



## Research report

# Normal composite face effects in developmental prosopagnosia

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## ABSTRACT

Upright face perception is thought to involve holistic processing, whereby local features are integrated into a unified whole. Consistent with this view, the top half of one face appears to fuse perceptually with the bottom half of another, when aligned spatially and presented upright. This 'composite face effect' reveals a tendency to integrate information from disparate regions when faces are presented canonically. In recent years, the relationship between susceptibility to the composite effect and face recognition ability has received extensive attention both in participants with normal face recognition and participants with developmental prosopagnosia. Previous results suggest that individuals with developmental prosopagnosia may show reduced susceptibility to the effect suggestive of diminished holistic face processing. Here we describe two studies that examine whether developmental prosopagnosia is associated with reduced composite face effects. Despite using independent samples of developmental prosopagnosics and different composite procedures, we find no evidence for reduced composite face effects. The experiments yielded similar results; highly significant composite effects in both prosopagnosic groups that were similar in magnitude to the effects found in participants with normal face processing. The composite face effects exhibited by both samples and the controls were greatly diminished when stimulus arrangements were inverted. Our finding that the whole-face binding process indexed by the composite effect is intact in developmental prosopagnosia indicates that other factors are responsible for developmental prosopagnosia. These results are also inconsistent with suggestions that susceptibility to the composite face effect and face recognition ability are tightly linked. While the holistic process revealed by the composite face effect may be necessary for typical face perception, it is not sufficient; individual differences in face recognition ability likely reflect variability in multiple sequential processes.

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## 1. Introduction

In recent years, research has revealed substantial individual differences in face processing ability. Whilst ‘super-recognisers’ make up the upper tail (Russell, Duchaine, & Nakayama, 2009), the lower-end of the distribution is composed of individuals with developmental prosopagnosia<sup>1</sup> (DP). DP is a neurodevelopmental condition characterised by difficulties recognising facial identity, despite normal intelligence, typical low level vision, and no history of brain damage (Behrmann & Avidan, 2005; Cook & Biotti, 2016; Duchaine & Nakayama, 2006b). DP was once thought to be extremely rare (McConachie, 1976), but one in every 50 people are now thought to experience lifelong face recognition difficulties severe enough to disrupt their daily lives (Kennerknecht, Ho, & Wong, 2008; Kennerknecht et al., 2006). Individuals with DP typically utilise non-face cues including voice, gait, and hairstyle to recognise others. Consequently, they often experience great difficulties when non-face cues are unavailable or changed, or when familiar people are encountered out of context.

Numerous papers have suggested that diminished holistic face processing may underlie the difficulties seen in DP (Avidan, Tanzer, & Behrmann, 2011; Carbon, Grüter, Weber, & Lueschow, 2007; DeGutis, Cohan, & Nakayama, 2014; DeGutis, Cohan, Mercado, Wilmer, & Nakayama, 2012; Liu & Behrmann, 2014; Lobmaier, Bölte, Mast, & Dobel, 2010; Palermo et al., 2011). Typical face perception appears to involve a rapid parallel analysis, whereby local features are integrated into a unified whole (Farah, Wilson, Drain, & Tanaka, 1998; Maurer, Le Grand, & Mondloch, 2002; McKone & Yovel, 2009; Piepers & Robbins, 2013). Evidence of holistic face perception is provided by the composite face effect, where the top half of one face appears to fuse perceptually with the bottom half of another, when the two halves are aligned and presented upright (Hole, 1994; Young, Hellawell, & Hay, 1987). The resulting illusion-induced interference disrupts observers’ ability to judge the identity (Young et al., 1987), physical resemblance (Hole, 1994), age (Hole & George, 2011), gender (Baudouin & Humphreys, 2006), and attractiveness (Abbas & Duchaine, 2008) of constituent face halves (for reviews see Murphy, Gray, & Cook, 2017; Rossion, 2013). When face halves are inverted, observers show little or no interference (McKone et al., 2013; Susilo, Rezlescu, & Duchaine, 2013). Importantly, the composite effect reveals a tendency to integrate feature information from disparate regions when faces are presented canonically, consistent with holistic theories of face perception (Farah et al., 1998; Maurer et al., 2002; McKone & Yovel, 2009; Piepers & Robbins, 2013).

The suggestion that DP results from disrupted holistic processing is closely related to the view that the whole-face binding process measured by the composite face effect contributes to face recognition ability (DeGutis, Wilmer, Mercado, & Cohan, 2013; Farah et al., 1998; Maurer et al., 2002; Piepers & Robbins, 2013). However, studies comparing observers’

susceptibility to the composite face effect and their face recognition ability have yielded mixed results (Murphy et al., 2017). In cases of acquired prosopagnosia (AP), individuals are left with face recognition difficulties following brain injury. While some APs exhibit reduced composite face effects relative to matched controls (Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010; Ramon, Busigny, & Rossion, 2009), others exhibit typical susceptibility to the original matching procedure (Finzi, Susilo, Barton, & Duchaine, 2016; Rezlescu, Pitcher, & Duchaine, 2012). Where composite face effects and face recognition ability have been compared in samples drawn from the general population, some authors have observed positive associations (DeGutis et al., 2013; Engfors, Jeffery, Gignac, & Palermo, 2017; Richler, Cheung, & Gauthier, 2011), whilst others have found little or no correlation (Konar, Bennett, & Sekuler, 2010; Rezlescu, Susilo, Wilmer, & Caramazza, 2017; Wang, Li, Fang, Tian, & Liu, 2012).

The literature is also inconsistent with respect to the relationship between individuals’ susceptibility to the composite face effect and other putative markers of holistic representation, including the part-whole (Tanaka & Farah, 1993) and face-inversion effects (Yin, 1969). For example, some authors have found associations between susceptibility to the composite face effect and the part-whole effect (DeGutis et al., 2013). However, other studies have found no association between susceptibility to the composite face effect and the part-whole effect (Rezlescu et al., 2017; Wang et al., 2012), or between composite face effects and perceptual decrements induced by face inversion (Rezlescu et al., 2017). These findings cast doubt on the view that a unitary process underlies holistic face processing. Where different measures of holistic processing are unrelated or weakly correlated in the typical population, neuropsychological dissociations might also be seen in the DP population.

Although studies have described a number of individuals with DP who exhibit composite effects comparable with those of matched controls (Le Grand et al., 2006; Schmalzl, Palermo, & Coltheart, 2008; Susilo et al., 2010), three studies have concluded that DP is associated with reduced susceptibility to the composite face effect at the group level (Avidan et al., 2011; Liu & Behrmann, 2014; Palermo et al., 2011). Nevertheless, the case for diminished composite effects in DP remains unconvincing. In at least one study, inspection of single-case data suggests that previously reported group results have been strongly influenced by the presence of outliers in DP samples (Palermo et al., 2011). In other studies, DP samples perform poorly in the baseline ‘misaligned’ condition making it hard to interpret putative differences in composite effect susceptibility (Liu & Behrmann, 2014).

Given the uncertainty about the functional significance of the holistic processes revealed by the composite face effect (Finzi et al., 2016; Konar et al., 2010; Rezlescu et al., 2017; Wang et al., 2012) and the popular view that DP may be caused by diminished holistic representation (Carbon et al., 2007; DeGutis et al., 2012, 2014; Lobmaier et al., 2010), obtaining a better understanding of composite face effects in DP is theoretically important. It may also have implications for interventions aimed at improving face recognition in DP (e.g., DeGutis et al., 2014). The present study therefore sought to confirm that DP is associated with reduced composite face

<sup>1</sup> We use the term *developmental prosopagnosia* instead of *congenital prosopagnosia* to indicate the possibility that in some cases the disorder may not be present at birth.

effects at the group level. We describe two experiments employing independent samples of DP participants collected in the UK and the USA ( $N = 16$  and  $N = 24$ ) and complementary paradigms (simultaneous and sequential matching). Contrary to previous group studies (Avidan et al., 2011; Liu & Behrmann, 2014; Palermo et al., 2011), we find no evidence for diminished composite face effects in DP.

## 2. Experiment 1

In our first experiment we compared the composite face effects of DPs and matched controls using a simultaneous matching procedure (Hole, 1994). Composite effects seen with upright faces were compared with those seen with inverted faces. Whereas strong effects of alignment are seen when composite faces are presented upright, interference is greatly reduced when composites are constructed from inverted faces (Susilo et al., 2013). This comparison is useful as it addresses the possibility that effects of misalignment found with upright faces are due to general factors rather than face-specific processes (McKone et al., 2013; Rossion, 2013). We also examined composite effects for pseudo-words which resemble the effects found for upright faces (Anstis, 2005). For the sake of brevity, however, details of the procedure and results for pseudo-words are provided as [supplementary material](#).

## 3. Methods

### 3.1. Participants

Two groups of observers completed the procedure; 16 individuals with DP ( $M_{\text{age}} = 43.56$  years,  $SD_{\text{age}} = 15.09$  years, 3 males), and a control group comprising 16 neurotypical adults ( $M_{\text{age}} = 39.81$  years,  $SD_{\text{age}} = 12.95$  years, 10 males). All observers were resident in the UK. Ethical approval was granted by the local ethics committee and the study was conducted in line with the Declaration of Helsinki. All participants provided informed consent prior to testing.

