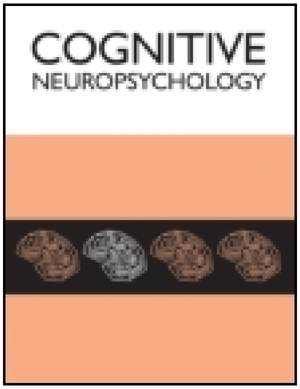

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Because holistic processing is a hallmark of normal face recognition, we ask whether such processing is reduced in developmental prosopagnosia (DP), and, if so, what the sources are of this deficit. Existing literature provides a mixed picture, with face inversion effects showing consistent holistic processing deficits but unable to locate their source and with some composite face studies showing reduced holistic processing and some not. We addressed this issue more thoroughly with a very large sample of DPs ($N = 38$) performing the part–whole task, a well-accepted measure of holistic processing that allows for the separate evaluation of individual face parts. Contrary to an expected overall reduction in holistic processing, we found an intact holistic advantage for the mouth and a complete absence of a holistic advantage for the eye region. Less severely impaired prosopagnosics showed significantly more holistic processing of the mouth, suggesting that holistic processing can aid them in recognizing faces.

Keywords: Developmental prosopagnosia; Holistic face processing; Part–whole task.

Face processing is distinct from general object processing in several ways, not only in the cognitive operations recruited but also in its neural substrates. One mechanism that consistently differs between object and face processing is that face components are more integrated into a global/holistic structure than are components of objects. Though definitions of this holistic processing vary (e.g., Farah, Wilson, Drain, & Tanaka, 1998; Garner, 1974; Richler, Tanaka, Brown, & Gauthier, 2008), holistic processing for faces has been commonly described as the simultaneous integration of parts and configural

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information into a single coherent visual representation (Rossion, 2008; Tanaka & Farah, 1993). Evidence suggests that in neurotypical individuals, greater holistic face processing abilities are associated with better face recognition (DeGutis, Wilmer, Mercado, & Cohan, 2013; Richler, Cheung, & Gauthier, 2011; Wang, Li, Fang, Tian, & Liu, 2012) and that holistic face processing underlies better visual short-term memory for faces than for objects (Curby & Gauthier, 2007).

Developmental prosopagnosia (DP)[1] is a disorder defined by severe lifelong face identification deficits with otherwise intact intellectual function. Developmental prosopagnosics (DPs) typically present with deficient face perceptual abilities that lead to subsequent impairments with encoding, consolidating, and recognizing faces (Duchaine & Nakayama, 2006a). Though a popular notion in both past and recent literatures in acquired prosopagnosia is that prosopagnosics' perceptual difficulties are rooted in deficits with holistic face processing (for example, Farah, Wilson, Drain, & Tanaka, 1995; Ramon, Busigny, & Rossion, 2010), the specific nature of holistic face processing deficits in both acquired and developmental prosopagnosia remains to be determined. In this paper, we review the evidence for holistic face processing deficits in DPs and, using a much larger DP sample than is typically studied ($N = 38$), conduct a study that aims to better characterize the source of these deficits.

Holistic face processing: Definitions and demonstrations

All definitions of holistic face processing have in common the idea that the whole of the face, its global structure determined by the spatial relations among its components, is greater than the sum of its parts (Tanaka & Farah, 1993; Yovel, Paller, & Levy, 2005). Though face theorists generally agree on this definition, what comprises this holistic representation continues to be debated. For example, researchers differ in their views of the contribution of feature shape and the spacing between features to the holistic representation (Rossion, 2008; Yovel, 2009).

In addition to the structure of the holistic representation, the importance of holistic processing in face perception relative to other operations (e.g., parts-based processing) is also currently under debate. One view suggests that holistic processing plays a dominant role in face processing, overshadowing explicit representations of discrete facial features (Rossion, 2008; Tanaka & Farah, 1993). Evidence for this comes from the difficulty, when imagining a familiar face, of conjuring up an image of just a single feature without the whole face. Correspondingly, empirical studies have found that feature changes within the context of the face are easier to detect than when features are shown in isolation (part–whole effect, see Figure 1 and below). In contrast to this view, others have suggested that holistic processing and parts processing of faces occur simultaneously and independently, with both being important to face perception (Bartlett & Searcy, 1993; Ingvalson & Wenger, 2005). Still, other face theorists believe that holistic face processing refers more to the integration of internal features and is distinct from the process of distinguishing the subtle spacing between features (i.e., second-order relations; Diamond & Carey, 1986; Maurer, Le Grand, & Mondloch, 2002). These researchers suggest that both holistic processing and computing second-order relations are important aspects of face perception.[2] Though these theories of face perception differ in their

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[1] We use the inclusive term developmental prosopagnosia instead of the more specific term congenital prosopagnosia, because we cannot rule out that prosopagnosia was caused by developmental abnormalities. We exclude individuals with acute brain damage from our definition of developmental prosopagnosia.

[2] However, holistic processing and computing second-order relations may not be independent processes. The enhanced ability to judge the spacing between features in faces could be a direct consequence of these features being efficiently combined into a holistic representation (e.g., Farah et al., 1998; Rossion, 2008). In other words, making feature spacing judgements is easier for faces because holistic processing allows one to consider multiple features at once.

emphasis of the role of holistic processing, they all agree that holistic processing is a major contributor to what makes face processing distinct from other types of visual processing.

Three widely used tasks demonstrate holistic face processing: the face inversion task (Yin, 1969), the composite face task (Young, Hellawell, & Hay, 1987), and the part–whole task (Tanaka & Farah, 1993; see Figure 1). Indicating that they measure phenomena specific to faces, each task has shown effects for upright faces that are either qualitatively or quantitatively different from those seen with objects and inverted faces (McKone & Robbins, 2007; Rossion, 2008; Sekuler, Gaspar, Gold, & Bennett, 2004). First, it had long been known that presenting a face upside-down makes it dramatically more difficult to discriminate and recognize (Attneave & Olson, 1967; Kohler, 1940), but Yin (1969) was the first to show that inversion affects the recognition of faces more so than object categories. Some evidence exists for inversion effects with objects of expertise, such as when dog experts view upright and inverted dogs (Diamond & Carey, 1986; Xu, Liu, & Kanwisher, 2005) and when novices are trained to become experts on novel objects (Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002), but these effects have not been replicated by others and are typically much smaller than those found with faces

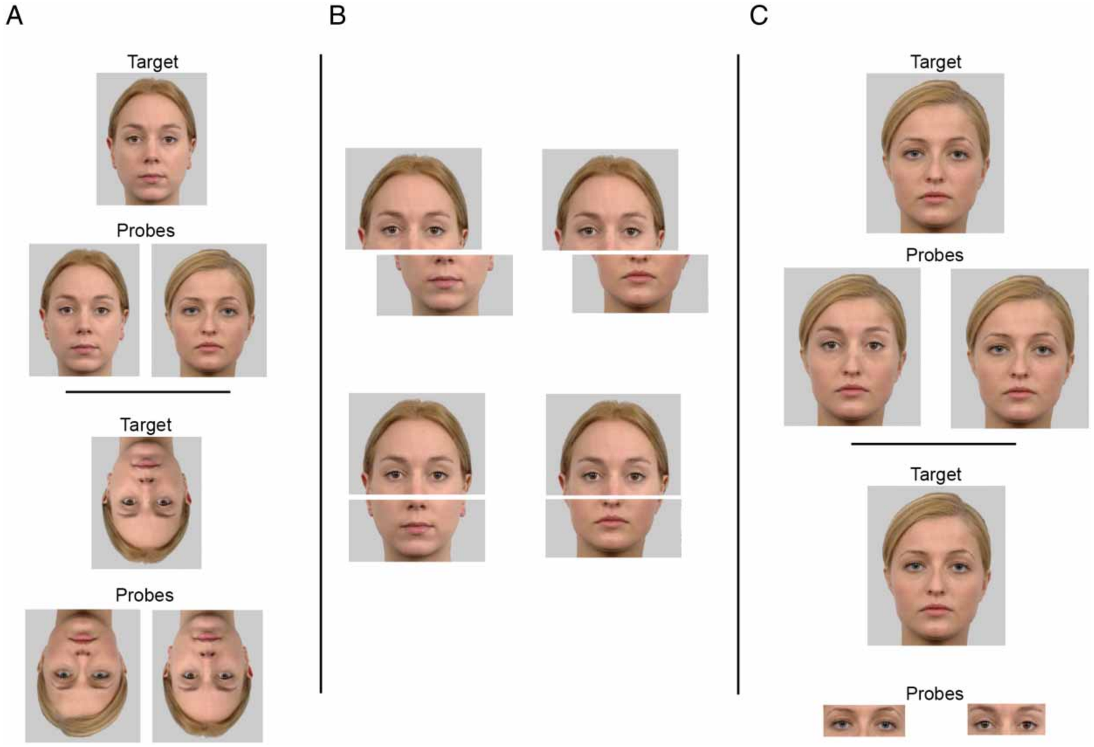

Figure 1. *A. Example of face inversion effect. It is much easier to match the target face to one of the probe faces when stimuli are upright than when they are inverted. B. Example of composite effect. The top halves of faces are the same while the bottom halves are different. When faces are misaligned, it is much easier to tell the top halves of the faces are the same than when the top halves are aligned with the different bottom halves. C. Example of the part–whole effect. It is much easier to match the eyes of the probe faces to the target face when the eyes are shown in the context of the whole face than when they are shown in isolation. Faces are from the Radboud Faces Database. Langner, O., Dotsch, R., Bijlstra, G., Wigboldus, D.H.J., Hawk, S.T., & van Knippenberg, A. (2010). Presentation and validation of the Radboud Faces Database.* Cognition & Emotion, 24*, 1377–1388.*

