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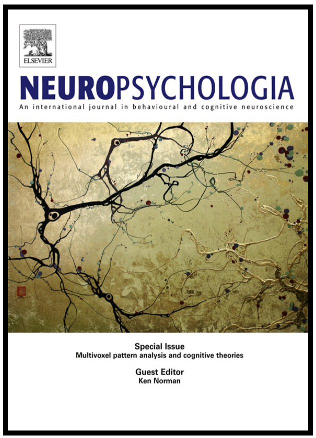
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Margaret C Jackson, Paul Counter, Jeremy J Tree

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Face working memory deficits in developmental prosopagnosia: Tests of encoding limits and updating processes

Margaret C Jackson[1*], Paul Counter[2], Jeremy J Tree[2]

[1]School of Psychology, University of Aberdeen

[2]School of Psychology, Swansea University

[*]Corresponding author: Dr Margaret C Jackson, School of Psychology, William Guild Building, Kings College, University of Aberdeen, Aberdeen, AB24 3FX.
m.jackson@abdn.ac.uk

Abstract

Developmental prosopagnosia (DP) is a condition in which individuals experience life-long problems recognising faces. In recent years, unpacking the nature of the impairments of this population has been the focus of numerous studies. One focus has been on the nature of face-based memory impairments for such individuals, with the onus being mainly on long-term memory deficits. Far fewer have considered the nature of face-based working memory (WM) impairments for DP cases, and the current study seeks to address this. One recent WM study (Shah et al., 2015) reported that the maintenance of faces over time in WM was spared among DPs, and argued instead that face encoding was limited in some way. Here we further explore the nature of face-based WM impairments in DP across two experiments designed to probe encoding limits (Experiment 1) and WM updating processes (Experiment 2). In Experiment 1 we manipulated the number of faces (1-4) to encode into WM and presented these simultaneously. We reasoned that if face encoding among DPs was inefficient or imprecise, then increasing encoding demands (WM load) would disproportionately impair WM accuracy compared to controls. However, we found that DP cases were consistently poorer than controls across all face load conditions, suggesting that front-end encoding problems are only part of the deficit. In Experiment 2, to measure updating four faces were shown sequentially for encoding into WM and accuracy was analysed as a function of whether the test face had been presented first, second, third or last in the encoding sequence. DPs had significantly poorer WM than controls for later faces but not the first face encoded in the sequence, and showed an attenuated recency effect. To account for these findings, we discuss the potential role of comparison processes at retrieval, impairments in configural face processing, and the impact of noise in the face identification system of individuals with DP.

Keywords: Developmental Prosopagnosia, Working Memory, Faces, Face Recognition, Memory

1.0 Introduction

Developmental prosopagnosia (DP) is a lifelong hereditary condition in which face recognition is severely impaired, while low level visual processing, intelligence, and general social cognition remain intact (for recent overviews see Bate & Tree, 2016, and Dalrymple & Palermo, 2016). Also known as 'face blindness', it is a disorder affecting approximately 2% of the population (Kennerknecht et al., 2006). It can impact on daily life and impede social interactions. The condition is still not fully understood, and the face processing challenges experienced by DP individuals warrants further exploration.

DP is heterogeneous, but is typically characterised by impairments in perceptual face matching tasks and/or face memory tasks. Regarding perceptual face processing, reported deficits are variable across different tasks. Using faces shown in different viewpoints, DP individuals can show impaired identity or gender matching of two simultaneously presented unfamiliar faces, producing more errors and slower response times than controls (same / different response; Behrmann, Avidan, Marotta, & Kimchi, 2005). Similar evidence was provided by Duchaine, Germine, and Nakayama (2007) who reported impaired DP face perception using the Cambridge Face Perception Test (CFPT; Duchaine, Yovel, & Nakayama, 2007), which requires individuals to sort 6 morphed face images (frontal view) in order of similarity to a three quarter profile view target face within one minute (see also White, Rivolta, Burton, Al-Janabi, & Palermo, 2016). However, although DP cases can be impaired at fundamental testing of face perception, this is not true of all such cases (Duchaine & Nakayama, 2004, 2006a). A more consistent pattern is reported on tests that involve memory, indicating that DP cases can show a dissociation between face perception and face memory. Using the CFPT and the Old/New Faces task (Duchaine & Nakayama, 2005), Dalrymple, Garrido, and Duchaine (2014) found that all DP participants showed memory deficits while only half showed perceptual deficits, thus the DP population may be sub-divisible into two subtypes. As such, it has recently been suggested that DP be defined as a specific face memory deficit that may or may not be accompanied by abnormal face perception (Dalrymple & Palermo, 2016).

However, characterising the form of face based memory impairments DP cases have is by no means clear. For example, it is well established that there are different forms of memory (long-term, short-term) and a large variety of ways in which memory can be tested. Regarding long-term memory (LTM) there is evidence of impairments for familiar or famous faces among DP individuals (Behrmann et al., 2005; Duchaine, Nieminen-von Wendt, New & Kulomaki, 2003; Le Grand et al., 2006). LTM impairments for unfamiliar faces have also been shown using the ‘Face one in ten’ test, in which participants were required to recognise 15 images of a target face (studied during a brief learning phase) among a set of 150 face alternatives presented sequentially during a test phase (identity old / new speeded response; Duchaine, et al., 2003). Short-term or working memory (WM) deficits are also reported. In one version of the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006b), three target faces in different views are sequentially presented for three seconds each, immediately after which participants must choose which face matches in identity to one of the previously studied faces. This task requires the temporary maintenance of each study face in WM for a few seconds until the match response is required. DP participants have been shown to perform 36% worse than controls on this task (Duchaine, et al., 2007). On balance then, there is clear evidence of LTM face based impairments for DP cases. However, we argue that more in-depth exploration of WM for faces is still needed, and that it is particularly important to understand how WM for faces is affected for DP cases as this shapes how these individuals interact with others from moment to moment. As a consequence, the focus of the work presented here is to further explore the nature of face based WM impairments in the context of DP.

1.1 Working Memory and Face Processing in Developmental Prosopagnosia.

Working memory is a fundamental aspect of human cognition. It is conceived as the glue which temporarily maintains and binds perceptual information during brief input disruptions in order to provide a cohesive and integrated representation of what is happening and unfolding from second to second. Without a functioning WM system we could not read, follow a conversation, or keep track of social interactions. While WM has been extensively studied over the decades using non-face stimuli (for overviews see Baddeley, 2012, and Logie & Cowan, 2015), WM for faces has only more recently been examined (Curby & Gauthier, 2007; Eng, Chen, & Jiang, 2005; Jackson & Raymond, 2008; Meconi, Luria, & Sessa, 2014; Scolari, Vogel, & Awh, 2008) and predominantly in the context of emotional expression effects on WM accuracy (Becker, Mortensen, Anderson, & Sasaki, 2014; Jackson, Linden, & Raymond, 2012, 2014; Jackson, Wolf, Johnston, Raymond, & Linden, 2008; Jackson, Wu

, Linden, & Raymond, 2009; Sessa, Luria, Gotler, Jolicoeur, & Dell’acqua, 2011; Stiernströmer, Wolgast, & Johansson, 2015; Thomas, Jackson, & Raymond, 2014).

The successful recognition of faces using visual WM requires a combination of perceptual and mnemonic processes. Front-end processing requires perceptual encoding of face information, followed by temporary maintenance of encoded representations in WM until such time at which memory is tested (normally 1-10 seconds after encoding). Retrieval requires the ability to accurately compare the visible test item(s) with the stored WM representation(s) held in the mind’s eye. For comparison processes at retrieval to be accurate therefore requires that faces are encoded sufficiently and also effectively maintained.

Due to the short time-course of WM, the stages of encoding, maintenance, and retrieval can be manipulated, controlled, and examined independently in various different ways to determine more specific elements of the process (e.g., with faces Jackson et al., 2012, 2014). This makes the WM paradigm an ideal task to probe both perceptual and memory face processing deficits among prosopagnosics, yet only one study has explicitly examined this to date. Shah, Gaule, Gaigg, Bird, and Cook (2015) explored whether face recognition deficits among developmental prosopagnosics were driven by deficits in maintaining face information in WM. In their study, participants were required to encode one face into WM and maintain its representation for either two or eight seconds. Immediately after the maintenance period, six test faces were presented simultaneously from which participants chose the one that matched in identity to the encoding face just seen. Shah and colleagues reasoned that if DP individuals were specifically impaired in maintaining face representations in WM, the longer interval would disproportionately impair their memory performance compared to controls. However, this was not found. Both groups showed a similar detrimental effect of the extended maintenance period and DP participants performed significantly worse than controls at both short and long maintenance intervals. They concluded that maintenance of face information was spared, but perceptual face encoding was impaired. They did not find a WM deficit among DPs for hands, butterflies, or chairs, indicating a face-specific impairment.

