, followed by a jittered inter-stimulus interval of 200-300ms, and the S2 face (300ms duration). The interval between successive trials was varied randomly between 1400ms and 1500ms. On each trial, the identity and the expression of the S1 face could either be the same or differ from the identity and expression of the S2 face. These two factors were varied orthogonally and randomly across trials, resulting in four equiprobable trial types (identity repetition/expression repetition (IRER); identity repetition/expression change (IREC); identity change/expression repetition (ICER); identity change/expression change (ICEC); see Figure 1). There were two blocked task conditions

(identity task and expression task). Each task consisted of 504 trials (126 trials for each of the four different trial types), and was performed in 8 consecutive blocks (63 trials per block). There was a rest period after each block, and participants initiated the next block by pressing a response button.

In the identity task, participants had to respond to an identity repetition or change between the S1 and S2 face by pressing one of two response buttons, and to ignore expression repetitions or change between these two faces. In the expression task, they had to respond to an expression repetition or change, and to ignore repetitions versus changes of facial identity. Responses were made with the index and middle finger, and the response-hand was counterbalanced across participants. Images of three different individuals with three different emotional expressions were shown in two different versions (mouth-open or mouth-closed) in each of the two tasks, resulting in 18 face images for the identity task, and 18 different face images for the expression task. The order in which the two tasks were performed was counterbalanced across participants within both the DP and Control groups. Participants completed one training block of 30 trials at the start of each task.

2.3. EEG recording and analyses

EEG was recorded using a BrainAmps DC amplifier with a 40Hz low-pass filter and a sampling rate of 500Hz 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 5kΩ. The EEG was epoched from 100ms before to 400ms after the onset of the second face image (S2) on each trial. Epochs with HEOG activity exceeding ±30μV (horizontal eye movements), activity at Fpz exceeding ±60μV (blinks and vertical eye movements), and voltages at any electrode exceeding

±80μV (movement artefacts) were removed from analysis. EEG was averaged relative to a baseline between 50ms prior to 50ms after S2 onset, for each combination of Identity (repetition versus change), Expression (repetition versus change), separately for the identity task and the expression task. Only trials with correct responses were included in the main ERP analyses.

N250r components were quantified on the basis of ERP mean amplitudes calculated during a window from 220 ms to 320 ms after S2 onset. ERP mean amplitudes were computed for four posterior electrodes over the right hemisphere (P8, PO8, P10 and P10), and for the equivalent four electrodes over the left hemisphere (P7, PO7, P9 and PO9). Mean amplitudes were then averaged separately for the four left-hemisphere and right-hemisphere electrodes. Repeated-measures ANOVAs were conducted on these mean amplitude values for the factors Group (DP versus Control), Identity (repetition versus change), Expression (repetition versus change), and Hemisphere (left versus right), separately for the identity and expression tasks. An additional ANOVA was conducted across both tasks, with Task (identity versus expression task) as an additional factor. Analogous analyses were conducted on behavioural performance measures (error rates and reaction times). When significant interactions between Identity and Expression were found in these analyses, these interactions were further explored with follow-up t-tests. Bonferroni corrections for multiple comparisons were applied when appropriate. Additional analyses were also conducted for N170 components in response to S2 faces. These were based on ERP mean amplitudes measured between 150 and 200 ms after S2 onset at the same four electrode pairs that were used for the N250r analyses.

To evaluate whether N250r components were reliable at the level of individual participants, additional analyses of individual ERP waveforms were conducted, using a non-parametric bootstrap procedure (Di Nocera & Ferlazzo, 2000). With this procedure, the reliability of ERP amplitude differences between two 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 was

repeated 10,000 times in the current study, resulting in a distribution of difference values with a mean value of zero, as both sample pairs were drawn from the same dataset. Based on this distribution, the reliability of an empirically observed ERP difference between conditions was 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, et al. 2012; Oruc et al., 2011; Towler et al., 2012; Towler et al. 2016; Fisher et al., 2016b, for previous applications of this procedure in ERP studies of prosopagnosia). In the present experiment, this bootstrap procedure was based on EEG mean amplitudes obtained between 220 and 320 ms after S2 onset on identity repetition and identity change trials where facial expression was repeated (collapsed the eight lateral posterior electrodes over the left and right hemisphere). Separate bootstrap analyses were conducted for the identity and expression tasks, for each participant with DP and each control participant.

3. Results

3.1 Behaviour

Figure 2 shows error rates and reaction times (RTs) for the four different trial types in the identity task (top panels) and expression task (bottom panels), separately for the DP group and the Control group. In order to test whether DPs were selectively impaired relative to Controls in a face matching task where identity is task-relevant, and whether this was also the case when they had to match emotional expression, analyses of error rates and reaction times were first conducted separately for the identity and expression tasks, with factors Group (DP, Control), Identity (repetition, change) and Expression (repetition, change). Additional analyses were then conducted across both matching tasks, with Task (identity, expression) as an additional factor.

