

**Neural responses in a fast periodic visual stimulation paradigm
reveal domain-general visual discrimination deficits in developmental prosopagnosia**

Fisher, K.^{1,2}, Towler, J.³, Rossion, B.⁴, & Eimer, M.^{1*}

¹Department of Psychological Sciences, Birkbeck, University of London, UK

²UCL Division of Psychology and Language Sciences, University College London, UK

³Department of Psychology, College of Human and Health Sciences, Swansea University,

⁴Université de Lorraine, CNRS, CRAN, F-54000 Nancy, France

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***Corresponding author's contact details:** Martin Eimer, Department of Psychological Sciences,
Birkbeck, University of London, Malet Street, London WC1E 7HX, UK. Phone: 0207 6316358.
Email: m.eimer@bbk.ac.uk.

Highlights

- Rapid neural identity discrimination responses to faces are attenuated in DPs
- DPs also show reduced identity discrimination responses to non-face objects (cars)
- Visual identity processing deficits in DP are not entirely face-specific
- DP is linked to a domain-general impairment in rapid visual object discrimination

Abstract

We investigated selective impairments of visual identity discrimination in developmental prosopagnosia (DP), using a fast periodic identity oddball stimulation paradigm with electroencephalography (EEG). In Experiment 1, neural responses to unfamiliar face identity changes were strongly attenuated for individuals with DP as compared to Control participants, to the same extent for upright and inverted faces. This reduction of face identity discrimination responses, which was confirmed in Experiment 2, provides direct evidence for deficits in the visual processing of unfamiliar facial identity in DP. Importantly, Experiment 2 demonstrated that DPs showed attenuated neural responses to identity oddballs not only with face images, but also with non-face images (cars). This result strongly suggests that rapid identity-related visual processing impairments in DP are not restricted to faces, but also affect familiar classes of non-face stimuli. Visual discrimination deficits in DP do not appear to be face-specific. To account for these findings, we propose a new account of DP as a domain-general deficit in rapid visual discrimination.

Keywords: face recognition, object recognition, developmental prosopagnosia, domain specificity, frequency tagging, FPVS

1. Introduction

Developmental prosopagnosia (DP) is a life-long severe deficit in the ability to recognise the identity of faces that cannot be accounted for by low-level visual or intellectual impairments, and without any known neurological history (McConachie, 1976; Behrmann & Avidan, 2005). Individuals with DP have difficulties remembering the faces of familiar individuals and many also have problems discriminating between pictures of different unfamiliar faces (e.g., Duchaine et al., 2007). In contrast, other aspects of face processing such as the ability to recognise and discriminate emotional expression or gender appear to operate relatively normally in DP (DeGutis, Chatterjee, Mercado, Wilmer, & Nakayama, 2012; Chatterjee and Nakayama 2012; Garrido et al., 2009; Lee, Duchaine, Wilson, & Nakayama, 2010).

The factors that are responsible for face identity recognition deficits in DP remain under intense investigation. It is still unclear which aspects of face processing are impaired, whether DP is a homogeneous or heterogeneous disorder, and to what degree it is face-specific. There is behavioural evidence suggesting that the face processing impairments in DP might be associated with a deficit in holistic face processing (i.e., the ability to form a unified visual representation of the face; see Rossion, 2013; Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987). In individuals with normal face recognition ability, presenting faces upside-down produces stronger recognition and discrimination deficits than inverting other types of objects that have a canonical orientation (Yin, 1969; McKone, Duchaine, & Kanwisher, 2007). Behavioural markers of holistic face processing tend to be reduced or absent for inverted faces, indicating that inverted faces are processed less holistically (e.g., Tanaka & Farah, 1993; Rossion, 2009; see also Susilo, Reslescu, & Duchaine, 2013, for evidence for some holistic processing of inverted faces). Individuals with DP are strongly impaired in matching the identity of simultaneously presented upright unfamiliar faces. However, they often show little additional performance costs when these faces are inverted (e.g. Duchaine, Yovel, & Nakayama, 2007, Duchaine, 2011; but see Biotti, Gray, & Cook, 2019, for evidence that most DPs show such costs in tests of perceptual face individuation). If face inversion effects were reduced in DP, this would suggest that DPs might be selectively impaired at processing upright faces holistically. While there is substantial evidence for this hypothesis (Avidan, Tanzer, & Behrmann, 2011; Palermo, Willis, Rivolta, McKone, Wilson, &

Calder, 2011; DeGutis, Cohan, Mercado, Wilmer, & Nakayama, 2012), some studies have found no differences in behavioural markers of holistic face processing between DPs and Controls (Ulrich et al., 2017; Biotti, Wu, Yang, Jiahui, Duchaine, & Cook, 2017). Overall, current empirical support for an impairment of holistic face processing in DP is suggestive, but by no means conclusive. Since holistic face processing is regarded as a hallmark of domain specificity, demonstrating that it is selectively impaired in DPs would imply that the underlying recognition deficits are face-selective and thus presumably domain-specific. In this case, DPs should only show deficits when processing the identity of faces, but not during the recognition of non-face objects.

While some authors have suggested that visual recognition impairments in DP are indeed strongly face-specific (e.g., Duchaine & Nakayama, 2005), two recent studies have challenged this assumption. Geskin & Behrmann (2017) examined more than 700 published cases of DP, to assess the prevalence of associations versus dissociations of face and non-face recognition performance. In most studies that measured both face and object recognition, the majority of DPs tested also showed some impairment in non-face object recognition tests. However, a smaller subset of DPs performed normally in object recognition tests and had apparently face-selective deficits. The overall results of this survey suggest that DP might not be as face-selective as has previously been assumed. Along similar lines, fMRI results by Jiahui, Yang, & Duchaine (2018) have indicated that the tuning of high-level visual regions to preferred object categories was reduced in DPs. Importantly, this was the case not only for face-selective areas, but also for regions that are selective for other types of objects (scenes and bodies). These observations challenge the idea that visual processing impairments in DP are restricted to a dedicated face processing network. Overall, the findings by Geskin & Behrmann (2017) and Juahui et al. (2018) provide behavioural and neural evidence that visual recognition deficits in DP are not exclusive to faces, but are usually also present to some degree for other non-face object categories.

The question of which aspects of face processing are impaired in DP, and the related question of whether these impairments are genuinely face-specific, are difficult to answer with behavioural tests alone. Behavioural performance in face processing tasks reflects the contribution of perceptual, attentional, memory-related, strategic control, and decisional processes. These tests also often suffer from floor or ceiling effects in one or more conditions, which could reduce their sensitivity to inversion effects for the worst

performers. For these reasons, the question of which aspects of face processing are impaired in DP needs to be thoroughly investigated with brain activity measures (e.g., Towler & Eimer, 2012; Towler, Fisher, & Eimer, 2017; Eimer, 2018; Towler & Tree, 2018). In spite of the manifest behavioural face processing impairments in DP, many functional neuroimaging studies of individuals with DP have found face-selective activity in core regions of the posterior face processing network (Avidan & Behrmann, 2009; Furl, Garrido, Dolan, Driver, & Duchaine, 2011; Avidan, Tanzer, Hadj-Bouziane, Liu, Ungerleider, & Behrmann, 2014). These regions are not only present in most DPs, but also show similar activity reductions to immediate face identity repetitions as in individuals with normal face recognition, suggesting that they are sensitive to face identity (Avidan & Behrmann, 2009; Furl et al., 2011). Face processing impairments in DP have been found to be more apparent in a face-selective anterior region in ventral temporal cortex (Avidan et al., 2014; but see Jiahui et al., 2018) that may be associated both with perceptual and post-perceptual stages of face processing (e.g. Collins, & Olson, 2014). This anterior temporal face-selective region may serve as a hub that provides important top-down signals to more posterior visual brain regions during face recognition and this hub and its connections may be disrupted in developmental prosopagnosia (Rosenthal, et al., 2017; Rosenthal & Avidan, 2018).

Clearer evidence for face-specific impairments in DP at early visual-perceptual processing stages comes from event-related brain potential (ERP) studies that measured the face-sensitive N170 component. The N170 is a negative-going component that is maximal over lateral posterior electrodes, peaks approximately 170 ms post-stimulus, and is larger for faces than for other non-face objects (Bentin et al., 1996; Jeffreys, 1989). Source localisation studies (e.g., Bötzel, Schulze, & Stodieck, 1995; Rossion, Joyce, Cottrell, & Tarr, 2003; Watanabe, Kakigi, & Puce, 2003), neuropsychological studies of acquired prosopagnosic patients (Dalrymple et al, 2011; Alonso-Prieto, et al., 2011), as well as correlations between the N170 amplitude and fMRI signal (Sadeh, Podlipsky, Zhdanov, & Yovel, 2010) or between the scalp and intracerebral N170 (Jacques et al., 2019) have suggested that the N170 is generated in occipito-temporal regions that are part of the posterior face-selective processing network (Haxby, Hoffman, & Gobbini, 2000). The N170 component is sensitive to image manipulations that impair the visual processing of faces and the subsequent extraction of facial identity, and a series of studies from our lab has demonstrated that this sensitivity is consistently reduced or absent in DP (Towler, Gosling,

Duchaine, & Eimer, 2012, Towler, Parketny, & Eimer, 2016; Fisher, Towler, & Eimer, 2016). Specifically, individuals with DP do not show the characteristic amplitude enhancements of the N170 component that are elicited in response to inverted faces or to faces with spatially scrambled or contrast-inverted internal features as compared to normal upright faces. Taken together, these results suggest that DPs have a deficit in the rapid sensitivity of posterior face-selective regions to fundamental aspects of facial structure.

While these N170 results suggest that relatively early perceptual processes within the core posterior face processing network operate atypically in DP, more direct ERP evidence for an impairment of face recognition comes from studies that measured N250/N250r components as markers of the activation of visual face memory representations DPs and Control participants (Eimer, Gosling, & Duchaine, 2012; Parketny, Towler, & Eimer, 2015; Fisher, Towler, & Eimer, 2017; Towler, Fisher, & Eimer, 2018). The N250 component reflects the difference in neural responses to familiar as compared to unfamiliar faces. The N250r computed by comparing ERPs to face images preceded by an image of the same individual with ERPs to faces preceded by the face of a different individual. These components emerge later than the N170 (typically 200 – 300 ms after stimulus onset), but has a similar focal lateral posterior scalp topography, suggesting that it is also generated within the occipito-temporal face processing network. Successfully recognized famous faces or previously unfamiliar learned target faces elicited N250 components of similar size in individuals with DP and in Control participants, but these components were delayed in DPs (Parketny et al., 2015). In sequential face identity matching tasks with unfamiliar faces, N250r components triggered by repetitions of identical faces were strongly attenuated for participants with DP (Fisher et al., 2017; Towler et al., 2018). For Control participants, N250r components to identical face repetitions were larger than the sum of the N250r responses to partial repetitions of either external (hair, head outline) or internal facial features (eyes, nose, mouth), whereas no such superadditive N250r was found for the DP group (Towler et al., 2018). This suggests that internal and external facial features were integrated during face matching for Control participants, whereas individuals with DP had a deficit in activating such integrated visual face representations.

These observations point to impairments in the visual processing of face identity in DP. However, ERP markers are not always sufficiently sensitive at the individual participant

level to allow strong conclusions about links between atypical ERP results and behavioural face recognition deficits in DP. ERP components such as the N170 and N250 also do not provide any direct insights into whether any processing deficits in DP are genuinely face-specific, or might also affect the recognition of non-face objects. In the present study, we employed EEG frequency-tagging or fast periodic visual stimulation (FPVS) to study the ability of the visual system to discriminate between the identities of faces and of non-face objects, in individuals with DP and in Control participants. FPVS typically measures neural responses to stimulus sequences lasting for tens of seconds (“runs”) that are presented at a relatively fast and constant (i.e. periodic) rate, by computing amplitudes at the specific stimulation frequency in the EEG frequency-domain (Regan, 1989; Norcia et al., 2015 for reviews¹). This approach has substantial advantages in terms of sensitivity (i.e., high signal-to-noise ratio) and objectivity (i.e., identification and quantification of the response of interest at the pre-defined stimulation frequency).

Importantly, such FPVS techniques can also be used to probe the neural processes involved in the detection of and discrimination of faces in a more targeted way than is possible with behavioural or ERP markers (see Rossion, 2014; Rossion, Retter, & Liu-Shang, in press, for reviews). Liu-Shuang, Norcia, & Rossion (2014) employed this method in an oddball paradigm to measure neural responses to face identity changes. When such changes occur periodically (e.g., every 5 stimuli) during the sequential presentation of the same unfamiliar face at 6 Hz, a visual evoked response is generated that is specific to the frequency at which the face identity change occurs (i.e., $6 \text{ Hz}/5 = 1.2 \text{ Hz}$). This face identity oddball discrimination response is maximal at lateral posterior electrodes, with a right hemisphere advantage (Liu-Shuang et al., 2014), and thus shows a similar scalp topography as the N170 and N250/N250r components. To ensure that this signal reflects high-level mechanisms involved in face identity discrimination rather than merely low-level responses to visual features of an oddball face or to image changes, each oddball face is chosen randomly from a set of multiple different faces, and the size of all face images in a run varies randomly, to prevent pixel-wise neural adaptation (see Rossion et al., in press, for details).

¹We use the term FPVS rather than “steady-state visual evoked potential” (SSVEP) because SSVEP refers to the type of response obtained rather than the approach, and because there remains some controversy about the precise definition of SSVEPs (see Retter & Rossion, 2016; Rossion et al., in press for discussion).

These neural responses to face identity oddballs are likely to be generated by mechanisms that are similar to those responsible for repetition suppression effects in neuroimaging studies (e.g., Henson, 2003; Nemrodov, Jacques, & Rossion, 2015; Retter & Rossion, 2016; Liu-Shuang et al., 2014). If different subgroups of face-selective neurons within the same posterior region respond to different facial identities, the presentation of oddball faces will result in a release from identity-selective suppression and thus in a periodic increase of neural responses at the oddball frequency. Evidence that the identity-selective responses obtained with FPVS procedures are generated in posterior regions of the face processing network comes from a recent intracerebral recording study which has shown that such responses are measured in the ventral occipito-temporal cortex, in particular the right fusiform face area (Jacques et al., 2020). The fact that these responses are strongly reduced by image manipulations that are known to impair the processing of face identity, such as orientation inversion and contrast reversal (Liu-Shuang et al., 2014), suggest that they reflect high-level face identity discrimination processes that go beyond the detection of mere physical differences between stimuli.

With FPVS procedures, face identity discrimination responses can be measured in the absence of behavioural responses and decision-making processes, thus providing a relatively pure measure of the ability of the visual system to discriminate between different face identities. Moreover, the high signal-to-noise ratio of EEG activity obtained with this approach allows a robust and reliable measure of visual discrimination processes based on a relatively small number of runs (see Rossion, 2014; Rossion et al., in press, for further discussion). Finally, the face identity discrimination oddball paradigm is associated with a high test-retest reliability. For example, Dzhelyova et al. (2019) found a very strong correlation ($r = 0.79$) between individual face identity discrimination response amplitudes between sessions separated by a two month interval. Given these advantages, the FPVS approach should also be useful to investigate face recognition impairments in prosopagnosic individuals. For example, the question whether face inversion effects are reduced in DPs relative to Controls is difficult to assess behaviourally, due to the possibility of floor or ceiling effects in performance. FPVS procedures offer a different way of measuring the effects of face inversion on identity discrimination processes that is not affected by such limitations.