Shah et al.’s (2015) DP sample also showed impaired face perception using the CFPT, so these DP cases fit the sub-type of this condition in which both face memory and face perceptual impairments go hand in hand. It is perhaps not surprising therefore that WM was impaired, argued to be driven by poor perceptual encoding of faces into WM. However, if perceptual encoding of faces into WM was impaired, it may be considered unusual that this did not lead to a disproportionately larger maintenance deficit (but see Bogartz, 1990 who argued that there is no link between the depth of encoding and the rate of forgetting). More generally, prior research with healthy individuals has shown a link between the effectiveness of encoding and the accuracy of recall, in that WM accuracy for faces improved given longer and more sufficient encoding time (Curby & Gauthier, 2007; Eng et al., 2005). Curby and Gauthier concluded that insufficient encoding time impaired perceptual encoding processes which thus impaired recall. If we make the assumption that sufficient representation in WM relies on effective encoding, then inadequate encoding (whatever the cause) could render the comparison between the test faces at retrieval with the face stored in WM particularly difficult.

More relevant in the current context of prosopagnosia is the consideration of clinical impairments in perceptual processing and how these impact WM. Individuals with schizophrenia have impaired WM that is not stimulus-specific or WM-domain specific (it presents in visual-spatial and verbal tasks). It has been proposed that inefficient encoding is partly responsible for this WM deficit, as it leads to poor or imprecise internal representations of the memoranda being stored in WM (Lee & Park, 2005). Furthermore, encoding among schizophrenia patients is considered to be imprecise because they fail to efficiently select or attend to the most relevant information for optimal processing (e.g., Braver et al., 1999; Adler et al., 1998). Using abstract shapes, Haenschel and colleagues found that increasing WM load from 1 to 3 shapes (using a serial presentation) disproportionately impaired WM among schizophrenia patients compared to controls (Haenschel et al., 2007, 2009). This suggests that poor perceptual encoding in a clinically impaired sample leads to more severe encoding limits than controls. ~~Control participants in these studies also showed a decline in WM accuracy as load increased, but the magnitude of impairment was not as large.~~ Similarly, using an n-back task in which coloured stimuli were serially presented, Jasnma, Ramsey, van der Wee, and Kahn (2004) found an interaction between load (how many items back a repeat occurred) and participant group, wherein schizophrenia patients became more impaired than controls as load increased. Interestingly, increasing the maintenance interval did not result in disproportionately larger WM deficits in schizophrenia than controls (Tek et al., 2002), which mirrors the findings from Shah et al.’s (2015) study of DP patients. Lee and Park point out that inefficient encoding may not be the sole contributor of WM deficits in schizophrenia, and that other mechanisms need to be considered.

1.2 The Present Study – Exploring Face Based WM Performance in a DP Population.

In the current study we sought to directly examine WM encoding deficits among DPs in two ways, by assessing encoding limits (Experiment 1) and updating processes (Experiment 2). WM is limited in capacity and many of the WM paradigms used to measure capacity present items simultaneously and manipulate WM load, i.e., the number of items to be remembered (Alvarez & Cavanagh, 2004; Bays, Catalao, & Husain, 2009; Jackson & Raymond, 2008; Luck & Vogel, 1997). There is ongoing debate as to whether the WM capacity limit is quantitative in nature - reflecting a limit to the number of discrete items we can store, or qualitative in nature - limited by the fidelity or precision with which we represent each item in WM (see Ma, Husain, & Bays, 2014 for a review). Quantitative (or slots-based) models propose that there is an upper limit of approximately four pieces of simple information such as colour or shape (e.g., Cowan, 2001; Vogel, Woodman, & Luck, 2001), and each item inhabits one WM slot. However, for more complex information, fewer than four items can be sufficiently remembered (Alvarez & Cavanagh, 2004; Eng et al., 2005; Luria, Sessa, Gotler, Jolicoeur, & Dell' Acqua, 2010). Regarding faces, WM capacity limits for healthy young adults have been estimated at between 1.5 to 3 faces (Curby & Gauthier, 2007; Eng et al., 2005; Jackson & Raymond, 2008). Qualitative WM models (known as flexible resource-based models) propose that performance is limited by the quality or precision with which each item is represented and that this is determined by the amount of resources available for each item (Bays et al., 2009; Bays & Husain, 2008). ~~Thus it is the resource pool that is limited in size.~~ The more items there are, the fewer resources each item will receive, and fewer resources degrades the fidelity of representation within WM (Ma et al., 2014). A third account, the interference model, proposes that similarity or overlap of features held in WM creates interference between items, which leads to the degradation (e.g., blurring or distortion) of these memory representations (Oberauer & Lin, 2017). The interference model aims to better reflect the binding of information in WM. The aim of the current study is not to test these models, but what is important to note is that all models predict (and show) that increasing the number of items to encode results in decreased WM accuracy.

In Shah et al. (2015) only one face was presented at encoding while six faces were shown at test (among which a match had to be identified). This may have placed very few demands on encoding but increased the difficulty of comparison processes at retrieval between the test faces and the face stored in WM. ~~While a DP deficit among DPs was observed in their study, it is worth considering whether this deficit was driven by impaired comparison processes at retrieval rather than front-end encoding impairments. Shah et al. used a large number of test faces (six) which themselves may have been inadequately perceived, making accurate discrimination between the test faces and the face held in WM particularly difficult.~~ We must therefore question whether the results of Shah and colleagues really do reflect front-end face encoding difficulties or a later stage deficit. ~~On balance then, interpreting the results of Shah et al. are somewhat limited by an inability to be certain whether the results do indeed speak to a perceptual face processing deficit at the early encoding stage or at some later stage, since the perceptual load of either was not considered or manipulated.~~

To explore whether DPs have impaired face WM encoding limits, in Experiment 1 we presented between one and four faces simultaneously at encoding to manipulate WM load. We chose a simultaneous presentation ~~(rather than the serial presentations used in Jansma et al., 2004 and Haenschel et al., 2007, 2009 to explore WM in schizophrenia)~~ so that we could examine load effects in isolation from WM updating effects (which are explored separately in a serial presentation task in Experiment 2). In Shah et al. (2015), one of the six faces always matched the face at encoding and performance relied on the ability to perceptually discriminate between the multiple faces at retrieval and locate the match among the non-match distracters. Here we specifically wanted to minimise these additional perceptual discrimination demands at retrieval and isolate task demands at encoding, and to do this we presented just a single face at retrieval which either matched or did not match in identity to one of the faces just seen. This paradigm was also used by both Curby & Gauthier (2007) and Scolari et al. (2008) to measure WM for faces. ~~Successful face recognition depends on both match and non-match decisions, and this single test item paradigm allows us to measure the ability of DPs to both detect when the face is present (match trials; hits) and importantly also to assess when the face is absent (non-match trials; false alarms). While the always match present design of Shah et al. (2015) (and notably also the CFMT) is very useful in telling us how well DP individuals are able to filter the noise from distracters at retrieval and locate the correct face, it does not tell us how well they can accurately detect the absence of this familiarity signal.~~ With consideration of the findings from the schizophrenia literature discussed above, if the DP deficit in WM is specifically due to impaired face encoding then we could predict that increasing the number of faces to encode should be disproportionately more difficult for DPs than controls, evidenced by an increasing magnitude of DP deficit as load increases. To pre-empt our results, we did not find this. DP individuals had poorer WM overall but this was not modulated by load.

In Experiment 2 we examined WM updating by using a serial presentation of faces, but importantly we kept load constant (4 faces) in order to isolate the updating effect from any load effect. Events and thoughts unfold over time, and an essential function of WM is to continuously add (and remove) items as they become relevant (or irrelevant) to current goals. This is particularly necessary when information is perceived in sequence, rather than in parallel. ~~In the laboratory, many studies of verbal and auditory WM present items one by one in sequence as this form of information cannot be processed adequately in parallel – we read and hear words and sentences in a temporal fashion.~~ ~~Such~~ Verbal and auditory WM studies, in which items are presented serially, ~~examine performance as a function of where in the encoding sequence the test item had appeared, and~~ find robust primacy and recency effects where the first and last items to be encoded respectively are recalled with significantly greater accuracy than items encoded in the middle of the sequence (e.g., Postman & Phillips, 1965; Baddeley, 2007). In visual WM there is evidence for a recency but not primacy effect, and only at higher WM loads in sequences of 4 or 5 items (Kool, Conway, and Turk-Browne, 2014). ~~used a colour matching task and showed that only a recency effect was elicited in visual WM and only at higher loads (i.e., with a sequence of 4 or 5 items but not 3 items).~~ This recency effect was also shown to not depend on the length of the maintenance interval, and instead suggests that items encoded early in the sequence suffered some degree of retroactive interference from later items. Kool et al. propose that visual WM is updated in a first in first out (FIFO) fashion when capacity limits are exceeded, which is clearly rooted in the slots model of WM. Recency effects are also thought to arise because the last item is held in the immediate focus of attention and thus receives special status (e.g., perhaps gains a larger share of resources according to the resource-based model) when retrieval is required (e.g., Allen, Baddeley, & Hitch 2014; Morrison, Conway, & Chein, 2014; Nee & Jonides, 2011; Oberauer, 2002). In terms of the lack of primacy effect in visual WM, Allen, Baddeley, and Hitch (2006) propose that retroactive interference from more recently presented items degrades or overwrites earlier presented representations.