(Robbins & McKone, 2007). Consistent inversion effects have been shown for bodies, though not headless bodies (Yovel, Pelc, & Lubetzky, 2010), calling into question whether the body inversion effect reflects holistic processing. Thus, inversion effects are seen as a hallmark of face-specific processing, are generally thought to reflect orientation-specific holistic processing (Rossion, 2008; except for bodies, Yovel et al., 2010), and are commonly used to evaluate whether other effects are specific to upright faces. The second demonstration of holistic processing is the composite face task (Young et al., 1987). In the most commonly used version, subjects are slower and less accurate to say that the top halves of two sequentially presented faces are the same when aligned with different bottom halves, compared to when the halves are misaligned (Hole, 1994). Composite effects are absent with objects and inverted faces (Macchi Cassia, Picozzi, Keufner, Bricolo, & Turati, 2009; Robbins & McKone, 2007; Rossion, 2008). Composite effects have been reported for objects of expertise (Wong, Palmeri, & Gauthier, 2009), but these effects are substantially smaller than those typically found with faces. Finally, holistic processing of faces has also been demonstrated by using the part–whole task (Tanaka & Farah, 1993). In this task, subjects are about 10% more accurate in recognizing the identity of a feature (e.g., Larry's nose) when it is presented in the context of the entire face (e.g., Larry's face with Larry's nose versus Bob's nose) rather than as an isolated feature (Larry's nose versus Bob's nose). Though researchers have shown a similar whole-over-part superiority effect for recognizing objects (i.e., object superiority effect, Davidoff & Donnelly, 1990) and body parts (Seitz, 2002), it is not found for all object categories (e.g., houses) or inverted faces, and the holistic advantage is much larger and more consistently observed for faces (Tanaka & Farah, 1993, for example, compare Experiments 1 and 2 in Seitz, 2002).

Though these tasks and their variants provide much of what we empirically know about holistic face processing, there have also been more recent behavioural demonstrations of holistic face processing, including investigations of whether right and left face halves are processed independently or interactively (Yovel et al., 2005) and the utilization of gaze-contingent masking (Van Belle, De Graef, Verfaillie, Rossion, & Lefevre, 2010). In the latter method, participants' gaze location is used to change the visual task in real time. Van Belle and colleagues (2010) found that when a small mask covers the participants' gaze location they show a marked impairment in discriminating inverted faces but are not impaired at upright faces, probably from integrating other information around the masked portion in the upright faces.

Recent functional magnetic resonance imaging (MRI) and electroencephalography (EEG) studies have also provided neural evidence for holistic face processing (Andrews, Davies-Thompson, Kingstone, & Young, 2010; Jacques & Rossion, 2009; Schiltz, Dricot, Goebel, & Rossion, 2010). Andrews and colleagues (2010) showed that changing only the external or only the internal features produced as much release from adaptation in the fusiform face area as changing the entire face, suggesting that internal or external feature changes affect the neural processing of faces as much as if unique individuals were being presented. Similarly, using EEG, Jacques and Rossion (2009) found that when observers experienced the composite face illusion (erroneously perceiving two physically identical top halves of faces as being different because of being paired with different bottom halves), there was a release from adaptation in the right hemisphere N170, similar to when they were shown two unique faces. This release from adaptation in an early brain potential is consistent with behavioural evidence that holistic face processing is a rapid, bottom-up process (Todorov, Loehr, & Oosterhof, 2010). Together these demonstrations provide robust evidence for holistic face processing and its recruitment of specialized face mechanisms.

Holistic face processing in prosopagnosia

Both acquired and developmental prosopagnosics commonly complain that they are unable to grasp the "whole" face, and, correspondingly, several face theorists posit that deficient holistic face processing is fundamental to prosopagnosia (Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010; Farah et al., 1998; Ramon et al., 2010). Researchers, for example, have described the experience of acquired prosopagnosia as an inability to integrate the features of a complex patterned display in order to arrive at a global perception of a face (Davidoff, Matthews, & Newcombe, 1986), as an impairment in integrating local part information with information about global shape (Riddoch & Humphreys 1987), and as having a reduced perceptual field for faces (Ramon et al., 2010). Though there exists good evidence that holistic processing is deficient in cases of acquired prosopagnosia (Busigny et al., 2010, Ramon et al., 2010), evidence for holistic processing deficits in DPs is incomplete and inconsistent, and the source(s) of whatever holistic processing impairments exist in DPs remains poorly understood. Strategic differences between DPs and controls on holistic processing tasks and the heterogeneity of DPs as a population (Le Grand et al., 2006; Minnebusch, Suchan, Ramon, & Daum, 2007) are probably obscuring the picture. Below we review the evidence for holistic processing deficits in DPs, focusing on the three traditional, well-characterized tests of holistic face processing. We restrict our review to holistic processing during face identity discrimination, since there are few reports measuring DPs' holistic processing abilities with other types of facial information such as gender and emotion (though see DeGutis, Chatterjee, Mercado, & Nakayama, 2012; Palermo et al., 2011).

Face inversion effect in developmental prosopagnosia

The face inversion effect was the first holistic processing task to be studied in prosopagnosia and has the greatest number of reports (see Table 1). In controls, countless variants of face inversion tasks have been performed (for reviews, see McKone & Yovel, 2009; Rhodes, Brake, & Atkinson, 1993; Rossion, 2008; Valentine 1988), with the typical effect being reduced accuracy with inverted faces, most often interpreted as face-specific holistic processing mechanisms not being engaged (for other interpretations of the face inversion effect, see Rhodes et al., 1993). In our review of the DP face inversion literature, we included studies where we could separately assess performance on upright and inverted conditions (e.g., excluded Rivolta, Palermo, Schmalzl, & Williams, 2012) and where ceiling/floor effects were not clearly problematic (e.g., floor effect in Susilo et al., 2010; ceiling effects in Righart & de Gelder, 2007). As can be seen from Table 1, reduced inversion effects in DPs compared to controls are found in 11 out of 14 studies examined. In all of these studies, controls exhibited robust inversion effects in accuracy, reaction times (RTs), or both. These reduced inversion effects in DPs occur across both simultaneous (Behrmann, Avidan, Marotta, & Kimchi, 2005) and sequential matching tasks (Nunn, Postma, & Pearson, 2001); with face part changes (de Gelder & Rouw, 2000), whole face changes (Avidan, Tanzer, & Behrmann, 2011), and feature spacing changes (Schmalzl, Palermo, & Coltheart, 2008); when blocking (nearly all the studies) or interleaving inverted and upright trials (Duchaine, Yovel, Butterworth, & Nakayama, 2006); and on accuracy (Lee, Duchaine, Wilson, & Nakayama, 2010) or reaction time measures (Behrmann, et al., 2005). These reduced inversion effects probably result from DPs receiving less of a benefit when processing upright faces, but another potential contributor could be that some DPs have an advantage over controls in processing inverted faces (for examples: Avidan et al., 2011; Behrmann et al., 2005; Duchaine, Murray, Turner, White, & Garrido, 2009), possibly due to compensatory enhanced parts-based processing in some DPs. Two of the three studies that show mixed results (some DPs have similar inversion effects to those of controls while the others show reduced effects), as well as two of the three studies that find significant but reduced inversion effects, use the Cambridge Face Perception Test (CFPT). Perhaps strategic

Table 1. *A summary of face inversion, composite, and part–whole studies with developmental prosopagnosics and comparison of performance between developmental prosopagnosics and controls*

Study	N	*Task*	*Results*	*ACC effect controls*	*ACC effect DPs*	*HP?*
Inversion						
de Gelder & Rouw (2000)	1 (M)	Simultaneous and sequential matching task, upright & inverted blocked, 2AFC; target frontal view, test 3/4 view. Exp. 1 - whole faces; Exp. 2 - target stim = wholes; test stim = parts	Exp. 1 - sim: no effects in ACC or RT. seq: evidence of inversion effect in ACC, and trend for RT. Exp. 2 - sim: evidence of inversion superi-orty effect in ACC, not RT. seq: no effects in ACC, trend for RT.	Exp. 1: .08/.26 Exp. 2: .02/.00	Exp. 1: .06/.22 Exp. 2: −.32/.04	No
Nunn et al. (2001)	1 (M)	Sequential matching task, upright & inverted mixed, 2AFC, unlimited duration, faces vs. houses	No inversion effects in ACC. RT not reported.	.38	−.10	No
Behrmann et al. (2005)	5 (2F)	Simultaneous matching task, upright & inverted blocked, 2AFC	ACC: no inversion effects; RT: inversion superiority effect	.18	.03	No
Duchaine et al. (2006)	1 (M)	Sequential matching task, upright & inverted mixed, 2AFC, target frontal view, test 3/4 view	No inversion effects in ACC or RT.	.34	−.03	No
Le Grand et al. (2006)	8 (4F)	Sequential Jane Task: same/different; featural, contour and eye spacing changes, upright & inverted blocked	Significant inversion effects for all three sets, larger for spacing than featural or contour. RT effect for spacing.	.42/.18/.18	.12/.14/.13	Yes <
Duchaine et al. (2007)	10 (7F)	CFPT upright & inverted	Significant but smaller inversion effect in ACC. RT not reported.	.30	.16	Yes <
Schmalzl et al. (2008)	4 (2F) A,D,H,C	Simultaneous Jane Task: same/different: configural spacing changes; upright & inverted blocked	All subjects showed no inversion effect in accuracy. RT not reported.	.41	.1	No
Garrido et al. (2008)	14 (10F)	CFPT upright & inverted	Significant but smaller inversion effect in ACC. RT not reported.	.30	.18	Yes <
Van den Stock et al. (2008)	3 (1F)	Simultaneous matching task, upright & inverted blocked, 2AFC; target frontal view, test 3/4 view. Exp. 1 - whole faces; Exp. 2 - target stim = wholes; test stim = parts	Ceiling effects in Controls and DPs in ACC. 2/3 DPs were slower for inverted than upright, while 1 DP was slower for upright than inverted.	Exp. 1: .04 Exp. 2: .02	Exp. 1: .09 Exp. 2: −.05	Mixed
Duchaine et al. (2009)	2 (M)	CFPT upright & inverted	1 subject showed no inversion effect, other showed inversion superi-ority effect. RT not reported.	.30	.10	No