### 3.2. Diagnostic testing

DP participants were recruited through [www.troublewithfaces.org](http://www.troublewithfaces.org). All members of the DP sample described lifelong face recognition difficulties that affected their daily lives. None of the DPs had a history of brain injury or psychiatric disorder (e.g., Schizophrenia, Autism Spectrum Disorder). Diagnostic evidence for the presence of DP was collected using the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006a) the Twenty-Item Prosopagnosia Index (PI20; Gray, Bird, & Cook, 2017; Shah, Gaule, Sowden, Bird, & Cook, 2015), and a Famous Face Test suitable for use with UK residents (FFT<sub>UK</sub>). Scores on the CFMT were compared against data from 50 typical observers reported by Duchaine and Nakayama (2006a). Participants also completed the Cambridge Face Perception Test (CFPT; Duchaine, Germine, & Nakayama, 2007) to determine whether face recognition deficits had an apperceptive origin (De Renzi, Faglioni, Grossi, & Nichelli, 1991). While participants were not

selected on the basis of these scores, the DP sample was impaired at the group level [ $t(22) = 2.34, p = .029$ ]. Scores on the CFPT and PI20 were compared with a group of 56 controls ( $M_{\text{age}} = 40.25$  years,  $SD_{\text{age}} = 13.71$  years, 24 males). Comparison data for the FFT<sub>UK</sub> was collected from a sample of 20 controls ( $M_{\text{age}} = 30.4$  years,  $SD_{\text{age}} = 10.27$  years, 9 males). When tested on the CFMT, all DPs scored at least 1.53 standard deviations below the mean performance of the comparison sample. All DPs tested<sup>2</sup> also scored at least 2 standard deviations below the mean of the comparison samples on the FFT<sub>UK</sub> and the PI20. Diagnostic information is presented in [Table 1](#).

### 3.3. The composite task

Face composites were constructed from images of emotionally neutral faces taken from the Karolinska Directed Emotional Faces database (Lundqvist, Flykt, & Öhman, 1998). Faces were cropped to exclude external facial features (e.g., ears, hairline). Face halves containing the eyes were used as target regions. Face composites subtended 8° of visual angle, vertically. The to-be-judged regions subtended 4°. In the misaligned conditions, the horizontal offset corresponded to approximately 25% the width of a face.

In total, 40 face composites were employed. Each composite was allocated a partner arrangement of the same type with which it would be presented simultaneously. For half the composite pairs, the target regions were identical, for half the pairs the target regions differed. Following the standard composite design (also referred to as the original design; Murphy et al., 2017; Rossion, 2013), the distractor regions within each pair were always different. The two target regions appeared at the same vertical position in the display (the lower edge of each target region was aligned to the vertical midpoint of the display). Two dashed guidelines were imposed over the arrangements to clearly delineate the stimulus regions to be judged. Example displays are presented in [Fig. 1a](#).

Testing took place at City, University of London. Participants judged whether the regions shown within the guidelines were identical or not. Composite displays were presented until a response was registered. Participants were asked to respond with both speed and accuracy. Each pair was presented twice in each alignment condition with side (left or right) counterbalanced, yielding 120 ‘same’ trials and 120 ‘different’ trials (10 pairs  $\times$  2 presentations  $\times$  2 levels of alignment  $\times$  3 composite types). Composite type (upright faces, inverted faces, pseudo-words) was interleaved randomly within blocks of 60 trials. Six practice trials were provided. The experiment was programmed in MATLAB (The MathWorks, Natick, MA) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

Prior to testing the DPs and age-matched controls, we piloted our novel procedure on a group of 25 young neurotypical adults ( $M_{\text{age}} = 18.92$  years,  $SD_{\text{age}} = 1.42$  years, 3 males) to ensure the tasks yielded the expected results. These data are provided in the [supplementary material](#). The sample

<sup>2</sup> In Experiment 1, two DPs did not complete FFT<sub>UK</sub>. In Experiment 2, two DPs did not complete the FFT<sub>US</sub> and two did not complete the ONFRT.

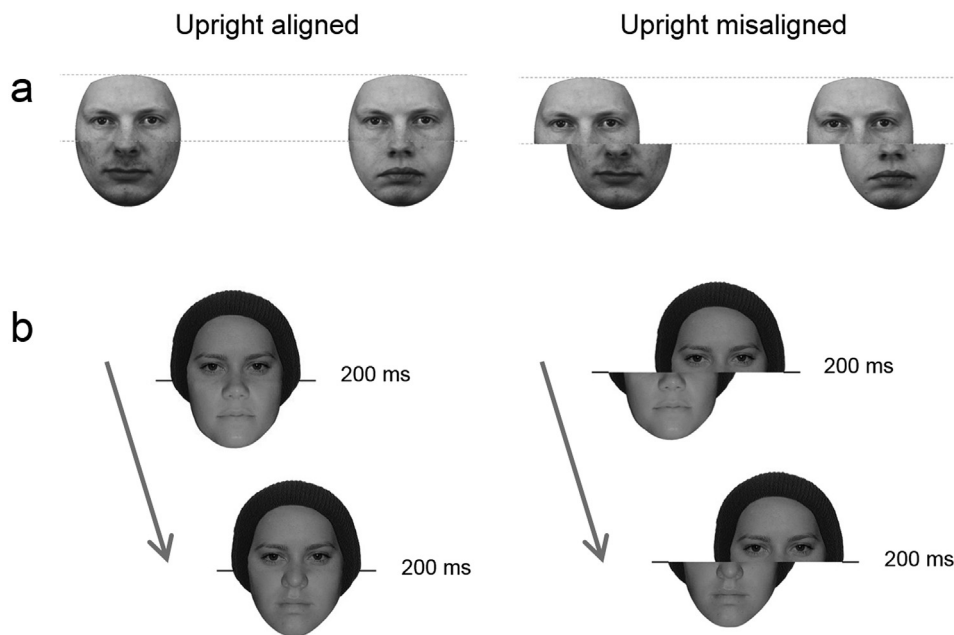
**Table 1 – Scores for each developmental prosopagnosic in Experiment 1 on the 20-Item Prosopagnosia Index (PI20), the Cambridge Face Memory Test (CFMT), the Cambridge Face Perception Test (CFPT), and the Famous Faces Test (FFT<sub>UK</sub>). Z-scores are shown in parentheses. Negative z-scores denote performance worse than the typical mean. The mean and standard deviation of the comparison samples are provided below.**

Participant	Age	PI20	FFT <sub>UK</sub> %	CFMT %	CFPT upright [errors]
F1	21	59 (−2.3)	25 (−4.2)	62.50 (−1.6)	30 (−.0)
F2	22	89 (−5.6)	–	50.00 (−2.8)	30 (−.0)
F3	25	87 (−5.4)	41 (−2.9)	63.89 (−1.5)	44 (−1.6)
F4	28	68 (−3.3)	48 (−2.3)	61.11 (−1.8)	32 (−.3)
F5	35	85 (−5.2)	34 (−3.4)	43.06 (−3.4)	46 (−1.8)
F6	42	92 (−5.9)	18 (−4.8)	45.83 (−3.1)	62 (−3.5)
F7	50	78 (−4.4)	30 (−3.8)	58.33 (−2.0)	34 (−.5)
F8	53	85 (−5.2)	42 (−2.8)	45.83 (−3.1)	74 (−4.8)
F9	55	85 (−5.2)	–	58.33 (−2.0)	36 (−.7)
F10	65	79 (−4.5)	14 (−5.1)	61.11 (−1.8)	40 (−1.1)
F11	65	81 (−4.7)	25 (−4.2)	59.72 (−1.9)	44 (−1.6)
F12	48	78 (−4.4)	45 (−2.5)	58.33 (−2.0)	26 (+.4)
F13	48	85 (−5.2)	37 (−3.2)	63.89 (−1.5)	60 (−3.3)
M1	28	62 (−2.6)	44 (−2.6)	62.50 (−1.6)	46 (−1.8)
M2	54	88 (−5.5)	48 (−2.3)	58.33 (−2.0)	66 (−3.9)
M3	58	92 (−5.9)	5 (−5.9)	44.44 (−3.3)	68 (−4.2)
DP mean		80.81	32.57	56.26	46.12
DP SD		9.97	13.53	7.66	15.31
Comparison mean		37.75	75.35	80.4	36.7
Comparison SD		9.16	12.00	11.0	12.2

exhibited a clear composite effect for upright faces that accords closely with the existing literature. Reassuringly, we found disproportionate effects of Alignment on ‘same’ trials, where the presence of the illusion makes it harder to detect that target regions are identical, consistent with previous reports (e.g., Le Grand, Mondloch, Maurer, & Brent, 2004). As expected, composite effects were greatly diminished when arrangements were constructed from inverted faces.