In Experiment 2 ~~we examined face WM updating by presenting~~ four faces were presented sequentially for encoding into WM, and we assessed WM accuracy as a function of serial position of the encoding item. ~~(Note that the same sample of DPs were used in both~~

~~Experiments 1 and 2, but a different control sample was used in each.)~~ As in Experiment 1, a single test face was shown at retrieval to isolate encoding and updating demands. We reasoned that if perceptual encoding of faces into WM is impaired among DPs, the recency effect may be magnified as indexed by a disproportionately larger WM deficit for items encoded early on than those encoded most recently, compared to controls. More specifically, we propose that if encoding of the first face in the sequence is impaired among DPs, then any subsequent faces then presented for (equally poor) encoding may cause significantly greater retroactive interference and dramatically degrade or overwrite the existing (poor) representations, compared to controls. To pre-empt our results, we did not find this pattern. DPs showed significantly poorer WM than controls for later faces but not for the first face presented in the encoding sequence, and DPs also showed an attenuated (but mildly spared) recency effect compared to controls.

Overall then, our two studies sought to more systematically evaluate the nature of face-based WM problems in DP cases. In so doing we demonstrate that while encoding impairments may party contribute to the deficit, they do not wholly explain our results. We consider in addition the role of comparison processes at retrieval, and inefficiencies within the face processing system as potential mechanisms for the WM face deficit among DPs.

2.0 Experiment 1: WM load

2.1 Material and Methods

2.1.1 Participants

Ten individuals with developmental prosopagnosia were recruited (3 females, 7 males; mean age 26 years; all were below the age of 37). Full details of the DP sample and their performance data on the neuropsychological test battery are provided in Table 1. Six out of ten DP individuals performed normally on the CFPT with upright faces and 9/10 performed normally on the CFPT with inverted faces. On all the non-face perceptual tasks (GNT, BORB, RMT-w) all DPs performed normally. Thirty three control participants were recruited from Swansea University (27 females, 6 males; mean age 21 years). All participants here and in Experiment 2 had normal or corrected-to-normal vision, reported no history of neurological or psychiatric disorders, were not aware of the purpose of the experiment, and provided signed consent prior to participation.

Table 1. Developmental prosopagnosia case scores on neuropsychological test battery. Scores which are two standard deviations outside of mean normal performance are in bold itallics, indicating an impairment.

DP Case	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
	NP	**KS**	**KC**	**AB**	**KL**	**DC**	**RK**	**BF**	**RW**	**AT**
Age	19	19	34	20	28	23	36	19	34	32
Gender	Female	Female	Male	Male	Female	Male	Male	Male	Male	Male
Face Testing										
FFT	**22/35**	**14/35**	**19/35**	**22/35**	**18/35**	**17/35**	**18/35**	**23/35**	**24/35**	**27/35**
CFPTu	**56/144**	46/144	**92/144**	**60/144**	38/144	**60/144**	43/144	40/144	53/144	42/144
CFPTi	86/144	70/144	**94/144**	60/144	54/144	80/144	36/144	62/144	48/144	64/144
CFMTu	**39/72**	**43/72**	**30/72**	**40/72**	**42/72**	**41/72**	**42/72**	**42/72**	**36/72**	**39/72**
CFMTi	32/72	44/72	**29/72**	30/72	36/72	32/72	36/72	42/72	37/72	36/72
RMT-f	**34/50**	**34/50**	**29/50**	**34/50**	**22/50**	39/50	**31/50**	**35/50**	36/50	**29/50**
Autism Screening										
Eyes	**17**	22	28	26	26	29	26	25	26	32
ASQ	25	30	14	25	14	25	14	14	12	14
Non-Face Testing										
GNT	21/30	20/30	20/30	20/30	22/30	20/30	29/30	21/30	22/30	24/30
BORB	55/64	57/64	53/64	56/64	55/64	56/64	58/64	55/64	51/64	56/64
RMT-w	44/50	48/50	45/50	46/50	40/50	43/50	42/50	45/50	45/50	48/50

FFT (Famous Faces Test; Duchaine & Nakayama, 2005); CFPTu/i (Cambridge Face Perception Task upright / inverted; Duchaine et al., 2007); CFMTu/i (Cambridge Face Memory Task upright / inverted; Duchaine & Nakayama, 2006b); RMT-f (Recognition Memory Test-faces; Warrington, 1984); Eyes (Reading the Mind in the Eyes task; Baron-Cohen, Jolliffe, Mortimore, & Robertson, 1997); AQ (Autism Spectrum Quotient; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001); GNT (Graded Naming Test; McKenna & Warrington, 1980); BORB (Birmingham Object Recognition Battery; Riddoch & Humphreys, 1993 – two difficult subtests used from test 10, 64 objects in total), RMT-w (Recognition Memory Test–words; Warrington, 1984).

2.1.2 Stimuli

Images of six individual males from the Ekman and Friesen (1976) database were cropped in an oval shape to remove hair and other outline contour details. Cropping served to minimise the use of certain featural cues to perform the task. All had a neutral expression and were presented in greyscale. As per Jackson et al. (2009), scrambled face images (see Figure 1B) were used to fill locations when fewer than four faces were presented for encoding. This ensured that there were always four items on screen on every trial (i.e., 1 face and 3 scrambled images for Load 1, 2 faces and 2 scrambled imaged for Load 2, and so on). Faces and scrambled images subtended a visual angle of 1.43 x 1.36 degrees and were displayed in random locations in a 2x2 grid in on each trial. On trials with fewer than four faces, the faces and scrambled images could appear at any of the four locations at random, so all grid locations could be occupied with faces in every load condition throughout the session (as per Jackson et al., 2008, 2014). Using small sets of items in WM tasks is considered more appropriate than larger sets as this constrains task performance to the images on a trial by trial basis, rather than running the risk of engaging long-term memory (LTM) accidentally. For example using a larger set there is the risk that a face never seen at all during the experimental session is presented for retrieval and the participant detects that they have never seen it before, so responds ‘nonmatch’ on this LTM basis rather than using WM. We used only male faces as per Shah et al. (2015) and Jackson & Raymond (2008) in order to create a more homogeneous stimulus set. The task was delivered via E-Prime (version 2.0) using a Dell Viglen 22-inch computer with 1280 x 1024 resolution, and viewing distance was approximately 50cm.

2.1.3 Design and Procedure

Participants completed a set of 10 practice trials before the main task began. The main experimental session comprised 120 trials in total, split into six blocks of 20 trials to allow for frequent rest breaks if required. There were four STM loads (1, 2, 3, 4) presented in a pseudo-random order (randomised between participants), with 30 trials per load condition. Within each load condition, half of trials presented a test face at retrieval that matched in identity to one of the faces at encoding, the other half of trials presented a face that did not match any of the faces at encoding (randomised). On match trials, the test face was the same image used at encoding (note that face perception deficits are found whether the same image or different image of the same person is used; see White et al., 2016). We are confident that our task design does tap into face processing mechanisms. Using a single test face which was the same image on match trials, two studies found a significant face inversion effect among healthy adults (Curby and Gauthier, 2007, Experiment 1; Jackson et al., 2009, Experiment 5). Inversion effects are taken to indicate that face processing mechanisms were engaged for upright faces. Participants initiated a trial by pressing the space bar. Between one and four faces were then presented simultaneously for encoding for 500ms per face: thus encoding durations were 500ms (Load 1), 1000ms (Load 2); 1500ms (Load 3), and 2000ms (Load 4). This ensured that ample time was provided to encode all faces, and meant that any effects of WM load on performance were not due to encoding time restrictions (see Jackson & Raymond, 2008). Following the encoding phase, a 1000ms maintenance interval was provided in which no information was present other than a central fixation cross. Then a single test face was presented in the centre of the screen and participants stated whether it matched or not in identity to one of the faces at encoding. There was no time limit imposed on the retrieval response. See Figure 1A for an example trial procedure.