Liu-Shuang, Torfs, & Rossion (2016) used the face identity oddball paradigm to test a well-known patient with acquired prosopagnosia (PS). This patient has damage to core posterior face processing regions and showed no face identity discrimination response, indicating a deficit in perceptual mechanisms that are involved in the rapid extraction of facial identity. More recent studies using the same rapid identity oddball procedure have found correlations between face identity oddball responses and behavioural measures of unfamiliar face learning (Xu et al., 2017) and unfamiliar face matching (Dzhelyova et al., 2020) in neurotypical individuals, and reduced identity oddball responses specifically for upright faces in a group of autistic individuals (Vettori et al., 2019).

The first question addressed in the present study was whether a similar reduction (or complete elimination) of face identity discrimination responses would also be found for participants with DP, and whether this deficit would be restricted to upright faces. This was investigated in Experiment 1, where a group of 10 participants with DP and 10 age-matched Control participants were tested with the face identity oddball paradigm. The second question addressed was whether any identity-related processing deficits in DP, as revealed by atypical neural responses to identity oddballs, reflect a genuinely face-selective impairment. This was tested in Experiment 2, which employed the same FPVS paradigm as Experiment 1, but now compared neural responses to identity oddballs in runs where sequences of faces were presented and other runs where non-face objects (cars) were shown instead. If the impairment of identity discrimination mechanisms in DP was exclusive to face processing, atypical identity oddball responses for DPs as compared to Controls should only be found for faces but not cars.

2. Experiment 1

This experiment used the same identity oddball procedure that was employed by Liu-Shuang et al. (2014). On each run, face images were presented sequentially at a base stimulation frequency of 5.88 Hz. An identity change occurred for every fifth images in this sequence, corresponding to an identity oddball frequency of 1.18 Hz. On some runs, these images appeared in an upright position. On other runs, all faces were inverted (see Figure 1 for an illustration of the experimental design). Participants' task was to attend to a central fixation cross to detect infrequent colour changes. The face images and their identity were

task-irrelevant. For Control participants, the pattern of identity oddball responses should confirm previous observations by Liu-Shuang et al. (2014). Reliable neural responses should emerge at the identity oddball frequency (1.18 Hz) and its harmonics on runs with upright faces. These responses should be maximal over lateral occipito-temporal cortex, and be strongly attenuated on runs with inverted faces. The critical question was whether a different pattern of neural responses to face identity changes would be found for individuals with DP. One possibility is that the results observed for the DP group mirror that of the Control group. This would be in line with previous observations that face-selective posterior regions show a similar sensitivity to repetitions versus changes of face images in DPs and Controls (e.g., Furl et al., 2011), and provide evidence that rapid identity-sensitive perceptual processes operate normally in DP. Another possibility is that identity oddball responses in the DP group are attenuated, but only for runs with upright faces. This would be in line with the hypothesis that DPs have specific impairments in the perceptual analysis of upright faces, possibly resulting from selective deficits in the tuning of holistic face processing mechanisms to the prototypical spatial configuration of faces (e.g. Towler et al., 2018). In this case, there should be no systematic differences between DPs and Control participants for the identity oddball responses observed on runs with inverted faces, as these faces are not processed in the same holistic fashion. A third possibility is that identity-sensitive EEG responses are generally attenuated in the DP group relative to the Control group, both for upright and for inverted faces. This would point to an impairment of identity-sensitive perceptual face processing in DP that cannot be attributed to a selective deficit of holistic face processing.

2.1. Methods

All materials required for any re-analyses of the data sets collected in Experiments 1 and 2 are available for open access in repositories provided and maintained by Birkbeck, University of London (Data: <http://brainb.psyc.bbk.ac.uk/cortex/Data/>; Materials: <http://brainb.psyc.bbk.ac.uk/cortex/Materials/>; ~~Analysis~~ codes: <http://brainb.psyc.bbk.ac.uk/cortex/Analysis Codes/>). No part of the study procedure or analysis was pre-registered prior to the research being conducted. We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether

inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1.1. Participants

Ten participants with developmental prosopagnosia (4 females; mean age 37.4, SD = 12.5) and ten age-matched Control participants (4 females, mean age 37.1, SD=12.66) took part in Experiment 1. This sample size was determined a priori, based on previous studies on face identity processing in DP (Eimer et al., 2012; Parketny et al., 2015; Fisher et al., 2017) and the study by Liu-Shuang et al. (2014) that used an identical FPVS oddball paradigm. Critically, we also report data for each individual participant in both groups, to document interindividual variability of the critical FPVS responses to identity oddballs. DP participants were recruited through two research websites (<http://www.faceblind.org>; <http://www.prosopagnosia.bbk.ac.uk>). All DP participants reported difficulties recognising faces since childhood. Their impairment was confirmed with a battery of behavioural tests. Z-scores for four behavioural tests are shown in Table 1 for each participant with DP. The Famous Faces Test (FFT) is a test of long-term face memory where participants have to identify 60 people who are famous in popular culture (e.g. actors, musicians, or politicians). The ability of the DP participants to learn new faces was assessed with the Cambridge Face Memory Test (CFMT). Here, participants are required to memorize faces of six target individuals shown from different viewpoints which then have to be identified 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 tests face learning. Participants have to memorize 10 faces, and then distinguish these learned faces from 30 novel faces by making an “old” (learned face) or “new” (novel face) judgement about each face. The Cambridge Face Perception Test (CFPT, Duchaine et al. 2007) assesses visual face processing. Participants are shown a target face together with six-front view morphed test faces that contain different proportions of the target face, and have to be rearranged in order of their similarity to the target face. This task was run both with upright and with inverted faces. As can be seen from Table 1, all ten DPs were impaired (defined as performance below 2 standard deviations of the estimated population mean; Duchaine & Nakayama, 2006) on the FFT and CFMT, and all except one were impaired on the

ONT. Performance on the CFPT was more variable, as observed before (Duchaine et al., 2007). Six of the ten DPs showed impaired CFPT performance with upright faces, and four were impaired with inverted faces. All Control participants reported that they were confident in their face recognition abilities. To verify this, they were tested with the CFMT. The scores for all ten participants in the Control group were within ± 1 standard deviation of the estimated population mean. All participants gave verbal and written consent prior to testing.

	Age	Gender	FFT	CFMT	CFPT Upright	CFPT Inverted	ONT Faces
DP1	35	F	-1.74	-1.88	-2.15	0.36	-3.03
DP2	31	M	-7.72	-4.29	-3.1	-2.89	-14.34
DP3	25	F	-7.34	-2.01	0.24	-0.36	-6.68
DP4	31	F	-8.49	-2.9	-0.92	-1.05	-9.03
DP5	45	M	-8.88	-2.77	-2.56	-0.63	-8.16
DP6	45	M	-5.21	-2.77	0.17	-0.77	-3.36
DP7	53	F	-8.49	-1.25	-2.01	-1.05	-2.72
DP8	59	M	-3.67	-2.14	-1.6	-0.2	-6.49
DP9	21	M	-8.49	-2.52	-1.33	-1.05	-6.41
DP10	29	M	-7.53	-3.27	-0.65	-0.91	1.04
Mean	37.40		-6.76	-2.58	-1.39	-0.86	-5.92

Table 1

Z-values for 10 DP participants in the Famous Faces Test (FFT), Cambridge Face Memory Test (CFMT), the Cambridge Face Perception Test (CFPT) for upright and inverted faces, and the Old-New Test (ONT), and mean values across all DPs.

2.1.2. Materials and procedure

Stimulus materials and procedure were identical to those used in a previous study (Liu-Shuang et al., 2014). Participants were seated in front of a CRT monitor at a viewing distance of 100 cm. Experimental stimuli consisted of full-front coloured photographs of 25 male and 25 female faces with a neutral expression. Photographs were taken under standardised conditions with respect to lighting, image background, and the distance of the model from the camera. External features such as hair and ears were cropped from the images using Adobe Photoshop. The resulting face images were resized to 250x186(± 11) pixels. They were displayed with a screen resolution of 800x600 pixels, and

occupied an average visual angle of $6.53 \times 4^\circ$. Face images were vertically flipped for the inverted face condition. The mean luminance of the faces was equalized online during stimulation and a gamma correction was applied.

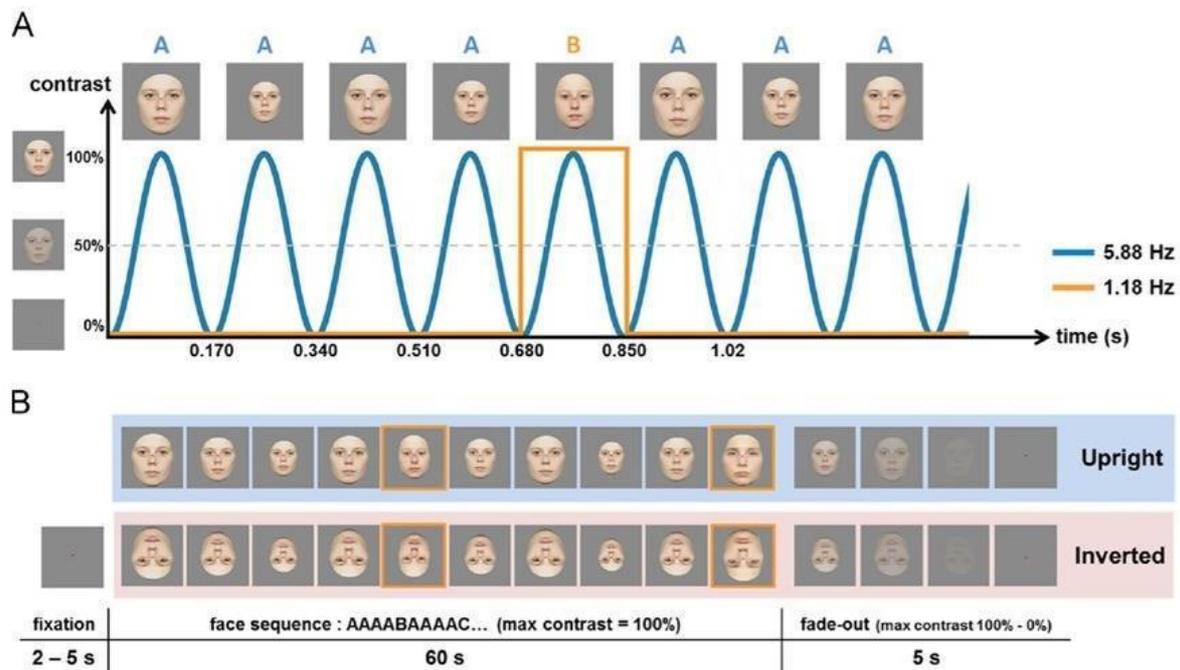


Figure 1. Schematic illustration of the experimental paradigm. **A.** Faces were presented via sinusoidal contrast modulation at a rate of 5.88 Hz. During each presentation sequence, four faces of the same individual (A) were followed by a face of a different individual (identity oddball; B). Because identity changed for every 5th face in the sequence, the identity oddball frequency for 1.18 Hz (5.88/5 Hz). To prevent pixel-wise adaptation, face size was randomly varied (between 74% - 120%). **B.** Time course of run: Following a fixation interval of 2 – 5 seconds, faces images were shown at 5.88 Hz for 60 seconds. At the end of the sequence, the maximal contrast of the sinusoidal stimulation decreased for 5 seconds, eventually resulting in stimulus fade-out. In different runs, all faces were presented in an upright or inverted orientation. Reproduced from Liu-Shuang et al. (2014), with permission.

Stimulus presentation was controlled using a custom script in MATLAB with PsychToolbox as well as custom graphics toolboxes. The beginning of each run was marked with the onset of a fixation cross at the centre of the display which was displayed for between 2 and 5 seconds (randomly jittered between runs). Following this fixation-only period, sequences of faces were presented for 60 s. Face images emerged with the fixation cross overlaid on the nasion region (between the two eyes) for both upright and inverted faces. Face stimuli were displayed at a rate of 5.88 cycles per second (a base stimulation frequency of 5.88 Hz) which corresponds to each cycle having a duration of 170ms (i.e., $1000 \text{ ms}/5.88$). In line with previous research, 5.88 Hz was chosen as the base stimulation

frequency because face adaptation/repetition suppression effects have been shown to be largest when faces are presented at this frequency (Alonso-Prieto et al., 2013). Because 5.88 Hz is exact integer submultiple of the 100 Hz frame-rate of the CRT monitor ($100/17=5.88$), it also avoids a mismatch between monitor refresh rate and presentation rate. Face images were presented using sinusoidal contrast modulation (Rossion & Boremanse, 2011; Rossion et al., 2012). Each face presentation began with a uniform grey background (40 cd/m^2) from which a face appeared as its contrast increased. Full contrast was reached at 85 ms and then decreased at the same rate (see Figure 1 for a schematic illustration of the experimental design). To ensure that face identity changes were not confounded by changes in the retinal image that only occurred at the identity discrimination frequency, the size of all face images was randomly varied between 74% and 120% of the original image size during every 5.88 Hz stimulation cycle (as illustrated in Figure 1B). This ensured that the low-level features of the faces did not visually overlap in retinotopic coordinates and changes in face identity could not be detected on the basis of local image changes.

The experiment consisted of eight runs. In half of all runs, all faces were presented in an upright orientation. In the other half, they were presented in an inverted orientation. The order of upright and inverted face runs was randomised. For each face orientation, there were two runs that contained only male faces and two runs that contained only female faces. For each run, one face was randomly selected as the base face. This face was repeated throughout the sequence. The identity of every fifth face in the sequence changed to a different face that was randomly selected from the remaining 24 faces. As a result, each run sequence contained face identity changes at a frequency of 1.18 Hz (the 5.88 Hz base frequency divided by 5). EEG amplitudes at the 1.18 Hz oddball frequency and its harmonics (i.e., 2.35 Hz, 3.53 Hz, etc.) were measured as markers of the visual discrimination of individual faces. At the end of each run, and following the 60 s sequence, visual stimulation faded out gradually by decreasing the contrast from 100% maximum contrast level to 0% over period of 5 s. Stimulus fade-out was used to avoid abrupt eye-movements or blinks near the end of each run. Triggers were sent via parallel port at the start of the each sequence and at the minima of each cycle (grey background, 0% contrast). New runs were manually initiated when participants showed an artifact-free EEG signal. Figure 1B illustrates the time-line of a single run.

Participants were instructed to fixate on a small red cross situated in the centre of the screen. Their task was to detect brief (200 ms) colour changes of the fixation cross (red to blue). Colour changes occurred at eight times within every run. This task served the purpose of ensuring that the participant maintained a constant fixation location and kept attention focused at that location throughout each run.

2.1.3. Electroencephalography recording and data pre-processing

EEG was DC-recorded with a BrainAmps DC amplifier (upper cut-off frequency 40 Hz, 500 Hz sampling rating) and Ag-AgCl electrodes mounted on an elastic cap from 27 scalp sites Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO8, Oz, P9, PO9, PO10, and P10 according to the extended international 10–20 system. Horizontal electrooculogram (HEOG) was recorded bipolarly from the outer canthi of both eyes. An electrode placed on the left earlobe served as reference for online recording and EEG was re-referenced offline to a common average. All electrode impedances were kept below 5 k Ω .