(*Continued overleaf*)

Table 1. *Continued*

Study	N	*Task*	*Results*	*ACC effect controls*	*ACC effect DPs*	*HP?*
Russell et al. (2009)	26 (14F)	CFPT upright & inverted	Range of ACC results showing normal, lessened, and no inversion effects. RT not reported.	n/a	n/a	Mixed
Lee et al. (2010)	3 (2F)	CFPT upright & inverted	ACC: 2 subjects show normal inversion effects (evidence suggests 1 shows smaller effect than controls), 1 no inversion effect. RT not reported.	.28	−.15	Mixed
Tree & Wilkie (2010)	4 (2F)	CFMT upright & inverted	No inversion effects in ACC. RT not reported.	.33	.08	No
Avidan et al. (2011)	14 (11F)	Simultaneous matching task, upright & inverted blocked, 2AFC	ACC: no inversion effects. RT: no inversion effects (6 subjects showed inverted inversion effects).	.07	.07	No
Composite						
Le Grand et al. (2006)	8 (4F)	Partial design, sequential matching	7/8 subjects showed composite effect in ACC and RT.	−.56	−.49	Yes =
Schmalzl et al. (2008)	4 (2F)	Partial design: simultaneous matching task	ACC not reported. RT results show lack of composite effect for 3/4 subjects.	–	–	Mixed
Susilo et al. (2010)	1 (F)	Exp. 1 - Speeded naming task, sequential, upright & inverted; Exp. 2 - Partial design, sequential, adult stimuli, upright & inverted; Exp. 3 - Partial design, sequential, child stimuli, upright only	Exp. 1 - ACC: No results. RT: normal composite effect for upright, no effect for inverted. Exp 2 - ACC: normal composite effect for upright, none with inverted. No RT results. Exp. 3 - ACC: Normal effect.	Exp. 1: – Exp. 2: ~ −.24 Exp. 3: ~ −.18	Exp. 1: – Exp. 2: ~ −.14 Exp. 3: ~ −.42	Yes =
Avidan et al. (2011)	14 (11F)	Partial design, sequential matching	No composite effects in ACC or RT.	−.19	−.03	No
Palermo et al. (2011)	12 (8F)	Partial design, sequential matching	No ACC results reported. RT Results show but significant composite effect.	−.21	−.24	Yes <
Part Whole						
DeGutis et al. (2011)	5 (3F)	2AFC, Caucasian male & Korean female stim, blocked	Part advantage on Korean faces; no holistic advantage on Caucasian faces	.18	.04	No

Note: DP = developmental prosopagnosics. ACC = accuracy. RT = reaction time. M = male. F = female. CFMT = Cambridge Face Memory Test. CFPT = Cambridge Face Perception Test. HP = holistic processing. 2AFC = two-alternative forced-choice test. A, D, H, C = subjects in the study by Duchaine et al. (2007). <, = indicates the magnitude of DPs' holistic processing in relation to controls.

differences between this task and the others, such as to where DPs attend, could explain these mixed results (for more about this, see Discussion).

Interestingly, 8 out of 14 studies demonstrate no inversion performance decrement, providing no evidence of holistic face processing in these DPs. Furthermore, 4 of these 8 studies show results where DP performance is actually better with inverted faces than with upright faces (i.e., inversion superiority: Avidan et al., 2011; Behrmann et al., 2005; de Gelder & Rouw, 2000; Duchaine et al., 2009). However, the four inversion superiority effects reported should be interpreted with caution. These effects are found in only one task in each study and found only with RTs in Behrmann et al. (2005) and Avidan et al. (2011). In fact, de Gelder and Rouw (2000) only found an inversion superiority effect in one out of their three tasks. Thus, similar to Busigny and Rossion's (2010) recent questioning of the inversion superiority effect in acquired prosopagnosics, the question still remains whether inversion superiority can be convincingly shown in DPs. However, it is evident that the majority of DP studies using face inversion show no evidence of holistic face processing.

Though DPs clearly have deficient inversion effects across a variety of paradigms, underscoring the generality of the finding, it remains unclear what leads to this deficit. For example, their deficits could conceivably arise from the inability to integrate, into a holistic face representation, the parts themselves, the spacing between parts, or the overall face shape/outer features. Thus, the results of inversion effect studies demonstrate robust holistic processing deficits in DPs but do not sufficiently characterize the precise nature of these deficits.

Composite effect in developmental prosopagnosia

Compared to the results from face inversion, studies employing the composite paradigm show a much less consistent pattern of results. Some studies show no or reduced effects relative to controls indicating reduced holistic processing, while others show completely normal performance. In four of the five studies using this task, DPs and controls judged whether two sequentially presented top halves of faces were the same or different when presented with an aligned or misaligned incongruent bottom half (i.e., partial design; similar to Hole, 1994). The remaining study (Schmalzl et al., 2008) had subjects judge two simultaneously presented composite faces. Susilo et al. (2010) also included an experiment in which a DP learned the identity of several top halves of faces over many trials and then had to judge the facial identity of the top half of faces with different bottom halves (similar to Young et al., 1987). Over the last several years, Richler et al. (2011) have provided evidence that the partial design, used in the above studies, may be confounded by response bias (responding "different" more often on incongruent aligned trials than incongruent misaligned trials; though note this criticism does not apply to Susilo et al., 2010) and that the complete design (testing for a Congruency × Alignment interaction) provides a more valid alternative. Indeed, recent work suggests that the complete design is more closely associated to face recognition ability than the partial design (Richler et al., 2011). Unfortunately, as of yet, no studies of DPs have used the complete design (though for cases of acquired prosopagnosia, see Busigny et al., 2010; Ramon et al., 2010).

Of the four studies that report accuracy results, three demonstrate that DPs have a significant composite effect, with all showing that the strength of the effect is not different from that of controls (LeGrand et al., 2006; Palermo et al., 2011; Susilo et al., 2010; though see Avidan et al., 2011). When examining reaction time in all five studies, three demonstrate that prosopagnosics have a significant composite effect (naming paradigm: Susilo et al., 2010; sequential matching: LeGrand et al., 2006; Palermo et al., 2011), with two showing performance similar to that of controls (Le Grand et al., 2006; Susilo et al., 2010) and the other showing a reduced composite effect relative to that of controls (Palermo et al., 2011). The remaining two studies show a lack of a reaction time composite effect at the group level (Avidan et al., 2011; Schmalzl et al., 2008). Highlighting the potential contribution of DP heterogeneity (see Minnebusch et al., 2007), or lack of consistency of the composite effect in this population, Le Grand et al. (2006) and Palermo et al. (2011) showed both normal and reduced composite effects, respectively, using the exact same task. Taken together, these results generally suggest preserved holistic processing mechanisms in DPs that are either equal to or slightly reduced from holistic processing mechanisms in controls (though see Avidan et al., 2011). Furthermore, Susilo et al.'s (2010) single case study provides the strongest evidence for a reliably normal composite effect in a DP, finding robust composite effects using both sequential matching tasks (with adult and children's faces) and a separate identification task, as well as demonstrating that these composite effects do not occur with inverted faces.

Holistic processing, as reflected in these composite effect results, may be inconsistent and vary across DPs, or the composite effect itself may not be the most valid measure of holistic face processing in this population. Multiple sources of evidence suggest the latter. First, within the same study, DP participants show a significantly and consistently reduced inversion effect, indicative of holistic processing deficits, while showing robust composite effects similar to those of controls (Le Grand et al., 2006). Further evidence for composite task inconsistencies in prosopagnosia comes from a well-characterized pure acquired prosopagnosic, P.S. P.S. has clearly demonstrated robust holistic processing deficits on the part–whole task (Ramon et al., 2010) and several face inversion tasks, as well as gaze-contingent masking tasks (Van Belle et al., 2010). In contrast, when performing the composite task partial design for top and bottom halves, in both versions P.S. showed a normal composite effect in accuracy and a present but slightly reduced effect in RT (though this could be from a speed/accuracy trade-off). Furthermore, when performing a separate complete design composite task, P.S. showed results quite challenging to interpret—substantially *better* performance on aligned incongruent trials (typically the condition with the lowest performance) than on the other trial types. It is difficult to think of a theoretically plausible mechanism that would produce such a result. Together, this casts some doubt on the validity of the composite task as a measure of holistic processing in prosopagnosics. One reason for this could be that prosopagnosics take a different strategic approach to the composite task than do controls, which produces holistic-like effects in the absence of normal holistic processing. For example, prosopagnosics could be attending to the nose region of the upper half of the face, which could receive interference from the lower part of the nose when the bottom half of the face is aligned. Using a measure of holistic processing, such as the part–whole task, that does not cut across features and that separately measures holistic processing effects for each feature (eyes, nose, mouth) may potentially yield more consistent results and better localize DPs' holistic processing deficits.