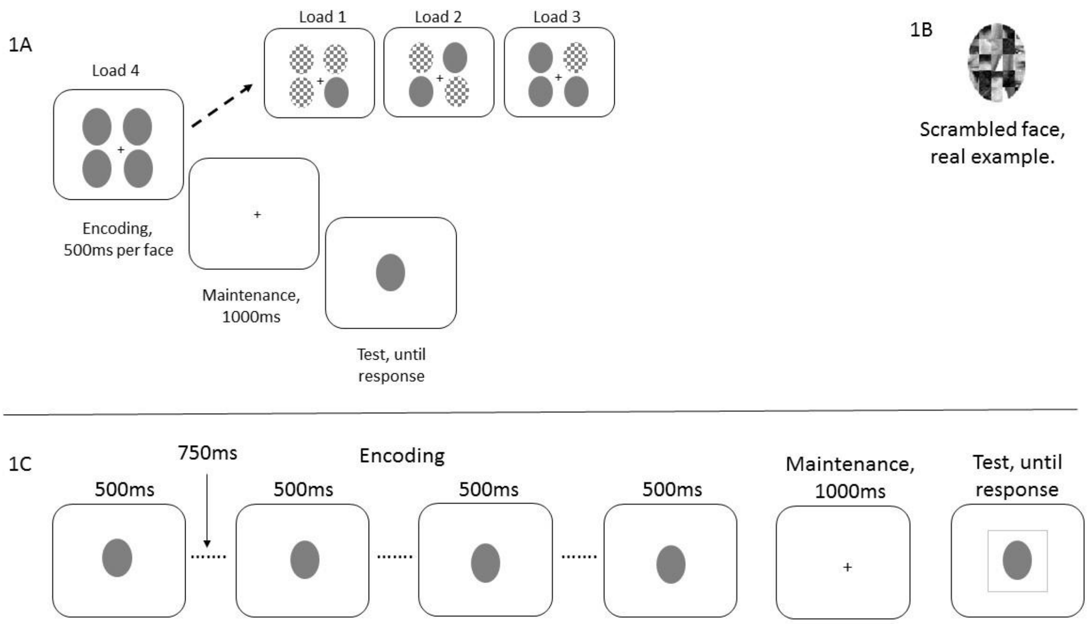

Figure 1. Example trials sequences for Experiment 1 (panel A) and Experiment 2 (panel C). [Real faces were used in the actual experiments and the oval shapes shown here are for illustration purposes only.] In Experiment 1, between 1 and 4 faces were presented simultaneously for encoding, for 500ms per face. Irrelevant scrambled faces filled in the positional gaps when fewer than 4 face were present (see panel B for an example scrambled face). In Experiment 2, four faces were presented sequentially for encoding for 500ms duration each with a 750ms interval between. In both experiments there was a 1000ms blank maintenance interval and a single test face presented at retrieval until a face identity match/non-match response was provided. In Experiment 2, face positions at encoding were jittered slightly off-centre so that each image did not entirely appear in the same foveal position as the other. A grey rectangle surrounded the test face in Experiment 2, in order to properly distinguish it from the encoding faces.

2.2 Results

We analysed WM accuracy in three different ways to provide a rich picture of task performance. We used d’ in order to assess memory accuracy as a combined function of both hits and false alarms (FA), where d’ = $_{Z}$Hits-$_{Z}$FA, considered to be a robust measure of the ability to discriminate information. Maximum d’ is 4.66 (100% correct) and a d’ of zero indicates chance performance (50%). We also analysed hits and FAs separately, as previous research has shown a dissociation between unfamiliar face matching performance on match trials (hits data) versus mismatch trials (FA data), suggesting that separate cognitive processes may underpin these performance measures (Attwood, Penton-Voak, Burton & Munafó, 2013; Megreya & Burton, 2007). We also analysed reaction times (RTs) on correct trials, excluding RTs greater than 6000ms given that this was not a speeded task per se. This trimming of RTs resulted in the removal of 13 trials in total from the DP group and 14 trials in total from the control group.

d’: A repeated measures ANOVA with WM load as a within factor (1, 2, 3, 4 faces) and group (DP, control) as a between factor showed that DP participants performed significantly poorer than controls overall ~~revealed a significant main effect of group~~ (F(1, 41) = 8.46, p = .006, $ŋ_p^2$ = .17, observed power = .81)~~, indicating that~~ (Figure 2). Importantly, the interaction between group and load was non-significant (F(3, 123) = 0.32, p = .81).[1] The main effect of load was significant, accuracy decreased as load increased (F(3, 123) = 45.83, p < .001, $ŋ_p^2$ = .53, observed power = 1.00).

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[1] To examine whether there were any power issues in using a larger control than DP sample that could account for these effects, we split the control sample data into three sets of 10 participants to match the DP sample size, using the first 10 tested, the second 10 tested, and the third 10 tested. In Experiment 1, there was still a significant main effect of group when using the first 10 controls (*F*(1, 18) = 10.74, *p* = .004), the second 10 controls (*F*(1, 18) = 4.97, *p* = .039) and the third 10 controls (*F*(1, 18) = 15.639, *p* = .001). All interactions remained non-significant (all *p*s > .35). Thus we conclude that the pattern of results found with the full sample is meaningful and not driven by a greater number of control participants.

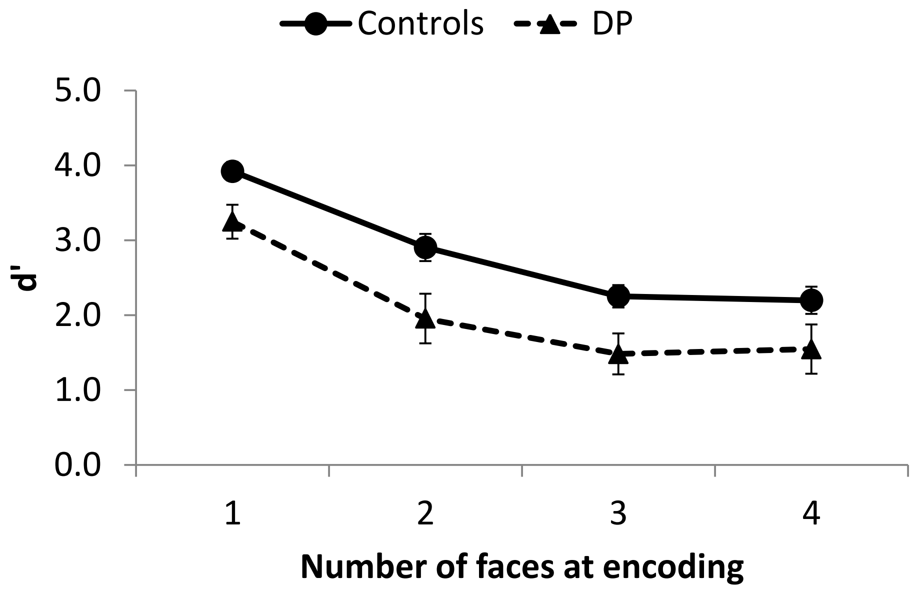


Figure 2. Results from Experiment 1, representing d’ scores for DPs and controls as a function of the number of faces at encoding (WM load). Error bars represent 1 Standard Error above and below the mean.

We ~~also~~ computed z scores for d’ performance (collapsed across load) in order to determine the homogeneity of the DP deficit in WM performance relative to the control group average (see Table 2). Nine out of the 10 DP individuals showed a WM deficit of a variety of magnitudes, and one of those (DP9) was significantly impaired at the threshold z < -1.65.

Table 2. z scores for each DP individual compared to the controls average, for d’ data collapsed across load in Experiment 1 and collapsed across serial encoding position in Experiment 2. Scores below zero indicate poorer performance than controls and scores that are below -1.65 indicate a significant impairment.

DP	Experiment 1	Experiment 2
1	-1.64	-2.07
2	-0.37	-0.25
3	-0.72	-1.20
4	-0.86	-1.31
5	-0.57	-1.16
6	-0.78	-1.10
7	-0.54	-0.64

8	0.04	-0.03
9	-1.92	-0.90
10	-0.52	-0.55

We also examined whether any response biases were present in the data and if so whether these differed between DPs and controls. ~~It is possible that this pattern of hits and FAs simply reflects a more liberal response bias among DPs than controls, they may have stated 'yes' more often which would boost hits but also increase the number of FAs. To assess this, we computed response bias scores (C)~~ To do this we used the formula $C = 0.5*({}_{Z}Hits+{}_{Z}FA)$, where a score closer to or greater than 1 indicates a 'yes' response bias and a score closer to or less than -1 indicates a 'no' response bias. We computed a repeated-measures ANOVA on this data and found a significant interaction between group and load ($F(3, 123) = 4.28$, $p = .007$, $\eta_p^2 = .09$, observed power = .85). This interaction reflected a significantly greater bias to respond yes among DPs ($C = 0.44$) than controls ($C = -0.11$) at load 1 only ($t(41) = -4.12$, $p < .001$). However, the group difference in response bias scores was non-significant at load 2 (DPs: $C = 0.28$; controls: $C = 0.01$; $t(41) = -1.59$, $p = .12$), load 3 (DPs: $C = 0.35$; controls: $C = 0.33$; $t(41) = -0.13$, $p = .90$), and load 4 (DPs: $C = 0.46$; controls: $C = 0.53$; $t(41) = 0.47$, $p = .64$). ~~We conclude therefore that poorer ability to make an accurate mismatch response among DPs than controls cannot account for poorer WM accuracy at loads 2 to 4, but may have caused the pattern of results found at load 1.~~

Finally to examine whether any learning effects occurred due to multiple face repetitions during the session, and crucially whether any learning effects differed among DPs versus controls, we split the d' data into the first three blocks (period 1) and the last three blocks (period 2). While participants did improve over time in general (significant main effect of period, $F(1, 40) = 15.41$, $p < .001$, $\eta_p^2 = .28$, observed power = .97), the period by group interaction was non-significant ($F < 0.01$), as was the period x group x load interaction ($F < 1$).