All EEG data processing was performed using Matlab 8.1 (Mathworks), and Letswave (<http://nocions.webnode.com/letswave>; Mouraux & Iannetti, 2008). Data was imported into Letswave for pre-processing. A high pass filter of 0.1 Hz with a cut-off width of 0.05 Hz and a low-pass filter of 30 Hz with a cut-off width of 5 Hz were applied to all individual EEG data offline. For each run, EEG data was initially segmented from 2 s prior to the start of a stimulation sequence to 2 s after the end of the fade-out period. EEG data within each of these 69 s segments was down-sampled to 250 Hz. The first 4 s of each segment (including the first 2 s after the start of a stimulation sequence) were removed to avoid contamination of EEG frequency signals by initial transient event-related neural responses. These pre-processed data segments were then cropped down to a constant length that corresponded to a multiple of the 1.18 Hz cycles, resulting in segments that were approximately 60 s long, captured 70 stimulation cycles per run (14,884 time bins in total), and covered the stimulation sequence until just before stimulus fade-out. For each participant, the four runs with upright faces and the four runs with inverted faces were averaged separately in the time-domain, to increase the signal-to-noise ratio by reducing EEG activity that is not phase-locked to the stimulus sequence. A Fast Fourier Transform (FFT) was then applied to these averaged segments, and amplitude spectra were extracted for all channels. Frequency

analysis yielded spectra with a high frequency resolution of 0.017 Hz (1/59.54), which allowed for an unambiguous identification of the response at the base frequency (5.88 Hz), the identity oddball frequency (1.18Hz), and its harmonics (2.35 Hz, 3.53 Hz, 4.70 Hz etc.).

2.1.4. Selection of electrodes and frequencies for the analysis of neural responses to face identity changes and to the base stimulation frequency

Preliminary analyses of frequency-domain EEG data obtained for Control participants were conducted in order to determine the electrodes and frequencies at which meaningful neural responses were recorded. Since evoked EEG responses to a particular critical frequency (i.e., the base stimulation frequency and the identity oddball frequency) are also observable at the corresponding harmonic frequencies, amplitudes at the critical frequency and its harmonics are both relevant for analysis (Norcia et al., 2015; Retter & Rosison, 2016). To determine which harmonics of the 1.18Hz oddball frequency and the 5.88Hz base frequency reflected the presence of a significant neural signal, FFT spectrum data obtained for all Control participants were averaged across runs with upright and inverted faces and across all scalp electrodes. Z-scores were then calculated for the signal at base and harmonic frequencies by subtracting the average of the 20 surrounding frequency bins, excluding the two bins immediately adjacent to the harmonic frequency (in case of remaining spectral leakage), and dividing by the standard deviation of these 20 surrounding bins. Harmonics were then selected for inclusion in subsequent analyses if these z-scores were above 1.64 ($p < .05$, one-tailed, signal above noise; see also Retter & Rossion, 2016). Based on these criteria, the oddball frequency (1.18 Hz) and three harmonics (2.35 Hz, 3.53 Hz, 4.70 Hz) were retained for oddball response analysis. Because the next harmonic of the oddball frequency (5.88 Hz) is confounded with the base stimulation frequency, this harmonic was not included. Exactly the same harmonics were selected when selection was based on the whole EEG data set obtained from DPs and Controls. For the analysis of the base frequency response, the fundamental frequency (5.88 Hz) and the second harmonic (11.76Hz) were selected, based on the same criteria.

Signal-to-noise-subtraction (SNS) amplitudes were calculated by subtracting from the signal at each harmonic the average of the 20 surrounding frequency bins, excluding the two bins immediately adjacent to the harmonic frequency. To combine amplitude values across these frequencies, the resulting SNS amplitudes for each harmonic were summed to

quantify overall oddball and base responses, respectively (see Retter & Rossion, 2016, for analogous procedures). To define the electrode channels of interest for the analyses of oddball responses, FFT spectra obtained for all Control participants were averaged across runs with upright and inverted faces. Summed oddball harmonics amplitudes were maximal at lateral occipito-temporal electrodes in the left hemisphere (P7, PO7, P9, PO9) and in the right hemisphere (P8, PO8, P10 and PO10), in line with previous studies using this paradigm (Liu-Shuang et al., 2014; Dzhelyova et al., 2019). These four electrode pairs were therefore selected for all analyses of oddball FPVS responses. To obtain single oddball EEG amplitude values for each participants (DPs and controls), face orientation (upright or inverted), and hemisphere, amplitudes were averaged across the four left-hemisphere and right-hemisphere electrodes, respectively. As a result of these processing steps, summed amplitude values (SNSs) for with upright and inverted face conditions were obtained for identity oddball responses (separately for the left and right hemisphere).

2.1.5. Analyses of FPVS data

To assess differences between the DP and Control groups, a repeated-measures analysis of variance (ANOVA) of summed SNS values for each individual participant was conducted, with the within-participant factors *Face Orientation* (upright versus inverted) and *Hemisphere* (left versus right), and the between-participant factor *Group* (DP Group versus Control Group). To explore the presence or absence of identity discrimination responses in DPs and Control participants, additional follow-up ANOVAs were conducted separately for each group. In addition, we also investigated the presence of reliable identity discrimination responses in response to upright and inverted faces at the level of individual DPs and Control participants, on the basis of individual Z-scores for raw FFT amplitudes (averaged across hemispheres and summed across harmonics), separately for upright and inverted faces. This procedure produced two Z-scores for each participant, representing the mean face identity discrimination response for this participant in response to upright and inverted faces, respectively. An individual Z-score of 1.96 ($p < 0.05$) was used as the significance threshold.

The summed base frequency response showed a focal maximum at midline electrode Oz, as expected on the basis of previous studies (e.g., Liu-Shuang et al., 2014; Dzhelyova et al., 2019). The analysis of differences in the size of this response between DPs

and controls was therefore conducted on summed SNS values obtained at Oz only, in response to either upright or inverted faces. These values were analysed in a separate ANOVA with the factors Face Orientation and Group.

To illustrate the profiles of identity oddball and base frequency responses, signal-to-noise ratios (SNRs) were computed to minimize the visible effects of random noise variations in the EEG data, based on absolute FFT amplitudes across the whole EEG spectrum. SNRs were calculated as the ratio of the FFT amplitude at each frequency to the average amplitudes of the 20 surrounding frequency bins on each side, excluding the two immediately adjacent bins (see Liu-Shuang et al., 2014, for analogous procedures). These SNR values were used for Figures 2 and 4, including the topographical scalp distribution maps. Because data analyses were based on signal-to-noise subtraction (SNS) amplitudes rather than SNRs, the corresponding EEG spectra based on SNS amplitudes for identity oddball responses in Experiment 1 are provided in supplementary figure (Figure S1).

2.2. Results

2.2.1. Behavioural data

Participants in both groups had near perfect performance in detecting colour changes in the fixation cross. Control participants detected 98% of all fixation colour changes, and participants with DP detected 96% of these changes. Mean response times (RTs) for detected colour changes were 422 ms in the Control group and 455 ms in the DP group. Neither accuracy nor RT differed reliably between the two groups, both $t < 1.23$.

2.2.2. The face identity discrimination response

Figure 2 shows grand-averaged SNR values obtained across the entire frequency spectrum up to 6 Hz for runs with upright faces (top panels) and inverted faces (bottom panels) over the left and right hemisphere (averaged across the four lateral posterior electrodes over each hemisphere). SNR values measured for the Control group (blue) and SNR values for the DP group (red) are overlaid, and the corresponding topographic scalp distribution maps are also shown (see Figure S1 for analogous results based on SNS amplitudes). As can be seen from this Figure, the largest response was present at the base stimulation frequency (5.88 Hz), but there were also clear face identity discrimination

electrodes over the left hemisphere (LH) and right hemisphere (RH). SNR spectra for the Control and DP groups are indicated by blue and red traces, respectively. Coloured circles mark amplitudes at the first four harmonics of the identity oddball frequency for the two groups. The scalp maps on the right show the topographical distribution of identity discrimination responses to upright and inverted faces (based on SNR values averaged across the first four harmonics), separately for Controls and DPs. Note the different scales between the maps for the Control and DP groups. For upright faces, identity discrimination responses at the identity oddball frequency (1.18 Hz) and its harmonics are visible for both groups, but are attenuated in the DP group. Identity discrimination responses to inverted faces were generally smaller, but were again reduced in the DP group.

These observations were confirmed by an ANOVA of SNS amplitude values for the factors Group, Hemisphere, and Face Orientation. Most importantly, there was a highly significant main effect of Group, $F(1,18) = 17.36$, $p < .001$, $\eta_p^2 = .49$, confirming the general reduction of identity discrimination responses in the DP Group as compared to the Control Group (.71 μ V versus .29 μ V). The presence of larger identity discrimination responses for upright as compared to inverted faces (.70 μ V versus .31 μ V) was reflected by a main effect of Face Orientation, $F(1,18) = 35.96$, $p < .001$, $\eta_p^2 = .67$. The interaction between Face Orientation and Group was not significant $F(1,18) = 1.92$, $p = .18$, indicating that the reduction of identity discrimination responses for inverted versus upright faces did not differ between the two groups. This was confirmed in an additional analysis where this face inversion effect was quantified as the reduction (in percent) of responses to inverted faces, which showed no effect of Group, $F < 1$. There was also a significant main effect of Hemisphere, $F(1,18) = 15.06$, $p < .001$, $\eta_p^2 = .46$, due to the fact that identity discrimination responses were generally more pronounced over the right hemisphere than the left hemisphere (.58 μ V versus .42 μ V). The interaction between Hemisphere and Group was not significant, $F(1,18) = 3.31$, $p = .09$, and no two or three way interactions with Hemisphere and Orientation or Hemisphere, Group and Orientation, all $F < 2$.

Separate analyses conducted for each group showed that upright faces produced larger identity discrimination responses than inverted faces not only in the Control Group, $F(1,9) = 24.51$, $p < .001$, $\eta_p^2 = .73$ (.95 μ V versus .47 μ V), but also in the DP Group, $F(1,9) = 11.97$, $p < .007$, $\eta_p^2 = .57$ (.43 μ V versus .14 μ V). For the Control group, a main effect of Hemisphere, $F(1,9) = 11.32$, $p < .008$, $\eta_p^2 = .56$, confirmed that identity discrimination responses were larger over the right hemisphere (.83 μ V versus .59 μ V). Although Figure 2 suggests that this was primarily the case for inverted faces, the interaction between

Hemisphere and Face Orientation was not significant for Control participants, $F(1,9) = 1.6$, $p = .24$. In the DP group, the main effect of Hemisphere approached significance, $F(1,9) = 3.76$, $p = .08$, reflecting a similar tendency for identity discrimination responses to be larger over the right hemisphere (.32 μ V versus .24 μ V).

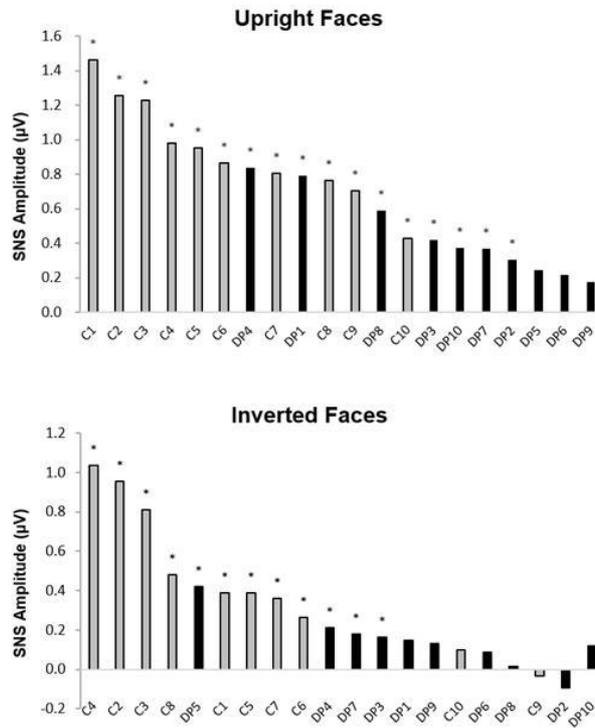


Figure 3. SNS amplitude values of the identity discrimination response (summed across the first four harmonics of the identity oddball frequency and averaged across hemispheres) on runs with upright faces (top panel) and inverted faces (bottom panel) obtained in Experiment 1 for each individual participant. Values for DPs are shown as dark bars, and values for Controls as light grey bars. Asterisks indicate the presence of a significant identity discrimination response for an individual participant, based on Z-scores computed on the basis of summed raw FFT amplitudes (see Methods section for details).

Finally, we conducted Z-score analyses (based on raw FFT amplitudes averaged across hemispheres and summed across harmonics) for face identity discrimination responses at the level of individual DP and Control participants (see Methods section for details). These analyses revealed that all ten Control participants had significant identity discrimination responses for upright faces. For inverted faces, eight of the ten Control participants showed significant identity discrimination responses. In contrast, only seven of the ten participants with DP had reliable identity discrimination responses to upright faces, and only four of the DPs showed a significant identity response to inverted faces. Individual

identity discrimination responses to upright and inverted faces, and the difference of these responses across the two groups are shown in Figure 3, which presents summed SNS values (averaged across both hemispheres) for upright faces (top panel) and inverted faces (bottom panel). Results for DPs are shown in black bars and for Control participants in grey bars, and are ordered from left to right for participants with larger versus smaller responses.

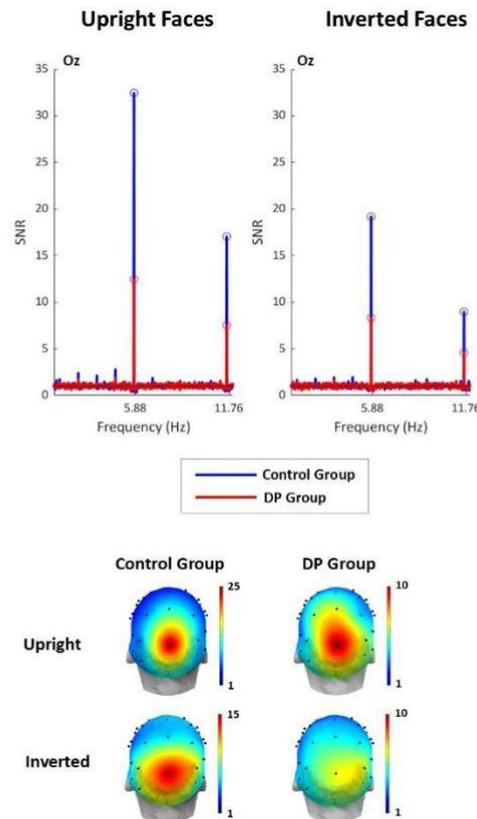


Figure 4. Top panels: SNR spectra of responses measured in Experiment 1 at the base stimulation frequency and its first harmonic at midline occipital electrode Oz on runs with upright or inverted faces, for the Control group (blue traces) and the DP group (red traces). Coloured circles mark amplitudes of base frequency responses for the two groups. Base stimulation frequency responses were reduced for inverted as compared to upright faces, and were generally smaller in the DP group. Bottom panels: Topographic maps showing the scalp distributions of the base frequency response and its first harmonic (based on averaged SNR values), separately for upright and inverted faces, and both groups. Note the scale difference between the maps for the two groups.

2.2.3. The base stimulation frequency response

Figure 4 shows summed SNR values obtained at the base stimulation frequency and its first harmonic (11.76 Hz) at midline occipital electrode Oz for upright faces (top panel) and inverted faces (bottom panel), for the Control group and the DP group. The topographical maps included in Figure 4 show that these base frequency responses were

maximal at Oz in both groups (note the different scale of the maps for Controls and DPs). Base frequency responses were generally larger for upright than for inverted faces, and larger in the Control Group relative to the DP Group. This was confirmed by an ANOVA of summed SNS values with the factors Face Orientation and Group, which revealed main effects of Face Orientation, $F(1,18) = 18.65$, $p < .001$, $\eta_p^2 = .51$, and Group, $F(1,18) = 14.29$, $p < .001$, $\eta_p^2 = .44$. The interaction between Face Orientation and Group approached significance $F(1,18) = 4.00$, $p = .06$, $\eta_p^2 = .18$, reflecting a tendency for the absolute effect of face inversion on base frequency responses to be larger in the Control Group (upright faces: $3.69\mu\text{V}$, inverted faces: $1.43\mu\text{V}$) than in the DP group (upright faces: $1.41\mu\text{V}$, inverted faces: $.81\mu\text{V}$). However, an additional analysis of face inversion effects in terms of the reduction (in percent) of responses to inverted as compared to upright faces showed no difference between the two groups, $t < 1.3$.