#### 4. Results

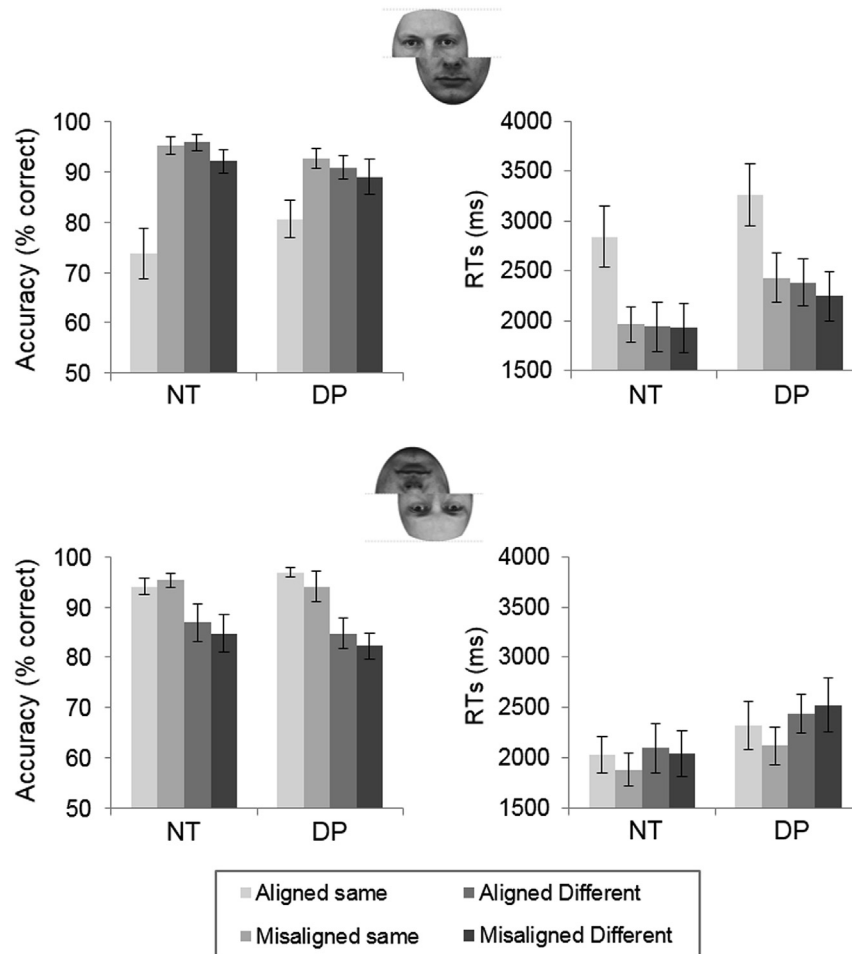
Where stimulus displays are visible until participants respond, there is a trade-off between response speed and response accuracy; slower responding allows observers to collect more perceptual evidence, and thereby reduce errors. Under these conditions, many observers approach ceiling on accuracy



**Fig. 1 – (a) In our first experiment, trials presented pairs of composite arrangements simultaneously. Composites were visible until a response was registered. (b) In our second experiment, trials presented pairs of face composites sequentially. Composites were presented for 200 msec each, with an inter-stimulus-interval of 400 msec during which a black display was presented.**

**Table 2 – Mean accuracy and response time measures from Experiment 1. Standard deviations are shown in parentheses.**

			Aligned same	Misaligned same	Aligned different	Misaligned different
Upright faces	Accuracy (%)	NT	73.8 (20.0)	95.3 (7.2)	95.9 (6.6)	92.2 (9.3)
		DP	80.6 (15.2)	92.8 (8.0)	90.9 (9.5)	89.1 (14.3)
	RT (ms)	NT	2840 (1228)	1964 (711)	1937 (992)	1925 (1006)
		DP	3257 (1241)	2430 (981)	2383 (945)	2243 (974)
Inverted faces	Accuracy (%)	NT	94.1 (6.4)	95.3 (5.9)	86.9 (14.6)	95.3 (14.8)
		DP	96.9 (4.0)	94.1 (12.3)	84.7 (12.3)	82.2 (10.6)
	RT (ms)	NT	2028 (741)	1882 (661)	2095 (990)	1882 (909)
		DP	2323 (969)	2120 (753)	2438 (787)	2522 (1068)

**Fig. 2 – Results from Experiment 1 for composite arrangements constructed from upright faces (top) and inverted faces (bottom). Error bars represent  $\pm 1$  standard error of the mean.**

measures (e.g., Calder, Young, Keane, & Dean, 2000; Palermo et al., 2011). To facilitate clear interpretation we therefore present both the response speed and accuracy data (Table 2).

#### 4.1. Accuracy

First, we compared the composite face effects exhibited by the groups in their accuracy data (Fig. 2). Our analyses revealed evidence of clear composite effects for upright faces. As expected, we observed a significant main effect of Alignment [ $F(1,30) = 19.04, p < .001, \eta^2 = .388$ ], a main effect of Trial Type [ $F(1,30) = 5.91, p = .021, \eta^2 = .165$ ], and an Alignment  $\times$  Trial

Type interaction [ $F(1,30) = 36.72, p < .001, \eta^2 = .550$ ]. The analysis indicated that the composite effects exhibited by the controls and DPs did not differ. We observed no main effect of Group [ $F(1,30) = .145, p = .706, \eta^2 = .005$ ], and the effects of Alignment [ $F(1,30) = .135, p = .254, \eta^2 = .043$ ], Trial Type [ $F(1,30) = 1.41, p = .245, \eta^2 = .045$ ], and the Alignment  $\times$  Trial Type interaction [ $F(1,30) = 2.99, p = .094, \eta^2 = .091$ ], did not interact with Group. We also note that the Alignment  $\times$  Group interaction failed to reach significance when the analysis was restricted to ‘same’ trials [ $F(1,30) = 2.61, p = .117$ ]. When considered separately, the neurotypical controls showed effects of Alignment [ $F(1,15) = 12.187, p = .003, \eta^2 = .448$ ] and an Alignment  $\times$  Trial

Type interaction [ $F(1,15) = 35.161, p < .001, \eta^2 = .701$ ]. Clear effects of Alignment [ $F(1,15) = 6.855, p = .019, \eta^2 = .314$ ] and an Alignment  $\times$  Trial Type interaction [ $F(1,15) = 8.238, p = .012, \eta^2 = .355$ ] were also seen in the DP group.

Neither group showed evidence of composite effects for inverted faces. The analysis revealed a significant effect of Trial Type [ $F(1,30) = 23.43, p < .001, \eta^2 = .439$ ], but the effects of Alignment [ $F(1,30) = 1.29, p = .264, \eta^2 = .041$ ], and the Alignment  $\times$  Trial Type interaction [ $F(1,30) = .41, p = .527, \eta^2 = .013$ ] failed to reach significance. As expected, the main effects of Trial Type [ $F(1,30) = 60.96, p = .000, \eta^2 = .670$ ] and Alignment [ $F(1,30) = 16.71, p = .000, \eta^2 = .358$ ] both varied significantly as a function of Composite Type (upright face, inverted face). We observed no main effect of Group [ $F(1,30) = .09, p = .763, \eta^2 = .003$ ], and none of the other main effects or interactions varied as a function of group [all  $F$ 's  $< .9, p$ 's  $> .35$ ].

#### 4.2. Response times

Next, we compared the composite face effects exhibited by the groups in their response time data (Fig. 2). Analysis of response latencies for the upright faces revealed main effects of Alignment [ $F(1,30) = 56.339, p < .001, \eta^2 = .653$ ], and Trial Type [ $F(1,30) = 28.80, p < .001, \eta^2 = .490$ ], and an Alignment  $\times$  Trial Type interaction [ $F(1,30) = 32.219, p < .001, \eta^2 = .518$ ]. The analysis indicated that similar composite face effects were seen for controls and DPs. No effect of Group was observed [ $F(1,30) = 1.496, p = .231, \eta^2 = .048$ ], and the effects of Alignment [ $F(1,30) = .101, p = .753, \eta^2 = .003$ ], Trial Type [ $F(1,30) = .101, p = .753, \eta^2 = .003$ ], and the Alignment  $\times$  Trial Type interaction [ $F(1,30) = .424, p = .520, \eta^2 = .014$ ], did not vary as a function of Group. Once again, the Alignment  $\times$  Group interaction failed to reach significance when the analysis was restricted to 'same' trials [ $F(1,30) = .043, p = .838$ ]. The neurotypical controls showed effects of Alignment [ $F(1,15) = 25.108, p < .001, \eta^2 = .626$ ] and an Alignment  $\times$  Trial Type interaction [ $F(1,15) = 14.720, p = .002, \eta^2 = .495$ ]. Highly significant effects of Alignment [ $F(1,15) = 31.517, p < .001, \eta^2 = .678$ ] and an Alignment  $\times$  Trial Type interaction [ $F(1,15) = 19.722, p < .001, \eta^2 = .568$ ] were also seen in the DP group.

Neither group showed evidence of a composite face effect for inverted faces in their response time data. The main effects of Trial Type [ $F(1,30) = 3.421, p = .075, \eta^2 = .102$ ] and Alignment [ $F(1,30) = 2.831, p = .103, \eta^2 = .086$ ], and the Alignment  $\times$  Trial Type interaction [ $F(1,30) = 2.808, p = .104, \eta^2 = .086$ ], all failed to reach significance. The main effect of Alignment [ $F(1,30) = 20.646, p < .001, \eta^2 = .408$ ] and the Alignment  $\times$  Trial Type interaction [ $F(1,30) = 10.638, p = .003, \eta^2 = .262$ ] varied significantly as a function of Composite Type (upright faces, inverted faces). No main effect of Group was observed [ $F(1,30) = 1.459, p = .236, \eta^2 = .046$ ] and none of the effects or interactions varied as a function of Group [all  $F$ 's  $< .8, p$ 's  $> .38$ ].

#### 4.3. Individual differences

Next we sought to determine how susceptibility to the composite face effect related to individual differences in face

processing ability in our sample of 16 DPs. Scores on the CFMT ( $r = -.186, p = .491$ ) and the upright CFPT ( $r = .219, p = .416$ ) failed to correlate with a measure of the composite effect based on accuracy ( $\Delta\text{accuracy} = \% \text{Correct}_{\text{aligned}} - \% \text{Correct}_{\text{misaligned}}$ ). Similarly, composite effects based on response time ( $\Delta\text{latency} = \text{RT}_{\text{aligned}} - \text{RT}_{\text{misaligned}}$ ), failed to correlate with performance on the CFMT ( $r = .194, p = .471$ ) or the upright CFPT ( $r = -.072, p = .792$ ). Finally, we sought to derive a single measure of performance that combined response times and accuracy. We therefore computed Inverse Efficiency Scores (IES; Fig. 3) by adjusting participants' response times (RTs) upwards in proportion to their error rate [ $\text{IES} = \text{RT}/\% \text{Correct}$ ] (Townsend & Ashby, 1978). No correlation was observed between composite face effects ( $\Delta\text{IES} = \text{IES}_{\text{aligned}} - \text{IES}_{\text{misaligned}}$ ) and their performance on the CFMT ( $r = .216, p = .422$ ) or their CFPT scores ( $r = -.176, p = .514$ ).