Hits and FAs: For hits data, the main effect of group was non-significant, ($F(1, 41) = 0.67$, $p = .42$), and the group by load interaction was non-significant ($F(3, 123) = 0.33$, $p = .80$) (see Figure 3, black lines). There was a significant main effect of load ($F(3, 123) = 9.89$, $p < .001$, $\eta_p^2 = .28$, observed power = .97). In contrast, DP participants had significantly more FAs than controls ~~for FA data there was a significant main effect of group~~ ($F(1, 41) = 7.15$, $p = .01$, η_p^2

= .149, observed power = .743) ~~, indicating that~~ (see Figure 3, grey lines). Similar to the d' data, the interaction between group and load for FAs was non-significant (F(3, 123) = 0.35, p = .79). The main effect of load was significant, showing increased FAs overall as load increased (F(1, 41) = 7.15, p = .01, η_p^2 = .14, observed power = .74).

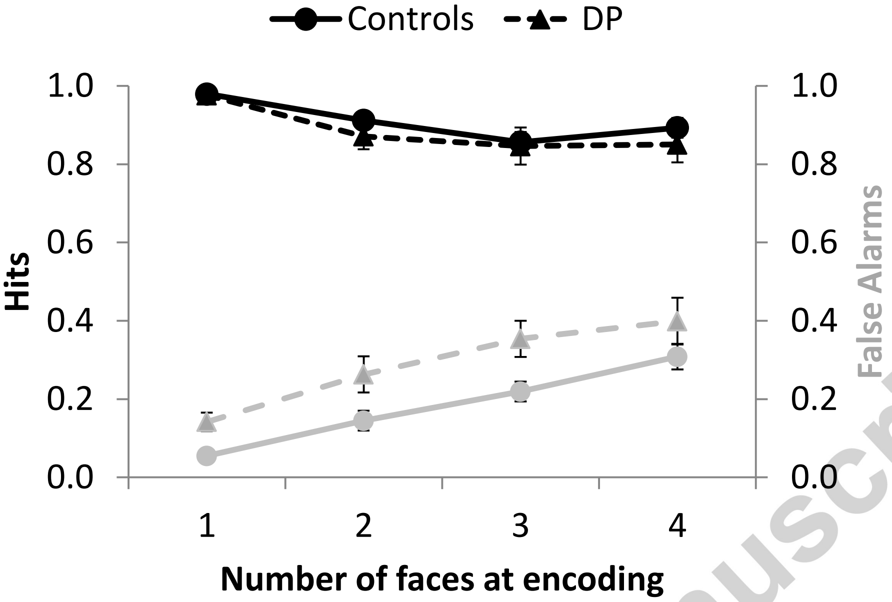


Figure 3. Results from Experiment 1, representing hit rates (black lines) and FA rates (grey lines) for DPs and controls, as a function of the number of faces at encoding (WM load). Error bars represent 1 Standard Error above and below the mean.

RTs: Analysis of RTs on correct trials showed that DPs (M = 1391.83, SE = 94.07) were 193ms slower than controls (M = 1198.712, SE = 51.782) on average, but this difference did not reach significance (F(1, 41) = 3.24, p = .08). There was no significant interaction between group and load (F(3, 123) = .36, p = .78).

In summary, these analyses show that overall DPs have impaired WM compared to controls, which is more specifically driven by a larger number of false alarms. Thus DPs appear to be particularly impaired in making a correct nonmatch response, but are not impaired in their ability to accurately determine a face match in WM. While greater response bias among DPs may account for the group difference at load 1, it cannot account for poorer WM accuracy among DPs at loads 2 to 4.

Drawing from the literature on WM impairments in schizophrenia (Haenschel et al., 2007, 2009; Jansma et al., 2004) we hypothesised that if the DP deficit for faces in WM is specifically due to impaired perceptual encoding, then increasing the number of faces to encode may be disproportionately more difficult for DPs than controls. Our results do not support this. DP individuals showed significantly impaired WM compared regardless of load, and did not show a steeper decline in WM accuracy with increasing load compared to controls. While this does not rule out the presence of face encoding deficiencies among DPs, it does suggest that a face encoding deficit cannot fully account for the WM deficit. ~~Furthermore, the WM deficit among DP individuals was driven by poorer ability to accurately discriminate a nonmatch test face from two or more face representations stored in WM.~~

3.0 Experiment 2: WM Updating

3.1 Material and Methods

3.1.1 Participants

We used the same ten DP individuals who took part in Experiment 1. A different sample of 32 control participants were recruited (26 females, 6 males; mean age 21 years).

3.1.2 Stimuli

To ensure that results across our two experiments were not constrained by specific face stimuli, we used a different set of six male faces taken from the Radboud database (Langner et al., 2010), similarly cropped in an oval shape to remove hair and other outline contour details. All face dimensions were the same as in Experiment 1.

3.1.3 Design and Procedure

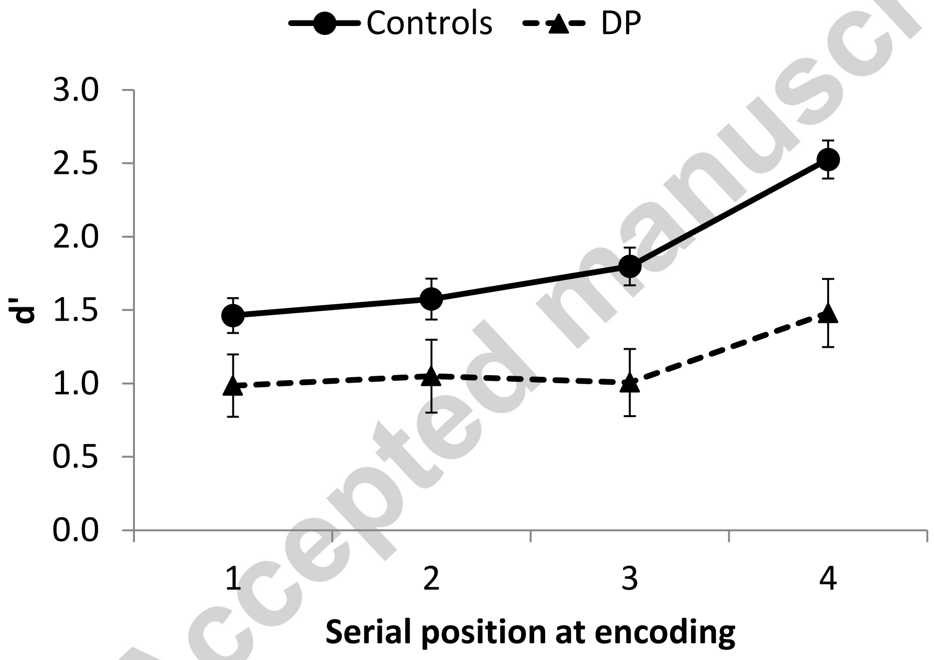
Participants completed a set of 10 practice trials before the main task began. The main experimental session comprised 120 trials in total, split into six blocks of 20 trials to allow for frequent rest breaks if required. Half of trials presented a test face at retrieval that matched in identity to one of the faces at encoding the other half of trials presented a face that did not match any of the faces at encoding (randomised; as in Experiment 1). On match trials there were four serial position conditions (1, 2, 3, 4) presented in a pseudo-random order, where the test face at retrieval matched in identity to a face at one of the four positions. On match trials, the serial position at which the to-be-tested face appeared in the encoding sequence was fully counterbalanced. Participants initiated a trial by pressing the space bar. Four faces were presented one by one for 500ms each for encoding into WM (equated to encoding time provided for each face in Experiment 1. A blank 750ms interval interceded between each face to minimise potential masking effects. After the last face in the sequence, a 1000ms maintenance interval was provided in which no information was present other than a central fixation cross. Then a single test face was presented in the centre of the screen and participants stated whether it matched or not in identity to one of the faces at encoding (no time limit). To reduce potential confusion among participants, this test face had a light grey rectangle around it to distinguish it from the encoding faces which had no border. See Figure 1C for an example trial procedure.