2.3. Discussion of Experiment 1

Using a FPVS procedure with face images, where identity changes occurred for every fifth face within the sequence, Experiment 1 revealed clear differences between participants with DP and age-matched Control participants in the size of face identity discrimination responses over occipito-temporal electrodes. Each individual Control participants showed reliable identity discrimination responses in runs with upright faces. These responses were attenuated for inverted faces, analogous to previous observations by Liu-Shuang et al. (2014). Two Control participants did not show significant identity oddball responses when faces were inverted. Critically, identity discrimination responses were strongly reduced for both upright and inverted faces in the DP group. Three DPs showed no significant response to upright faces, and responses to inverted faces were absent for six DPs (see Figure 3).

The presence of strongly reduced identity discrimination responses in the DP group contrasts with results from most fMRI studies, which have found no systematic differences between DPs and Control participants in the activation and adaptation effects of face-selective posterior occipitotemporal regions that are involved in the visual processing of faces and facial identity (e.g., Avidan & Behrmann, 2009; Furl et al., 2011; Avidan et al., 2014). The fact that DPs showed reduced face identity discrimination responses in Experiment 1 suggests that FPVS procedures can reveal visual impairments in the rapid

processing of unfamiliar face identity. However, there was little evidence that these impairments were linked to a specific deficit of holistic face processing in the DP group. If this had been the case, the reduction of face identity discrimination responses for DPs relative to Controls should have been more pronounced in runs with upright faces as compared to runs with inverted faces. In fact, upright face identity oddballs produced larger responses than inverted faces in both groups, and the absolute and relative sizes of these face inversion effects did not differ between the two groups. Since these observations were based on a relatively small sample, links between face orientation and the reduction of identity-sensitive FPVS responses in DPs were investigated again in Experiment 2.

The absence of evidence for a specific deficit of holistic face processing in Experiment 1 could suggest that the deficits reflected by the reduction of identity oddball responses for DPs might not be domain-specific. One possibility is that this reduction is due to generic attentional factors. For example, participants with DP might generally have a stronger tendency to avoid attending to face images, which were task-irrelevant in Experiment 1. Such a tendency could have produced attenuated identity-specific neural responses in DPs. If this was the case, differences between DPs and Controls should be smaller or perhaps even absent under task conditions where attention has to be actively focused on the face image stream. This was tested in Experiment 2. Another possibility is that there are genuine impairments in the rapid processing of identity in DPs, but that they are not face-specific, but are also present for non-face objects. Given recent suggestions that many DPs show impairments in the visual processing and recognition of non-faces (Geskin & Behrmann, 2017; Jiahui et al., 2018), individuals with DP might also show reduced responses to identity oddballs in FPVS streams with non-face objects. The main goal of Experiment 2 was to test this hypothesis.

Unexpectedly, DPs not only showed reduced identity discrimination responses in Experiment 1, but also smaller neural responses than Control participants at the base stimulation frequency and its first harmonic (see Figure 4). As in previous studies with this paradigm (e.g., Liu-Shuang et al., 2014; Dzhelyova et al., 2019), this response was maximal at midline occipital electrode Oz, consistent with a main neural generator in early visual cortical regions. However, this base rate response is not merely a low-level visual response but also reflects activity in high-level visual regions, including face-selective areas. The attenuation of this response for inverted as compared to upright faces might suggest the

involvement of face-selective neural generators, but could also reflect low-level differences in the retinotopic location of upright and inverted faces. With fixation centred between the eyes, the larger part of face images appeared in the lower visual field for upright and in the upper visual field for inverted faces (Di Russo et al., 2007, for evidence that EEG amplitudes to fast periodic visual stimulation differ between stimuli in the upper versus lower visual field). The fact that base frequency responses were smaller in the DP group relative to the Control group in Experiment 1 could suggest the presence of low-level sensory processing deficits in DP. This would be surprising, given that DPs generally perform normally in intermediate-level visual tasks that require the perception and discrimination of visual shapes (Lee, Duchaine, Wilson, & Nakayama, 2010; see also Le Grand et al., 2006), indicating that they do not have any generic visual-perceptual impairment. Alternatively, attenuated base frequency responses for DPs might reflect their tendency to avoid attending to the face images. Since EEG amplitudes to fast periodic visual stimuli are known to be modulated by attention (e.g., Müller & Hillyard, 2000), this could have reduced the size of the base frequency response in the DP group relative to the Control Group. This was tested in Experiment 2. Alternatively, this group difference could simply be a sampling artefact, resulting from the small sample size ($n=10$) for both groups in Experiment 1. As there are substantial individual differences in the size of base frequency responses to periodic stimuli (which ranged from $.27\mu\text{V}$ to $6.5\mu\text{V}$ for upright faces in Experiment 1), the Control group may have incidentally included many individuals with larger responses relative to the individuals in the DP group. If this was the case, systematic group differences in the size of base frequency responses should disappear in Experiment 2, where a different sample of DPs and Control participants was tested.

3. Experiment 2

This second experiment was conducted to investigate the questions raised by the findings of Experiment 1. As before, we employed FPVS streams with identity oddballs, and tested participants with DP and age-matched Control participants. On some runs, upright or inverted faces were presented, and participants' task was to attend to the fixation cross, as in Experiment 1. Face identity discrimination responses were expected to be attenuated in the DP group, and the question was whether this attenuation would again be similar for

upright and inverted faces. We also included runs where participants were instructed to attend to upright face stimuli (attend-stimuli runs), in order to identify them in a subsequent old-new memory test. If the attenuation of face identity discrimination responses observed for DPs relative to Controls in Experiment 1 was due to their tendency to avoid attending to face images, this attenuation should be smaller in attend-stimuli as compared to attend-fixation runs. Base frequency responses were also measured on these two types of runs. If the reduction of these responses for DPs in Experiment 1 was a sampling artefact, no such group differences should be found for the new sample of participants in Experiment 2. If it was due to attentional factors, these differences should be smaller or absent on attend-stimuli runs.

To address the critical question whether the reduction of neural responses to face identity changes observed for DPs in Experiment 1 reflects a domain-specific face-selective phenomenon, Experiment 2 also included runs where a sequence of non-face objects (upright cars) was presented (see Lochy et al., 2018; Hagen & Tanaka, 2019, for previous FPVS oddball studies with non-face stimuli). As with faces, every fifth image within this sequence was an identity oddball (i.e., a different car), and sequences of car images were also presented under attend-fixation and attend-stimuli instructions. Neural responses at the frequency of these car oddballs were compared between DPs and Controls, to find out whether DPs show attenuated identity discrimination responses also for non-face stimuli. To determine whether any such attenuation for DPs versus Controls would be more pronounced for faces, we also compared runs with upright faces and upright cars. If identity discrimination deficits in DP were strictly face-specific, DPs should show reduced neural responses to identity oddballs exclusively in runs with faces, and no such group differences should emerge for runs with car images. If this deficit was domain-general, smaller identity-sensitive responses in the DP group should also be found for cars, although this attenuation might still be stronger on runs with face images.

3.1. Methods

3.1.1. Participants

Twelve participants with developmental prosopagnosia (9 females; mean age 31, SD = 4.35) took part in Experiment 2. Only one of them (DP9) took part in both experiments. This participant was DP10 in Experiment 1. Twelve age-matched Control participants (9

females, mean age 31, SD=4.65) were also tested, and none of these took part in Experiment 1. The sample size was increased relative to Experiment 1 in order to make the counterbalancing of conditions equal across participants, and to improve the power for detecting any group-level differences between DPs and Controls in the effects of face inversion on face identity discrimination responses. Critically, and analogous to Experiment 1, we also report FPVS identity oddball responses for all individual participants. DP participants were recruited and pre-tested behaviourally in the same way as described in Experiment 1. Table 2 shows their Z-scores for four behavioural tests with faces. Because Experiment 2 also investigated neural correlations of identity processing for non-face objects, behavioural results for all DPs in the Old-New Recognition Tests with cars, houses, and horses are also shown. These tests were identical to those previously used by Duchaine & Nakayama (2005). As can be seen from Table 2, all twelve DPs were impaired on the FFT and CFMT, and all except one were impaired on the ONT with faces. Performance on the CFPT was again more variable, as in Experiment 1, with many but not all DPs performing within the normal range. There was also evidence for non-face object recognition deficits in some DPs. Four out of twelve DPs were impaired with cars, five with houses, and one with horses. All Control participants reported that they were confident in their face recognition abilities. This was confirmed by their CFMT scores, which were all within ± 1 standard deviation of the mean (Duchaine & Nakayama, 2006).

	Age	Gender	FFT	CFMT	CFPT Upright	CFPT Inverted	ONT Faces	ONT Cars	ONT Houses	ONT Horses
DP1	32	F	-7.5	-2.1	-0.1	-0.2	-9.3	-3.4	-3.6	-0.1
DP2	28	F	-8.9	-2.1	-2.3	0.5	-10.4	-1.7	-1.2	0.1
DP3	33	M	-8.3	-3.2	-3.2	-1.5	-5.7	-2.2	-3.2	-1.9
DP4	39	F	-5.6	-2.5	-0.9	1.4	-6.5	-1.7	0.3	0.4
DP5	31	F	-5.8	-2.1	-0.9	0.4	-2	-4.7	-2.2	0.7
DP6	26	F	-8.9	-3.4	-1.3	-1.6	-10.4	-1.2	1.7	0.9
DP7	24	F	-5.8	-4	0.5	-1.5	-8.4	-4.6	-0.7	0.1
DP8	27	F	-7.9	-2.1	-0.8	1.8	-4.6	0.8	-0.6	-0.6
DP9*	33	M	-7.5	-3.3	-0.7	-0.9	1	-1.9	-7.9	-1.4
DP10	30	M	-7	-2.9	-3.1	-1.5	-6.5	-1.6	-2.2	-4.3
DP11	37	F	-8.7	-2.9	-1.3	-1.2	-4.6	-1.1	-3.8	-1
DP12	31	F	-4.8	-3	-1.2	1.1	-4.9	-0.6	-0.6	-1.4
Mean	30.92		-7.23	-2.80	-1.28	-0.27	-6.03	-1.99	-2.00	-0.71

Table 2

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, and

the Old-New Test (ONT) with face, car, house and horse images, plus mean values across all DPs.

3.1.2. Materials and procedure

The face stimuli were taken from the same set that was used in Experiment 1. To make the old-new discrimination test that was run after attend-stimuli blocks (see below) less challenging, the face stimulus set was limited to the 24 photographs of male faces employed in Experiment 1. In addition, photographs of 24 blue cars (shown in side view) were also used. These were taken from free-to-use online images of car advertisements (see example in Figure 5), and were processed in Adobe Photoshop. The contrast and brightness of the images was balanced across images and all were resized to an average 453 (s.d.=24) x153 (s.d.=8) pixels. Any writing, emblems and logos were removed from the images. For both face and car stimuli, mean luminance was equalized online during stimulation, and a gamma correction was applied.



Figure 5. Examples of car images shown in Experiment 2.

The oddball discrimination paradigm used was identical to Experiment 1 (see Figure 1). In separate runs, stimulus sequences contained either faces or non-face objects (cars). In addition, attention was also manipulated, by including both “attend-fixation” and “attend-stimuli” conditions. The task on attend-fixation runs was the same as in Experiment 1. Participants were instructed to ignore the stimulus objects, and to detect colour changes of the fixation cross. On attend-stimulus runs, participants were instructed to attend to and remember the face or car stimuli in the sequence, in order to identify them in a subsequent old-new memory test (see below). Participants were told to focus gaze on the fixation cross, and to ignore the task-irrelevant colour changes at this location, in order to equate eye gaze and stimulus parameters with attend-fixation runs. To retain previously unseen new face or

car stimuli for the old-new memory tests, the stimulus selection procedures employed in Experiment 1 were modified. The total sets of 24 and 24 car stimuli were divided into three sets of 8 images. One set was used in the attend-fixation runs, one set was used in the attend-stimulus runs, and the third set was used for new stimuli in the old-new tasks. The allocation of stimulus sets to tasks was counterbalanced across participants.

Experiment 2 included five different types of runs. There were two successive attend-fixation and attend-stimulus runs, with either faces or cars (eight runs in total), and additionally two successive runs with inverted faces and attend-fixation instructions. At the end of the second attend-stimulus run with faces, participants were given an immediate old-new memory test consisting of 8 successive runs. On each run, an “old” face (i.e., one of the eight faces that were shown in the two preceding attend-stimulus runs) was presented next to a “new” face (i.e., a face that did not appear in these runs), against a grey background. Old and new face stimuli were presented to the left or right of fixation (randomized across runs), and participants responded by pressing the corresponding left or right arrow key on the computer keyboard. Stimuli remained on the screen until a response was recorded, at which point the next stimuli pair were immediately presented. On each run, one old and one new face stimulus was selected randomly and without replacement. An analogous old-new memory test was presented following the second attend-stimulus run with cars. The car memory test was identical to the face memory test except that the two car stimuli were presented above and below fixation, and participants indicated the location of the old car image by pressing the corresponding up or down arrow key. EEG was not recorded during these old-new tasks, and participants were free to move their eyes between the stimuli. In the two successive runs where inverted face images were presented under attend-fixation instructions, face stimuli were the same as in attend-fixation runs with upright faces.

In summary, there were three types of runs with face stimuli, which were presented in the following order: attend-fixation with upright faces; attend-fixation with inverted faces; attend-stimuli with upright faces, followed by the old-new face memory test. There were two types of runs with car stimuli (attend-fixation followed by attend-stimuli followed by the old-new car memory test). Participants completed two successive 60 s runs for each task condition. For half of all participants with DP and half of all Control participants, runs with face images preceded runs with car images, and this order was reversed for the other participants.

3.1.3. Electroencephalography recording data pre-processing, selection of electrodes and frequencies, and analyses

These were all analogous to Experiment 1. For the oddball response analyses, the frequencies used for identity discrimination responses (1.18 Hz, 2.35 Hz, 3.53 Hz, 4.70 Hz), and base frequency responses (5.88 Hz and 11.76Hz) and the electrodes selected for these analyses were identical to Experiment 1. Summed SNS values were computed for each individual participant. To assess identity discrimination responses for faces and cars in DPs and Controls, a repeated-measures analysis of variance (ANOVA) was conducted for SNS amplitudes obtained on all runs with upright stimuli, with the between-participant factor Group (DP Group versus Control Group), and the within-participant factors *Stimulus Type* (faces versus cars), *Attention Condition* (attend-fixation versus attend-stimuli), and *Hemisphere* (left versus right). A separate ANOVA was conducted for attend-fixation runs with upright and inverted faces, with the factors *Group*, *Face Orientation* (upright versus inverted) and *Hemisphere*. Summed SNS amplitudes for the base frequency response were analysed in an ANOVA with the factors *Group*, *Stimulus Type*, and *Attention Condition*. Analogous to Experiment 1, EEG spectra profiles for identity oddball and base frequency responses shown in Figures were computed on the basis of signal-to-noise ratios (SNRs), based on absolute FFT amplitudes across the whole EEG spectrum. The corresponding EEG spectra based on SNS amplitudes for identity oddball responses are provided as supplementary material (Figure S2 and S3).