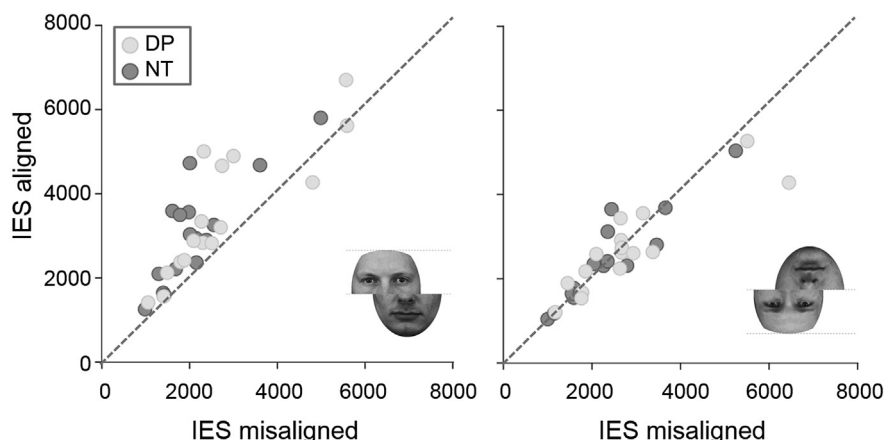
## 5. Experiment 2

In our first experiment, we examined whether 16 individuals with DP exhibited diminished composite face effects using a simultaneous matching paradigm. Contrary to previous reports (Avidan et al., 2011; Liu & Behrmann, 2014; Palermo et al., 2011), we found that the DPs and controls exhibited comparable composite face effects. However, DP is known to be a heterogeneous condition (Eimer, Gosling, & Duchaine, 2012; Stollhoff, Jost, Elze, & Kennerknecht, 2011; Susilo & Duchaine, 2013). For example, some individuals appear to perceive facial expressions normally, whereas others exhibit impaired expression recognition (Biotti & Cook, 2016; Duchaine, Parker, & Nakayama, 2003; Duchaine, Yovel, Butterworth, & Nakayama, 2006; Humphreys, Avidan, & Behrmann, 2007). Similarly, some individuals with DP recognize objects normally, while others exhibit broader object recognition deficits (Behrmann, Avidan, Marotta, & Kimchi, 2005; Biotti, Gray, & Cook, 2017; Dalrymple, Elison, & Duchaine, 2017; Duchaine, Germine et al., 2007). In light of this heterogeneity, it is possible that a subgroup of the DP population exhibits diminished composite effects, but is under-represented in our first sample. Moreover, the use of simultaneous matching in Experiment 1 differs from the sequential matching tasks employed in the previous studies that have reported group differences (Avidan et al., 2011; Liu & Behrmann, 2014; Palermo et al., 2011). In our second experiment, we therefore tested a different group of DPs with a sequential matching composite task.

## 6. Methods

### 6.1. Participants

Twenty-four individuals with DP ( $M_{\text{age}} = 40.1$  years,  $SD_{\text{age}} = 13.2$  years, 6 males) participated in the study. The performance of the DPs was compared to a control group comprising 22 neurotypical adults ( $M_{\text{age}} = 45.8$  years,  $SD_{\text{age}} = 13.9$  years, 5 males). All observers were US residents. Ethical approval was granted by the local ethics committee and the study was



**Fig. 3 – Inverse efficiency scores (IES) for aligned composites plotted against those seen for misaligned composites, for upright faces (left), inverted faces (middle), and pseudo-words (right). Points lying to the left of the dashed line are indicative of typical composite effects (performance misaligned > performance aligned).**

conducted in line with the Declaration of Helsinki. All participants provided informed consent prior to testing.

### 6.2. Diagnostic testing

DP participants were recruited through the Dartmouth/Harvard/UCL Prosopagnosia Research Center website ([www.faceblind.org](http://www.faceblind.org)). All complained of lifelong face recognition difficulties that affected their daily lives. Convergent diagnostic evidence for the presence of DP was collected using the CFMT, the Old-New Face Recognition Test (ONFRT; Duchaine & Nakayama, 2005), and a Famous Faces Test suitable for use with US residents (FFT<sub>US</sub>; Duchaine & Nakayama, 2005). When tested on the CFMT, all DPs scored at least 1.7 standard deviations below the mean performance of the comparison sample described by Duchaine and Nakayama (2006a). All DPs tested<sup>2</sup> also scored at least 2 standard deviations below the mean of the controls on the FFT<sub>US</sub> and the ONFRT (comparison data taken from Duchaine, Yovel, & Nakayama, 2007; Susilo, Wright, Tree, & Duchaine, 2015). DPs also completed the CFPT and the Leuven Perceptual Organization Screening Test (L-POST; Torfs, Vancleef, Lafosse, Wagemans, & de-Wit, 2014). All DPs scored within the normal range on the L-POST, suggesting typical mid-level vision. Detailed diagnostic results are provided in Table 3.

### 6.3. Composite task

The stimuli and procedure were adapted from the composite task employed by Susilo et al. (2013; Experiment 3). Face composites were constructed from greyscale photographs of Caucasian male children posing neutral expressions (Fig. 1b). The children were photographed wearing a black ski-cap to occlude their hairline. When viewed from 40 cm, aligned faces

subtended 10° vertically and 6.5° horizontally, and misaligned faces 10° × 9°. All subjects were tested remotely via [www.testable.org](http://www.testable.org), a platform that enables precise control of experiments conducted online.<sup>3</sup> Participants were asked to do the task in an environment in which they would not be disturbed and to employ a viewing distance of around 40 cm.

Experimental trials presented two face composites sequentially for 200 msec each, with an inter-stimulus interval of 400 msec during which a black display was presented. Composites were either both aligned or both misaligned, both upright or both inverted (Fig. 1b). Participants were asked to indicate with a keypress whether the target regions (the face halves containing the eyes) were the “same” (identical) or “different” (not identical) while ignoring the distractor regions, which were always different. There were 90 trials per orientation; 60 in which the target regions were the same (30 aligned, 30 misaligned) and 30 where the target regions were different (15 aligned, 15 misaligned), making 180 trials in total. Orientation (upright, inverted), Alignment (aligned, misaligned), and Trial Type (same, different) were randomly interleaved. Six practice trials were provided.

## 7. Results

Matching procedures that present composites sequentially for pre-determined intervals (in this case 200 msec) afford less opportunity for a trade-off between speed and accuracy, because participants cannot accumulate more perceptual evidence by responding slowly. In Experiment 2, our primary analyses focus on accuracy (% correct). Descriptive statistics for accuracy scores and RTs achieved by the two groups are presented in Table 4.

### 7.1. Accuracy

The combined dataset was subjected to ANOVA with Alignment (misaligned, aligned) and Orientation (upright, inverted) as within-subjects factors, and Group (DP, NT) as a between-subjects factor (Fig. 4). The analysis revealed main effects of

<sup>3</sup> One DP had technical difficulties, but a switch to another browser resolved the issue. This individual completed approximately one third of the trials before the task crashed, at which point the individual switched browsers and did the full task on the new browser.

**Table 3 – Scores for each developmental prosopagnosic in Experiment 2 on the Cambridge Face Memory Test (CFMT), The Famous Faces Test (FFT<sub>US</sub>), and the Old-New Faces Test (ONFT). Z-scores are shown in parentheses. Negative z-scores denote performance worse than the typical mean. The mean and standard deviation of the comparison samples are provided below.**

Participant	Age	FFT <sub>US</sub> %	ONFT A'	CFMT %	CFPT upright [errors]
F1	23	8 (−7.2)	.87 (−4.5)	45.83 (−3.1)	54 (−1.4)
F2	26	23 (−5.9)	–	58.33 (−2.0)	–
F3	27	27 (−5.5)	.81 (−7.5)	51.39 (−2.6)	54 (−1.4)
F4	27	–	.83 (−6.5)	55.56 (−2.3)	66 (−2.4)
F5	29	63 (−2.2)	.69 (−13.5)	50.00 (−2.8)	54 (−1.4)
F6	31	61 (−2.4)	.98 (1.0)	56.94 (−2.1)	52 (−1.3)
F7	32	51 (−3.3)	.89 (−3.5)	54.17 (−2.4)	78 (−3.4)
F8	34	–	.77 (−9.5)	56.94 (−2.1)	48 (−.9)
F9	38	58 (−2.7)	.87 (−4.5)	61.11 (−1.8)	62 (−2.1)
F10	38	36 (−4.7)	.77 (−9.5)	47.22 (−3.0)	56 (−1.6)
F11	41	28 (−5.4)	.87 (−4.5)	38.89 (−3.8)	92 (−4.5)
F12	41	40 (−4.3)	.91 (−2.5)	47.22 (−3.0)	42 (−.4)
F13	44	61 (−2.4)	.82 (−7.0)	52.78 (−2.5)	–
F14	44	40 (−4.3)	.90 (−3.0)	51.39 (−2.6)	34 (+.2)
F15	46	50 (−3.4)	.81 (−7.5)	58.33 (−2.0)	62 (−2.1)
F16	51	45 (−3.9)	.91 (−2.5)	61.11 (−1.8)	42 (−.4)
F17	60	33 (−5.0)	.75 (−10.5)	51.39 (−2.6)	70 (−2.7)
F18	62	48 (−3.6)	.81 (−7.5)	50.00 (−2.8)	70 (−2.7)
M1	23	26 (−5.6)	.90 (−3.0)	47.22 (−3.0)	92 (−4.5)
M2	28	24 (−5.8)	.94 (−1.0)	51.39 (−2.6)	62 (−2.1)
M3	34	56 (−2.9)	–	45.83 (−3.1)	80 (−3.5)
M4	58	33 (−5.0)	.81 (−7.5)	50.00 (−2.8)	78 (−3.4)
M5	62	43 (−4.0)	.93 (−1.5)	56.94 (−2.1)	62 (−2.1)
M6	63	40 (−4.3)	.87 (−4.5)	56.94 (−2.1)	50 (−1.1)
DP mean		40.64	.85	52.37	61.82
DP SD		14.63	.07	5.47	15.48
Comparison mean		87.5	.96	80.4	36.7
Comparison SD		11.0	.02	11.0	12.2