Part–whole effect in developmental prosopagnosia

Though there is the least amount of data from DPs on the part–whole task (only one report using the standard version, DeGutis, DeNicola, Zink, McGlinchey, & Milberg, 2011), out of the three traditional holistic processing measures it may have the most potential in quantifying and localizing DPs' deficits. Two advantages of the part–whole task over the other measures of holistic processing are that it requires attending to all the inner components of the face at once and also that it can allow for measurement of subjects' strategy. In a standard part–whole task, the subject briefly studies a whole target face and is required to identify this face when tested on either two whole faces that differ in the eyes, nose, or mouth parts or two sets of eyes, noses, or mouths in isolation (see Figures 1C & Figure 2). As the part tested for each trial is randomized, to succeed subjects must attend to the entirety of the initial target face. One can roughly verify how subjects' attention is allocated by comparing

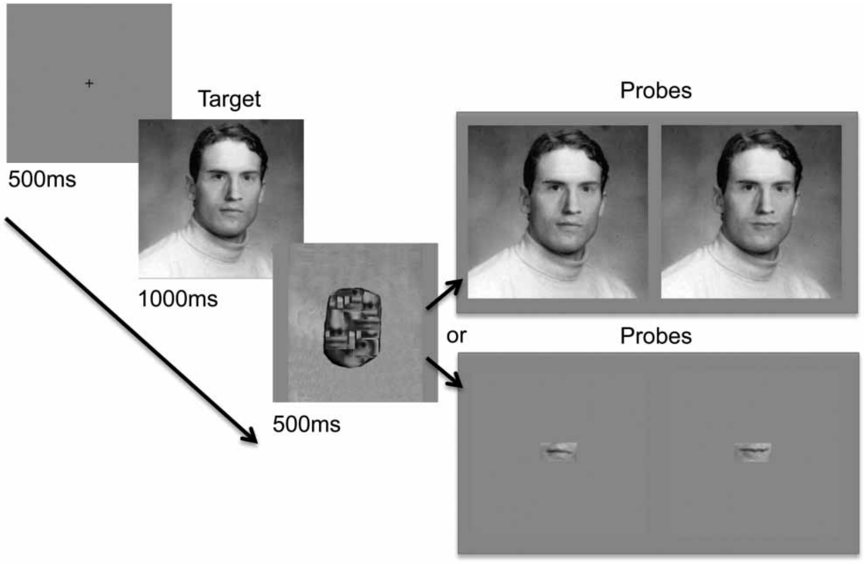

Figure 2. *Timeline of an example trial from the part–whole task. First, a fixation display is presented for 500 ms, followed by a to-be-remembered target face shown for 1,000 ms, and then a scrambled face mask is presented for 500 ms. Next, subjects must match one of the probe stimuli to the target face (indicated by pressing 1 or 2) and are tested either with isolated parts (lower) or with parts in the context of the whole face (upper). For descriptive purposes, target and probe stimuli are shown here larger than they appeared on the display screen.*

the relative accuracy on eyes, nose, and mouth part trials.

There is only one report of the standard part–whole task in a small group of Caucasian DPs (DeGutis et al., 2011), who showed a lack of a holistic advantage for both Korean and Caucasian faces (though DPs' overall holistic advantage for Caucasian faces was not significantly different from that of controls, who did show a significant advantage). De Gelder and Rouw (2000) used an incomplete variant of the part–whole task where they compared a DP's ability to discriminate between part changes in two whole faces with the ability to discriminate between part changes in two whole houses. Using both simultaneous and sequential matching presentations, they found their DP to be significantly worse at discriminating part changes in faces than controls, though the DP showed performance comparable to that of controls for discriminating part changes in houses. Though this study does not include trials in which parts are shown in isolation, it does provide indirect evidence that this DP did not receive a benefit from the context of the face when making part judgements. Additionally, in a 15-year-old prosopagnosic with congenital brain abnormalities due to hypocephalus (not technically a developmental prosopagnosic), using a simultaneous matching task Schmalzl and colleagues (Schmalzl, Palermo, Harris, & Coltheart, 2009) demonstrated normal parts discrimination ability in isolation but impaired parts discrimination ability in the context of the whole face (Van den Stock, van de Riet, Righart, & de Gelder, 2008, used a similar paradigm with three DPs, though controls were at ceiling on both part and whole conditions so the results are difficult to interpret). Similar to DeGutis et al. (2011), this provides evidence that, in prosopagnosia, the whole face context does not enhance part discrimination.

In addition to these reports, two recent studies using the part–whole task with acquired prosopagnosics (APs) are notable. Busigny et al. (2010) and Ramon et al. (2010) performed the part–whole task with two well-characterized APs that have shown holistic processing deficits on a variety of measures including gaze contingency and inversion. In their version of the part–whole task, they included eyes, nose, and mouth trials during the test, though they only assessed performance on eyes trials. Both reports found a slight part-over-whole face advantage for eyes trials, in contrast to whole-over-part advantage found in controls, suggesting that these prosopagnosics have severe holistic processing deficits, at least for the eye region. Since the eye region contains a great amount of discriminative information with regards to identity (Butler, Blais, Gosselin, Bub, & Fiset, 2010; Caldara et al., 2005; Schyns, Bonnar, & Gosselin, 2002; Vinette, Gosselin, & Schyns, 2004), a deficiency in holistic processing of the eyes may be an important contributing factor to prosopagnosics' recognition problems.

Current study

There is sufficient evidence throughout the literature to justify a basic claim that some aspect of holistic face processing differs in DPs, but the nature of this difference remains largely a mystery. The face inversion effect is consistently reduced or absent in DPs, though this could be from deficits with integrating parts, spacing between parts, or the outer facial elements into a holistic representation. In contrast to the inversion results, studies of the composite task are highly inconsistent, showing impairments in some studies on certain measures (Avidan et al., 2011; Palermo et al., 2011) and showing completely normal composite effects in others (LeGrand et al., 2006; Susilo et al., 2010). This may be due to strategic differences between DPs and controls, which could be masking their impairments in holistic processing. Finally, studies using the part–whole task show clear holistic processing deficits in DPs and APs, and, when splitting up the task into eyes/nose/mouth trials, this task has the potential to clarify the source of these holistic deficits. However, studies have yet to break up the trials in this manner, and the part–whole task has only been performed with a limited number of DPs.

In the current study, we recruited a very large sample of DPs ($N = 38$), two to three times what is typically reported in studies of DP. This not only ensured that the current findings would generalize to the rather heterogeneous DP population, but also allowed us to examine individual differences amongst DPs and measure whether the relative severity of their face recognition deficits (as measured by the Cambridge Face Memory Test) are linked to differences in holistic processing. We also broke the analysis of the part–whole task into eyes, nose, and mouth trials to determine whether patterns of holistic processing in DPs and controls differ in separate areas of the face.

Method

Control participants

A total of 38 Caucasian control participants (19 females) with an average age of 33.90 years (*SD* = 13.81) participated in experiments for compensation. All participants had normal or corrected-to-normal vision, reported having never experienced difficulties with face recognition, and scored higher than 2 standard deviations below the mean on the Cambridge Face Memory Test (CFMT; see Figure 3). Those scoring between 1.7 and 2 were also removed if their score on the part–whole task (PW, see below) was also more than 1.7 standard deviations below the mean. This resulted in removing one participant. All participants gave informed consent in compliance with the Institutional Review Boards of the VA Boston Healthcare System and Harvard University and were tested at either the VA Boston Medical Center in Jamaica Plain, MA, or the Vision Sciences Laboratory at Harvard University in Cambridge, MA. All participants had normal or corrected-to-normal vision.

Developmental prosopagnosics

A total of 38 developmental prosopagnosics (19 female) with an average age of 34.76 years (*SD* = 9.13) participated in the study (see Figure 3 and Table 2). In recruiting participants, we first began with a pool of approximately 4,500 individuals who completed a survey at www.faceblind.org and complained of face recognition problems. Based on questions that our lab has found to reflect daily-life face recognition abilities (see supplementary materials, which are available via the supplementary tab on the article's online page at

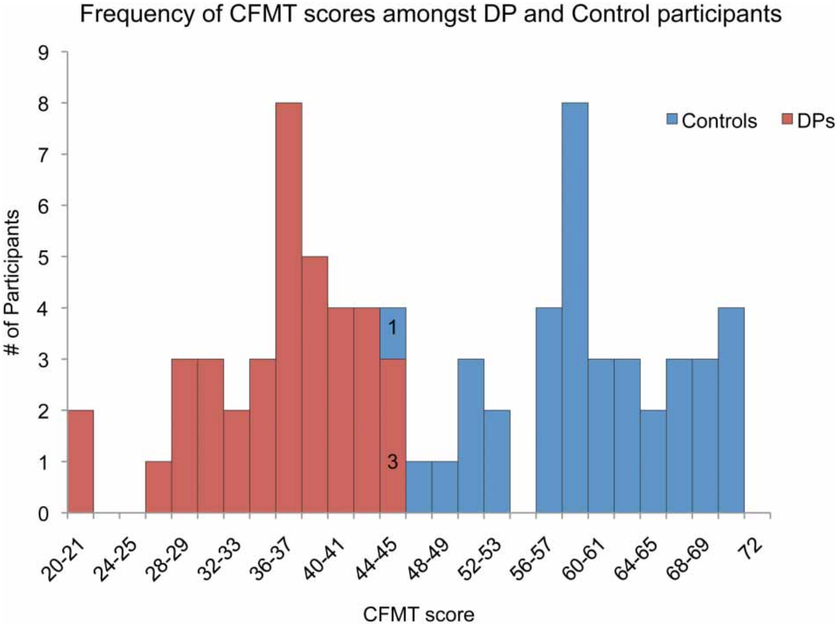

Figure 3. *Frequency of Cambridge Face Memory Test (CFMT) scores amongst DP (developmental prosopagnosics) and control participants.*

http://dx.doi.org/10.1080/02643294.2012.754745), and proximity to our lab's location in Cambridge, MA, we further filtered this pool down to 143 participants.