3.2 Results

Again, we report data analysed in the form of d', hits, and FA. Note that FA data cannot be linked to serial position as the test face was absent, so only one score is extracted here for overall FAs. As in Experiment 1, for RT analysis trials with RTs greater than 6000ms were removed, and this resulted in the exclusion of 41 trials from the DP group and 22 trials from the control group in total.

d': A repeated measures ANOVA with serial position at encoding (1, 2, 3, 4) as a within factor and group (DP, control) as a between factor revealed that DP participants performed poorer than controls overall ~~a significant main effect of group~~ (F(1, 40) = 9.70, p = .003, η_p^2 = .20, observed power = .86)~~, indicating~~ (Figure 4). The interaction between group and serial position was also significant (F(3, 120) = 2.84, p = .04, η_p^2 = .067, observed power = .68). To explore this interaction we first compared performance across groups at each serial position. We predicted that DPs would show a disproportionately greater WM deficit than controls for early versus later encoded items in the sequence. As can be seen in Figure 2, our data show the opposite pattern where the WM deficit among DPs is significant for items presented later in the sequence (position 2: t(40) = 2.64, p = .012; position 3: t(40) = 3.02, p = .004; position 4: t(40) = 3.94, p < .001), but non-significant for the very first item presented (position 1: t(40) = 1.96, p = .057) (note, these and all other t-tests reported here were not corrected for multiple comparisons).

To explore recency effects further, we examined the main effect of serial position in each group separately. Controls showed a significant main effect of serial position ($F(3, 93) = 39.05$, $p < .001$, $\eta_p^2 = .56$, observed power = 1.00). Paired t-tests revealed significantly poorer WM for test faces presented at position 1 compared to test faces that appeared at later positions 3 ($t(31) = 4.25$, $p < .001$) and 4 ($t(31) = 8.42$, $p < .001$). Performance steadily improved between positions 2 and 3 ($t(31) = 2.61$, $p = .014$), positions 2 and 4 ($t(31) = 7.31$, $p < .001$), and positions 3 and 4 ($t(31) = 5.60$, $p < .001$). DPs showed a significant but attenuated serial position effect ($F(3, 27) = 3.25$, $p = .037$, $\eta_p^2 = .27$, observed power = .68), and ~~DPs showed~~ a markedly weaker recency effect than controls.[2] Among DPs, significantly improved WM performance was only observed between positions 1 and 4 ($t(9) = 2.4$, $p = .038$) with marginal, non-significant improvements between positions 2 and 4 ($t(9) = 2.08$, $p = .068$) and positions 3 and 4 ($t(9) = 2.00$, $p = .077$). ~~Thus,~~



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[2] To check whether the weaker serial position effect for DPs than controls could simply be due to the larger control sample size, we again split the control sample into three sets of 10 participants and re-ran the position effects analyses with each of these smaller groups. There was a significant main effect of serial position in all three control sub-samples, which were larger in effect size (η_p^2) to the DP sample of equivalent size (first 10 controls: $F(3, 57) = 11.51$, $p < .001$, $\eta_p^2 = .38$; second 10 controls: $F(3, 57) = 10.16$, $p < .001$, $\eta_p^2 = .35$; third 10 controls: $F(3, 57) = 16.08$, $p < .001$, $\eta_p^2 = .46$). In addition, we assessed whether the larger difference in performance between the first and last items seen in controls than DPs could be due to more power to detect this in the larger control sample. We find no evidence of this: first 10 controls (mean difference = 0.90, $t(9) = 4.71$, $p = .001$); second 10 controls (mean difference = 0.88, $t(9) = 5.06$, $p = .001$); third 10 controls (mean difference = 1.24, $t(9) = 4.32$, $p = .002$). Thus, we conclude that there are no problematic power issues here.

Figure 4. Results from Experiment 2, representing d’ scores for DPs and controls as a function of the serial position of the test face at encoding. Error bars represent 1 Standard Error above and below the mean.

In Table 2 it can be seen that most DP individuals were impaired to varying degrees on this sequential task overall, with one participant significantly impaired (DP1).

As per Experiment 1, we computed response bias scores (C) and found no evidence that response bias could account for any group differences found. There was a significant interaction between group and position (F(3, 120) = 2.87, p = .04, $ŋ_p^2$ = .07, observed power = .68). However, post-hoc tests showed that the group difference was non-significant at all positions (all ps > .23). Finally, to examine learning effects we split the d’ data into the first three blocks (period 1) and the last three blocks (period 2) as we did for Experiment 1. Here there was no evidence of learning overall (non-significant main effect of period, F < 1), and there were non-significant interactions for period x group (p = .28), or for period x group x position (F < 1).

Hits and FAs. For hits data, the main effect of group was non-significant, (F(1, 40) = 1.52, p = .23) and the group by position interaction was also non-significant (F(3, 120) = 1.57, p = .20). Although the main effect and interaction were non-significant, we a priori examined group differences at each serial position based on the pattern of results found in d’ data. While hit rates between groups were non-significant for test faces that were encoded first (t(40) = 0.55, p = .59), second (t(40) = 0.29, p = .78), or third (t(40) = 1.66, p = .11) in the sequence, memory for the last face was significantly impaired among DPs (t(40) = 2.31, p = .03) (see Figure 5). Overall, DPs had significantly greater FAs (M = 0.29; SE = 0.43) than controls (M = 0.18; SE = 0.18), t(40) = 2.66, p = .01) as found in Experiment 1.

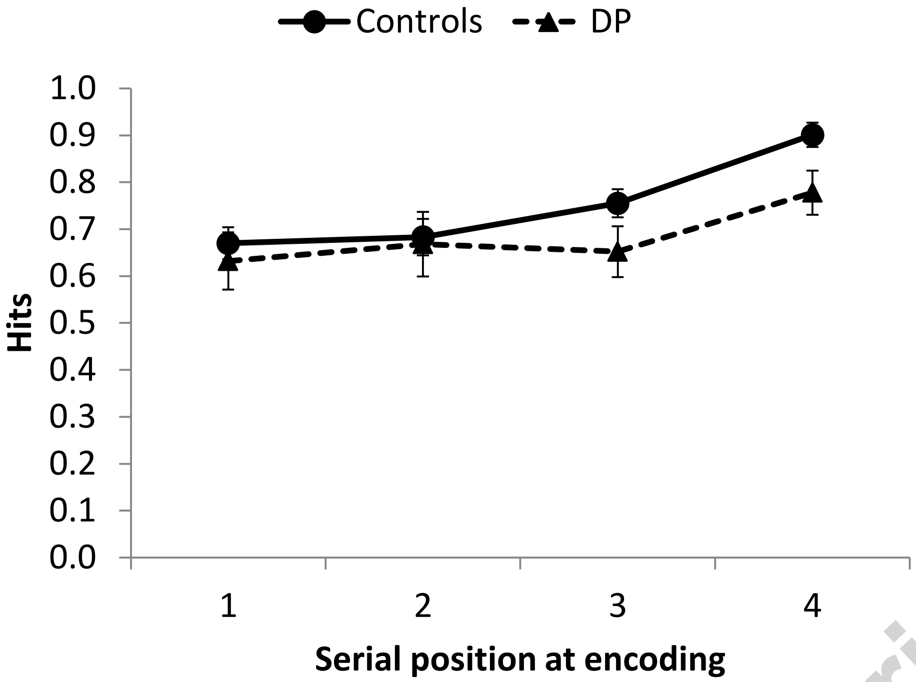

Figure 5. Results from Experiment 2, representing hit rates for DPs and controls as a function of the serial position of the test face at encoding. Error bars represent 1 Standard Error above and below the mean.

RTs: Analysis of RTs overall showed that DPs (M = 1832.86, SE = 171.64) were 356ms slower than controls (M = 1476.64, SE = 68.23) on average, and this difference was significant (t(40) = 2.31, p = .03). An analysis of RTs from match trials in which serial position effects could be analysed, showed a non-significant interaction between group and serial position (F(3, 120) = .56, p = .64). Interestingly RTs were significantly slower overall for test faces that were positioned earlier than later in the sequence (F(3, 120) = 17.21, p < .001). Bonferroni-corrected post-hoc tests showed that RTs were significantly slower for test faces presented at position 1 vs. 4 (p < .001), position 2 vs. 3 (p = .017), position 2 vs. 4 (p < .001), and position 3 vs. 4 (p < .001) (pos 1: M = 1734.78, SE = 103.78; pos 2: M = 1735.03, SE = 92.82; pos 3: M = 1578.44, SE = 80.26; pos 4: M = 1311.86, SE = 72.66).