**Table 4 – Mean accuracy and response time measures from Experiment 2. Standard deviations are shown in parentheses.**

		Aligned		Misaligned
Upright faces	Accuracy (%)	NT	65.9 (16.5)	92.0 (9.4)
		DP	67.6 (16.9)	91.2 (8.0)
	RT (ms)	NT	1105 (362)	874 (234)
		DP	1090 (277)	978 (255)
Inverted faces	Accuracy (%)	NT	88.0 (12.9)	88.8 (13.8)
		DP	86.7 (11.2)	91.7 (8.6)
	RT (ms)	NT	928 (247)	889 (215)
		DP	991 (260)	999 (303)

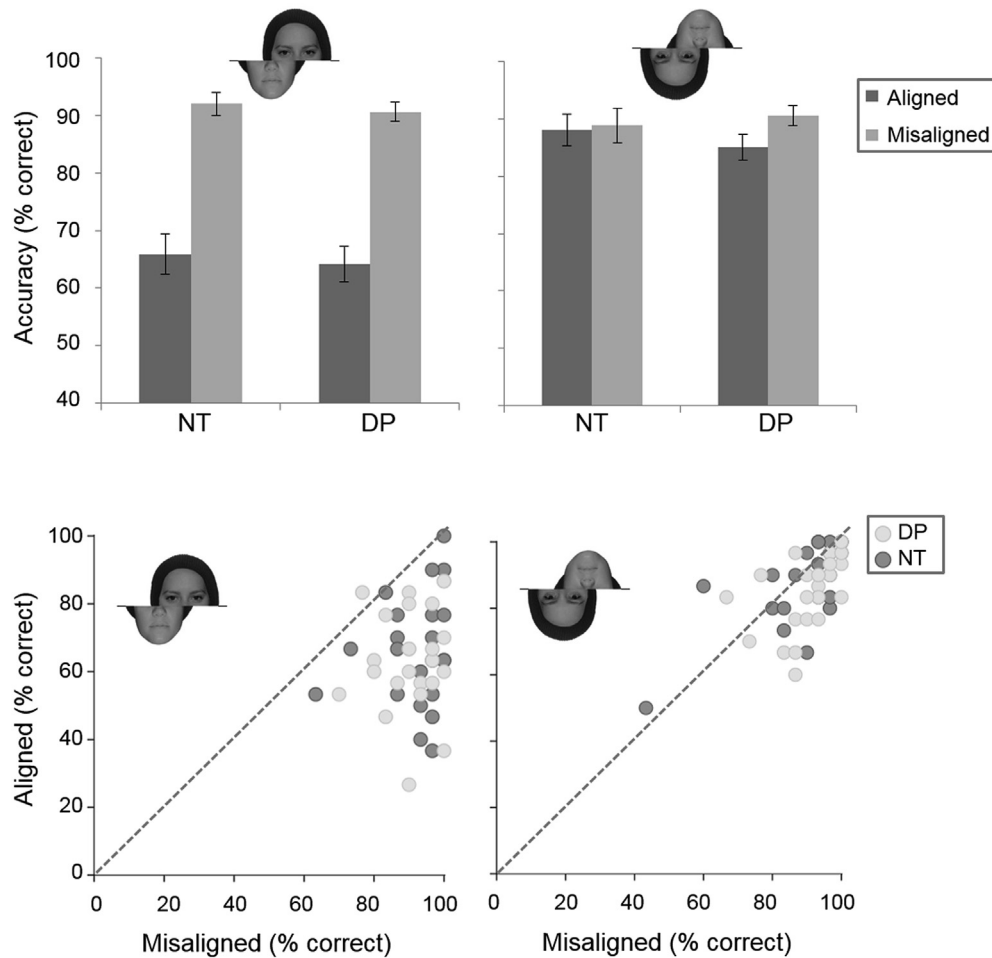
Orientation [ $F(1,44) = 30.96, p < .001, \eta^2 = .413$ ] and Alignment [ $F(1,44) = 84.33, p < .001, \eta^2 = .65$ ], as well as a highly significant Alignment  $\times$  Orientation interaction [ $F(1,44) = 75.21, p < .001, \eta^2 = .63$ ], reflecting a larger difference between aligned and misaligned trials when composites were shown upright. The main effect of Group was not significant [ $F(1,44) = .20, p = .65$ ], and neither the Group  $\times$  Orientation interaction [ $F(1,44) = .07, p = .79$ ], nor the Group  $\times$  Alignment interaction [ $F(1,44) = .61, p = .44$ ] reached significance. Most critically, however, the Orientation  $\times$  Alignment interaction did not vary as a function of Group [ $F(1,44) = .75, p = .39$ ]. As expected, controls' ability to discriminate the misaligned target regions exceeded their discrimination of the aligned targets when the faces were upright [ $t(21) = 6.95, p < .001, \text{Cohen's } d = 1.48$ ], but not when

arrangements were inverted [ $t(21) = .33, p = .75$ ]. The DPs exhibited a similar pattern, but their ability to discriminate the misaligned target regions exceeded their discrimination of the aligned targets in both the upright [ $t(23) = 7.78, p < .001, \text{Cohen's } d = 1.59$ ] and inverted [ $t(23) = 2.70, p = .013, \text{Cohen's } d = .55$ ] conditions.

Unlike controls, DPs showed an effect of alignment for inverted trials. Nevertheless, we do not believe this difference is indicative of qualitatively differently face processing. First, the Alignment  $\times$  Orientation interaction did not vary as a function of Group; both the DP and NT controls showed much larger alignment effects for upright faces than for inverted faces. Second, it is not uncommon for typical observers to show small but significant composite effects for inverted faces.<sup>4</sup> For example, [Susilo et al. \(2013\)](#) used the same inverted composite task used here and found a significant alignment effect in a large sample of typical observers ( $N = 242$ ) with a magnitude similar to that exhibited by the DPs in this experiment (Typical observers: 4.0%, DPs: 5.0% respectively).

<sup>4</sup> Composite face stimuli that include a gap of a few pixels between the target and distractor regions may be less likely to produce composite effects when arrangements are inverted ([Rossion & Retter, 2015](#)). It remains unknown how the presence or absence of this feature affects composite face processing in observers with DP. Addressing this issue in future studies of the composite effect in DP may prove worthwhile.





**Fig. 4 – Results of Experiment 2. Top panels present accuracy scores for the two groups on the upright (left) and inverted composites (right). Error bars represent  $\pm 1$  standard error of the mean. Bottom panels show accuracy scores seen for aligned composites plotted against those seen for misaligned composites, for upright faces (left) and inverted faces (right). Points lying to the right of the dashed line are indicative of typical composite effects (performance misaligned > performance aligned).**

### 7.2. Response times

The response latency data was analysed using a mixed-model ANOVA with Orientation (upright, inverted) and Alignment (aligned, misaligned) as within-subjects factors, and Group (DP, NT) as a between-subjects factor. Main effects of Orientation [ $F(1,44) = 12.71, p = .001, \eta^2 = .22$ ] and Alignment [ $F(1,44) = 22.04, p < .001, \eta^2 = .32$ ] were observed, as well as a significant Orientation  $\times$  Alignment interaction [ $F(1,44) = 21.80, p < .001, \eta^2 = .32$ ]. However, no main effect of Group was observed [ $F(1,44) = .46, p = .50$ ]. The effects of Orientation [ $F(1,44) = .60, p = .44$ ], Alignment [ $F(1,44) = 2.58, p = .12$ ], and the Orientation  $\times$  Alignment interaction failed to interact with Group [ $F(1,44) = .88, p = .35$ ].

### 7.3. Individual differences

Once again, no correlation was observed between the DPs' composite face effects ( $\Delta\text{accuracy} = \% \text{Correct}_{\text{aligned}} - \% \text{Correct}_{\text{misaligned}}$ ) seen in the upright condition and their scores on the CFMT ( $r = -.05, p = .81$ ) or CFPT ( $r = -.07, p = .77$ ). We

present the individual effects seen for the DPs and age-matched controls (Fig. 4) to illustrate that the failure to find a group difference is not due to the presence of outliers.

Some cases of developmental prosopagnosia appear to have an apperceptive profile – whereby individuals have problems forming perceptual descriptions of faces – while other cases may have selective problems with face learning or face memory (De Renzi et al., 1991). Insofar as the whole-face binding revealed by composite face effect has been characterised as a face encoding process (Murphy et al., 2017; Rossion, 2013), it is possible that susceptibility to the composite face effect is reduced only in apperceptive cases of DP. We took advantage of the large sample size employed in Experiment 2 to examine this possibility in more detail. The DPs were split into apperceptive ( $N = 12$ ) and non-apperceptive ( $N = 12$ ) subgroups. Members of the apperceptive subgroup performed at least 2 SDs below the mean of the comparison sample on the CFPT. Contrary to the foregoing speculation, however, we found no difference in the size of the composite effects ( $\Delta\text{accuracy}$ ) exhibited by the subgroups in the upright [ $t(22) = .324, p = .749$ ] or inverted [ $t(22) = .273,$

$p = .787$ ] conditions. The lack of relationship between scores on the CFPT and composite effect sizes accords with previous findings with typical observers (Rezlescu et al., 2017) and DPs (Palermo et al., 2011).