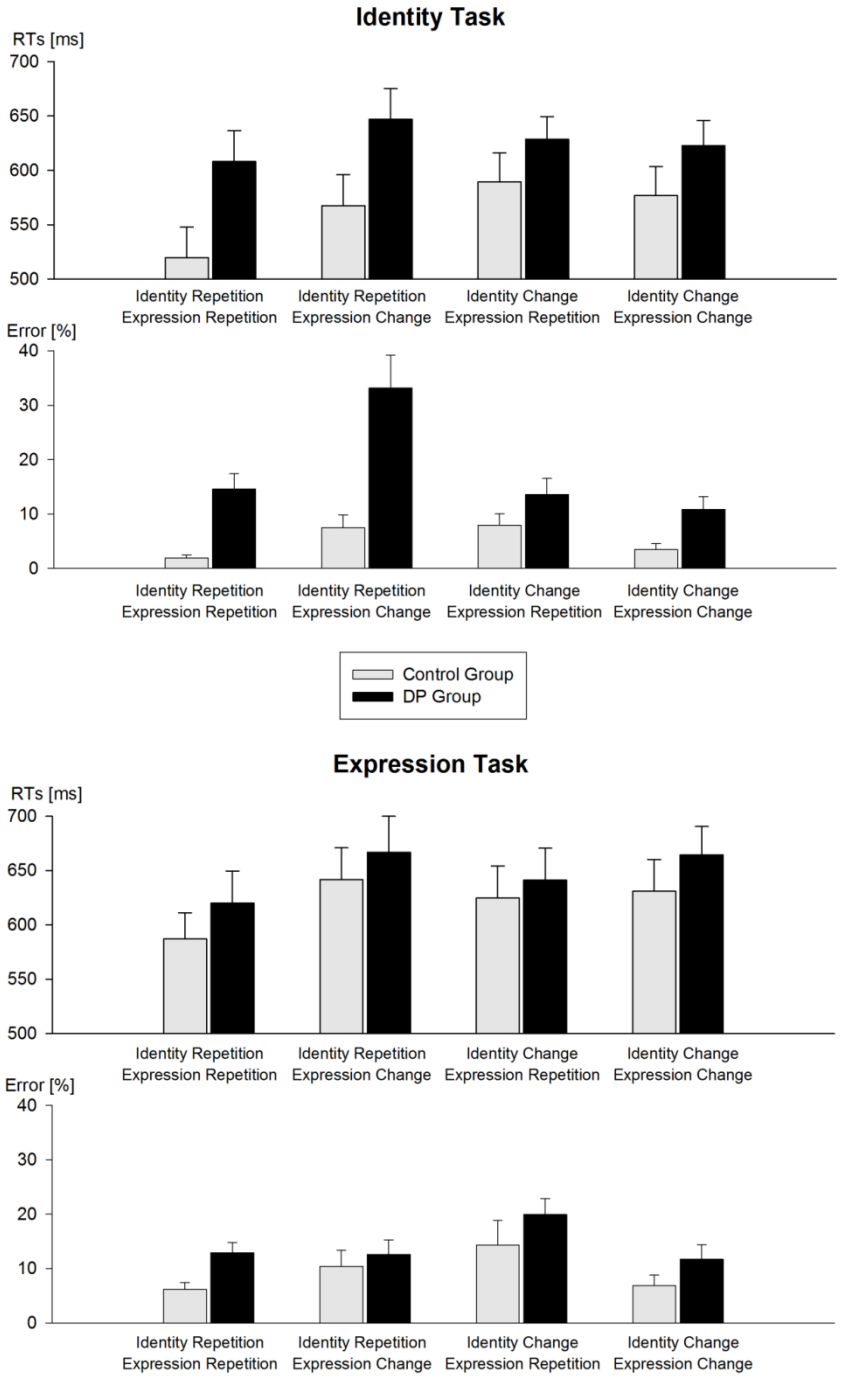


Figure 2. Mean reaction times and error percentages in the identity task (top panels) and the expression task (bottom panels), for the Control group (grey bars) and the DP group (black bars). Results are shown separately for each of the four combinations of identity (repetition versus change) and expression (repetition versus change). Error bars depict standard errors of the mean.

3.1.1 Error rates

Identity task. Participants with DP performed significantly worse than Controls, with an overall error rate of 18% as compared to 5% ($F(1,22)=23.47$, $p<.001$, $\eta_p^2=.52$). This was also reflected in d' values, which were reliably lower for DPs relative to Controls (2.12 versus 3.49; $t(22)=4.32$, $p<.001$). There was also an interaction between Group and Identity ($F(1,22)=5.59$, $p<.03$, $\eta_p^2=.20$). Participants with DP were more likely to incorrectly report an identity change on identity repetition trials than to incorrectly report an identity repetition on identity change trials (24% versus 12%), whereas there was no such difference for the Control group (5% versus 6%). As a result, the DP group showed a response bias towards "different" judgments, whereas this was not the case for control participants (C = 0.25 versus -.03; $t(22)=2.2$, $p<.04$). In addition, there was also an interaction between Group and Expression ($F(1,20)=6.38$, $p<.02$, $\eta_p^2=.23$). DPs made more errors on expression change trials relative to expression repetition trials (21% versus 14%), while no such difference was found for the Control Group (5% errors on both types of trials). Finally, a significant three-way interaction between Group, Identity and Expression was present ($F(1,22)=5.10$, $p<.04$, $\eta_p^2=.19$). To further explore this interaction, separate ANOVAs were carried out for both groups, with the factors Identity (repetition, change), and Expression (repetition, change). Both groups demonstrated significant interactions between Identity and Expression (Controls: $F(1,11)=14.03$, $p<.003$, $\eta_p^2=.56$; DPs: $F(1,11)=27.28$, $p<.001$, $\eta_p^2=.71$). This was due to an impairment in detecting identity repetitions when expression changed relative to trials where expression repeated, which was present both for Controls (8% versus 2% errors $t(11)=2.35$, $p<.04$) and DPs (33% versus 14% errors; $t(11)=4.52$, $p<.001$). A between-groups comparison demonstrated that this increase in identity matching errors across changes of expression was significantly larger in the DP group relative to the Control group (19% versus 6%; $t(22)=2.7$, $p<.02$). On identity change trials, a repetition of the task-irrelevant expression resulted in more errors in the Control group (8% versus 3% for

expression change versus expression repetition trials ($t(11)=2.81$, $p<.02$). In the DP group, there was a similar tendency for more errors on trials where an identity change was accompanied by an expression repetition, but this difference was not reliable (14% versus 11%; $t(11)=1.6$, $p=.14$).

Expression task. There was no reliable differences between DPs and Controls in their ability to match facial expression, with error rates of 10% for Control group and 14% for the DP group ($F(1,22)=2.21$, $p=.16$). Perceptual sensitivity (d') and response bias (C) did not differ between DPs and Control participants (d': 2.3 versus 2.99; $t<1.80$, $p=.09$; C: .11 versus .06; $t<1$). No reliable two-way interactions with Group and either Identity or Expression, or three-way interaction with all factors were found (all $F<1.25$). There was an interaction between Identity and Expression ($F(1,22)=11.82$, $p<.002$, $\eta_p^2=.35$), reflecting impaired expression matching performance when identity changed than when it repeated (17% versus 9%; $t(23)=3.86$, $p<.001$). Error rates on expression change trials were higher when identity was repeated than when identity changed (12% versus 9%), but this difference only approached significance ($t(1,23)=1.87$, $p=.07$).

Analysis across both tasks. In the overall analysis where Task was included as an additional factor, a significant interaction between Group and Task emerged ($F(1,22)=4.80$, $p<.04$, $\eta_p^2=.18$), reflecting the fact that DPs were less accurate than controls in the identity task but not in the expression task. There were also three-way interactions between Group, Task, and Identity ($F(1,22)=6.21$, $p<.03$ $\eta_p^2=.22$), and between Group, Task, and Expression ($F(1,22)=6.43$, $p<.02$ $\eta_p^2=.23$), reflecting the fact that the performance impairments for the DP group in the Identity task were most pronounced on trials where an identity match had to be detected, and when this match was accompanied by a change in facial expression. To further investigate this, the impairments produced in both tasks by a change in the currently irrelevant attribute on trials where there was a match in the relevant dimension were assessed separately for both groups. For

DPs, there were asymmetric interference effects. In the identity task, expression changes increased error rates relative to expression repetitions on match trials by 19%, whereas identity changes versus repetitions increased error rates on expression match trials in the expression task by only 7%, and this difference was reliable ($t(11)=2.34$, $p<.04$). In the Control group, symmetrical interference effects were found, as the increase in error rates on match trials triggered by a change in the irrelevant attribute did not differ between the identity and expression tasks (6% versus 8%; $t < 1$).

3.1.2 Reaction Times

Identity task. There was no overall significant RT difference between DPs and Controls in this task (627 ms versus 563 ms; $F(1,22)=3.01$, $p=.1$). However, there was an interaction between Group and Identity ($F(1,22)=5.94$, $p<.03$, $\eta_p^2=.21$). On identity repetition trials, RTs were delayed in the DP group relative to the Control Group (628 ms versus 543 ms; $t(22)=2.11$, $p<.05$). On identity change trials, this RT delay for the DP group was smaller (626 ms versus 583 ms) and not statistically reliable ($t(22)=1.24$, $p<.3$). There was no interaction between Group and Expression, and no three way interaction between Group, Identity, and Expression, both $F<1.7$ for RTs, suggesting that task-irrelevant repetitions or changes of expression did not differentially effect the groups' response times. Across both groups, a highly significant interaction between Identity and Expression ($F(1,22)=71.88$, $p<.001$, $\eta_p^2=.77$) reflected the fact that RTs on identity repetition trials were slower when expression changed than when it repeated (607 ms versus 564 ms; $t(1,23)=9.72$, $p<.001$), while RTs on identity change trials were faster when expression also changed than when it repeated (600 ms versus 609 ms; $t(23)=2.71$, $p<.02$).