Next, we contacted the eligible participants via email and set up clinical interviews with those participants who responded (approximately 87), during which we characterized participants' general medical history as well as their experience of prosopagnosia. If the source of their prosopagnosia was an acquired brain injury or the source was unclear, they were excluded. This resulted in excluding one participant. Any participant who had been diagnosed with or suspected themselves of having Asperger's syndrome or autism, or who stated that they had difficulty recognizing emotions from faces, was given the Autism Spectrum Quotient questionnaire (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). Any participant who scored above a clinical cut-off of 32 on the Autism Spectrum Quotient questionnaire was excluded. This resulted in the exclusion of 8 participants. At this point we also excluded those who were no longer interested in participating in our cognitive training study (see below), approximately 29 people. Finally, to be considered a developmental prosopagnosic and included in the study, each participant had to score at least 1.7 standard deviations below the mean on the Cambridge Face Memory Test (see Figure 1).[3] This resulted in the exclusion of 4 additional participants. A total of 12 participants that made it to this point (participating in initial behavioural assessments) chose not to participate in the study because of scheduling constraints, and/or they were unwilling to complete the cognitive training protocol (see below). This process resulted in 33 participants.

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[3] We chose −1.7 standard deviations (*SD*s) for two reasons. First, we recognize the limitations of the CFMT in that some people report symptoms of severe prosopagnosia, but score close to the normal range on the CFMT. Because of this, we wanted to be slightly more inclusive than a −2.0-*SD* cut-off. Our second reason is that we wanted to examine individual differences in prosopagnosia and avoid restriction of range effects. All group effects remain significant when using a −2.0 cut-off; see supplementary materials.

Table 2. *Subject demographics, scores for the CFMT and CFPT, and accuracy scores on the FOBPT*

Subject	*Age (years)*	*Sex*	*CFMT*	*CFPT*	*Faces (%)*	*Objects (%)*	*Bodies (%)*
S1	48	M	28 (−3.78)	80 (−3.55)	65	99	75
S2	22	M	31 (−3.40)	76 (−3.22)	58	89	76
S3	35	F	37 (−2.64)	70 (−2.73)	70	90	78
S4	35	M	27 (−3.91)	80 (−3.55)	61	84	86
S5	32	M	41 (−2.14)	62 (−2.07)	56	84	73
S6	46	F	38 (−2.52)	54 (−1.42)	69	80	84
S7	24	M	40 (−2.27)	52 (−1.25)	75	94	94
S8	52	F	32 (−3.28)	92 (−4.53)	61	70	76
S9	35	F	35 (−2.90)	66 (−2.40)	68	79	64
S10	47	F	34 (−3.02)	60 (−1.91)	59	85	79
S11	44	F	21 (−4.67)	54 (−1.42)	54	94	78
S12	19	M	44 (−1.76)	52 (−1.25)	70	91	84
S13	34	M	33 (−3.15)	74 (−3.06)	80	95	85
S14	32	M	36 (−2.77)	70 (−2.73)	80	94	91
S15	49	M	29 (−3.66)	44 (−0.60)	70	93	80
S16	27	F	30 (−3.53)	72 (−2.89)	58	94	85
S17	29	F	38 (−2.49)	68 (−2.57)	76	94	86
S18	47	M	42 (−2.01)	62 (−2.07)	71	90	80
S19	35	F	29 (−3.66)	68 (−2.57)	70	89	75
S20	28	M	38 (−2.52)	58 (−1.75)	61	88	74
S21	23	M	37 (−2.64)	60 (−1.91)	70	95	89
S22	28	M	21 (−4.67)	84 (−3.88)	—	—	—
S23	28	M	34 (−3.02)	90 (−4.37)	64	93	80
S24	40	F	42 (−2.01)	80 (−3.55)	59	88	81
S25	26	M	36 (−2.77)	60 (−1.91)	68	90	78
S26	25	F	44 (−1.76)	70 (−2.73)	—	—	—
S27	35	F	44 (−1.76)	68 (−2.57)	—	—	—
S28	43	M	41 (−2.14)	60 (−1.91)	—	—	—
S29	52	M	37 (−2.64)	68 (−2.57)	—	—	—
S30	30	F	37 (−2.64)	84 (−3.88)	—	—	—
S31	33	F	38 (−2.52)	78 (−3.39)	66	92	89
S32	24	F	42 (−2.01)	38 (−.11)	56	95	70
S33	31	F	41 (−2.14)	64 (−2.23)	76	94	81
S34	39	F	31 (−3.40)	56 (−1.58)	76	90	66
S35	40	M	37 (−2.64)	76 (−3.22)	63	83	78
S36	38	F	36 (−2.77)	54 (−1.41)	63	86	88
S37	43	M	39 (−2.39)	78 (−3.38)	58	90	81
S38	23	F	42 (−2.01)	54 (−1.41)	74	94	89
Mean	34.76		35.84	66.74	66.41	89.56	80.41
SD	9.13		5.86	12.41	7.37	5.90	6.98

Notes: Raw scores for CFMT and CFPT, with *z* scores in parentheses. Accuracy scores on the FOBPT in percentages. CFMT = Cambridge Face Memory Test. CFPT = Cambridge Face Perception Test. FOBPT = Faces−Objects−Bodies Test. M = male. F = female.

These 33 DP subjects were tested online, and 5 additional DPs were tested in lab (participants reported in DeGutis et al., 2011). The 33 DP subjects tested online were part of a large web-based cognitive training study aimed at improving face processing in DPs. All but one of these subjects tested online completed a faces/objects/bodies perceptual discrimination task (from Pitcher, Charles, Devlin, Walsh, & Duchaine, 2009; see Table 2), while the in-lab DPs did not. Because of the challenge of completing the 5-week online protocol, great care was taken with each participant to ensure that they were motivated and compliant, including dozens of email exchanges and occasional phone calls. Unsurprisingly, when comparing either our entire sample of 38 DPs, or just the 33 tested online, to a separate set of 19 developmental prosopagnosic subjects tested in lab, independent *t* tests showed no significant differences in CFMT scores. Also supporting our use of a partial online sample, Wilmer et al. (2010) and Germine et al. (2012) have shown online testing to yield the same mean performance and reliability as in-lab testing.

Cambridge Face Memory Test

The Cambridge Face Memory Test (CFMT) is a widely used test of face recognition ability (Duchaine & Nakayama, 2006b) and an established method for determining the severity of DP (for more details see Duchaine & Nakayama, 2006b).

Part–whole task

The part–whole task assesses the ability to use the face context when discriminating changes in individual facial features. After encoding a target face (e.g., Roger's face), neurotypical subjects demonstrate an advantage for discriminating a feature change (e.g., discriminating Roger's nose from Ken's nose) when features are shown within the context of the target face compared to when discriminating features shown in isolation.

In the current task (from Tanaka, Kiefer, & Bukach, 2004, used with permission of Jim Tanaka, University of Victoria), target faces were created using the outline of one Caucasian male face. By inserting a combination of six different pairs of eyes, noses, and mouths (see Figure 2), six unique target faces were created. For whole trials, foil faces were created by switching one of the three facial features (eyes, nose, or mouth) with that of a different target face. For part trials, foil stimuli were an isolated facial feature (eyes, nose, or mouth) from another target face.

Each trial began with a central fixation display presented for 500 ms (see Figure 2). Next, one of the six target faces was centrally presented for 1,000 ms, and subjects attempted to encode this face. Next, a scrambled face mask was displayed for 500 ms. During the subsequent test period, participants were presented with a pair of probe images side by side, either whole faces (whole trials) or isolated features (part trials). One of these images matched the target, and the other image was a foil (therefore the proportion of foils to targets was 50/50). Stimuli remained on the screen until participants indicated with a button press which probe stimulus matched the target face (subjects responded 1 for left image, 2 for right image). For whole trials, subjects chose between the whole target face and a whole foil face, which was the same as the target face except that one of the features (eyes, nose, or mouth) was replaced with a foil feature. For part trials, subjects chose between a face part from the target face (eyes, nose, or mouth) and the same facial feature from a foil face. On a given trial, subjects had no indication on which feature they would be tested, nor did they know whether isolated features or whole faces would be shown during the test period. There were 72 trials (36 parts trials and 36 whole trials), 24 for each feature type.

Individual differences in holistic processing ability

We sought to determine whether DPs with better face recognition abilities (as measured by the CFMT) tend to process the eyes, nose, or mouth, more or less holistically. To accomplish this, in DPs and controls, we performed individual differences correlations between measures of holistic processing and CFMT scores. Previous work in our lab with normal college undergraduates has shown that holistic processing measures obtained using regression are more related to each other and to face recognition ability than holistic processing measures obtained using subtraction (see DeGutis, Wilmer, et al., 2013, for a more thorough discussion). We therefore used regression scores as our primary measure, though for completeness and ease of comparison to prior literature, we also computed subtraction scores. Both regression and subtraction scores were computed separately for overall accuracy as well as accuracy broken down by each feature.