## 8. Discussion

The present study assessed whether individuals with DP exhibit diminished composite face effects at the group level. Across two experiments conducted on separate samples and using different paradigms, we find no evidence for diminished composite-face effects in this population. In our first experiment, a group of 16 DPs showed typical composite face effects when tested on a simultaneous matching procedure. In our second experiment, a separate group of 24 DPs also showed typical composite face effects when tested on a sequential matching procedure. Contrary to previous reports (Avidan et al., 2011; Liu & Behrmann, 2014; Palermo et al., 2011), these findings indicate that diminished composite face effects are not a characteristic feature of DP. These results have important implications, both for our understanding of DP and for our interpretation of the composite face effect.

### 8.1. Composite face effects in developmental prosopagnosia

Our results accord with findings from previous case studies that have described typical composite face effects in individual DPs (Le Grand et al., 2006; Schmalzl et al., 2008; Susilo et al., 2010). In particular, Le Grand et al. (2006) described typical composite effects in seven out of eight DPs tested. Similarly, having tested seven family members with DP, Schmalzl et al. (2008) found typical composite effects in the four youngest cases (aged 4–40 years) and atypical composite effects only in the three oldest cases (aged 66–87 years). Interestingly, we note recent findings from typical observers suggesting that composite face effects may behave differently in samples of older adults; for example, the composite processing of older observers may be less efficient (Wiese, Kachel, & Schweinberger, 2013) and be more susceptible to general factors (Meinhardt, Persike, & Meinhardt-Injac, 2016). In contrast, our results are inconsistent with previous reports of reduced composite face effects in DP at the group level (Avidan et al., 2011; Liu & Behrmann, 2014; Palermo et al., 2011). Having examined the processing of upright and inverted face composites in 40 individuals with DP (aged 21–63 years), our results suggest most members of this population exhibit normal composite face effects. On the other hand, close examination of the previous group studies calls their conclusions into doubt.

In their first experiment, Palermo et al. (2011) found that a sample of 12 DPs were slower to name the emotion of a target region when aligned with a distractor region expressing an incongruous emotion. However, inspection of the distribution suggests this difference was strongly influenced by the results from a single DP whose aligned RTs were considerably faster than their misaligned RTs – a reversed composite effect (see Palermo et al., 2011, Fig. 5). Further complicating interpretation, neither the DPs nor the controls showed composite

effects in their error rates. In their second experiment, controls and nine DPs were required to match the top halves of face composites presented sequentially for 200 msec each. Given the short presentations, accuracy is the most critical measure of composite effects, and the DPs and controls showed clear and nearly identical composite effects in their accuracy data. The evidence for atypical composite effects cited by the authors is derived from RTs. However, the Alignment  $\times$  Group interaction seen in the RT data failed to reach significance when analysed in the standard manner ( $p > .3$ ). The group difference was only significant when adjusted for performance in the baseline misaligned condition, a point we discuss further below.

Avidan et al. (2011) reported that a sample of 14 individuals with DP showed diminished effects of alignment both in their RTs and error rates, when matching upright composites presented sequentially. The age of the DP sample is older than is typical in this literature; half the DP participants were aged 60 years or older (mean age = 52.5 years; range 31–79 years). Inspection of the single-case data is further complicated by the fact that aligned and misaligned trials were blocked, and completed in a different order by different DPs. Whilst this treatment may have little effect on the performance of typical observers (e.g., Le Grand et al., 2004), DPs may be prone to order effects resulting from practice, fatigue, or test anxiety. Within their DP sample, those individuals who showed weaker composite face effects showed greater local bias ( $r = .52$ ) on a compound letter task (Navon, 1977). Where observed, weaker composite face effects therefore seem to be related to wider global processing difficulties. It is possible that a subgroup exists within the DP population characterized by a global processing deficit affecting performance on composite face and compound letter tasks. However, the present results together with previous reports, suggest that this profile is relatively uncommon. For example, many DPs exhibit typical perception of global motion and Glass patterns (Le Grand et al., 2006), typical Gestalt completion (Duchaine, 2000; Duchaine et al., 2006), and process compound ‘Navon’ stimuli typically (Duchaine, Germine et al., 2007; Duchaine, Yovel et al., 2007; Schmalzl et al., 2008).

Lastly, Liu and Behrmann (2014) reported that eight DPs showed reduced composite effects for left and right face halves when tested using the complete design. However, several factors undermine our confidence in these findings. First, the three DPs with the lowest holistic processing index, exhibited surprisingly normal performance on the diagnostic tests (e.g., MN and SH had CFMT scores of 73.6% and 79.2%, and WA exhibited above average famous face recognition). Second, inspection of the composite results indicates that the DPs performed much worse in the baseline misaligned condition than the matched controls. This feature of the data suggests that the reduced composite effects described reflect problems encoding local regions rather than aberrant integration processes. Distractor halves perceived as homogenous or nondescript by prosopagnosics may afford weaker perceptual prediction, and thereby exert less illusory bias in the aligned condition, than distractor halves perceived as distinctive. In an attempt to factor in baseline differences, the authors computed a holistic processing index, where modulation in the aligned condition is expressed relative to

misaligned performance. Crucially, this measure and similar indices (see Avidan et al., 2011; Palermo et al., 2011) make unfounded assumptions about the relationship between performance in misaligned conditions and susceptibility to the composite effect; it is not clear what constitutes a “typical” composite effect where observers exhibit atypical misaligned performance.

Traditionally, it has been assumed that the face inversion (Yin, 1969), composite face (Young et al., 1987), and part-whole effects (Tanaka & Farah, 1993), reflect the operation of a single process or mechanism (Farah et al., 1998; Maurer et al., 2002; McKone & Yovel, 2009; Piepers & Robbins, 2013). However, mounting evidence suggests that individuals' susceptibility to the composite face effect not only fails to correlate with their face recognition ability, but also appears weakly related to other putative measures of holistic face processing (Rezlescu et al., 2017; Wang et al., 2012; but see; DeGutis et al., 2013). As a result, we do not wish to claim that every facet of holistic face processing is typical in DP. Given that different measures of holistic processing are unrelated or weakly correlated in the typical population, neuropsychological dissociations might also be seen in the DP population. While DPs may show typical susceptibility to the composite face effect, other effects attributed to holistic face processing may be aberrant; for example, many DPs may show diminished face inversion effects (Duchaine et al., 2006; Shah, Gaule, Gaigg, Bird, & Cook, 2015; Tree & Wilkie, 2010), absent part-whole effects for the eye region (DeGutis et al., 2012), and commonly report excessive reliance on local features for identity recognition (DeGutis et al., 2012; Shah, Gaule, Sowden et al., 2015).

It is worth noting an interesting inconsistency in the DP literature highlighted by our findings. In both experiments, our DPs showed large composite effects with upright faces yet little or no composite effects with inverted faces (see also Susilo et al., 2010). Most DPs also show better performance with upright faces than inverted faces when tasks are sensitive and performance is not affected by restrictions of range (Duchaine, Germine et al., 2007; Duchaine, Yovel et al., 2007; Garrido, Duchaine, & Nakayama, 2008). Similarly, a study comparing event-related potentials (ERPs) indicated upright and inverted Mooney faces were processed differently by DPs (Towler, Gosling, Duchaine, & Eimer, 2016). These results indicate that DPs process upright and inverted faces differently, however they are inconsistent with findings from an ERP study of face processing in DP (Towler, Gosling, Duchaine, & Eimer, 2012). In typical observers, inverted faces reliably elicit larger N170 potentials than upright faces (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Eimer, 2000; Rossion et al., 1999). A group of 16 DPs, however, showed no difference in their N170s to upright and inverted faces at the group level (Towler, Fisher, & Eimer, 2017; Towler et al., 2012). While the reason for the discrepancy between these findings is unclear, it appears that behavioural inversion effects and the N170 inversion effect are measuring different aspects of face processing.

## 8.2. Composite face effect and face recognition ability

The view that individual differences in holistic face processing, inferred from susceptibility to the composite face effect,

predict face recognition ability is widespread (DeGutis et al., 2013; Farah et al., 1998; Maurer et al., 2002; Piepers & Robbins, 2013; Richler et al., 2011). This interpretation owes much to the correlated observations that orientation inversion renders faces harder to recognise (Yin, 1969) and greatly reduces the composite face effect (Young et al., 1987). Consistent with this view, composite studies employing the congruency design have found a positive correlation between composite effects and face recognition ability (DeGutis et al., 2013; Richler et al., 2011). However, the functional significance of the composite face effect has been called into question by other studies that have found little or no correlation between typical observers' composite face effects – measured using the standard design – and their face recognition ability (Konar et al., 2010; Rezlescu et al., 2017; Wang et al., 2012). Reports of diminished composite face effects in DP (Avidan et al., 2011; Liu & Behrmann, 2014; Palermo et al., 2011) have been cited as evidence that the process responsible for the composite face effect makes a necessary contribution to face recognition ability (Murphy et al., 2017). Our findings suggest this inference is potentially misleading.