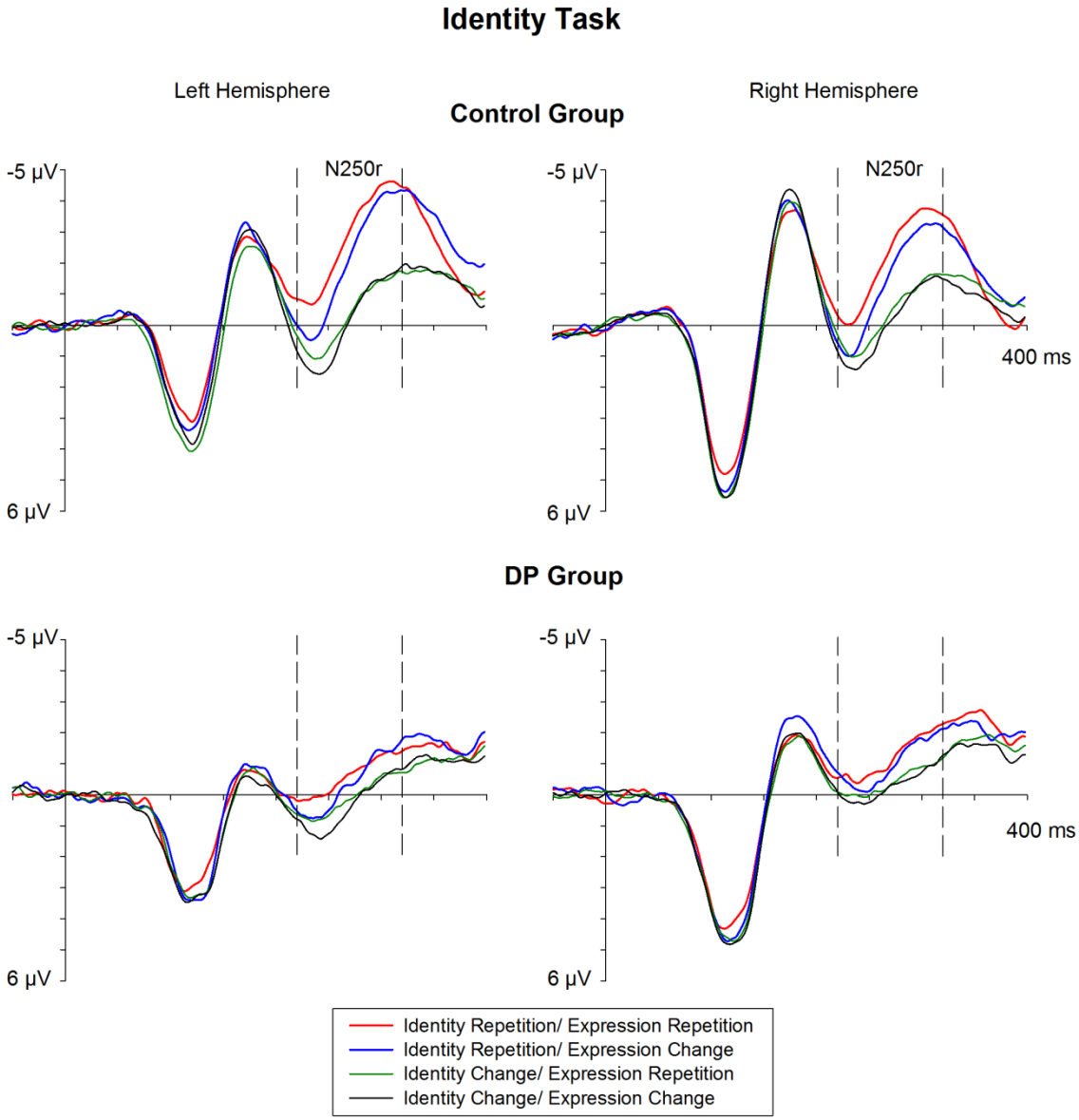
Expression task. RTs in this task did not differ significantly between DPs and Controls (648 ms versus 621 ms; $F<1$). There were also no interactions involving the factor Group, all

$F<2$. Across both groups, there was again an interaction between Identity and Expression, ($F(1,22)=16.93$, $p<.001$, $\eta_p^2=.44$), reflecting delayed RTs on expression repetition trials when identity changed than when it was repeated (632 ms versus 603 ms; $t(1,23)=4.75$, $p<.001$). RTs on expression change trials were also numerically slower when identity was repeated than when it changed, but this difference was not significant (654 ms versus 647 ms; $t(1,23)=1.3$, $p=.2$).

Analysis across both tasks. In the overall analysis with Task as an additional factor, a main effect of Task ($F(1,22)=9.05$, $p<.01$, $\eta_p^2=.29$) reflected the fact that RTs were generally faster in the identity task than in the expression task (595 ms versus 634 ms). There was no significant interaction between Task and Group, $F<2$. However, the interaction between Group, Task and Identity was reliable ($F(1,22)=4.40$, $p<.05$, $\eta_p^2=.17$), confirming that the RT delay in the DP group was most pronounced on identity repetition trials in the identity task.

3.2. N250r components

Figure 3 shows ERPs elicited in the identity task at lateral posterior electrodes over the left and right hemispheres for the four different trial types, separately for the Control Group (top panel) and the DP group (bottom panel), together with the scalp topographies of the N250r component. The corresponding ERP waveforms for the expression task are shown in Figure 6. N250r amplitudes were strongly reduced for DPs as compared to control participants, but showed the same typical scalp distribution in both groups, with a lateral posterior negativity accompanied by a more broadly distributed frontocentral positivity. ERPs were initially analysed separately for the two tasks, followed by an overall analysis across both tasks.


Identity Task
Left Hemisphere
Right Hemisphere
Control Group
-5 µV
N250r
6 µV
400 ms
DP Group
Identity Repetition/ Expression Repetition
Identity Repetition/ Expression Change
Identity Change/ Expression Repetition
Identity Change/ Expression Change

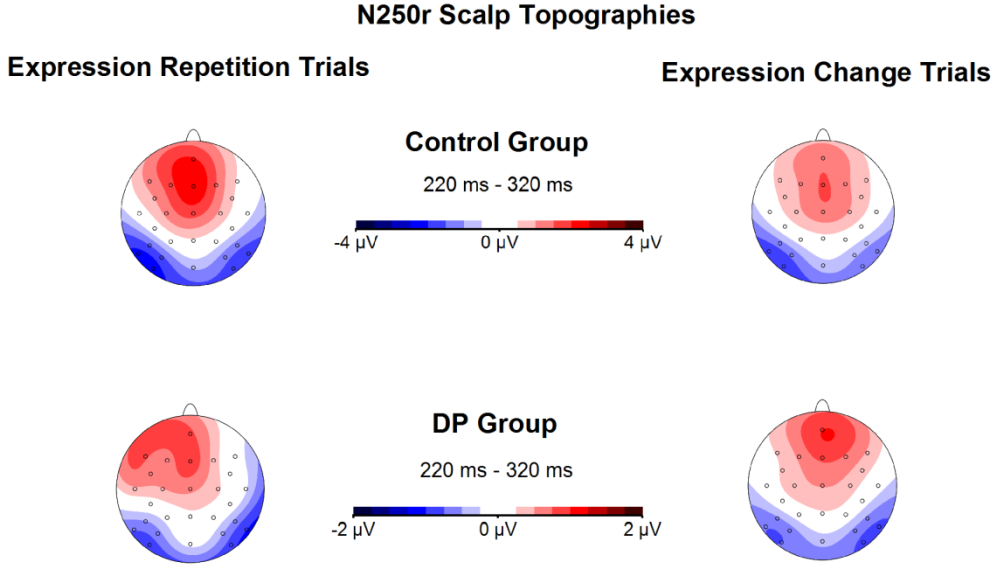

N250r Scalp Topographies
Expression Repetition Trials
Expression Change Trials
Control Group
220 ms - 320 ms
-4 µV
0 µV
4 µV
DP Group
220 ms - 320 ms
-2 µV
0 µV
2 µV