To summarise, we predicted that if perceptual encoding of faces into WM is impaired among DPs, the recency effect may be magnified in this group as indexed by a disproportionately larger WM deficit for items encoded early on than those encoded most recently, compared to controls. Our pattern of data does not support this. Instead, we find no WM deficit among DPs for the first item encoded into WM, but marked deficits for later items presented and an attenuated recency effect.

4.0 General Discussion

Across two experiments we sought to examine in more depth the nature of WM impairments for faces among developmental prosopagnosics (DPs), focusing on the role of perceptual encoding. In Experiment 1 we measured encoding limits by simultaneously presenting 1, 2, 3 or 4 faces for encoding into WM. After a 1000ms maintenance interval a single test face was presented at retrieval which either matched or mismatched one of the encoding faces. While this is the first direct assessment of face WM load effects in prosopagnosia, prior research with schizophrenia patients showed that they suffered a disproportionately larger decrease in WM accuracy as WM load increased, compared to controls (Haenschel et al., 2007, 2009; Jansma et al., 2004). WM deficits in schizophrenia are considered to partly reflect encoding deficits, where the memoranda are encoded in an inefficient or imprecise manner. Drawing a broad parallel with this research and known perceptual processing deficits for faces among DPs, we reasoned that if DPs were unable to encode effective perceptual representations of faces into WM, then increasing the number of faces to encode (increasing WM load) would disproportionately impair WM performance compared to controls. However, we found no evidence for this, and instead our data showed a more general WM impairment that was not modulated by face WM load. In Experiment 2 we assessed WM updating processes by presenting four faces sequentially for encoding into WM. Maintenance and retrieval elements and the match/mismatch task were the same as in Experiment 1. This serial paradigm requires that participants add faces to the WM storage facility while protecting those already encoded. Based on WM research which shows that items encoded early on in a sequence suffer some degree of retroactive interference from later presented items (culminating in a recency effect; Kool et al., 2014; Allen et al., 2006), we predicted that perceptual encoding deficits among DPs may disproportionately impair WM for faces that were presented early on in the sequence than those faces seen most recently, compared to controls. However, instead, we found an attenuated recency effect among DPs that was driven by impaired WM for later faces shown in the encoding sequence, and no DP impairment for the first face presented.

Overall, while we do not dispute that perceptual processing of faces is impaired among DPs, and that encoding of faces into WM is inadequate to some degree, our results cannot be fully explained by a face encoding deficit, at least not one that is sensitive to the cumulative effect of increasing WM load and serial updating. The nature of face recognition WM impairments among DPs appears more complex and we will address the results of each experiment in turn.

4.1 Face WM Load, Experiment 1

While we found that comparing the test face with four faces encoded into WM (load 4) is harder than comparing the test face with just one face held in WM (load 1) overall, this was not disproportionately more difficult for DPs than controls. DPs were similarly unable to encode just one face into WM as they were four faces. Our load effect among controls is comparable to those found in Curby and Gauthier (2007) who used a very similar paradigm with multiple faces at encoding and a single face at test, so there is nothing unusual about our baseline measure of 'normal' WM face performance. If encoding faces into WM were particularly difficult for those with DP, then the requirement to encode and store four versus one face should have been especially taxing, but it was not. This contrasts with the pattern of WM deficits reported in schizophrenia (Haenschel et al., 2007, 2009; Jansma et al., 2004), and this may be due to a difference in memoranda presentation style (serially in the schizophrenia studies, simultaneously here). As stated earlier, we wanted to isolate the effects of load from the effects of updating on WM performance among DPs versus controls, thus we used a simultaneous presentation with varied load in Experiment 1 and a serial presentation with constant load in Experiment 2. Perhaps the disproportionately larger load effects among schizophrenia patients than controls may have resulted from an interactive effect of serial updating plus increased load, but further research is required to investigate this. In Haenschel et al. (2007, 2009) and Jansma et al. (2004) serial position effects among schizophrenia patients versus controls are not reported and this would be an interesting focus for future study. Our results provide an important contribution to the literature on WM deficits in DP by showing that when the demands of serial updating are absent, DP individuals are not any more disadvantaged when they are required to encode multiple faces versus just one face into WM. It is notable that the overall WM deficit among DPs here appears smaller than that reported by Shah et al. (2015), despite the fact that encoding demands were substantially greater here. While this could be due to relatively low retrieval demands by using a single test face in our study, it suggests that DPs do not suffer drastic limits in front-end face encoding into WM..

Successful face recognition depends on both match and non-match decisions, and the single test item paradigm used here allows us to measure the ability of DPs to both detect when the face is present (match trials; hits) and importantly also to assess when the face is absent (non-match trials; false alarms). While the always match present design of Shah et al. (2015) (and notably also the CFMT) is very useful in telling us how well DP individuals are able to filter the noise from distracters at retrieval and locate the correct face, it does not tell us how well they can accurately detect the absence of this familiarity signal. It is of note here that the general WM deficit we find for DPs versus controls is indexed by the false alarm rate rather than hit rate (and we showed that this was not a response bias). Spared hit rates indicate that delayed matching of same identity faces is unimpaired in this particular task. But the ability to accurately dismiss a face as a nonmatch is impaired here across all loads equivalently, indicating that DPs find it hard to tell different faces apart when WM processes are engaged. This pattern of results contrasts with White et al. (2016) who showed the opposite effect using a perceptual task called the Local Heroes Task (LHT). In their task DPs were not impaired at telling two different faces apart than controls, but were impaired in their ability to tell that two faces were of the same person. The LHT involves the presentation of two familiar or unfamiliar faces side by side that either depict the same person or not. In contrast to our study, there is no memory component to the LHT and the images vary in low-level image properties. Perhaps an important distinction between White et al. and our study is that while their faces had hair present, our faces had hair removed and the same external, oval outline imposed. Spared ability to determine that two faces differed in White et al.'s task may therefore have been driven by reliance on external feature differences, while our task forced participants to engage with the central details of the faces which are more diagnostic for face identification. Furthermore, White and colleagues used full colour images while we used black and white images, so their findings might also reflect reliance on differences in skin colour, tone, and texture.

Our finding that DPs are impaired on non-match trials specifically, highlights an important facet of how faces are less able to be discriminated in WM among this group of individuals when familiarity signals are absent. We cannot determine whether spared DP ability to detect a matching test face reflects an explicit familiarity judgement or a response to a more unspecific familiarity signal that could be triggered by the reappearance of a face just seen. However, establishing that DPs have poorer non-match face recognition abilities in WM is important because false positives can be just as detrimental to social interaction as can a lack of positive identification. The fact that the presence or absence of perceptual or mnemonic face deficits among DPs appears to depend on the match / non-match condition of an experimental trial, highlights the importance of probing more in-depth the root of the deficit in relation to specific task demands and recall conditions. Closer examination of this kind of data in other face memory and perception tasks which allow for this may yield some important clues to help disentangle the heterogeneity of face processing deficits across different tests.

With evidence here that the WM deficit among DPs may be driven by more than just perceptual face encoding difficulties, we consider whether there may also be a deficit in the face comparison process at retrieval. Prior research using healthy young adults and non-face stimuli show that retrieval accuracy is influenced by the similarity between the physically present test item and the stored item representation(s). For complex (but not simple) abstract shapes, Jackson and colleagues found poorer WM when the test item was similar to but different from one of the faces at encoding (i.e., a similar nonmatch), relative to when the test item was a dissimilar nonmatch (Jackson, Linden, Roberts, Kriegeskorte, & Haenschel, 2015). The paradigm used in that study was identical to the one used here in Experiment 1, presenting 1-4 shapes simultaneously for encoding and a single test item at retrieval. Faces are a very complex stimulus (certainly compared to butterflies or chairs for example), and this raises the possibility that individuals with DP perceive faces to look very similar to one another, and this could account for the inability to accurately tell different faces apart when there is reliance on WM during the comparison process. Different faces were used in Experiment 1 and 2 in order to mitigate any potential danger that DP deficits could be face-set specific – having found a deficit in both tasks using different faces this is not of concern. However, future work could examine whether there are any differences in WM performance between face sets in a more controlled and systematic manner, by measuring how similar or dissimilar the faces are from one another psychometrically and/or via use of computer algorithms. An interesting question here might be whether face memory could be improved among prosopagnosic individuals if face distinctiveness is enhanced.