Clearly, a person with unusually robust holistic processing should obtain a better than expected whole trial score, whereas an individual with unusually weak holistic processing should obtain a worse than expected whole trial score. The theoretical reason for favouring regression scores is that they enable a direct, data-driven approach to determining expected whole trial performance, given part trial performance. Expected whole trial performance is calculated simply as the regression line predicting whole trial scores from part trial scores across individuals. Each regression score is then computed as a residual, or signed deviation, from this line. We computed regression scores for both DPs and controls as the deviation from the control regression line because we consider control performance to be normative (see Figure 4) We therefore want to know whether, and to what degree, each individual—whether DP or control—deviates from that norm.

Subtraction scores are computed by subtracting part trials from whole trials. The theoretical reason for disfavouring subtraction scores is that they disregard the empirically observed relationship between part and whole scores that determines what wholes score should be expected for an individual with a given parts score. Statistically, this means that subtraction scores generally correlate with their parts control condition. Conceptually, this means that a correlation (or lack thereof) between the part−whole task subtraction scores and some other measure need not reflect the

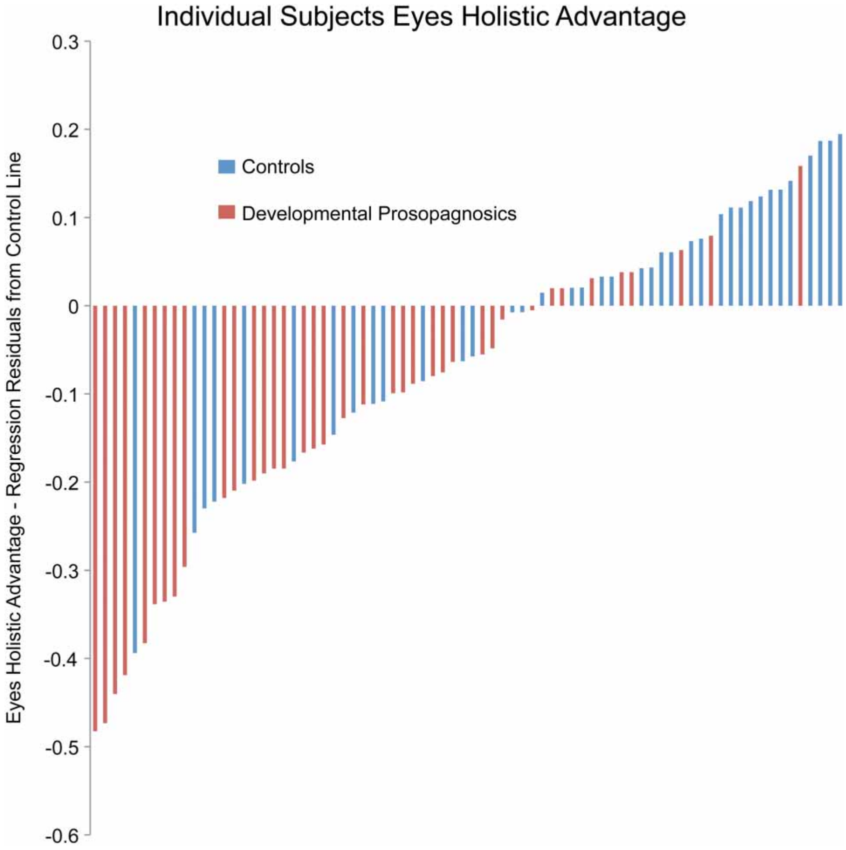

Figure 4. *Individual subject data showing regression residuals of the eyes holistic advantage, based on the regression line from the control group only. Developmental prosopagnosia participants are shown in red, while control participants are shown in blue.*

holistic processing mechanism that is theorized to enhance performance in the whole trial condition. It could instead reflect some mechanism that drives performance in the parts condition.

Results

Group characteristics

The DP group did not differ from the control group in age (DPs: $M = 34.76$ years; controls: 33.76 years), $t(74) = 0.32$, $p = .75$, and both groups had equal numbers of males and females (DPs: 19 males/19 females; controls: 19 males/19 females).

Cambridge Face Memory Test and Cambridge Face Perception Test

As can be seen by the negative *z* scores in Table 2, DPs scored substantially worse on the CFMT and CFPT than previous reported neurotypical subjects (Duchaine, Germine, & Nakayama, 2007; Duchaine & Nakayama, 2006b). Correspondingly, DPs performed significantly worse on the CFMT than did the current sample of controls (DPs: $M = 35.84$, $SD = 5.87$; controls: $M = 59.81$, $SD = 7.01$), $t(74) = 16.19$, $p < .0001$.

Part–whole task

Figure 5 summarizes our main results, comparing the performance on whole and part trials for all features combined (Figure 5a) and then for each feature separately (Figures 5b, 5c, 5d). Controls (in blue) demonstrate the classic holistic advantage, with greater accuracy on whole trials than on part trials, $t(37) = 5.25$, $p < .0001$. This holistic advantage is seen in controls when all the features are assessed

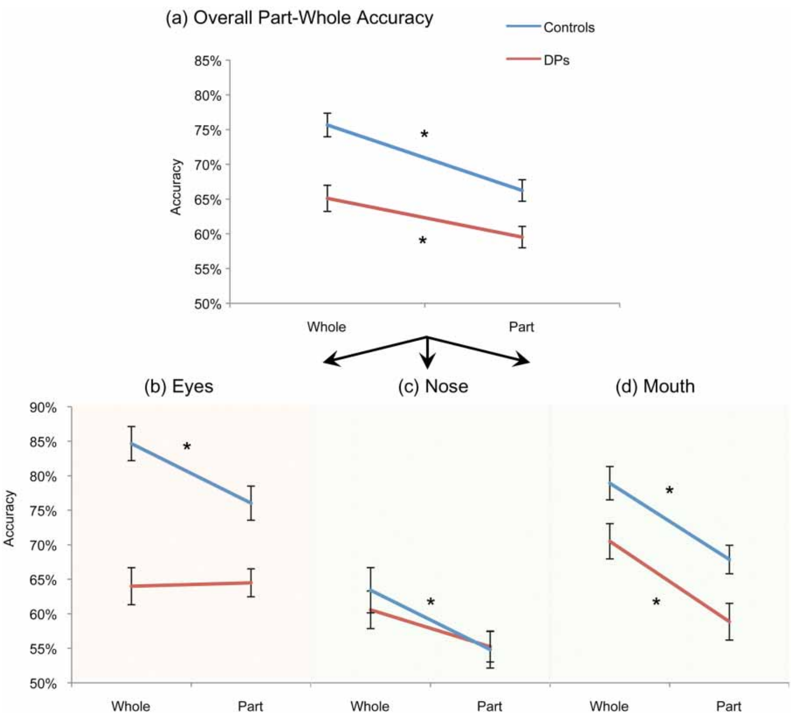

Figure 5. *Accuracy scores for whole and part trials in controls (blue lines) and developmental prosopagnosics (DPs; red lines) on the part–whole test for (a) overall score, (b) eyes trials only, (c) nose trials only, and (d) mouth trials only. Within-group comparisons significant at* p $<$ *.05 are indicated with* *.

together (Figure 5a) and when they are broken down by feature (Figures 5b, 5c, 5d): eyes, $t(37) = 3.80$, $p < .001$; nose, $t(37) = 2.09$, $p < .05$; and mouth, $t(37) = 4.11$, $p < .0005$.

Collapsing across all trials, DPs were significantly less accurate than controls, $t(74) = 4.61$, $p < .001$. However, when comparing part trials collapsed across features and whole trials collapsed across features (Figure 5a), DPs (in red) demonstrated a normal whole-over-part (holistic) advantage that was not significantly different from the control group: Group × Part/Whole interaction, $F(1, 74) = 1.78$, $p = .19$; whole versus part in DPs, $t(37) = 2.48$, $p < .05$. However, breaking down the results into the separate features indicates that regarding DPs' holistic advantage as "normal" is overstated. Instead, we see two distinct patterns of holistic processing depending on which feature of the face is considered. As demonstrated in Figures 5c and 5d, DPs demonstrate a significant holistic advantage for mouth trials, $t(37) = 3.28$, $p < .005$, and an effect that is just beyond a trend for nose trials, $t(37) = 1.63$, $p = .11$. These holistic advantages are not significantly different from those for controls: Group × Part/Whole interaction for nose, $F(1, 62) = 0.38$, $p = .54$, and mouth, $F(1, 74) = 0.02$, $p = .89$.

As can be seen in Figure 5b, eyes trials in DPs show a very different pattern. Instead of receiving a boost in accuracy when judging eye changes in whole face trials, their performance was no different from that in eyes alone (part) trials, $t(37) = 0.16$, $p = .87$. In contrast to nose and mouth trials, this pattern of results was significantly different from that for controls: Group × Part/Whole interaction, $F(1, 74) = 5.84$, $p < .05$. The comparison between individual controls' and DPs' eye results can be seen in Figure 4, in which we present the data of each individual subject ordered by their holistic advantage scores, derived from a regression approach using the control group (for the holistic advantage scores derived from subtraction and regression approaches using the entire group, see supplementary materials). It is clear that DP subjects (in red) as a group show less holistic advantage for the eye region than do the normal controls (in blue). Considering that the modest reliability of the eyes holistic advantage score (e.g., for regression, $\lambda 2 = .15$) adds a substantial amount of noise to the each score (eyes holistic advantage score = eyes holistic ability + noise in the measure), these individual results are quite consistent. In sum, the separate analysis of each facial feature demonstrates a different pattern from the overall results, with evidence of intact holistic processing in DPs for mouth and nose regions but not for the eyes.