Figure 3. Top panels: Grand-averaged ERPs elicited at lateral posterior electrodes over the left and right hemisphere during the 400 ms interval after the onset of the S2 face in the identity task, shown separately for the Control group (top panel) and the DP group (bottom panel). ERPs were averaged across four electrodes over the left (P7, PO7, P9 and PO9) and right hemisphere (P8, PO8, P10 and PO10). Waveforms are shown separately for each of the four combinations of identity repetition versus change and expression repetition versus change. Bottom panel: Scalp distribution of N250r components in the identity task on expression repetition and expression change trials, for the Control group and the DP group. These topographic maps were generated by subtracting ERP mean amplitudes in the 220-320 ms post-stimulus time window on identity change trials from ERPs on identity repetition trials. Note the different voltage scales for the two groups.

Identity task. Across both groups, there was a significant effect of Identity ($F(1,22)= 31.08$, $p<.001$, $\eta_p^2=.59$), with more negative lateral posterior ERPs on identity repetition as compared to identity change trials during the 220 – 320 ms time window after S2 onset, reflecting the presence of N250r components on trials where the identity of the S2 face matched the identity of the preceding S1 faces. Importantly, there was a significant interaction between Group and Identity ($F(1,22)=6.20$, $p<.03$, $\eta_p^2=.22$). As can be seen in Figure 3, N250r components were much larger in the Control group than in the DP group. The overall mean amplitude difference between identity repetition and identity change trials was -1.90 μV for control participants, and -.73 μV for participants with DP. These components showed the characteristic scalp topography in both groups, with a lateral posterior negativity accompanied by

an anterior positivity (see Figure 3, bottom panel; note the different voltage scales for the two groups to account for the reduced size of the N250r in the DP group).

To investigate whether a reliable N250r was elicited at all in the DP group, separate analyses were conducted for both groups. As expected, there was a highly significant main effect of Identity ($F(1,11)=19.47$, $p<.001$, $\eta_p^2=.64$) in the Control group. An interaction between Identity and Hemisphere ($F(1,11)=10.02$, $p<.01$, $\eta_p^2=.48$), was due to the fact that N250r components to identity repetitions versus changes were larger over the left relative to the right hemisphere in Controls (-2.22 μV versus -1.59 μV). There were no other interactions involving the factor Hemisphere, both $F<1$. In addition, there was a strong trend towards an interaction between Identity and Expression ($F(1,11)=4.70$, $p=.053$, $\eta_p^2=.30$) in the Control group. N250r components to identity repetitions tended to be larger when expression also repeated relative to trials where expression changed (see Figure 3), although reliable N250r components were present both on expression repetition trials ($t(11)=5.25$ $p<.002$) and on expression change trials ($t(11)=3.44$ $p<.01$). Critically, a reliable a main effect of Identity was also found for the DP group ($F(1,11)=14.55$, $p<.003$, $\eta_p^2=.57$), demonstrating that N250r components were reliably elicited for this group, albeit in an attenuated fashion. There was no interaction between Identity and Expression ($F<1$) in the DP group. Reliable N250r components were observed for participants with DP both on trials where expression was also repeated ($t(11)=4.36$ $p<.002$) and trials where expression changed ($t(11)=2.86$ $p<.02$). Finally, and unlike the Controls, DPs showed no interaction between Identity and Hemisphere ($F<1$). The presence of a left-hemisphere bias of the N250r component in the Control group and the absence of such a bias in the DP group was also reflected by significant interaction between Group, Identity, and Hemisphere ($F(1,22)=6.00$, $p<.03$, $\eta_p^2=.21$) in the overall analysis across both groups.

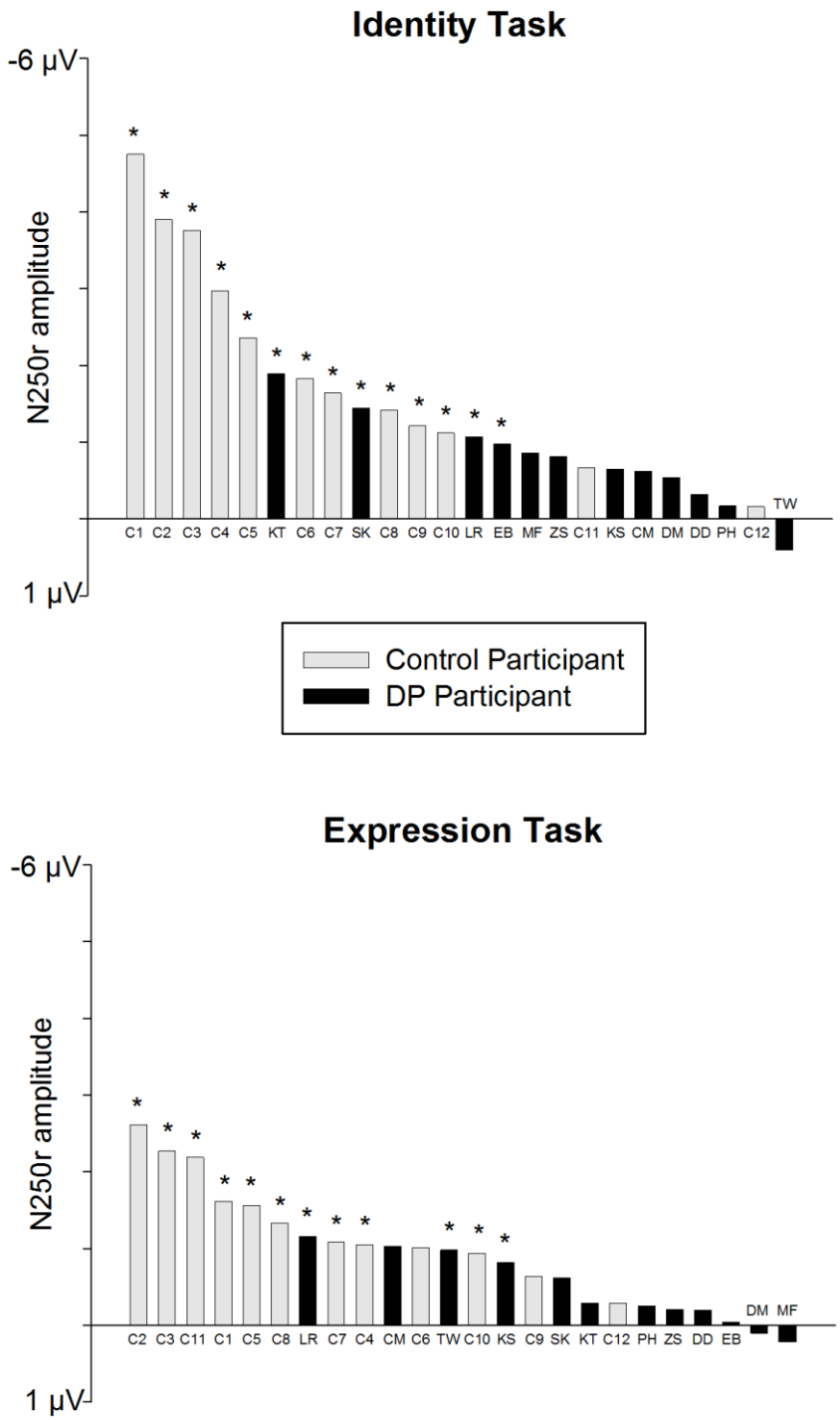


Figure 4. N250r amplitudes for individual participants with DP (black bars) and control participants (grey bars) in the identity task (top panel) and the expression task (bottom panel). These amplitude values were calculated by

subtracting ERP mean amplitudes in the N250r time window on identity change trials from mean amplitudes on identity repetition trials (for trials where expression was repeated), and collapsed across all eight lateral posterior electrodes over the left and right hemispheres. Individual DP participants are labelled with their initials, corresponding to Table 1. Asterisks indicate reliable N250r components, as determined by bootstrap analyses.