3.2. Results

3.2.1. Behavioural data

Attend-fixation runs: Similar to Experiment 1, participants in both groups performed close to ceiling in detecting colour changes in the fixation cross. Accuracy and RTs were analysed in two ANOVAs with the factors Stimulus Type (Faces, Cars) and Group (DPs, Controls). Neither accuracy nor RTs differed between runs with face or car images (both $F < 1$), and there were also no interactions between Stimulus Type and Group (both $F < 1$). There was no main effect of Group for accuracy ($F < 1$). Mean accuracy was 97% in the Control group, and 96% in the DP group. Mean RTs for detected colour changes were 412

ms in the Control group and 420 ms in the DP group, and this difference was not reliable (main effect of group: $F < 1$).

Old-new memory test performance following attend-stimuli runs: Accuracy in this test was analysed in an ANOVA with the factors Stimulus Type and Group. There was a main effect of Stimulus Type, $F(1,22)=7.18, p=.01, \eta^2=.25$, reflecting on overall reduction of accuracy for faces across both groups. The main effect of Group approached significance, $F(1,18)=3.61, p=.07, \eta^2=.14$. Critically, these effects were qualified by a highly significant interaction between Group and Stimulus Type, $F(1,22)=11.22, p=.003, \eta^2=.34$. Follow-up tests showed that the mean accuracy in the old-new face memory test was lower for DPs (58%; $sd= 14\%$) than for Control participants (78%; $sd= 14\%$), and this difference was reliable ($t(22)=3.8, p=.003$). In contrast, accuracy in the old-new car memory test was virtually identical for DPs (77%; $sd= 14\%$) and for Control participants (76%; $sd=14\%$; $t<1$).

3.2.2. Identity discrimination responses to upright faces and cars

Figure 6 shows grand-averaged SNR values obtained for runs with upright faces (top panels) and upright cars (bottom panels) over the left and right hemisphere (averaged across the four lateral posterior electrodes over each hemisphere) in attend-fixation runs. The corresponding results for attend-stimuli runs are shown in Figure 7. SNR values measured for the Control group (blue) and for the DP group (red) are overlaid, and topographic scalp distribution maps are included (see Figures S2 and S3 for corresponding results based on SNS amplitudes). As in Experiment 1, the face identity discrimination response to upright faces in attend-fixation runs was strongly attenuated in the DP group relative to the Control group (Figure 6, top panel). A similar difference between the two groups was also present for faces in attend-stimuli runs (Figure 7, top panel). Importantly, DPs also showed smaller identity discrimination responses than Controls on runs with images of cars, and this was the case both in attend-fixation and in attend-stimuli runs (Figures 6 and 7, bottom panels). This apparently domain-unspecific reduction in the size of identity oddball responses for DPs is further illustrated in Figure 8 (left and middle panels) for summed SNS amplitudes (collapsed across hemispheres, and across attend-fixation and attend-stimuli runs). Identity discrimination responses were larger for cars relative to faces in both groups. Critically, these responses are clearly generally attenuated for DPs as

compared to Controls, and this was the case not only for upright faces, but also for upright cars.

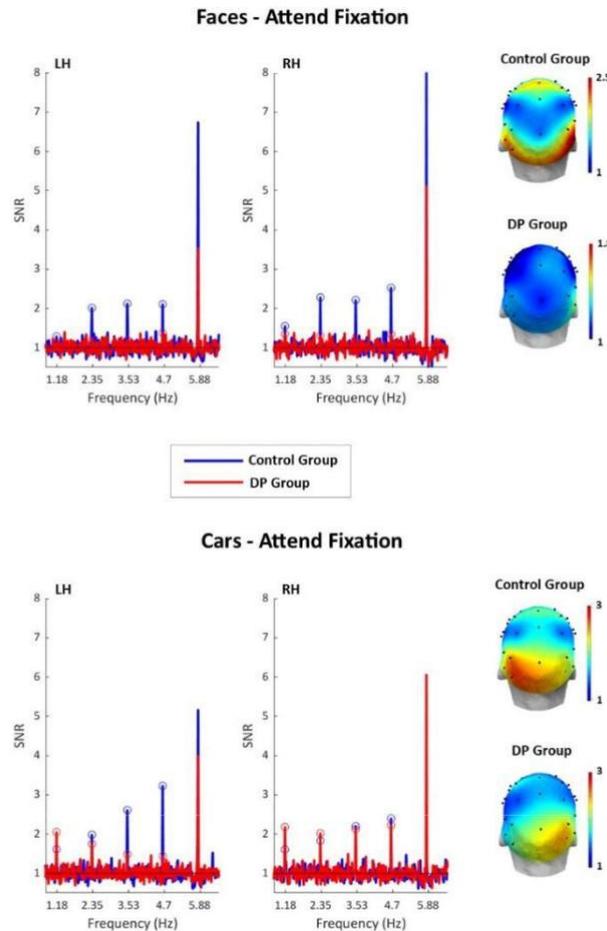


Figure 6. SNR spectra for identity discrimination responses measured in Experiment 2 on attend-fixation runs with upright faces (top panels) and upright cars (bottom panels). SNRs are averaged across the four occipito-temporal electrodes over the left hemisphere (LH) and right hemisphere (RH), and are shown separately for the Control and DP groups (blue and red traces). Circles mark amplitudes at the first four harmonics of the identity oddball frequency for the two groups. The corresponding topographical scalp distribution maps for identity discrimination responses to faces and cars (based on SNR values averaged across the first four harmonics of the identity oddball frequency) are also included. Note the different scales of the maps for runs with faces in the two groups. Relative to Controls, DPs showed attenuated identity discrimination responses not only for faces, but also for cars.

To confirm these observations, summed SNS amplitude values measured for attend-fixation and attend-stimuli runs with upright faces or cars were analysed in an ANOVA with the factors Group (DP versus Control), Stimulus Type (faces versus cars), Hemisphere (left versus right), and Attention Condition (attend-fixation versus attend-stimuli). This analysis revealed a main effect of Stimulus Type, $F(1,22)=12.58$, $p<.002$, $\eta^2=.36$. As can be seen in

Figure 8, SNS amplitudes to identity oddball stimuli were generally larger in runs with cars than in runs with faces (.79 μ V versus .51 μ V). There was also a main effect of Hemisphere, $F(1,22)=5.12$, $p=.03$, $\eta^2=.19$, as responses to identity oddballs were larger over the right hemisphere (.76 μ V, as compared to .56 μ V over the left hemisphere). No significant interactions were found between Hemisphere and Group, $F<1$, and between Hemisphere and Stimulus Type, $F<2$. A main effect of Group was present, $F(1,22)=11.32$, $p<.003$, $\eta^2=.34$, confirming that DPs generally showed smaller identity discrimination responses to upright faces or cars as compared to Control participants (.91 μ V versus .37 μ V). Critically, there was no interaction between Group and Stimulus Type, $F(1, 22)=1.5$, $p=.23$, suggesting that the attenuation of identity discrimination responses in the DP group was present not only for faces, but also on runs where images of cars were shown. However, a significant Stimulus Type x Hemisphere x Group interaction was present, $F(1,22)=4.56$ $p<.04$, $\eta^2=.17$).

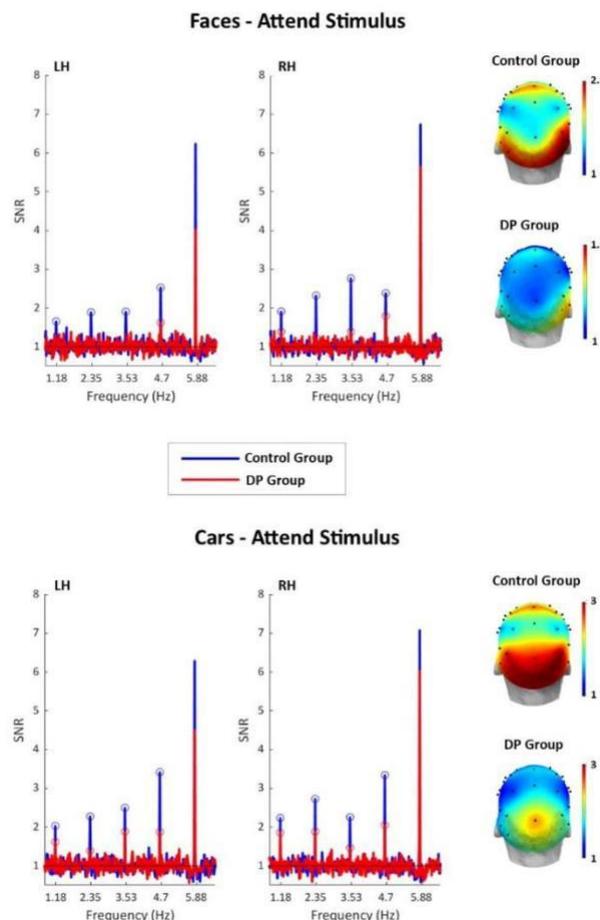


Figure 7. SNR spectra for identity discrimination responses measured in Experiment 2 on attend-stimuli runs with upright faces (top panels) and upright cars (bottom panels). The

layout of SNR values and topographical maps for DPs and Controls is analogous to Figure 6. DPs showed attenuated identity discrimination responses for faces as well as for cars.

To further confirm that DPs showed smaller identity oddball responses not only to faces but also to cars, follow-up analyses were conducted separately for runs with face and with car images. For faces, a main effect of Group, $F(1,22)=12.00$, $p<.002$, $\eta p^2=.35$, confirmed the reduction of face identity discrimination responses in the DP group (.19 μ V, as compared to .84 μ V for the Control group). Responses were larger in the right hemisphere (.64 μ V), as compared to .39 μ V in the left hemisphere; main effect of Hemisphere: $F(1,22)=6.44$, $p<.02$, $\eta p^2=.21$, and this asymmetry did not differ between the two groups (Hemisphere x Group: $F<2$). Crucially, a main effect of Group was also present for runs with car images, $F(1,22)=6.80$, $p<.02$, $\eta p^2=.24$, demonstrating that responses to car identity oddballs were attenuated for the DP group relative to the Control group (.55 μ V as compared to 1.02 μ V; see also Figure 8). There was no reliable left-right asymmetry for these responses to cars, and no interaction between Hemisphere and Group, both $F<2$.

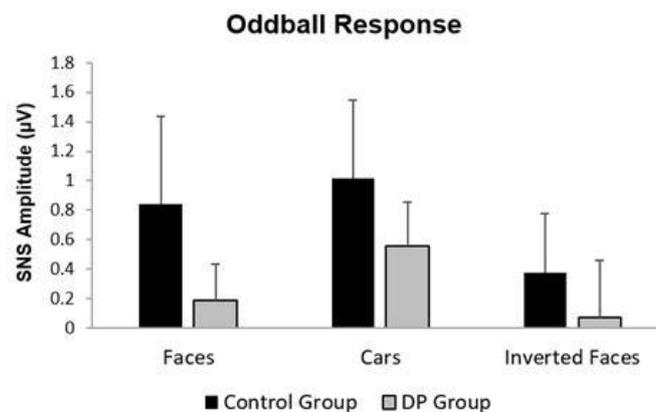


Figure 8. Averaged summed SNS amplitudes for identity discrimination responses in Experiment 2 in the Control group (black bars) and the DP group (grey bars). SNS values are shown separately for runs with upright faces and cars (left and middle panels; collapsed across attend-fixation and attend-stimuli runs), and for attend-fixation runs with inverted faces (right panel). Relative to Controls, DPs showed reduced identity discrimination responses for all types of stimuli.

Allocating attention to either the fixation cross or to the stimulus images had no overall effect on the size of identity oddball responses in Experiment 2 (main effect of Attention Condition: $F<1$). However, there was an interaction between Attention and Group, $F(1,22)=6.27$, $p<.02$; $\eta p^2=.22$, and a three-way interaction (Attention Condition x Stimulus Type x Group: $F(1,22)=6.88$, $p<.02$, $\eta p^2=.24$). This was further explored in separate ANOVAs

conducted for the two groups. For the Control group, there was a strong trend for identity oddball responses to be larger on attend-stimuli runs relative to attend-fixation runs ($.80 \mu\text{V}$ versus $1.05 \mu\text{V}$; $F(1, 11)=4.73$, $p=.052$, $\eta p^2=.3$). The interaction between Attention Condition and Stimulus Type was not significant, $F(1,11)=2.64$, $p=.13$. For the DP group, no reliable main effect of Attention Condition was present, $F(1,11)=2.36$, $p=.15$. However, the interaction between Attention and Stimulus Type approached significance, $F(1,11)=4.50$, $p=.06$, $\eta p^2=.29$, reflecting a trend for a smaller oddball response to cars on attend-stimuli as compared to attend-fixation runs ($.47\mu\text{V}$ versus $.72\mu\text{V}$), with no difference between these runs for faces ($.19\mu\text{V}$ versus $.19\mu\text{V}$).

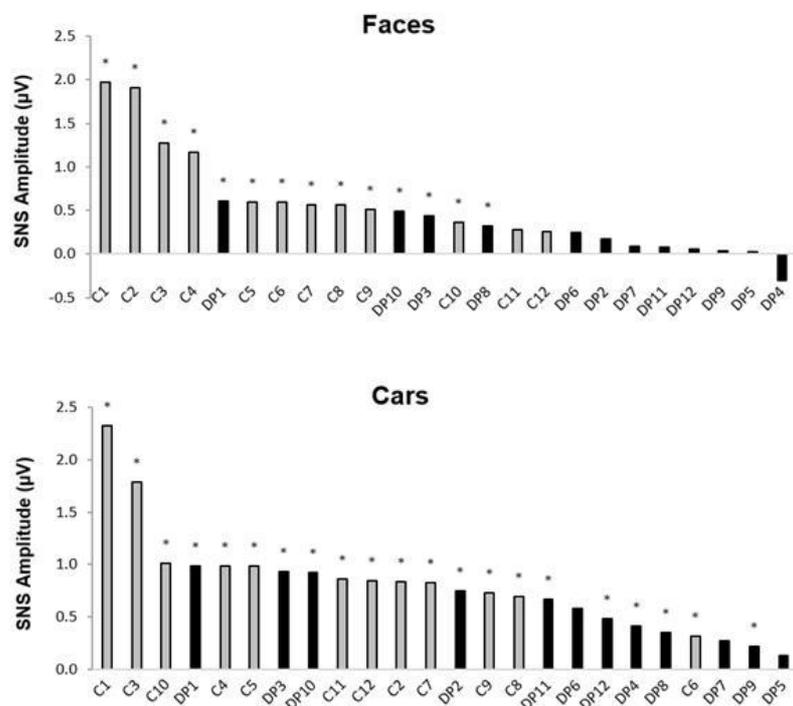


Figure 9. SNS amplitude values of the identity discrimination response (summed across the first four harmonics of the identity oddball frequency and averaged across hemispheres) on runs with upright faces (top panel) and upright cars (bottom panel) obtained in Experiment 2 for each individual participant. Values for DPs and Controls are shown as dark and light grey bars, respectively. Asterisks indicate the presence of a significant identity discrimination response for an individual participant, based on Z-scores computed on the basis of summed raw FFT amplitudes.

As in Experiment 1, we also assessed identity discrimination responses at the level of individual DP and Control participants, but now separately for runs with upright face or car images (collapsed across attend-fixation and attend-stimuli runs and across hemispheres, and excluding runs with inverted faces), based on Z-scores for summed raw FFT values.

Individual results are shown in Figure 9 for DPs (black bars) and Control participants (grey bars), on runs with upright faces (top panel) and upright cars (bottom panel), ordered from left to right for participants with larger versus smaller responses. For both face and car identity oddball responses, most participants with DP clustered on the right (i.e., small identity oddball responses) and Control participants on the left (large responses). All but two of the Control participants showed a significant oddball response to face identity changes, whereas only four out of twelve DP participants showed a significant response. All Control participants but only nine of the twelve DPs produced a reliable response to car identity changes.