In a review of the cognitive and neural basis of DP, Towler and colleagues report that neuroimaging and electroencephalography studies of DP show intact early, structural perceptual processing of faces among DPs, and suggest that face recognition impairments may be driven more by post-perceptual and higher cognitive processes (Towler, Fisher, & Eimer, 2016). The dual-route hypothesis of face recognition proposes that faces are processed using a combination of configural and featural analyses, but that configural processes are the hallmark of most efficient recognition (Bartlett, Searcy, & Abdi, 2003; Rhodes, Brake, & Atkinson, 1993). Strong evidence is cited for abnormal configural processing of faces among DPs (Towler et al., 2016), an inability to adequately process the visuo-spatial relationship between facial features. We propose that perhaps the WM deficit for faces among DPs found here may be driven by the inability to compare integrated, holistic representations of the test face with face representations stored in WM. Reliance on poorly integrated individual features to discriminate between the test face with those faces encoded earlier might be sufficient to accurately detect the reappearance of a matching test face (as reflected in spared hit rates for DPs), but insufficient to accurately discriminate a non-matching test face (as reflected in more false alarms for DPs). In perceptual face processing tasks, the physical presence of the faces during the comparison process may support the ability to distinguish between same or different features, which could account for the heterogeneity of DP performance found across different studies. The more consistent face memory deficits found among DPs suggests that the ability to recall a face, to compare who we see before us with the variety of face representations we hold in our mind's eye, may especially rely on configural information. ~~With configural information considered diagnostic for face identification and discrimination (e.g., Bartlett, Searcy, & Abdi, 2003; Rhodes, Brake, & Atkinson, 1993), s~~Studies have shown perceptual impairments in holistic processing of non-face stimuli among DP individuals (Avidan, Tanzer, & Behrmann, 2011; Behrmann et al., 2005; Tanzer, Freud, Ganel, & Avidan, 2013). Therefore impaired configural/holistic processing and greater reliance on feature processing in general may render faces to appear more similar to one another and thus degrade the accuracy of comparison during retrieval from WM.

We reiterate that individuals with DP in Experiment 1 here showed the same degree of WM impairment when there was one face to encode into WM compared to when there were four faces to encode. Thus, comparing the test face with one stored face versus multiple stored faces is not impaired per se. This suggests that the comparison deficit, if indeed this is part of the problem in WM, is immune to increased mnemonic load. It is possible that individuals with DP have some form of greater noise in their face processing system. Ma et al. (2015) highlight the role of noise within our internal WM representations, and that the level of noise increases with increasing WM load. They also state that, according to flexible resource theory increasing the resource allocated to an item can decrease the noise in its representation and improve the fidelity with which it is encoded and stored. Thus, perhaps DPs have a poorer signal-to-noise ratio for face representations in WM. At present, it remains unclear how to operationalize this 'noise' in face WM specifically, but it could be speculated to derive from greater reliance on featural than configural/holistic processing (Avidan et al., 2011; Behrmann et al., 2005; Tanzer et al., 2013). Greater reliance on featural than configural processes may reflect weaker binding between features and their configurations, which in turn could degrade the ability to process individual faces effectively and to recognise a face via memory comparison processes. If we consider the resource-based model of WM, it is also possible that featural face processing may consume a greater proportion of WM encoding resources than holistic face processing. Binding multiple pieces of information contained within a single object can serve to reduce or compress the amount of information that needs to be processed/encoded, so that objects with multiple features can be retained just as well as objects with one feature (e.g., Luck & Vogel, 1997; Raffone & Wolters, 2001; Wheeler & Treisman, 2002; Vogel et al., 2001). Thus inefficient binding of face features (i.e., impaired configural/holistic processing) among DPs may increase encoding demands per face and thus lower the signal-to noise ratio. Alternatively, the interference theory of WM (Oberauer & Lin, 2017) might posit that DPs suffer greater interference between faces in WM than controls, which increases confusion between the memory contents and thus impairs the comparison process at retrieval. Interference in this context could likely derive from inefficient encoding strategies that renders each face representation unstable and liable to overlapping from other faces so that they distort or blur. However, more in-depth research into feature binding, resource demands, and interference effects in WM using face and non-face objects among DPs is required to investigate these proposals.

It remains unclear why increasing the number of faces to encode, and thus potentially increasing the amount of noise in the system, did not result in more severe WM deficits among DPs than controls at higher loads. But what we can conclude is that any effect of noise in the system is not additive, and may thus be a constant rather than associated directly with the encoding of each individual face. Shah et al. (2015) found that WM for non-face objects was not impaired among DPs, and our sample of DPs showed no impairments on tests of object or word recognition. So it is possible that this noise, in whatever form it takes, is face-specific. Computational modelling may enable future work to investigate and systematically operationalize whether a face versus non-face noise constant could account for our pattern of results.

We turn now to the results from Experiment 2, in which faces were serially presented for encoding into WM.

4.2 WM Updating, Experiment 2

In Experiment 2, our data show that when required to encode four faces serially into WM, DPs were not impaired at remembering the first face in the sequence compared to controls, but were impaired for later presented faces and relatedly showed a weaker recency effect. The serial nature of the encoding phase means that there are n intervening faces presented before the test face is shown and a retrieval response is required. Performance was poorest in both groups for faces shown in positions 1 and 2, indicating that having two or three intervening faces to encode before the test phase places greater restrictions on WM retrieval ability. The most likely explanation is that retroactive interference degrades prior face representations and thus substantially disrupts the WM system (Allen et al., 2006; Kool et al., 2014). For DPs, we show here that any number of intervening faces degrades WM ability, indicated by flat performance for faces tested from positions 1, 2, and 3. However, for controls, one intervening face (position 3) is less problematic than two or three intervening faces (data from positions 2 and 1 respectively), suggesting that there is some protective (disruption reduction) mechanism they can use that DPs cannot.

Both groups showed a recency effect and no primacy effect, which parallels previous reports of visual WM performance as a function of serial position (Kool et al., 2014). However, the recency effect was attenuated among DPs and they showed a marked deficit in WM for the last face in the sequence (the most recently seen face). Why did the locus of relative impaired DP performance occur here? It is possible that, in addition to retroactive interference DPs also suffered proactive interference. Inefficient (i.e., featural) encoding of early presented faces (in particular the face which was third in the sequence) may have disrupted the ability of the last face to receive special status in the focus of attention. This account would also fit within the interference account of WM (Oberauer & Lin, 2017). Another account of recency effects in visual WM is that WM resources can be dynamically and flexibly allocated and re-allocated during updating (Gorgoraptis, Catalao, Bays, & Husain, 2011), to prioritise or deprioritise items. Thus, it is possible that our DP data from Experiment 2 reflects impaired flexibility or efficiency of resource allocation during updating of faces in WM. Noise in the face processing system may account for this inefficiency if we consider perhaps that it is the allocation of resources required for face identification that are ineffectively allocated, rather than general WM resources per se. From the perspective of the flexible resource-based model, the attenuated recency effect found in Experiment 2 may be argued to result from over-use of resources to inefficiently encode the first 2-3 faces in the sequence, leaving insufficient resources left available to place the last face in a particularly special focus of attention. Thus, the significantly weakened recency effect among DPs may result from an additive effect of WM-specific noise plus face-specific noise. Controls, with an intact face processing system, may only suffer WM-general noise in this serial task. What is clear is that some updating mechanism for faces in WM is disrupted among individuals with DP.

We also found in this sequential paradigm that DPs were significantly slower in making a correct response than controls by 356ms overall. (DPs were also slower than controls in Experiment 1 but this did not reach significance.) Slowed decision-making on this task suggests that DPs may have engaged in a less efficient and more laboured face comparison process at retrieval, perhaps resulting from more feature-based processing. Despite taking longer to respond, DPs were still impaired in memory accuracy relative to controls, indicating that whatever strategy they did take more time to engage in, it was not optimal. It could be argued that slower RTs served to degrade the representations held in WM to a greater degree among DPs compared to controls, and this impaired accuracy. However, this is unlikely given that Shah et al. (2015) found no disproportionate decrease in WM accuracy among DPs as maintenance interval increased from 2s to 8s, and given that the difference in response times here was less than 400ms.

To conclude, individuals with DP show face WM impairments but these are specific to certain encoding and retrieval conditions. We propose that noise in the face processing system, plus noise and interference in the WM updating system when engaged, leads to fragile and fragmented face representations in WM which are difficult to discriminate from the test face at retrieval. Our study highlights the importance of task parameters and demands when assessing face memory. The nature of face WM deficits described here may also adequately account for memory impairments documented using other commonly used face memory tasks, but closer inspection of this is required to fully understand the root(s) of face memory problems in developmental prosopagnosia.

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Highlights

- Poor face WM in developmental prosopagnosia (DP) is not just an encoding deficit.
- Additional comparison difficulties at retrieval are proposed.
- The recency effect in WM for faces shown sequentially is attenuated in DP.
- Resource demands of inefficient face processing in WM are discussed.
- The nature of task demands at encoding and retrieval should be better considered.