Figure 4 (top panel) shows N250r mean amplitudes for identity repetitions versus changes on trials where facial expression was repeated (collapsed across hemispheres) for each individual participant with DP (black bars) and each control participant (grey bars), ordered from left to right as a function of the size of individual N250r components. As can be seen from this figure, control participants tended to cluster on the left, and DPs on the right, reflecting the overall attenuation of N250r components in the DP group. There was however some overlap between the two groups, with some DPs showing N250r amplitudes in the normal range, and some control participants with small N250r components. The presence of significant N250r components at the level of individual participants, as determined with a non-parametric bootstrap analysis (Di Nocera & Ferlazzo, 2000), is indicated in Figure 4 by asterisks. Ten of the twelve control participants tested showed a reliable N250r to task-relevant face identity repetitions. In contrast, only four of the twelve DPs had a significant N250r.

To assess whether the size of these individual N250r components was associated with participants' face recognition performance in the CFMT, raw CFMT scores were correlated with individual N250r mean amplitudes on expression repetition trials in the identity task (computed by subtracting ERPs on identity change trials from ERPs on identity repetition trials). Across all participants tested, there was a reliable correlation between N250r amplitude and performance on the CFMT (r=.68, p<.001). This is illustrated in Figure 5, where scores for DP participants are shown in black, and scores for control participants in grey. Larger N250r components were

associated with better CFMT performance. This correlation remained reliable when only participants with DP were considered (r=.71, p<.01). A similar link between N250r amplitudes and CFMT scores was also apparent for Control participants, but this correlation was not significant (r=.44, p=.15). Analogous results were obtained when N250r components to identity repetitions versus changes were collapsed across expression repetition and expression change trials. Again, N250r amplitudes correlated with CFMT performance across all participants (r=.61, p<.001) and when only participants with DP were considered (r=.60, p<.05). In addition to predicting the performance of participants with DP in the CFMT, N250r mean amplitudes on expression repetition trials in the identity task for the DP group were also reliably correlated with performance in the CFPT (collapsed across upright and inverted faces; r=.61, p<.04). There was also a nearly significant correlation between N250r amplitudes and ONT performance for DPs (r=.55, p=.07), whereas no reliable correlation was found with FFT scores (r=.33, p=.3).

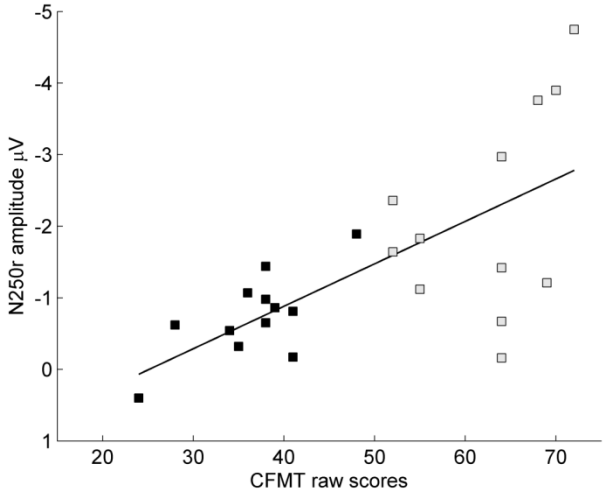
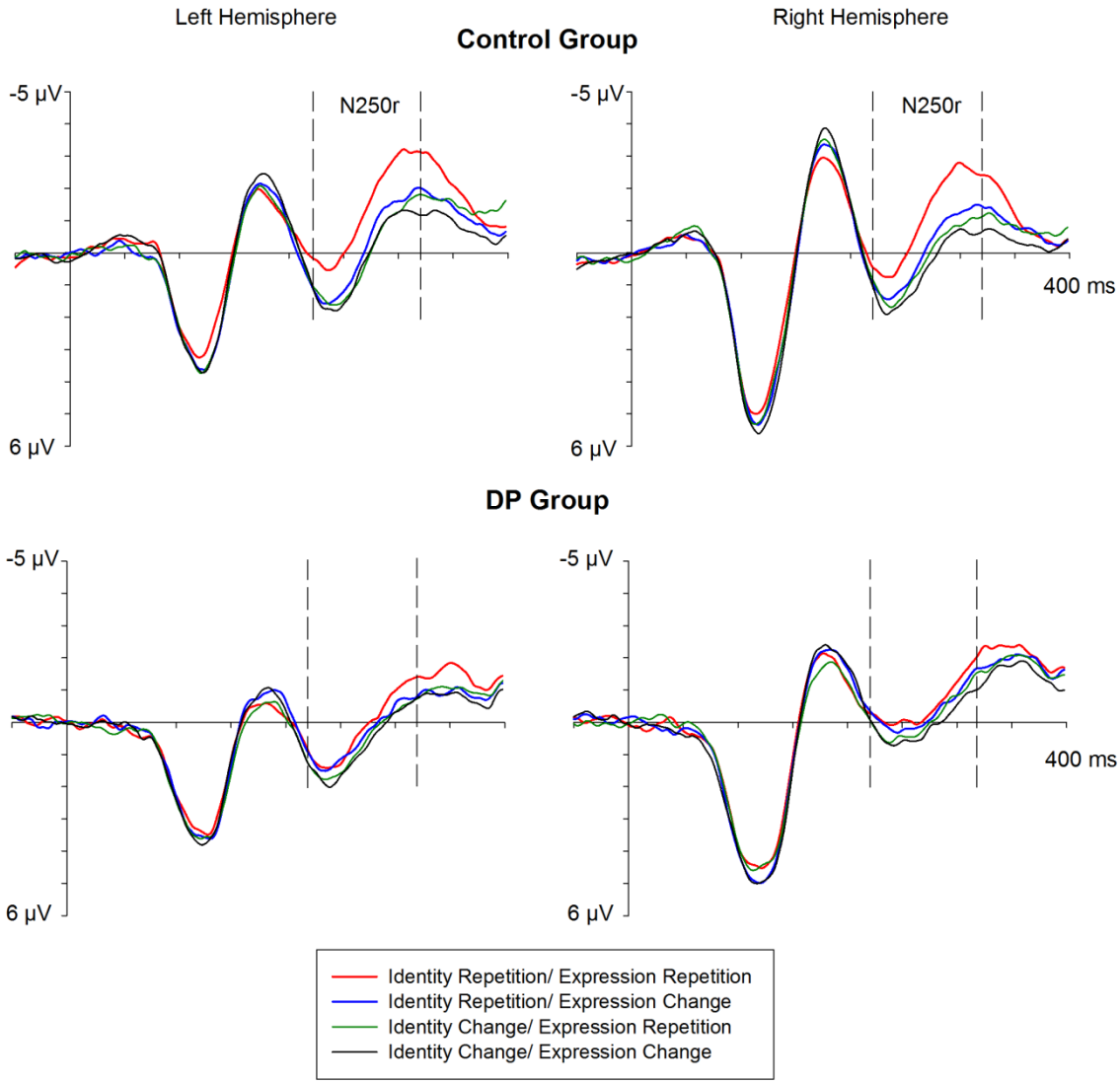


Figure 5. Correlation between individual performance in the Cambridge Face Memory Test (CFMT) and N250r amplitudes to identity repetitions versus changes on expression repetition trials in the identity task. DP participants are represented by black squares, and control participants by grey squares.