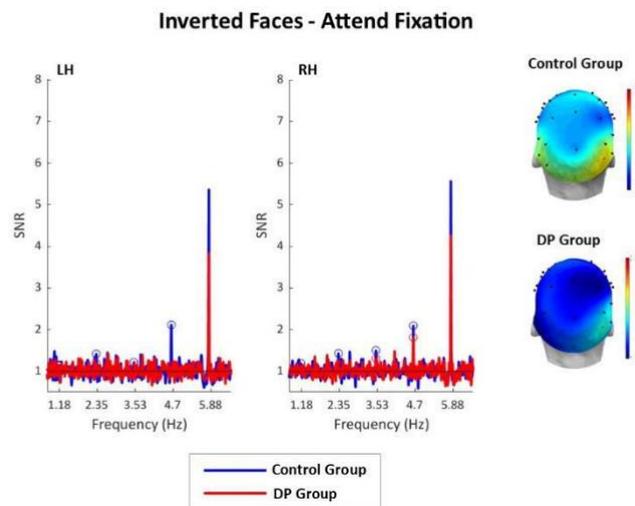


Figure 10. SNR spectra for identity discrimination responses and corresponding topographical maps measured in Experiment 2 for DPs and Controls on attend-fixation runs with inverted faces, showing attenuated responses for DPs.

3.2.3. Identity discrimination responses to upright and inverted faces

To confirm the finding from Experiment 1 that identity discrimination responses are reduced for inverted as compared to upright faces, and to further assess whether face inversion reduces the difference in these responses between DPs and Control participants, we compared identity oddball responses measured on attend-fixation runs with upright or inverted faces. Figure 10 shows SNR values and scalp maps for oddball responses to inverted face sequences, separately for DPs and Controls. The corresponding results for upright faces are shown in Figure 6 (top panel). As in Experiment 1, identity discrimination responses to inverted faces were attenuated in the DP group relative to the Control group (see also

Figure 8, right panel). In an ANOVA with the factors Group, Face Orientation (upright versus inverted), and Hemisphere, a main effect of Face Orientation was found, $F(1,22)=4.57$, $p<.05$, $\eta^2=.17$, reflecting larger identity discrimination responses for upright as compared to inverted faces (.48 μ V versus .22 μ V). There was a main effect of Hemisphere, $F(1,22)=4.96$, $p<.04$, $\eta^2=.18$, as the face oddball response was larger in the right (.43 μ V) than the left (.28 μ V) hemisphere. A main effect of Group, $F(1,22)=14.07$, $p<.001$, $\eta^2=.39$, again reflected the reduced face oddball response in the DP group. The interaction between Face Orientation and Group was not reliable, $F(1,22)=1.36$, $p=.26$, indicating that the difference in the size of face identity discrimination responses between DPs and Controls was not modulated by face orientation.

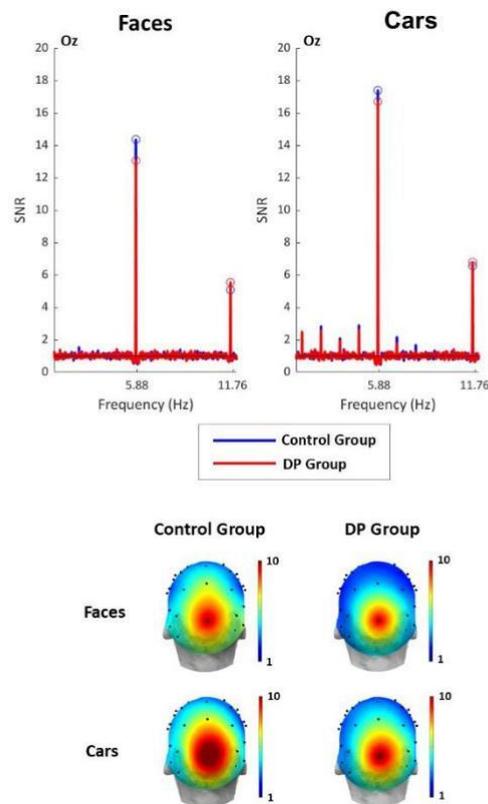


Figure 11. Top panels: SNR spectra of responses measured in Experiment 2 at the base stimulation frequency and its first harmonic at electrode Oz on runs with upright faces or upright cars, for the Control group (blue traces and circles) and the DP group (red traces and circles). Bottom panels: Topographic maps showing the scalp distributions of the base frequency response and its first harmonic (based on averaged SNR values), separately for faces and cars, and both groups. Base stimulation frequency responses did not differ reliably between DPs and Controls.

3.2.4. The base stimulation frequency response

In Experiment 1, the base frequency response to face images was attenuated in DPs relative to Control participants. To test whether this was also the case in Experiment 2, we compared summed SNS amplitudes at the base stimulation frequency and its first harmonic (11.76 Hz) at midline occipital electrode Oz between the Control group and the DP group, obtained on attend-fixation and attend-stimuli runs with upright faces or upright cars (runs with inverted faces were not included). Figure 11 shows the corresponding SNR values at these frequencies for faces and cars (top and bottom panels, collapsed across attend-fixation and attend-stimuli runs), together with topographical maps showing that base frequency responses were again maximal at Oz. Base frequency responses again tended to be slightly larger in the Control Group relative to the DP group, but these differences were much less pronounced than in Experiment 1. An ANOVA of summed SNS scores for the base frequency response with the factors Group, Stimulus Type, and Attention Condition revealed a main effect of Stimulus Type, $F(1,22)=5.03$, $p<.04$, $\eta^2=.19$. The base frequency response was larger for runs with car images than for runs with face images (2.6 μ V versus 2.11 μ V), which most likely reflects low-level visual differences between these two types of images. However, there was no main effect of Group, or interaction between Group and Stimulus Type, both $F<1.5$, indicating that DPs and Control participants did not differ systematically in the size of their base frequency responses in Experiment 2. There was no reliable main effect or interactions involving the factor Attention Condition, all $F < 3$.

3.2.5. Correlations between individual identity oddball responses to faces and cars

Figure 12 shows correlations between the size of individual identity oddball responses to upright faces and cars, separately for the DP group (in black) and the Control group (in grey). These responses appear to be strongly correlated in both groups. However, these correlations could simply be due to individual differences in generic FPVS responsiveness, and not be specifically related to links in identity discrimination processes in response to faces and cars. Such generic individual differences in FPVS amplitudes should also affect base frequency responses. To test this, partial correlations were calculated across both groups, and also separately within the DP and Control groups. These correlations investigated the relationship between individual identity oddball responses to upright faces and cars, whilst controlling for the amplitude of individual base frequency responses to these stimuli by including these base frequency responses as covariates. Across both groups,

a strong positive partial correlation between face and car identity oddball responses was obtained, which was statistically significant, $r(20) = .751$, $N = 24$, $p < .001$. This positive partial correlation was significantly present within the DP group, $r(8) = .878$, $N = 12$, $p < .001$, and also within the Control group, $r(8) = .674$, $N = 12$, $p = .033$. In addition, a zero-order correlation between base frequency responses and identity oddball responses to upright faces conducted across both groups. This analysis showed that the amplitudes of these responses were not significantly correlated, $r(24) = -.103$, $p = .663$, further indicating that the size of the base frequency response to faces had no significant impact on individual face identity oddball responses. For cars, base frequency responses and identity oddball responses were also not significantly correlated, $r(24) = .281$, $p = .184$.

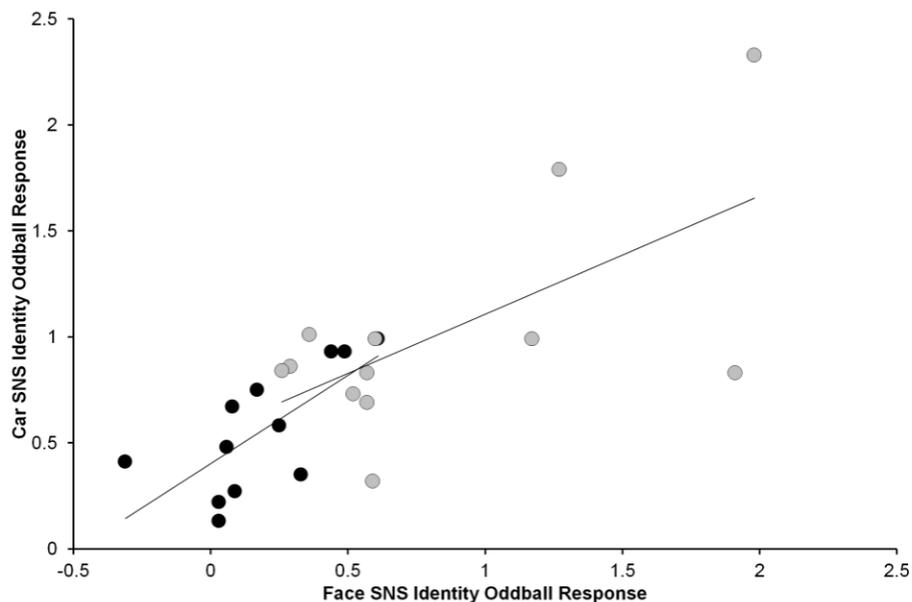


Figure 12. Correlations between the size of individual identity oddball responses on runs with upright faces and on runs with cars in Experiment 2. Scores for DP participants are shown in block, and scores for Control participants in grey, and lines of best fit are shown separately for each group.

Analogous partial correlations with the corresponding base frequency responses as covariates were calculated in both groups to investigate links between identity oddball responses for upright and inverted faces, and between inverted faces and cars. For identity oddball response to upright and inverted faces, a moderate significant positive correlation was present, $r(20) = .474$, $N = 24$, $p < .026$. Identity oddball responses to inverted faces and cars were more strongly correlated, $r(20) = .622$, $N = 24$, $p = .002$. In contrast, identity oddball and base frequency responses for inverted faces were not significantly correlated,

$r(24) = .343$, $p = .101$, further indicating that the size of individual base frequency responses had no significant association with the amplitude of identity oddball responses to inverted faces.

3.3. Discussion of Experiment 2

Confirming the results of Experiment 1, DPs showed reduced face identity discrimination responses relative to Control participants. Importantly, this attenuation again remained unaffected by face orientation (upright versus inverted). As neural responses obtained with the FPVS paradigm are not subject to the same limitations that affect the measurement of face inversion effects in behavioural tests, this result provides new and strong evidence that the face processing impairment in DP is not related to a selective deficit of a neural mechanism tuned to upright faces, such as holistic face processing. The absence of any differential effects of face orientation contrasts with the results a recent study (Vettori et al., 2019), where autistic individuals showed reduced identity oddball responses relative to neurotypical controls only for upright but not for inverted faces, pointing towards a specific impairment in holistic face processing in autism. Our results suggest that deficits in the perceptual processing of identity-related visual signals from faces in individuals with DP differs from those present in autism spectrum disorders.

Directing attention either towards the face images or towards the fixation cross had no impact whatsoever on the size of face identity responses in the DP group. This suggests that the attenuation of these responses for participants with DP was not a result of any tendency to avoid allocating attention to task-irrelevant face images on attend-fixation runs. For Control participants, identity discrimination responses tended to be generally larger on attend-stimuli runs (see also Yan, Liu-Shang, & Rossion, 2019, for similar results). In contrast to Experiment 1, base frequency responses to either face or car stimulus sequences did not differ reliably between DPs and Controls, and were also unaffected by our attention manipulation. This suggest that the group difference in the size of these responses observed in Experiment 1 might have been a sampling artefact, and did not reflect an objective difference in low-level visual or attentional processes between DPs and Controls.

The critical new finding of Experiment 2 was that DPs showed reliably attenuated identity discrimination responses not only in response to sequences of face images, but also

on runs where images of cars were shown. Although the absolute size of the difference in the size of this response between DPs and Controls was numerically larger for faces than for cars (.65 μ V and .47 μ V, respectively), there was no statistical evidence that its reduction in DPs was more pronounced for face identity changes. These observations strongly suggest that the reduction of rapid face identity discrimination responses observed for DPs in both experiments does not reflect a genuinely face-specific deficit, but an impairment that also affects the identity-related processing of non-face objects. Further support for this hypothesis comes from the observation that the size of individual identity oddball responses to faces and cars was correlated across individual DPs and also across Control participants, even when the amplitude of base frequency responses was taken into account. The implications of these observations will be further considered below.

It should be noted that while the FPVS results of Experiment 2 revealed the existence of a face-unspecific impairment in the processing of object identity in DP, behavioural results showed a more face-specific pattern. While all twelve DPs tested performed poorly in standardised face recognition and memory tests (FFT and CFMT), only some of them showed impaired performance in tests with non-face objects (although deficits were most widespread for cars). Moreover, in the old-new memory tests that followed attend-stimuli runs, DPs performed worse than Controls only for faces, but at the same level as Control participants for cars. This dissociation between neural and behavioural markers underlines the importance of employing multiple measures to assess object recognition deficits in DP, and suggests that identity oddball responses obtained with FPVS procedures might be more sensitive to underlying visual impairments than behavioural tests, which could be susceptible to compensatory strategies.

4. General Discussion

The goal of the current study was to find evidence for impaired unfamiliar face identity discrimination processes in DP, by using fast periodic visual stimulation procedures and measuring responses to identity oddballs. In Experiment 1, neural identity discrimination responses were strongly attenuated for DPs as compared to Controls, for both upright and inverted faces. This was confirmed in Experiment 2 with a different sample of DPs and Control participants. This experiment also showed that the reduction of face

identity discrimination responses for the DP group did not result from a tendency to avoid attending to task-irrelevant faces. Overall, these findings demonstrate that FPVS procedures can rapidly identify deficits in the rapid identity-sensitive processing of face stimuli in DP, in the absence of any requirement to process and identify these stimuli.

However, and importantly, Experiment 2 revealed that the identity processing impairment in DPs, as reflected by reduced neural responses at the identity oddball frequency and its harmonics, was not specific to faces, but was also apparent for sequences of non-face (car) images. The size of this reduction for DPs as compared to Control participants was not reliably larger for face oddballs than car oddballs, suggesting that the underlying impairment in rapid perceptual identity processing affects face and non-face stimuli to a comparable degree. Liu-Shang et al. (2014) suggested that FPVS responses to identity oddballs are generated by similar mechanisms to those that produce neural repetition suppression effects ([see also Rossion et al., 2020, for a recent discussion of this issue](#)). For faces, increased neural responses at the identity oddball frequency and its harmonics are likely to reflect the activation of clusters of face-selective neurons within posterior occipitotemporal cortex that are sensitive to facial identities. These neurons are suppressed when the same face is presented repeatedly, and released from suppression when an oddball face with a different identity appears. In this scenario, the reduction of face identity oddball responses observed for DPs in both experiments suggests that these face-selective neurons are less well tuned to changes in facial identities. As a result, any release from suppression in response to these oddballs is reduced in DPs relative to Control participants, as reflected by attenuated neural responses at the oddball frequency and its harmonics.

Because repetition suppression effects in ventral visual areas are elicited by faces as well as by non-face objects (e.g., Henson, 2003; Weiner, Sayres, Vinberg, & Grill-Spector, 2010), the neural responses measured for car identity oddballs in Experiment 2 are likely to be generated in an analogous fashion, by a release from suppression of neurons in areas involved in the high-level visual processing of object images. Thus, the observation that these responses were attenuated in DPs relative to Controls suggests that deficits in the tuning of visual areas to changes in the identity of visual objects in DP are not restricted to the processing of faces in face-selective regions, but also affect the processing of other types of objects in different regions of ventral visual cortex. This would be in line with

recent fMRI results by Jiahui et al. (2018), who found widespread reductions in the category selectivity of occipitotemporal areas in DP. Importantly, these reductions were not only evident in face-selective regions, but also in scene-selective and body-selective areas (although general object-selective regions in this study showed normal selectivity). It is possible that the reduced category selectivity for faces as well as non-face objects in DPs reported by Jiahui et al. (2018) and the presence of reduced identity oddball responses to both faces and cars observed for DPs in the current Experiment 2 reflect similar underlying deficits. If both face and non-face areas are less well tuned to their preferred object categories in individuals with DP, these areas may also be generally less sensitive to visual information that signals the presence of an identity change between objects within these categories. This could be tested in future studies where reductions in the category selectivity of specific occipitotemporal areas and the attenuation of identity oddball responses for objects within these categories are measured independently for individual DPs, in order to assess whether these two deficits are correlated.