Reaction time results are in line with the accuracy results, with DPs and controls performing similarly on mouth and nose trials, but differing on eyes trials (see Table 3). When collapsing across features, DPs showed slower RTs on whole trials than on part trials, $t(37) = 2.90$, $p < .01$. Controls showed *similar* RTs on part and whole trials, but the patterns between DPs and controls were not significantly different: Group × Part/Whole interaction, $F(1, 74) = 3.36$, $p = .71$. The pattern of DPs being slower on whole trials than on part trials but not differing from that of controls was also found for nose and mouth trials. In contrast, for eyes trials, DPs and controls showed opposing patterns of reaction time results: DPs were slower on whole trials than on part trials, while controls were faster on whole trials than on part trials: Group × Whole/Part interaction, $F(1, 74) = 5.86$, $p < .05$. This is consistent with the accuracy results and provides additional evidence that DPs, compared to controls, are disadvantaged when processing the eyes in the context of the whole face.

One explanation for DPs' slower and less accurate performance than that of controls when processing the eyes in the context of the whole face might be that DPs simply attend less to the eye region of the initial target face than do controls. Less attention to the eye region could drive down accuracy for both part and whole eyes trials. We reasoned that if, compared to controls, DPs attend less to the eyes and more to the mouth of the target face, then they should have a greater proportion of their total number of

Table 3. *Reliabilities of the Cambridge Face Memory Test, part–whole measures, and the correlations between part–whole measures and CFMT in developmental prosopagnosics*

Test	*Reliability*		*Upper bound with CFMT*	*Observed CFMT correlation*	*Corrected correlation*
CFMT	.81	(.84)	–	–	–
Part–whole face test					
Overall					
Whole	.62	(.54)	.72 (.66)	.19	.26 (.29)
Parts	.45	(.35)	.62 (.53)	−.02	−.03 (−.04)
HP subtraction	.24	(.09)	.45 (.27)	.17	.38 (.63)*
HP regression	.45	(.34)	.62 (.53)	.19	.31 (.36*)
Eyes					
Whole	.58	(.50)	.70 (.64)	.05	.07 (.08)
Parts	.44	(.36)	.61 (.54)	.09	.15 (.17)
HP subtraction	−.09	(−.27)	–	−.02	–
HP regression	.15	(.00)	.36 (—)	.01	.03 (—)
Nose					
Whole	.57	(.49)	.69 (.63)	.09	.13 (.14)
Parts	.37	(.24)	.56 (.45)	.02	.04 (.04)
HP subtraction	.44	(.33)	.61 (.52)	.06	.10 (.12)
HP regression	.57	(.49)	.69 (.63)	.09	.13 (.14)
Mouth					
Whole	.46	(.38)	.62 (.56)	.27	.44 (.48)*
Parts	.08	(−.11)	–	−.12	–
HP subtraction	−.02	(−.21)	–	.28	–
HP regression	.33	(.23)	.53 (.43)	.30	.57 (.70)*

Notes: Reliabilities are Guttman's λ2 with Cronbach's α in parentheses. Upper bound is the highest possible correlation given the reliability of the two measurements (square root of product of two reliabilities). Corrected correlation is the observed / upper bound. HP = Holistic Processing. *indicates a significant correlation (p < .05).

correct part trials being mouth trials than eye trials. We chose not to include nose part trials in this analysis because both groups were quite close to chance on these trials, and floor effects could spuriously create group differences. As can be seen in Figure 6a, controls and DPs had a similar pattern of performance across features. A Group (DPs/controls) × Feature (eyes/mouth) analysis of variance (ANOVA) demonstrated a main effect of controls performing better than DPs on part trials, $F(1, 74) = 10.62$, $p < .005$. This shows not only that DPs have impaired holistic processing, but that they are also impaired at either processing isolated face parts or allocating attention to multiple face parts in the target face. Despite this lower performance on part trials, DPs and controls performed relatively similar on eyes and mouth part trials: Group × Eyes/Mouth interaction, $F(1, 74) = 0.36$, $p = .55$. Both DPs and controls showed a significantly different pattern of performance across all three features: DPs, $F(2, 36) = 5.39$, $p < .01$; controls: $F(2, 36) = 16.37$, $p < .001$. In particular, as can be seen in Figure 6b, for both groups the largest proportion of total correct part trials was eye trials followed by mouth and nose trials. These similar proportions suggest that DPs and controls roughly allocate attention to the initial target face in a similar manner.

Associations with individual and subgroup differences in face recognition ability

Next we sought to determine whether DPs with better face recognition abilities, as measured by higher CFMT scores, process the eyes, or some

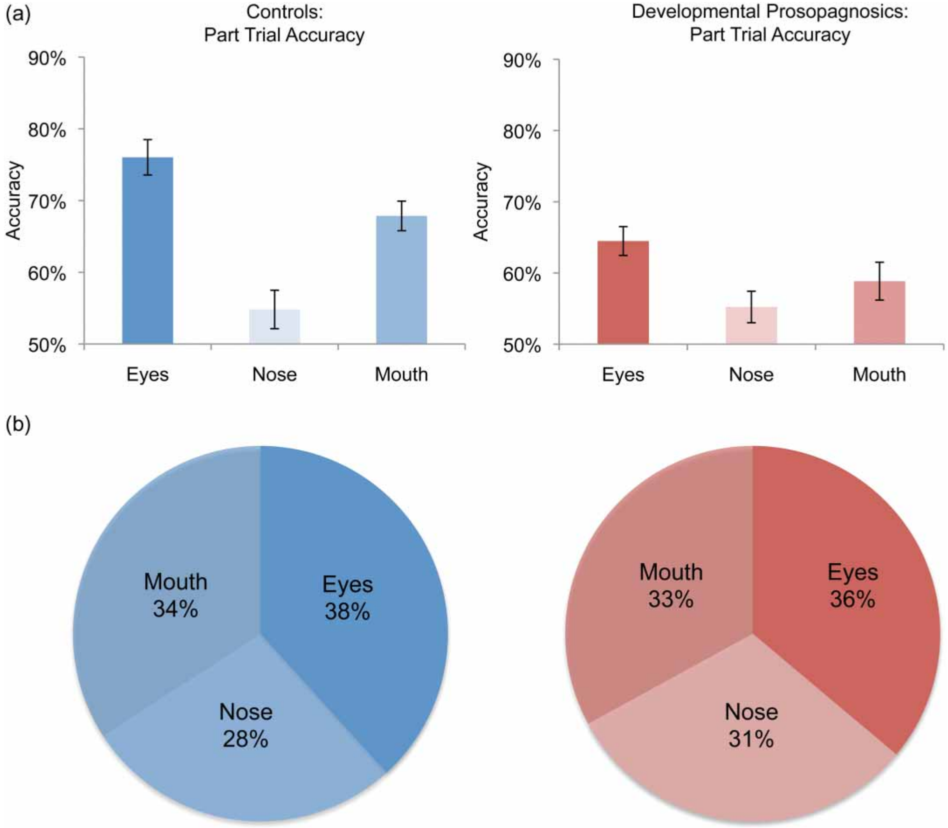

Figure 6. *(a) Accuracy on part trials in controls (blue) and developmental prosopagnosics (red) broken down by eyes, nose, and mouth. (b) Proportion of correct part trials broken down by eyes, nose, and mouth, for both groups.*

other feature, more holistically (for analysis of the CFPT in DPs, see supplementary materials). To address this issue, we used an individual differences approach where, for each DP, we calculated the overall holistic advantage and holistic advantage for each feature using both subtraction and regression approaches (see Method) and correlated these measures with DPs' CFMT scores using the Pearson product–moment correlation coefficient. To help with interpretation of these correlations by providing a measure of the upper limit of the correlation based on each test's reliability, we also calculated the reliabilities of the CFMT as well as the holistic advantage scores (see Table 4 and supplementary materials). Additionally, as a source of comparison we also performed the same analyses with controls.

As is shown in Figure 7a and Table 3, the only DP correlations with the CFMT that approached significance were the holistic mouth advantage scores: regression, $r = .30$, $p = .07$; subtraction, $r = .28$, $p = .09$. Figure 7b further exemplifies this holistic mouth advantage/CFMT relationship by splitting up the DP group based on CFMT scores into the upper and lower quartiles and middle half. The best scoring DPs clearly show a larger holistic advantage for the mouth than do the lowest and middle scoring DPs. One reason why the observed mouth holistic advantage/CFMT correlations did not reach significance is that the mouth holistic advantage scores have relatively low reliability (e.g., when using regression $\lambda^2 = .33$, see Table 4). When taking into account these low reliabilities and the upper bound

Table 4. *Part whole face test: accuracy and reaction times*

	Controls		*DP*	
Stimuli	*Percentage correct*	*Mean RT (ms)*	*Percentage correct*	*Mean RT (ms)*
Overall				
Whole	**76***	1,975	**65***	2,123
Parts	**66***	1,908	**60***	1,875
Eyes				
Whole	**85***	1,769	**64***	2,099
Parts	**76***	1,837	**64***	1,962
Nose				
Whole	63	2,243	61	2,303
Parts	55	1,998	55	1,875
Mouth				
Whole	**79***	1,912	**71***	1,974
Parts	**68***	1,888	**59***	1,791

Note: Between group comparisons significant at $p < .05$ are indicated with *.

correlations with the CFMT (highest correlation possible considering the reliabilities of the constituent tests), the link between holistic mouth processing and face recognition ability in DPs emerges as quite robust (e.g., when using regression, the corrected $r = .57$).