Expression Task



N250r Scalp Topographies

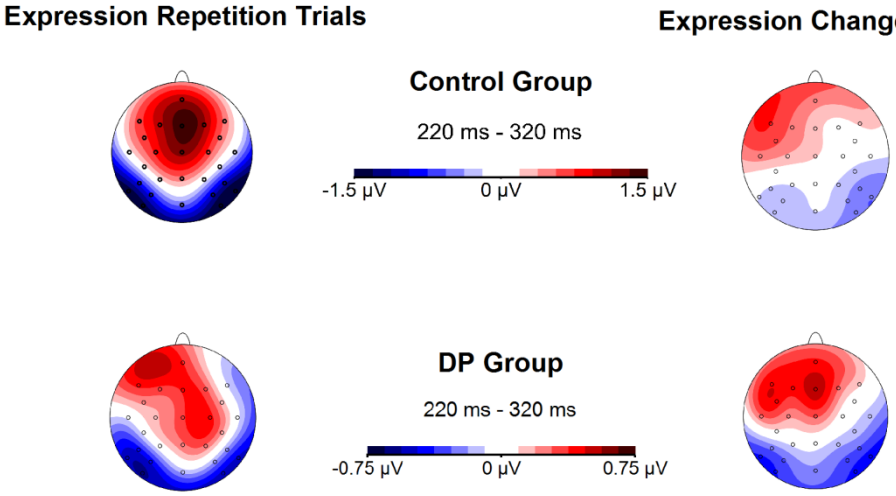


Figure 6. Top panels: Grand-averaged ERPs elicited at lateral posterior electrodes over the left hemisphere (P7, PO7, P9 and PO9) and right hemisphere (P8, PO8, P10 and PO10) during the 400 ms interval after the onset of the S2 face in the expression task, shown separately for the Control group (top panel) and the DP group (bottom panel). Waveforms are shown separately for each of the four combinations of identity repetition versus change and expression repetition versus change. Bottom panel: Scalp distribution of N250r components in the expression task on expression repetition and expression change trials, for the Control group and the DP group. These topographic maps were generated by subtracting ERP mean amplitudes in the 220-320 ms post-stimulus time window on identity change trials from ERPs on identity repetition trials. Note the different voltage scales for the two groups.

Expression task. Even though identity was irrelevant, N250r components were still elicited in response to identity repetitions versus changes (see Figure 6), demonstrating that facial identity was processed and maintained when participants' matched the expression of face pairs. Across both groups, a significant main effect of Identity ($F(1,22)=45.15$, $p<.001$, $\eta_p^2=.67$) was present, which confirms that N250r components were reliably present in the expression task. Importantly, and analogous to the results from the identity task, there was an interaction between Group and Identity ($F(1,22)=6.97$, $p<.02$, $\eta_p^2=.24$), which confirmed that N250r amplitudes were attenuated in the DP group relative to the Control group in this task (-.40 μV versus -.93 μV). This is further illustrated in Figure 4 (bottom panel, which shows N250r mean amplitudes for identity repetitions versus changes in the expression task on trials where facial expression was repeated (collapsed across hemispheres) in the expression task for each individual DP and control participant (black versus grey bars). As was the case in the identity task, control

participants clustered on the left (larger N250r components) and DPs on the right (smaller N250r amplitudes), reflecting the general attenuation of the N250r in the DP group. A non-parametric bootstrap analysis showed that ten of the twelve control participants but only three of the twelve DPs showed a significant N250r components to identity repetitions in the expression task (as indicated by asterisks in Figure 4, bottom panel).

Analyses conducted separately for the two groups revealed a significant main effect of Identity in the Control group ($F(1,11)=32.68$, $p<.001$, $\eta_p^2=.75$), confirming the presence of N250r components in the expression task. For this group, there was also an interaction between Identity and Expression ($F(1,11)=16.44$, $p<.002$, $\eta_p^2=.60$), as N250r components were considerably larger on trials where expression was repeated (-1.38 μV; $t(11)=6.87$, $p<.002$), than on expression change trials (-.47 μV; $t(11)=2.42$, $p<.03$). Importantly, a significant main effect of Identity was also found for the DP group ($F(1,11)=12.61$, $p<.005$, $\eta_p^2=.53$), confirming that an N250r component was triggered by identity repetitions in this group even though identity was task-irrelevant. The scalp maps in Figure 6 (bottom panel) show that the topography of the N250r component was similar in both groups (note the different voltage scales for the Control and DP groups). There was no interaction between Identity and Expression for the DP group ($F<1$), suggesting that in contrast to the N250r in Controls, the small N250r component elicited by identity repetitions in the DP group was not affected by repetitions versus changes of facial expression. This difference between the two groups was also reflected by a three-way interaction between Group, Identity, and Expression ($F(1,22)=7.44$, $p<.02$, $\eta_p^2=.25$) in the overall analysis conducted across both groups.

Analysis across both tasks. When ERP mean amplitudes during the N250r time windows from both tasks were analysed together, an interaction between Task and Identity was present ($F(1,22)=10.93$ $p<.003$, $\eta_p^2=.33$), as N250r components were generally larger in the identity task than in the expression task. Furthermore, there was a significant interaction between Group and

Identity ($F(1,22)=7.82$, $p<.02$, $\eta_p^2=.26$), again demonstrating that N250r components were attenuated in the DP group relative to the control group. Importantly, there was no three-way interaction between Task, Group, and Identity $F(1,22)=2.75$, $p=.11$, which shows that this attenuation of N250r amplitudes in the DP group was present regardless of whether facial identity was task-relevant or had to be ignored.

3.3. N170 components

To assess any effects of our experimental manipulation on N170 components to S2 faces, N170 mean amplitudes (measured between 150 and 200 ms after S2 onset) were analysed, separately for the identity and expression tasks, with the factors Group, Identity, Expression and Hemisphere. In the identity task, there were no significant main effects or interactions (all $F < 4.1$). In the expression task, a significant main effect of Expression was found for N170 amplitude ($F(1,22)=5.47$, $p<.03$, $\eta_p^2=.2$), which was 0.25 μV larger on expression change as compared to expression repetition trials (-1.5 μV versus -1.25 μV). However, there was no interaction between Expression and Group, and no other reliable main effect or interaction (all $F < 2.7$).

4. Discussion

The goal of the present study was to test whether face recognition impairments in DP are linked to a selective deficit in matching representations of facial identity in visual working memory with perceptual representations of currently seen faces. In two task conditions, participants with DP and age-matched control participants had to match either the identity or

the expression of two successively presented face images, and to ignore repetitions or changes of the other currently task-irrelevant attribute.