A domain-general perceptual deficit in DP

It is clear that the current results are incompatible with current accounts which assume that visual deficits in DP are domain-specific. If these deficits reflected impaired holistic face processing, they should primarily affect upright faces, but not inverted faces or non-face objects such as cars (e.g., Duchaine et al., 2006; Duchaine et al., 2007; DeGutis et al., 2012). If they represented a more general face-selective deficit, impairments should be observed for the processing of both upright and inverted faces, but not with cars. Instead, the current study demonstrated that DP participants are generally impaired at rapid visual discrimination, for upright faces, inverted faces, and also for cars. If visual processing deficits in DP are more domain-general than is often assumed, this would explain why many (although not all) individuals with DP also have some problems in non-face recognition tasks (Geskin & Behrmann, 2017). In Experiment 2 of the current study, four DPs showed impairments on two out of three old/new object recognition tasks, three additional DPs were clearly impaired on at least one object recognition task, and as a group DPs were impaired with cars and houses, but not horses (see Table 2).

This raises the question which factors could explain the co-occurrence of face and non-face identity processing deficits in DP. One possibility is that the core problem occurs further upstream, during the earliest sensory processing stages, resulting in impaired visual input to all higher-level category-selective areas (e.g. Lohse et al., 2016). The observation in Experiment 1 that FPVS base frequency responses were reduced in DPs as compared to Controls would be in line with such a low-level sensory account. However, this observation was not confirmed in Experiment 2, which suggests either that the group difference found in Experiment 1 was a sampling artefact, or that different DP individuals can have impairments at different stages in the visual hierarchy. In support of the former interpretation, there is little if any behavioural evidence in the literature suggesting that DPs generally have low-level visual impairments. In addition, ERP studies have consistently shown apparently normal early sensory P1/N1 components to visual objects in DP (e.g., Towler, et al., 2012).

Alternatively, DP might be regarded as a particular form of within-category visual object agnosia where the recognition of faces is most strongly impaired, but other non-face object processing is also often affected (see also Gauthier, Behrmann, & Tarr, 1999; Rossion, 2018) . With respect to the nature of this domain-general deficit, important clues are provided by the dissociation between the clear attenuation of identity oddball responses to both faces and cars observed for the DP groups in the present study, and the apparently normal performance of many individual DPs in some behavioural tests of face and object processing. Although virtually all DPs performed poorly in memory-based face recognition tests, most of them were within the normal range in the CFPT. Furthermore, although DPs as a group were impaired in tests of car and house memory (but not horse memory; see Table 2), many individual DPs showed no clear deficits in these tests. There was also a strong dissociation in the old/new recognition tests that followed attend stimuli runs in Experiment 2, where DPs showed strong impairments for faces, but performed as well as Control participants when their memory for car images was tested. To understand this pattern of results, it is important to contrast the temporal demands imposed on identity-related perceptual processing in the oddball FPVS paradigm and in behavioural tests of face and non-face perception and recognition. Given the rapid image presentation in the FPVS procedure, neural identity oddball responses reflect the ability of ventral visual areas to extract identity-sensitive signals from the visual stream within less than 170 msec. In contrast, behavioural tests typically used to assess face and non-face perception and

recognition allow much more time to extract and encode task-relevant information, and to provide responses. In addition, behavioural tests that are commonly employed to assess face and object visual discrimination abilities in DPs, as also used here, do not measure response speed. Neuropsychological studies have shown that some patients with acquired prosopagnosia can achieve normal levels of accuracy in discriminating unfamiliar face identities, at the expense of unusually long response times (e.g., Davidoff & Landis, 1990; Delvenne, Seron, Coyette, & Rossion, 2004).

This key difference may go some way to explaining the partial dissociations in the behavioural and neural profiles of some of the DPs tested here. The core impairment in DP may be a domain-general perceptual deficit in the ability to rapidly extract visual information that is relevant for individual object discriminations that applies to both faces and non-face object categories. However, when sufficient time is available, they are able to employ compensatory attentional strategies that enable them to perform relatively normally in some behavioural tasks such as the CFPT and old/new recognition tasks with non-face objects. Such an impairment in rapid perceptual processing is consistent with a growing number of studies that have found slower response times for non-face object recognition tasks for DP participants in conditions where accuracy is apparently normal (e.g. Rivolta, Lawson, & Palermo, 2017; Bate et al., 2019). It would also explain why DPs were found to show evidence for delayed processing of the global form of Navon stimuli, which correlated with both face and object recognition ability (Gerlach et al., 2017).

The hypothesis that DPs have a specific deficit in rapid visual object discrimination might also explain why identity adaptation effects in face-selective brain regions have consistently been shown to be normal in fMRI studies of DP. These studies have employed relatively long face stimulus presentation durations (between 300-1700 ms) and even longer interstimulus intervals in which face images can be consolidated (Furl et al., 2011; Avidan, Hasson, et al., 2005; Avidan & Behrmann, 2009), allowing DP participants ample time to engage compensatory mechanisms. In contrast to fMRI measures, more temporally precise ERP markers of markers of face identity processing (N250/N250r components) have consistently found identity-specific face matching and recognition deficits in DPs (Parketny et al., 2016; Fisher et al., 2017; Towler et al., 2018). Also in line with a rapid perceptual discrimination deficit, we previously found impaired sensitivity to the canonical spatial configuration of facial features in DPs at the level of the N170 component (140-190 ms post-

stimulus) that was no longer evident from around 200 ms after face stimulus onset (Towler et al., 2016).

The rapid visual discrimination deficit (RVDD) hypothesis of DP

To put our findings into a wider context, theories of rapid auditory discrimination deficits have been used to explain perceptual and memory deficits in neurodevelopmental disorders such as specific language impairment (e.g. Benasich et al., 2002), dyslexia (e.g. Hari, & Renval, et al., 2001), and amusia (e.g. Albuoy et al., 2016). Here we propose an analogous account for the visual modality. According to our domain-general rapid visual discrimination deficit hypothesis of developmental prosopagnosia (RVDD hypothesis), individuals with DP tend to have a generally slower and less precise visual-perceptual discrimination system located within posterior occipito-temporal cortex. This category-general deficit affects the ability to rapidly encode and discriminate between exemplars from within familiar and visually complex object categories such as faces and cars.

DP is likely to be associated with atypical developmental trajectories of occipitotemporal brain areas, as a result of genetic as well as environmental influences (e.g., Towler & Eimer, 2012; Towler et al., 2017). Atypical development can affect both face-selective and other category-selective areas, and can result in different individual patterns of associations and dissociations between face and object recognition deficits. The co-occurrence of these deficits in many DPs therefore reflects a general predisposition for atypical development of higher-level ventral visual areas (excluding visual word-form areas; Gerlach et al, 2019; see also Towler & Tree, 2018; Gray & Cook, 2018, for similar suggestions). Our hypothesis makes the specific proposal that these atypical trajectories primarily affect rapid object discrimination processes in these areas, and that this is a major risk factor for DP. It assumes that such impairments in rapid perceptual discrimination are domain-general, and affect early identity-sensitive neural responses to faces and non-face objects (cars) in similar ways, as was demonstrated by the current results. If this was the case, why would such deficits have a particularly profound impact on the development of a normal face processing system, and less so on the ability to recognize other common object categories? General rapid perceptual discrimination ability may be more important for faces than for other objects because of the temporal demands placed on recognising conspecifics

in real world situations, and also because different face exemplars are generally much more similar to each other than exemplars from other object categories. Such factors are usually considered as reasons why face processing should be based on domain-specific mechanisms. According to the RVDD hypothesis, they explain why faces place higher demands on domain-general visual discrimination processes than other types of objects, thus resulting in apparently face-specific patterns of recognition impairments.

The RVDD hypothesis can be experimentally tested in several ways. For example, a previous study (Alonso-Prieto et al., 2013) has found that for neurotypical participants without face processing impairments, the optimal stimulation frequency for identity discrimination is approximately 5.88Hz (as in the present study). We predict that individuals with DP should have a slower optimal oddball face discrimination frequency than Control participants, and this can be readily assessed by parametrically varying FPVS oddball stimulation frequencies (e.g., Retter, Jiang, Webster, & Rossion, 2020). Another empirical test is to manipulate encoding durations in matching and recognition tasks for face and non-face objects. DPs should be most disproportionately impaired for the shortest stimulus durations (in the range of 100-200 ms), for both objects and faces, and these impairments should become smaller when stimuli are presented for longer.

The RVDD hypothesis does not just provide a new account of developmental prosopagnosia, but also has more general and testable implications for the cognitive architecture of visual cognition. It is often assumed that oddball identity discrimination responses reflect the activity of domain-specific encoding and representational systems (particularly in the case of human faces; e.g., Jonas et al., 2018; Liu-Shuang, Torfs, & Rossion, 2016; Jacques, Retter, & Rossion, 2016). If there are functionally separate discrimination systems for faces and for cars, individual differences in the efficiency of these systems should be largely independent, even for neurotypical individuals. In this case, one would expect little if any correlations in the size of oddball discrimination responses for these two object categories. The fact that these responses were reduced in the DP group relative to the Control group in Experiment 2 for both faces and objects provides initial evidence against domain-specificity, and suggests common or shared visual-perceptual discrimination mechanisms. More direct evidence was provided by the results of the partial correlation analyses of individual identity oddball responses to faces and cars in Experiment 2. The amplitudes of these responses were strongly associated, even when the size of

individual base frequency responses were taken into account, demonstrating that these correlations do not reflect individual differences in generic FPVS responsiveness.

These findings not only provide further support for the RVDD hypothesis, but also have implications for the more general question whether there are shared and overlapping perceptual representation systems for faces and other familiar object classes (Haxby et al., 2001) or whether these systems are separate and domain-specific (Kanwisher, 2010). While the current results suggest strong associations between face and object discrimination ability, it remains an open question at which stage of the perceptual and cognitive hierarchy these associations are generated. For example, a strong domain-general account of face and object recognition could claim that face and object recognition are underpinned by the same general visual recognition system. The observed impairments in DPs in the present study are consistent with this account, but are difficult to reconcile with the strong evidence for category-selectivity from neuroimaging and intracranial recording studies (e.g. Kanwisher, 2010). Alternatively, a strong version of the domain-specific account could suggest that face recognition and object recognition are independent disorders that are underpinned by separate cognitive and neural systems (e.g., Gray & Cook, 2018). According to this account, DP is caused by physical brain pathology within the occipito-temporal cortex, and this brain pathology varies in its spatial extent between individual DPs. When it is present exclusively within face-selective regions, DPs will have face-specific impairments. More often, this pathology affects wider occipito-temporal regions, and causes separate impairments in independent face and object recognition systems.

Our results are difficult to interpret within such a strong domain-specific account. If face and object recognition were entirely independent, there would be no reason to assume that face and object oddball discrimination responses should be strongly and systematically linked across individual DPs. Perhaps even more importantly, no such links should be found across individual control participants without any brain pathology which impairs face and/or object recognition. However, our results are consistent with an alternative hybrid account which assumes that face and object recognition are separate at high levels of the visual hierarchy (consistent with strong evidence for category-selectivity in visual processing), but are closely linked at shared lower-level sensory-perceptual stages. These stages are impaired in DP, and this has downstream effects at higher levels on both face and object recognition ability. Our results also suggest that low-level visual processes which generate

base frequency responses for faces and non-face objects are not reliably impaired in DP (Experiment 2), and that these low-level responses are not systematically associated with higher-level identity oddball responses for faces and non-face objects. Overall, our findings support the notion of a domain-general visual learning mechanism that is involved in the rapid perceptual discrimination of faces and of other familiar object categories such as cars (e.g., Richler, Wilmer, & Gauthier, 2017). There may be individual differences in the efficiency of this domain-general learning process, and it might be particularly impaired in many individuals with DP (e.g., Towler & Tree, 2018). In order to distinguish between these competing theoretical accounts, future EEG and behavioural studies should investigate the degree to which DPs might also be impaired in the rapid discrimination of low- and intermediate-level visual features and patterns, and of novel objects for which they have not acquired visual experience and expertise.

In summary, the results of this study demonstrate that FPVS procedures can be an important tool for the investigation of visual object recognition processes, which also provides insights into the domain-specificity versus generality of these processes. Our findings provide new evidence in support of recent suggestions that impairments in DP are not restricted to the processing of faces and facial identity, but also affect non-face object recognition. They strongly suggest that one source of the common associations between face and object recognition in DP (Geskin & Behrman, 2017) is an early rapid visual discrimination stage for different types of objects, which is particularly important for successful face recognition. It is entirely possible that there are also other points of association or divergence between face and object recognition systems, at the level of lower-level visual perceptual systems, or higher-level memory and attention systems, which need to be investigated in future studies.

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References

- Albouy, P., Cousineau, M., Caclin, A., Tillmann, B., Peretz, I. (2016). Impaired encoding of rapid pitch information underlies perception and memory deficits in congenital amusia. *Scientific Reports*, 6:18861.
- Alonso-Prieto, E., Caharel, S., Henson, R. N., & Rossion, B. (2011). Early (N170/ M170) face-sensitivity despite right lateral occipital brain damage in acquired prosopagnosia. *Frontiers in Human Neuroscience*, 5, 138.
- Alonso-Prieto, E., Belle, G. V., Liu-Shuang, J., Norcia, A. M., & Rossion, B. (2013). The 6Hz fundamental stimulation frequency rate for individual face discrimination in the right occipito-temporal cortex. *Neuropsychologia*, 51(13), 2863–2875.
- Avidan, G., & Behrmann, M. (2009). Functional MRI reveals compromised neural integrity of the face processing network in congenital prosopagnosia. *Current Biology*, 19(13), 1146–1150.
- Avidan, G., Tanzer, M., & Behrmann, M. (2011). Impaired holistic processing in congenital prosopagnosia. *Neuropsychologia*, 49(9), 2541–2552. <http://doi.org/10.1016/j.neuropsychologia.2011.05.002>
- Avidan, G., Tanzer, M., Hadj-Bouziane, F., Liu, N., Ungerleider, L. G., & Behrmann, M. (2014). Selective dissociation between core and extended regions of the face processing network in congenital prosopagnosia. *Cerebral Cortex*, 24(6), 1565–1578.
- Bate, S., Bennetts, R. J., Tree, J. J., Adams, A., & Murray, E. (2019). The domain-specificity of face matching impairments in 40 cases of developmental prosopagnosia. *Cognition*, 192, 104031.
- Behrmann, M., & Avidan, G. (2005). Congenital prosopagnosia: face-blind from birth. *Trends in Cognitive Sciences*, 9(4), 180-187.
- Benasich, A. A., & Tallal, P. (2002). Infant discrimination of rapid auditory cues predicts later language impairment. *Behavioural Brain Research*, 136, 31–49.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8(6), 551–565.
- Biotti, F., Wu, E., Yang, H., Jiahui, G., Duchaine, B., & Cook, R. (2017). Normal composite face effects in developmental prosopagnosia. *Cortex*, 95, 63-76.
- Biotti, F., Gray, K. L., & Cook, R. (2019). Is developmental prosopagnosia best characterised as an apperceptive or mnemonic condition? *Neuropsychologia*, 124, 285-298.
- Bötzel, K., Schulze, S., & Stodieck, S. G. (1995). Scalp topography and analysis of intracranial sources of face-evoked potentials. *Experimental Brain Research*, 104(1).
- Chatterjee, G., & Nakayama, K. (2012). Normal facial age and gender perception in developmental prosopagnosia. *Cognitive Neuropsychology*, 29(5-6), 482–502.
- Collins, J. A., & Olson, I. R. (2014). Beyond the FFA: The role of the ventral anterior temporal lobes in face processing. *Neuropsychologia*, 61, 65–79.
- Davidoff, J., & Landis, T. (1990). Recognition of unfamiliar faces in prosopagnosia. *Neuropsychologia*, 28(11), 1143-1161.
- Dalrymple, K. A., Oruc, I., Duchaine, B., Pancaroglu, R., Fox, C. J., Iaria, G., et al. (2011). The anatomic basis of the right face-selective N170 in acquired prosopagnosia: A combined ERP/fMRI study. *Neuropsychologia*, 49, 2553–2563.
- DeGutis, J., Chatterjee, G., Mercado, R. J., & Nakayama, K. (2012). Face gender recognition in developmental prosopagnosia: Evidence for holistic processing and use of configural information. *Visual Cognition*, 20(10), 1242–1253.