Typical composite effects in the DPs tested here, and in other cases described previously (Le Grand et al., 2006; Schmalz et al., 2008; Susilo et al., 2010), as well as evidence that some acquired prosopagnosics exhibit normal face composite effects (Finzi et al., 2016), suggest a complex relationship between susceptibility to the composite face effect and face recognition ability. Face recognition is thought to depend on a processing stream that can be fractionated at several stages (Bruce & Young, 1986). The whole-face binding indexed by the composite effect appears to be intact in individuals with DP suggesting that the locus of their impairment lies elsewhere in the face processing stream. However, the binding process revealed by the composite effect may still make a causal contribution to face recognition ability; i.e., the composite process may be necessary, but not sufficient, for typical face perception. Cases of acquired prosopagnosia have been described where face recognition deficits are associated with aberrant composite effects (e.g., Busigny et al., 2010, 2014; Ramon et al., 2009), and no neuropsychological cases have been described who show no evidence of a composite effect but normal performance on tests of face perception and face recognition.

Typical composite face effects in DP and in some cases of acquired prosopagnosia (Finzi et al., 2016; Rezlescu et al., 2012), accord with other evidence that the processes underlying the composite effect are difficult to disrupt. Photographic negation disrupts observers' ability to encode 3D face shape (Kemp, Pike, White, & Musselman, 1996), but has little effect on the strength of the composite face effect (Hole, George, & Dunsmore, 1999; Taubert & Alais, 2011). Similarly, composite effects can be seen with abstract cartoon faces that contain only schematic facial features, but bear little resemblance to naturalistic faces (Murphy et al., 2017). Moreover, several markers of face processing, notably the ability to use the internal features (Ellis, Shepherd, & Davies, 1979; Osborne & Stevenage, 2008; Young, Hay, McWeeny, Flude, & Ellis, 1985) and achieve view-point invariance (Longmore, Liu, & Young, 2008), are strongly modulated by facial familiarity. In contrast, compelling composite effects can be seen with

entirely unfamiliar faces (Hole, 1994). Together with the findings from prosopagnosia, insensitivity to negation, abstraction, and familiarity, suggest that the composite face effect is resilient and disrupted only by gross changes to the faciotype (e.g., misalignment, inversion) or catastrophic damage to the face processing stream.

### 8.3. Face composite designs

Like most previous studies of composite effects in DP (e.g., Avidan et al., 2011; Le Grand et al., 2006; Palermo et al., 2011; Schmalzl et al., 2008), we employed the standard design in both experiments, where the distractor regions always differ. There has been considerable debate about the merits of an alternate congruency design, employing a full factorial combination of target regions (same, different) and distractor regions (same, different) (Richler & Gauthier, 2014; Rossion, 2013). Some authors have suggested that congruency designs mitigate the effects of response bias (for discussion see Richler & Gauthier, 2014). However, congruency designs have been criticized because the predicted effect on congruent-different trials – where different distractor halves are paired with different target halves – is unclear (Robbins & McKone, 2007), and because the congruency design produces composite effects for stimuli that do not yield demonstrable composite illusions (Rossion, 2013). The additional trials may induce domain-general facilitation/interference effects that differ from the illusory interference seen for upright-aligned face composites (Murphy et al., 2017; Rossion, 2013). Crucially, because the standard design is thought to limit the domain-general effects of congruency, the present findings represent a conservative test of the hypothesis that composite face effects are diminished in DP. Where observed, domain-general congruency effects may be expected to attenuate a group difference arising from a face-specific deficit.

## 9. Conclusion

In summary, we have described two experiments that sought to compare the composite face effects seen in typical observers and those with DP. Having employed complementary procedures and independent samples we find convergent results: evidence of highly significant composite effects in typical controls and DP groups that were indistinguishable. Contrary to previous reports, these results suggest that the whole-face binding process indexed by the composite face effect is intact in DP, indicating that the locus of this condition lies elsewhere in the face processing stream.

## 10. Author note

FB and EW contributed equally to the work described.

## Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cortex.2017.07.018>.

## REFERENCES

- Abbas, Z. A., & Duchaine, B. (2008). The role of holistic processing in judgments of facial attractiveness. *Perception*, 37(8), 1187–1196.
- Anstis, S. (2005). Last but not least. *Perception*, 34, 237–240.
- Avidan, G., Tanzer, M., & Behrmann, M. (2011). Impaired holistic processing in congenital prosopagnosia. *Neuropsychologia*, 49(9), 2541–2552.
- Baudouin, J. Y., & Humphreys, G. W. (2006). Configural information in gender categorisation. *Perception*, 35(4), 531–540.
- Behrmann, M., & Avidan, G. (2005). Congenital prosopagnosia: Face-blind from birth. *Trends in Cognitive Sciences*, 9(4), 180–187.
- Behrmann, M., Avidan, G., Marotta, J. J., & Kimchi, R. (2005). Detailed exploration of face-related processing in congenital prosopagnosia: 1. Behavioral findings. *Journal of Cognitive Neuroscience*, 17(7), 1130–1149.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8, 551–565.
- Biotti, F., & Cook, R. (2016). Impaired perception of facial emotion in developmental prosopagnosia. *Cortex*, 81, 126–136.
- Biotti, F., Gray, K. L. H., & Cook, R. (2017). Impaired body perception in developmental prosopagnosia. *Cortex*, 93, 41–49.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433–436.
- Bruce, V., & Young, A. W. (1986). Understanding face recognition. *British Journal of Psychology*, 77, 305–327.
- Busigny, T., Joubert, S., Felician, O., Ceccaldi, M., & Rossion, B. (2010). Holistic perception of the individual face is specific and necessary: Evidence from an extensive case study of acquired prosopagnosia. *Neuropsychologia*, 48(14), 4057–4092.
- Busigny, T., Van Belle, G., Jemel, B., Hosen, A., Joubert, S., & Rossion, B. (2014). Face-specific impairment in holistic perception following focal lesion of the right anterior temporal lobe. *Neuropsychologia*, 56, 312–333.
- Calder, A. J., Young, A. W., Keane, J., & Dean, M. (2000). Configural information in facial expression perception. *Journal of Experimental Psychology: Human Perception and Performance*, 26(2), 527–551.
- Carbon, C. C., Grüter, T., Weber, J. E., & Lueschow, A. (2007). Faces as objects of non-expertise: Processing of Thatcherised faces in congenital prosopagnosia. *Perception*, 36(11), 1635–1645.
- Cook, R., & Biotti, F. (2016). Developmental prosopagnosia. *Current Biology*, 26(8), R312–R313.
- Dalrymple, K. A., Elison, J. T., & Duchaine, B. (2017). Face-specific and domain-general visual processing deficits in children with developmental prosopagnosia. *Quarterly Journal of Experimental Psychology*, 70(2), 259–275.
- De Renzi, E., Faglioni, P., Grossi, D., & Nichelli, P. (1991). Apperceptive and associative forms of prosopagnosia. *Cortex*, 27(2), 213–221.
- 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.
- DeGutis, J., Cohan, S., & Nakayama, K. (2014). Holistic face training enhances face processing in developmental prosopagnosia. *Brain*, 137(Pt 6), 1781–1798.
- DeGutis, J., Wilmer, J., Mercado, R. J., & Cohan, S. (2013). Using regression to measure holistic face processing reveals a strong link with face recognition ability. *Cognition*, 126(1), 87–100.
- Duchaine, B. (2000). Developmental prosopagnosia with normal configural processing. *NeuroReport*, 11(1), 79–83.
- Duchaine, B., Germine, L., & Nakayama, K. (2007). Family resemblance: Ten family members with prosopagnosia and