The behavioural results provided clear evidence that DPs have a selective deficit in matching facial identity. Participants with DP were much less accurate than control participants in the identity task, but performed at the same level as controls in the expression task. The same pattern was also found for d' as a measure of perceptual sensitivity. This dissociation is in line with previous observations that the recognition of facial expression is generally unimpaired in DP (e.g., Duchaine et al., 2003, 2007; Palermo et al., 2011), and also supports cognitive and neural models which assume that the processing of facial identity and expression are mediated by anatomically and functionally distinct systems (e.g., Bruce & Young, 1986; Haxby et al., 2000). The performance deficits for DPs in the identity task were particularly pronounced on trials where the two faces had the same identity, where participants with DP were both slower and less accurate than controls participants. As a result, DPs showed a bias towards more frequent "different" responses relative to Controls in the identity task. However, no difference in response bias between DPs and control participants was found in the expression task, showing that there was no general more conservative response bias in the DP group. Recent work on unfamiliar face recognition in participants with unimpaired face processing abilities (Andrews, Jenkins, Cursiter, & Burton, 2015; Burton, Kramer, Ritchie & Jenkins, 2015) has highlighted the importance of distinguishing the effects of within-person variability, which provides cues to identity during face learning but can be a source for error when images of the same individual have to be matched, and between-person variability, which is the basis for telling faces of different individuals apart. The fact that DPs were specifically impaired in reporting identity repetitions in the present study suggests that they have a selective deficit in utilizing within-person variability to recognise an individual face, and in discounting variability between face images that is unrelated to identity. To investigate whether impairments in reporting an identity match in participants with DP group had a more general impact on their face recognition

abilities, we correlated error rates on identity match trials and performance on the CFMT. A significant negative correlation was obtained (r=-.72, p<.01), showing that DPs who were less accurate in detecting identity repetitions also performed worse in the CFMT. Interestingly, no such link was found when individual error rates on identity change trials were correlated with CFMT scores for DP participants (r=-.32, p=.32), which suggests that the face recognition deficit in DP might be primarily associated with difficulties in discounting within-person variability. In line with this interpretation, Garner interference effects from changes in the currently irrelevant dimension on error rates were symmetrical across both tasks for control participants, but were asymmetrical in the DP group. For DPs, changes in facial expression interfered more strongly with their ability to match face identity relative to the effects of irrelevant identity changes in the identity task. On one third of all trials where an identity repetition was accompanied by an expression change, DPs incorrectly reported that the face pair showed two different individuals. This shows that it is clearly wrong to assume that all faces look the same for individuals with DP. In contrast, it appears as if DPs tend to perceive face images as different even when they belong to the same individual.

If face identity matching processes are impaired in DP, this should be demonstrated by the N250r component, which reflects the activation of working memory representations of individual faces by matching perceptual input (Schweinberger & Burton, 2003). At the cognitive level, the N250r corresponds to the activation of FRUs in visual memory in response to an identity match (e.g., Bruce & Young, 1986). If the ability to activate FRUs in response to identity repetitions was severely disrupted in DP, N250r components might have been entirely absent. This was clearly not the case. In the identity task, N250r components to face identity repetitions were reliably present for the DP group on trials where these repetitions were successfully detected. The presence of N250r components in both Controls and DPs suggests that there are no fundamental qualitative differences in face identity matching processes between DPs and Controls. This conclusion is in line with previous DP studies that investigated the activation of

longer-term memory representations during the recognition of famous faces or previously learned target faces (Eimer et al., 2012; Parketny et al., 2015), and found that such recognition processes give rise to N250 components in participants with DP (see Towler & Eimer, 2012, Towler et al., 2016, for further discussion).

A central finding of the current study was that N250r amplitudes were strongly attenuated for DPs as compared to control participants in the present study. This suggests that the activation level of FRUs triggered by an identity match was generally reduced in DPs. Although this difference in the size of N250r components between DPs and Controls was reliable at the group level, there was considerable variation between individual participants with DP, with a minority of DPs showing N250r amplitudes in the normal range (see Figure 4, top panel). Bootstrap analyses of N250r amplitudes for individual participants showed that only four of the 12 DPs tested had reliable N250r components in the identity task, and only three showed a reliable N250r in the expression task, whereas all except two of the control participants had significant N250r components in the two tasks. Notably, individual N250r amplitudes in the identity task were correlated with face recognition performance, as measured in the CFMT. Participants with higher CFMT scores generally had larger N250r components for identity repetition versus identity change trials (Figure 5), and this correlation was reliable across all participants tested, and also when only participants with DP were considered. For control participants, a similar albeit non-reliable tendency towards links between CFMT scores and N250r amplitudes was found. This suggests that face identity matching processes that are reflected by the N250r in the present study (e.g., the activation of specific FRUs) and the processes involved in successfully detecting a match between a test face and one of several memorized faces in the CFMT may rely on shared mechanisms. A selective impairment in these mechanisms can therefore result both in poor CFMT performance and in reduced N250r amplitudes.

Even though identity was task-irrelevant in the expression task, identity repetitions still triggered small but reliable N250r components in the Control group, in line with previous findings (Fisher et al., 2016a). This suggests that face identity matching processes were activated in a task-independent automatic fashion (see also Zimmermann & Eimer, 2014). Importantly, participants with DP also showed significant N250r components in the expression task, indicating that similar to Controls, they did not completely ignore identity when matching facial expression. This was also underlined by the fact that incongruent identity repetitions or changes interfered with performance in the expression matching task in both groups. As in the identity task, N250r amplitudes were again attenuated in the DP group relative to the Control group in the expression task, with some variability in the size of N250r components between individual DPs (see Figure 4, bottom panel). The fact that the attenuation of N250r components in the DP group was present in both tasks suggests that impairments in the activation of working memory representations by an identity match are unaffected by top-down strategies to selectively attend or ignore the identity of face images. It is important to note that in all trials of the present study, the lower part of the face image pairs was always different (mouth-open versus mouth-closed). As individuals with DP tend to focus more on the mouth than the eye region during the visual exploration of faces (e.g., Bobak, Parris, Gregory, Bennetts & Bate, 2016), this image change may have disproportionally affected face identity matching processes in the DP group, and may have been partly responsible for the reduction of N250r components in this group.

Although N250r components were generally smaller for DPs as compared to control participants, there was no evidence for an additional reduction of N250r amplitudes in the DP group on trials where an identity repetition was accompanied by an expression change. This may seem surprising, as the ability to match facial identity was particularly impaired on these trials in the DP group, with one third of all identity matches incorrectly reported as identity changes (see above). It is important to note that the N250r components for the identity task (as shown in Figure 3) were all based on trials with correct responses, and thus cannot provide direct insights

into why DPs often failed to report identity repetitions on expression change trials. One possibility is that a face identity match was not registered at all on these trials. Another possibility is that such a match was in fact detected, triggering an activation of corresponding FRUs in visual memory, but that this did not result in an explicit report of an identity repetition. To investigate this, we computed additional ERPs for the DP group, based on identity repetition/expression change trials with incorrect responses in the identity task, and compared them to ERPs for identity change/expression change trials in the same task. One participant with DP (SK) was excluded from this analysis, because their error rate on identity repetition/expression change trials was less than 2%, which is too low to compute meaningful ERPs for these trials. The ERPs for the remaining 11 participants with DP are shown in Figure 7 (collapsed across the lateral posterior electrodes over the left and right hemisphere). As can be seen from this Figure, there was indeed an enhanced negativity in the N250r time range for non-reported face identity repetitions that were accompanied by an expression change relative to trials where both identity and expression changed. The scalp distribution of this difference (shown in Figure 7, right panel) was similar to the typical topography of the N250r component. A comparison of ERP mean amplitudes in the N250r time window (220-320 ms post-stimulus) showed that this difference was reliable ($t(10)=1.85$, $p<.05$, one-tailed).