- DeGutis, J., Cohan, S., Mercado, R. J., Wilmer, J., & Nakayama, K. (2012). Holistic processing of the mouth but not the eyes in developmental prosopagnosia. *Cognitive Neuropsychology*, *29*(5-6), 419–446.
- Delvenne, J. F., Seron, X., Coyette, F., & Rossion, B. (2004). Evidence for perceptual deficits in associative visual (prosop) agnosia: A single-case study. *Neuropsychologia*, *42*(5), 597-612.
- Di Russo, F., Pitzalis, S., Aprile, T., Spitoni, G., Patria, F., Stella, A., ... Hillyard, S. A. (2007). Spatiotemporal analysis of the cortical sources of the steady-state visual evoked potential. *Human Brain Mapping*, *28*(4), 323–334.
- Duchaine, B. (2011). Developmental prosopagnosia: Cognitive, neural and developmental investigations. In A. J. Calder, G. Rhodes, M. H. Johnson, & J. V. Haxby (Eds.), *The Oxford handbook of face perception* (pp. 329-366). Oxford, UK: Oxford University Press.
- Duchaine, B., & Nakayama, K. (2005). Dissociations of Face and Object Recognition in Developmental Prosopagnosia. *Journal of Cognitive Neuroscience*, *17*(2), 249–261.
- Duchaine, B., & Nakayama, K. (2006). The Cambridge Face Memory Test: Results for neurologically intact individuals and an investigation of its validity using inverted face stimuli and prosopagnosic participants. *Neuropsychologia*, *44*(4), 576–585.
- Duchaine, B., Yovel, G., & Nakayama, K. (2007). No global processing deficit in the Navon task in 14 developmental prosopagnosics. *Social Cognitive and Affective Neuroscience*, *2*(2), 104–113.
- Dzhelyova, M., Jacques, C., Dormal, G., Michel, C., Schiltz, C., & Rossion, B. (2019). High test-retest reliability of a neural index of rapid automatic discrimination of unfamiliar individual faces. *Visual Cognition*, *27*(2), 127-141.
- Dzhelyova, M., Schiltz, C., Rossion, B. (2020). The Relationship Between the Benton Face Recognition Test and Electrophysiological Unfamiliar Face Individuation Response as Revealed by Fast Periodic Stimulation, *Perception*, *49*, 210-221.
- Eimer, M. (2018). What do associations and dissociations between face and object recognition abilities tell us about the domain-generalty of face processing? *Cognitive Neuropsychology*, *35*(1–2), 80–82.
- Eimer, M., Gosling, A., & Duchaine, B. (2012). Electrophysiological markers of covert face recognition in developmental prosopagnosia. *Brain*, *135*(2), 542–554.
- Fisher, K., Towler, J., & Eimer, M. (2016). Reduced sensitivity to contrast signals from the eye region in developmental prosopagnosia. *Cortex*, *81*, 64 –78.
- Fisher, K., Towler, J., & Eimer, M. (2017). Face identity matching is selectively impaired in developmental prosopagnosia. *Cortex*, *89*, 11-27.
- Furl, N., Garrido, L., Dolan, R. J., Driver, J., & Duchaine, B. (2011). Fusiform gyrus face selectivity relates to individual differences in facial recognition ability. *Journal of Cognitive Neuroscience*, *23*(7), 1723–1740.
- Garrido, L., Furl, N., Draganski, B., Weiskopf, N., Stevens, J., Tan, G. C.-Y., ... Duchaine, B. (2009). Voxel-based morphometry reveals reduced grey matter volume in the temporal cortex of developmental prosopagnosics. *Brain*, *132*(12), 3443–3455.
- Gauthier, I., Behrmann, M., & Tarr, M. J. (1999). Can face recognition really be dissociated from object recognition? *Journal of Cognitive Neuroscience*, *11*(4), 349-370.
- Geskin, J., & Behrmann, M. (2017). Congenital prosopagnosia without object agnosia? A literature review. *Cognitive Neuropsychology*, *22*, 1-51.
- Gerlach, C., Klargaard, S. K., Petersen, A., & Starrfelt, R. (2017). Delayed processing of global shape information in developmental prosopagnosia. *PLoS ONE*, *12*(12), 1–20.

- Gerlach, C. Klargaard, S.K. Alnæs, D. Kolskår, K.K. Karstoft, J. Westlye, L.T., & Starrfelt, R. (2019). Left hemisphere abnormalities in developmental prosopagnosia when looking at faces but not words. *Brain Communications*, 1, fcz034.
- Gray, K. L. H., & Cook, R. (2018). Should developmental prosopagnosia, developmental body agnosia, and developmental object agnosia be considered independent neurodevelopmental conditions? *Cognitive Neuropsychology*, 35(1-2), 59-62.
- Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, 4(6), 223–233.
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science*, 293(5539), 2425–2430.
- Hari, R., & Renvall, H. (2001). Impaired processing of rapid stimulus sequences in dyslexia. *Trends in Cognitive Sciences*, 5(12), 525-532.
- Jacques, C., Retter, T.L., Rossion, B., (2016). A single glance at natural face images generates larger and qualitatively different category-selective spatio-temporal signatures than other ecologically-relevant categories in the human brain. *NeuroImage* 137, 21–33.
- Jacques, C., Jonas, J., Maillard, L., Colnat-Coulbois, S., Koessler, L., Rossion, B. (2019). The inferior occipital gyrus as a major cortical source of the face-evoked N170: evidence from simultaneous scalp and intracerebral human recordings. *Human Brain Mapping*, 40, 1403-1418.
- Jacques, C., Rossion, B., Volfart, A., Brissart, H., Colnat-Coulbois, S., Maillard, L., & Jonas, J. (2020). The neural basis of rapid unfamiliar face individuation with human intracerebral recordings. *NeuroImage*, 117174.
- Jeffreys, D.A. (1996). Evoked potential studies of face and object processing. *Visual Cognition*, 3, 1–38.
- Jiahui, G., Yang, H., & Duchaine, B. (2018). Developmental prosopagnosics have widespread selectivity reductions across category-selective visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*.
- Jonas, J., Brissart, H., Hossu, G., Colnat-Coulbois, S., Vignal, J.-P., Rossion, B., Maillard, L. (2018). A face identity hallucination (palinopsia) generated by intracerebral stimulation of the face-selective right lateral fusiform cortex. *Cortex*, 99, 296-310.
- Kanwisher, N. (2010). Functional specificity in the human brain: A window into the functional architecture of the mind. *Proceedings of the National Academy of Sciences of the United States of America*, 107(25), 11163–11170.
- Hagen, S., & Tanaka, J. W. (2019). Examining the neural correlates of within-category discrimination in face and non-face expert recognition. *Neuropsychologia*, 124, 44-54.
- Henson, R. N. (2003). Neuroimaging studies of priming. *Progress in Neurobiology*, 70(1), 53– 81.
- Le Grand, R., Cooper, P.A., Mondloch, C.J., Lewis, T.L., Sagiv, N., de Gelder, B., & Maurer, D. (2006). What aspects of face processing are impaired in developmental prosopagnosia? *Brain and Cognition*, 61, 139–158.
- Lee, Y., Duchaine, B., Wilson, H. R., & Nakayama, K. (2010). Three cases of developmental prosopagnosia from one family: Detailed neuropsychological and psychophysical investigation of face processing. *Cortex*, 46(8), 949–964.
- Liu-Shuang, J., Norcia, A. M., & Rossion, B. (2014). An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic oddball stimulation. *Neuropsychologia*, 52, 57–72.

- Liu-Shuang, J., Torfs, K., & Rossion, B. (2016). An objective electrophysiological marker of face individualisation impairment in acquired prosopagnosia with fast periodic visual stimulation. *Neuropsychologia*, 83, 100–113.
- Lochy, A., Jacques, C., Maillard, L., Colnat-Coulbois, S., Rossion, B., & Jonas, J. (2018). Selective visual representation of letters and words in the left ventral occipito-temporal cortex with intracerebral recordings. *Proceedings of the National Academy of Sciences*, 115(32), E7595-E7604.
- Lohse, M., Garrido, L., Driver, J., Dolan, R.J., Duchaine, B.C., Furl, N., (2016). Effective connectivity from early visual cortex to posterior occipitotemporal face areas supports face selectivity and predicts developmental prosopagnosia. *J. Neurosci.* 36, 3821–3828.
- McConachie, H. R. (1976). Developmental prosopagnosia. A single case report. *Cortex*, 12(1), 76-82.
- McKone, E., Kanwisher, N., & Duchaine, B. C. (2007). Can generic expertise explain special processing for faces? *Trends in Cognitive Sciences*, 11(1), 8–15.
- Mouraux, A., & Iannetti, G. D. (2008). Across-trial averaging of event-related EEG responses and beyond. *Magnetic Resonance Imaging*, 26, 1041 –1054.
- Müller, M. M., & Hillyard, S. (2000). Concurrent recording of steady-state and transient event-related potentials as indices of visual-spatial selective attention. *Clinical Neurophysiology*, 111(9), 1544–1552.
- Nemrodov, D., Jacques, C., & Rossion, B. (2015). Temporal dynamics of repetition suppression to individual faces presented at a fast periodic rate. *International Journal of Psychophysiology*, 98(1), 35-43.
- Norcia, A. M., Appelbaum, L. G. G., Ales, J. M. J. M., Cottureau, B. R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research: a review. *Journal of Vision*, 15(6), 4.
- Palermo, R., Willis, M. L., Rivolta, D., McKone, E., Wilson, C. E., & Calder, A. J. (2011). Impaired holistic coding of facial expression and facial identity in congenital prosopagnosia. *Neuropsychologia*, 49(5), 1226–1235.
- Parketny, J., Towler, J., & Eimer, M. (2015). The activation of visual face memory and explicit face recognition are delayed in developmental prosopagnosia. *Neuropsychologia*, 75, 538–547.
- Regan, D. (1989). *Human brain electrophysiology: Evoked potentials and evoked magnetic fields in science and medicine*. New York: Elsevier.
- Retter, T. L., & Rossion, B. (2016). Visual adaptation provides objective electrophysiological evidence of facial identity discrimination. *Cortex*, 80, 35-50.
- Retter, T. L., Jiang, F., Webster, M. A., & Rossion, B. (2020). All-or-none face categorization in the human brain. *NeuroImage*, 116685.
- Richler, J. J., Wilmer, J. B., & Gauthier, I. (2017). General object recognition is specific: Evidence from novel and familiar objects. *Cognition*, 166, 42 –55.
- Rivolta, D., Lawson, R. P., & Palermo, R. (2016). More than just a problem with faces: altered body perception in a group of congenital prosopagnosics. *The Quarterly Journal of Experimental Psychology*, 1-11.
- Rosenthal, G., Tanzer, M., Simony, E., Hasson, U., Behrmann, M., (2017). Altered topology of neural circuits in congenital prosopagnosia. *Elife*, 6, e25069.
- Rosenthal, G., & Avidan, G. (2018). A possible neuronal account for the behavioural heterogeneity in congenital prosopagnosia. *Cognitive Neuropsychology*, 35(1–2), 74–77.
- Rossion, B. (2009). Distinguishing the cause and consequence of face inversion: The

- perceptual field hypothesis. *Acta Psychologica*, 132(3), 300–312.
- Rossion, B. (2013). The composite face illusion: A whole window into our understanding of holistic face perception. *Visual Cognition*, 21(2), 139–253.
- Rossion, B. (2014). Understanding individual face discrimination by means of fast periodic visual stimulation. *Experimental Brain Research*, 232(6), 1599–1621.
- Rossion, B. (2018). Damasio's error—Prosopagnosia with intact within-category object recognition. *Journal of Neuropsychology*, 12(3), 357–388.
- Rossion, B., Alonso Prieto, E., Boremanse, A., Kuefner, D., & Van Belle, G. (2012). A steady-state visual evoked potential approach to individual face perception: Effect of inversion, contrast-reversal and temporal dynamics. *NeuroImage*, 63, 1585–1600.
- Rossion, B., & Boremanse, A. (2011). Robust sensitivity to facial identity in the right human occipito-temporal cortex as revealed by steady-state visual-evoked potentials. *Journal of Vision*, 11(2), 16–16.
- Rossion, B., Joyce, C. A., Cottrell, G. W., & Tarr, M. J. (2003). Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *NeuroImage*, 20(3), 1609–1624.
- Rossion, B., Prieto, E. A., Boremanse, A., Kuefner, D., & Van Belle, G. (2012). A steady-state visual evoked potential approach to individual face perception: Effect of inversion, contrast-reversal and temporal dynamics. *NeuroImage*, 63(3), 1585–1600.
- Rossion, B., Retter, T.L. , & Liu-Shuang, J. (in press). Understanding human individuation of unfamiliar faces with oddball fast periodic stimulation and electroencephalography. *European Journal of Neuroscience*.
- Sadeh, B., Podlipsky, I., Zhdanov, A., & Yovel, G. (2010). Event-related potential and functional MRI measures of face-selectivity are highly correlated: a simultaneous ERP- fMRI investigation. *Human Brain Mapping*, 31(10), 1490-1501.
- Susilo, T., Rezlescu, C., & Duchaine, B. (2013). The composite effect for inverted faces is reliable at large sample sizes and requires the basic face configuration. *Journal of Vision*, 13(13), 1–9.
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *The Quarterly Journal of Experimental Psychology. A, Human Experimental Psychology*, 46(2), 225– 245.
- Towler, J., Eimer, M., 2012. Electrophysiological studies of face processing in developmental prosopagnosia: neuropsychological and neurodevelopmental perspectives. *Cognitive Neuropsychology*. 29, 503–529.
- Towler, J., Gosling, A., Duchaine, B., & Eimer, M. (2012). The face-sensitive N170 component in developmental prosopagnosia. *Neuropsychologia*, 50(14), 3588–3599.
- Towler, J., Parketny, J., & Eimer, M. (2016). Perceptual face processing in developmental prosopagnosia is not sensitive to the canonical location of face parts. *Cortex*, 74, 53–66.
- Towler, J., Fisher, K., & Eimer, M. (2017). The cognitive and neural basis of developmental prosopagnosia. *Quarterly Journal of Experimental Psychology*, 70(2), 316-344.
- Towler, J., Fisher, K., Eimer, M. (2018). Holistic face perception is impaired in developmental prosopagnosia. *Cortex*, 108, 112–126.
- Towler, J. R., & Tree, J. J. (2018). Commonly associated face and object recognition impairments have implications for the cognitive architecture. *Cognitive Neuropsychology*, 35(1–2), 70–73.

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