- within-class object agnosia. *Cognitive Neuropsychology*, 24(4), 419–430.
- 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. (2006a). 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., & Nakayama, K. (2006b). Developmental prosopagnosia: A window to content-specific face processing. *Current Opinion in Neurobiology*, 16, 166–173.
- Duchaine, B., Parker, H., & Nakayama, K. (2003). Normal recognition of emotion in a prosopagnosic. *Perception*, 32(7), 827–838.
- Duchaine, B., Yovel, G., Butterworth, E., & Nakayama, K. (2006). Prosopagnosia as an impairment to face-specific mechanisms: Elimination of the alternative hypotheses in a developmental case. *Cognitive Neuropsychology*, 23(5), 714–747.
- 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.
- Eimer, M. (2000). Effects of face inversion on the structural encoding and recognition of faces – evidence from event-related brain potentials. *Cognitive Brain Research*, 10, 145–158.
- Eimer, M., Gosling, A., & Duchaine, B. (2012). Electrophysiological markers of covert face recognition in developmental prosopagnosia. *Brain*, 135(Pt 2), 542–554.
- Ellis, H. D., Shepherd, J. W., & Davies, G. M. (1979). Identification of familiar and unfamiliar faces from internal and external features: Some implications for theories of face recognition. *Perception*, 8, 431–439.
- Engfors, L. M., Jeffery, L., Gignac, G. E., & Palermo, R. (2017). Individual differences in adaptive norm-based coding and holistic coding are associated yet each contributes uniquely to unfamiliar face recognition ability. *Journal of Experimental Psychology: Human Perception and Performance*, 43(2), 281–293.
- Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. N. (1998). What is “special” about face perception? *Psychological Review*, 105(3), 482–498.
- Finzi, R. D., Susilo, T., Barton, J. J. S., & Duchaine, B. (2016). The role of holistic face processing in acquired prosopagnosia: Evidence from the composite face effect. *Visual Cognition*, 24(4), 304–320.
- Garrido, L., Duchaine, B., & Nakayama, K. (2008). Face detection in normal and prosopagnosic individuals. *Journal of Neuropsychology*, 2(1), 119–140.
- Gray, K. L. H., Bird, G., & Cook, R. (2017). Robust associations between the 20-item prosopagnosia index and the Cambridge face memory test in the general population. *Royal Society Open Science*, 4(3), 160923.
- Hole, G. (1994). Configurational factors in the perception of unfamiliar faces. *Perception*, 23(1), 65–74.
- Hole, G., & George, P. (2011). Evidence for holistic processing of facial age. *Visual Cognition*, 19(5), 585–615.
- Hole, G., George, P. A., & Dunsmore, V. (1999). Evidence for holistic processing of faces viewed as photographic negatives. *Perception*, 28(3), 341–359.
- Humphreys, K., Avidan, G., & Behrmann, M. (2007). A detailed investigation of facial expression processing in congenital prosopagnosia as compared to acquired prosopagnosia. *Experimental Brain Research*, 176(2), 356–373.
- Kemp, R., Pike, G., White, P., & Musselman, A. (1996). Perception and recognition of normal and negative faces: The role of shape from shading and pigmentation cues. *Perception*, 25(1), 37–52.
- Kennerknecht, I., Grüter, T., Welling, B., Wentzek, S., Horst, J., Edwards, S., et al. (2006). First report of prevalence of non-syndromic hereditary prosopagnosia (HPA). *American Journal of Medical Genetics*, 140A(15), 1617–1622.
- Kennerknecht, I., Ho, N. Y., & Wong, V. C. N. (2008). Prevalence of hereditary prosopagnosia (HPA) in Hong Kong Chinese population. *American Journal of Medical Genetics*, 146A(22), 2863–2870.
- Konar, Y., Bennett, P. J., & Sekuler, A. B. (2010). Holistic processing is not correlated with face-identification accuracy. *Psychological Science*, 21(1), 38–43.
- Le Grand, R., Cooper, P. A., Mondloch, C. J., Lewis, T. L., Sagiv, N., de Gelder, B., et al. (2006). What aspects of face processing are impaired in developmental prosopagnosia? *Brain and Cognition*, 61(2), 139–158.
- Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2004). Impairment in holistic face processing following early visual deprivation. *Psychological Science*, 15(11), 762–768.
- Liu, T. T., & Behrmann, M. (2014). Impaired holistic processing of left-right composite faces in congenital prosopagnosia. *Frontiers in Human Neuroscience*, 8, 750.
- Lobmaier, J. S., Bölte, J., Mast, F. W., & Dobel, C. (2010). Configural and featural processing in humans with congenital prosopagnosia. *Advances in Cognitive Psychology*, 6, 23–34.
- Longmore, C. A., Liu, C. H., & Young, A. W. (2008). Learning faces from photographs. *Journal of Experimental Psychology: Human Perception and Performance*, 34, 77–100.
- Lundqvist, D., Flykt, A., & Öhman, A. (1998). *The Karolinska directed emotional faces – KDEF*. CD ROM from department of clinical neuroscience, psychology section. Karolinska Institutet, ISBN 91-630-7164-9.
- Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences*, 6(6), 255–260.
- McConachie, H. R. (1976). Developmental prosopagnosia. A single case report. *Cortex*, 12(1), 76–82.
- McKone, E., Davies, A. A., Darke, H., Crookes, K., Wickramaryatne, T., Zappia, S., et al. (2013). Importance of the inverted control in measuring holistic face processing with the composite effect and part-whole effect. *Frontiers in Psychology*, 4(33), 1–21.
- McKone, E., & Yovel, G. (2009). Why does picture-plane inversion sometimes dissociate the perception of features and spacing in faces, and sometimes not? Toward a new theory of holistic processing. *Psychonomic Bulletin & Review*, 16(5), 778–797.
- Meinhardt, G., Persike, M., & Meinhardt-Injac, B. (2016). The composite effect is face-specific in young but not older adults. *Frontiers in Aging Neuroscience*, 8, 187.
- Murphy, J., Gray, K. L. H., & Cook, R. (2017). The composite face illusion. *Psychonomic Bulletin & Review*, 24(2), 245–261.
- Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology*, 9(3), 353–383.
- Osborne, C. D., & Stevenage, S. V. (2008). Internal feature saliency as a marker of familiarity and configural processing. *Visual Cognition*, 16, 23–43.
- 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.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Piepers, D. W., & Robbins, R. A. (2013). A review and clarification of the terms “holistic,” “configural,” and “relational” in the face perception literature. *Frontiers in Psychology*, 3(559), 1–11.

- Ramon, M., Busigny, T., & Rossion, B. (2009). Impaired holistic processing of unfamiliar individual faces in acquired prosopagnosia. *Neuropsychologia*, 48(4), 933–944.
- Rezlescu, C., Pitcher, D., & Duchaine, B. (2012). Acquired prosopagnosia with spared within-class object recognition but impaired recognition of degraded basic-level objects. *Cognitive Neuropsychology*, 29(4), 325–347.
- Rezlescu, C., Susilo, T., Wilmer, J. B., & Caramazza, A. (2017). The inversion, part-whole, and composite effects reflect distinct perceptual mechanisms with varied relationship to face recognition. *Journal of Experimental Psychology: Human Perception and Performance*. <http://dx.doi.org/10.1037/xhp0000400>.
- Richler, J. J., Cheung, O. S., & Gauthier, I. (2011). Holistic processing predicts face recognition. *Psychological Science*, 22(4), 464–471.
- Richler, J. J., & Gauthier, I. (2014). A meta-analysis and review of holistic face processing. *Psychological Bulletin*, 140(5), 1281–1302.
- Robbins, R., & McKone, E. (2007). No face-like processing for objects-of-expertise in three behavioural tasks. *Cognition*, 103(1), 34–79.
- 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., Delvenne, J. F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., et al. (1999). Spatio-temporal localization of the face inversion effect: An event-related potentials study. *Biological Psychology*, 50, 173–189.
- Rossion, B., & Retter, T. L. (2015). Holistic face perception: Mind the gap! *Visual Cognition*, 23(3), 379–398.
- Russell, R., Duchaine, B., & Nakayama, K. (2009). Super-recognizers: People with extraordinary face recognition ability. *Psychonomic Bulletin & Review*, 16(2), 252–257.
- Schmalzl, L., Palermo, R., & Coltheart, M. (2008). Cognitive heterogeneity in genetically based prosopagnosia: A family study. *Journal of Neuropsychology*, 2(Pt 1), 99–117.
- Shah, P., Gaule, A., Gaigg, S. B., Bird, G., & Cook, R. (2015a). Probing short-term face memory in developmental prosopagnosia. *Cortex*, 64, 115–122.
- Shah, P., Gaule, A., Sowden, S., Bird, G., & Cook, R. (2015b). The 20-item prosopagnosia index (PI20): A self-report instrument for identifying developmental prosopagnosia. *Royal Society Open Science*, 2(6), 140343.
- Stollhoff, R., Jost, J., Elze, T., & Kennerknecht, I. (2011). Deficits in long-term recognition memory reveal dissociated subtypes in congenital prosopagnosia. *PLoS One*, 6(1), e15702.
- Susilo, T., & Duchaine, B. (2013). Advances in developmental prosopagnosia research. *Current Opinion in Neurobiology*, 23, 423–429.
- Susilo, T., McKone, E., Dennett, H., Darke, H., Palermo, R., Hall, A., et al. (2010). Face recognition impairments despite normal holistic processing and face space coding: Evidence from a case of developmental prosopagnosia. *Cognitive Neuropsychology*, 27(8), 636–664.
- 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), 14.
- Susilo, T., Wright, V., Tree, J. J., & Duchaine, B. (2015). Acquired prosopagnosia without word recognition deficits. *Cognitive Neuropsychology*, 32(6), 321–339.
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology*, 46(2), 225–245.
- Taubert, J., & Alais, D. (2011). Identity aftereffects, but not composite effects, are contingent on contrast polarity. *Perception*, 40(4), 422–436.
- Torfs, K., Vancleef, K., Lafosse, C., Wagemans, J., & de-Wit, L. (2014). The Leuven Perceptual Organization Screening Test (L-POST), an online test to assess mid-level visual perception. *Behavior Research Methods*, 46(2), 472–487.
- 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., Gosling, A., Duchaine, B., & Eimer, M. (2012). The face-sensitive N170 component in developmental prosopagnosia. *Neuropsychologia*, 50(14), 3588–3599.
- Towler, J., Gosling, A., Duchaine, B., & Eimer, M. (2016). Normal perception of Mooney faces in developmental prosopagnosia: Evidence from the N170 component and rapid neural adaptation. *Journal of Neuropsychology*, 10(1), 15–32.
- Townsend, J. T., & Ashby, F. G. (1978). Methods of modeling capacity in simple processing systems. In J. C. F. Restle (Ed.), *Cognitive theory* (Vol. 3, pp. 200–239). Hillsdale, N.J.: Erlbaum.
- Tree, J. J., & Wilkie, J. (2010). Face and object imagery in congenital prosopagnosia: A case series. *Cortex*, 46(9), 1189–1198.
- Wang, R., Li, J., Fang, H., Tian, M., & Liu, J. (2012). Individual differences in holistic processing predict face recognition ability. *Psychological Science*, 23(2), 169–177.
- Wiese, H., Kachel, U., & Schweinberger, S. R. (2013). Holistic face processing of own-and other-age faces in young and older adults: ERP evidence from the composite face task. *NeuroImage*, 74, 306–317.
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, 81(1), 141–145.
- Young, A. W., Hay, D. C., McWeeny, K. H., Flude, B. M., & Ellis, A. W. (1985). Matching familiar and unfamiliar faces on internal and external features. *Perception*, 14, 737–746.
- Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception*, 16(6), 747–759.