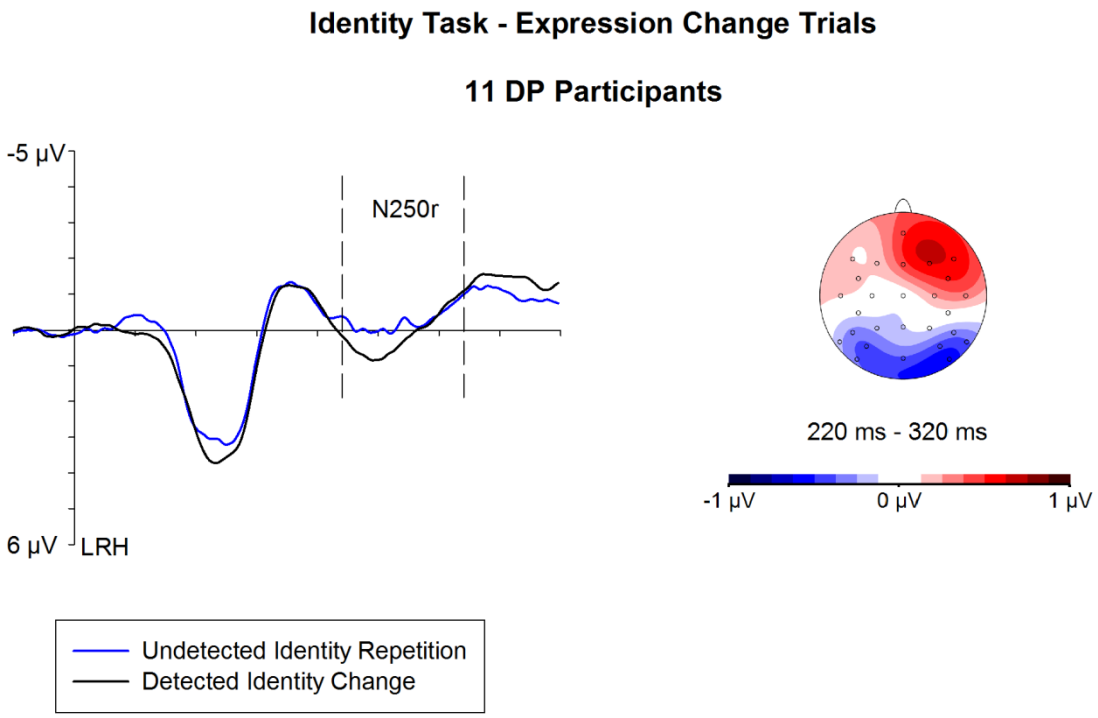


Figure 7. Grand-averaged ERPs elicited at lateral posterior electrodes over the left hemisphere (P7, PO7, P9 and PO9) and right hemisphere (P8, PO8, P10 and PO10) during the 400 ms interval after the onset of the S2 face, on expression change trials in the identity task, for 11 participants with DP in the identity task. ERPs for trials with an undetected identity repetition are shown together with ERPs on trials with a correctly detected identity change. The scalp topography of ERP mean amplitude differences between these two types of trials in the N250r time window is shown on the right.

The presence of an N250r component for undetected face identity repetitions on expression change trials for these DP participants shows that a successful identity match took place on at least some of these trials, but that this was not sufficient for the subsequent conscious detection and report of an identity repetition. This dissociation may be explained in the context of cognitive models of face recognition (Bruce & Young, 1986; Burton, Bruce & Johnston, 1990), which assume that explicit face recognition will take place once the activation

of particular FRUs in visual memory exceeds a certain threshold. The fact that N250r components on trials with correct responses were smaller in the DP group and were reliable only for a minority of individual DPs suggests that FRU activation levels were reduced and more variable across trials for DPs relative to control participants. If average FRU activation levels are generally close to the threshold required for the explicit report of an identity match in DPs, it is likely that they will fall below this threshold on a subset of trials, in particular when there is an expression change between the two faces. On these trials, a below-threshold activation of FRUs will result in a low level of confidence with respect to the presence of an identity repetition, which increases the likelihood that DPs will report an identity change instead.

An unexpected finding of the current study was that N250r components were larger over the left hemisphere in control participants. A similar non-significant tendency was also observed in our previous study (Fisher et al., 2016a) for young unimpaired participants. The left hemisphere has been linked to the part-based processing of faces (e.g. Rossion et al., 2000), whereas the right hemisphere is assumed to be more strongly activated during holistic face processing (e.g., Schiltz, Dricot, Goebel, & Rossion, 2010). It is possible that the current face matching task placed greater emphasis on part-based face processing, resulting in a left-hemisphere bias for the N250r (see also Towler & Eimer, 2016, for larger N250r components over the left hemisphere in response to inverted faces).

The current study has provided new evidence that visual working memory impairments in individuals with DP are specific to facial identity, and do not affect their ability to retain and match facial expressions. This raises important theoretical questions about the links between representations of identity and expression in the face processing system. The presence of symmetrical behavioural interference effects from task-irrelevant identity on expression or vice versa in the control group shows that selective attention could not be entirely focused on one of these dimensions, and suggests that facial identity and expression were not represented independently (see also Fisher et al., 2016, for similar results and interpretations). In contrast, the

fact that DPs showed a selective impairment of identity processing but intact processing of facial expression as well as asymmetrical Garner interference effects suggests a substantial degree of independence between these two dimensions.

The presence of asymmetrical interference effects by facial expression versus identity in the DP group is in line with previous suggestions that such effects are mediated by discriminability within the currently relevant dimension, with larger interference effects when discriminability is low (Wang, Fu, Johnston, & Zan, 2013). A general impairment in processing facial identity for DPs will reduce the discriminability of identity-related signals, and this may result in asymmetric interference effects. Importantly, instead of being generated at the stage where working memory representations are formed, identity-related deficits in DP may already emerge at earlier sensory-perceptual stages of face processing (see also Shah et al., 2016, for similar suggestions). Previous ERP studies of DP that focused on the N170 component have found evidence that DPs are less sensitive to the prototypical spatial configuration of upright faces (Towler, et al., 2012; 2016) and to contrast signals from the eye region (Fisher et al., 2016b). Such spatial-configural and contrast-related related signals, in particular from the eyes, provide important cues to identity (e.g., Gilad, Meng, & Sinha, 2009), because they remain invariant across changes in expression and other image changes (e.g., Burton, 2013). If the perceptual analysis of such image-invariant visual identity cues was selectively impaired, DPs would have to rely more strongly on low-level image-dependent features. Identity-related information will thus be poorly encoded in visual face representations, whereas other dimensions such as expression can be encoded normally. In the current study, where the intervals between face pairs were very short and perceptual encoding was therefore emphasized, such identity-specific perceptual deficits will result in selective impairments for face identity matching, in particular in the presence of additional identity-unrelated visual changes. The fact that N250r amplitudes for individual DPs in the identity task were reliably correlated with their performance

in the CFPT provides additional evidence for the involvement of perceptual processes during face identity matching.

Overall, we propose that facial identity and expression are generally represented together, not only in control participants but also in DPs. For individuals with DP, such visual face representations are less well suited for determining individual identity than for discriminating facial expressions. As a result, the ability to detect face identity matches is selectively impaired, and this may be an important contributing factor to the general face recognition problems that are the defining characteristic of DP.

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