The specific link between greater holistic mouth processing and improved face recognition ability in DPs is particularly notable considering the pattern of results found in controls. Similar to DPs, controls demonstrated a nonsignificant correlation between overall holistic processing and CFMT (controls, $r = .13$, $p = .44$; DPs, $r = .10$, $p = .55$). These control results contrast recent reports of significant correlations between the part–whole holistic advantage and face recognition ability in younger neurotypical subjects (Wang et al., 2012; *M* age = 20.4 years; DeGutis et al., 2012, *M* age = 24.4 years). This may be due to effects of age in our current sample—older controls, *M* age = 49.1 years, showed an absence of a holistic processing/CFMT link ($r = .08$, $p = .63$), whereas our younger controls, *M* age = 24.0 years, showed a stronger association ($r = .17$, $p = .31$; see supplementary materials for more older/younger comparisons). When breaking down our entire control group results by features, we found a nonsignificant holistic advantage/CFMT correlation for the eyes ($r = .09, p = .59$), a significant correlation for the nose ($r = .37, p < .05$), and a negative correlation for the mouth ($r = -.23$, $p = .16$). Rather than indicating that the eyes holistic advantage is unrelated to face recognition ability, this nonsignificant correlation could be driven by a ceiling effect on these trials—individuals with better eye part performance who perform better on the CFMT (correlation between CFMT and eye part trials: $r = .32$, $p = .05$) have less room to demonstrate a holistic advantage. For the mouth trials, controls demonstrated that *less* holistic mouth processing related to *improved* CFMT scores ($r = -.23, p = .16$). This relationship was significantly different from that of DPs who showed that *more* holistic mouth processing was related to *improved* CFMT ($r = .28, p = .09$; significance of difference between DPs and control correlations: $z = 2.16$, $p < .05$). This suggests that holistic processing of the mouth region may provide a useful tool for recognition in DPs but not controls.

Discussion

The current results show that DPs exhibit both preserved and deficient patterns of holistic face processing. On mouth trials, DPs showed a significant holistic advantage that is nearly identical to that of controls. However, in contrast to controls who show a trend towards worse face recognition ability with greater mouth holistic processing, an individual differences analysis of DPs revealed that those who are more proficient at face recognition show more holistic processing of the mouth region. This suggests that those DPs who are able to process the mouth holistically may use that intact aspect of holistic processing to better recognize faces. In contrast to the results for the mouth, on eyes trials DPs demonstrated a complete absence of a holistic advantage. These differences in holistic processing between eyes and mouth trials could not be explained by DPs overattending to the mouth at the expense of the

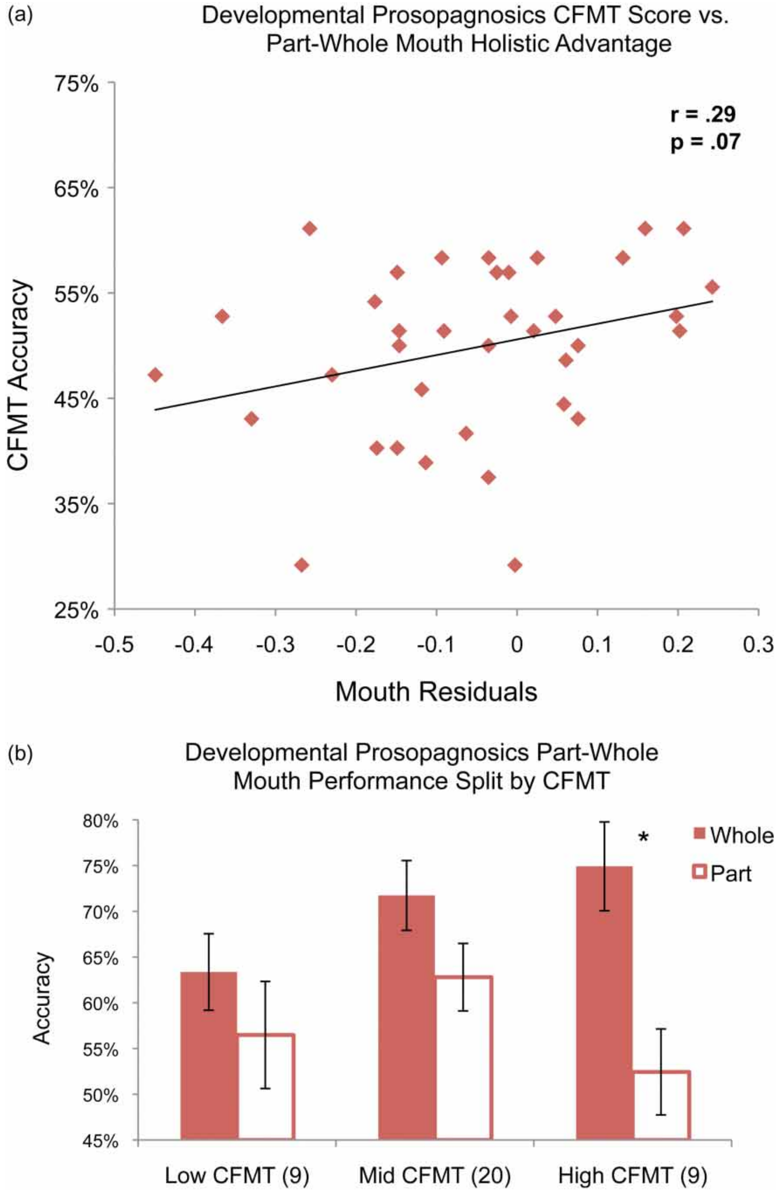

Figure 7. *(a) Correlation between accuracy on the Cambridge Face Memory Test (CFMT) and part–whole task holistic advantage residuals for mouth trials. (b) Whole and part mouth trial accuracy in developmental prosopagnosics with low CFMT (lower quartile* N*), mid CFMT (middle half* N*), and high CFMT (upper quartile* N*) scores. Significant within-group comparisons (*$p < .05$*) are indicated with *.*

eyes. Together, these results suggest that DPs possess preserved holistic processing capacity for the mouth that can facilitate some degree of face recognition, yet they have insufficient capacity to holistically process the more complex eye region. These findings with such a large sample of DPs, alongside previously reported holistic eye processing deficits in cases of acquired prosopagnosia (Busigny et al., 2010; Ramon et al., 2010), provide compelling evidence that a deficit in holistically processing the eye region is a fundamental aspect of prosopagnosia.

The current results indicating that DPs can successfully integrate the mouth, but not the eyes, into a holistic percept and that DPs use this holistic mouth information for successful face recognition contrast results of neurotypical individuals showing that they rely primarily on the eye region for successful face recognition (Butler et al., 2010). DPs' reliance on holistic mouth processing is consistent with recent findings in acquired prosopagnosia showing that successful recognition depends on processing the lower halves of faces (Barton, Cherkasova, Press, Intriligator, & O'Connor, 2003; Bukach, Le Grand, Kaiser, Bub, & Tanaka, 2008; Caldara et al., 2005). For example, in two cases of acquired prosopagnosia, Bukach and colleagues (2008) found both normal featural processing and configural processing of the mouth region (they did not assess configural processing of the nose) alongside disrupted configural and featural processing of the eyes. Additionally, in a well-studied acquired prosopagnosic, P.S., eye movement data and classification images revealed an increased reliance on the mouth during successful identification (Caldara et al., 2005), consistent with our results here that those DPs who holistically process the mouth recognize faces better than those who do not. Furthermore, this result is also consistent with a report of a DP by Barton and colleagues (2003; patient G.A., prosopagnosia possibly caused by a fall at one year of age, cardiopulmonary arrest, and coma, though MRI is normal), who showed relatively normal sensitivity to mouth position changes, though impairment when mouth and eye positions and eye brightness all changed together, perhaps distracting from the potential benefit to be gained from the mouth information. The current study extends these findings by demonstrating in a large and more representative sample of DPs that the degree to which prosopagnosics holistically process the mouth is directly related to their face recognition abilities. This not only reinforces the privileged role of the lower half of the face in prosopagnosia, but also suggests that an increased ability to integrate the mouth into a representation of the whole face may provide a useful crutch that some prosopagnosics may rely on to attenuate their face recognition difficulties.

Because there may be more useful recognition-related information in the mouth region for DPs, it is tempting to interpret the current results as implying that DPs attend more to that region. Indeed, previous AP studies have suggested that prosopagnosics may attend to the lower part of the face as a general recognition strategy (Bukach et al., 2008; Caldara et al., 2005; Orban de Xivry, Ramon, Lefevre, & Rossion, 2008). However, evidence argues that the current results are more due to DPs' limited perceptual integration abilities rather than to simply where they allocate their attention. Since for each trial participants do not know on which feature they will be tested, the proportion of eyes/nose/mouth correct parts trials can be used as a rough measure of where participants are attending. As can be seen in Figure 6b, DPs show a similar proportion of eyes/nose/mouth correct parts trials to that of controls, with eyes trials as the highest proportion correct. Even after considering that controls' generally enhanced holistic processing abilities allow them to more efficiently attend to the eyes, nose, and mouth at once (Hsiao & Cottrell, 2008; Orban de Xivry et al., 2008), the current results suggest that in this task DPs distribute their attention across features in a similar manner to that of controls (though work by Orban de Xivry and colleagues, 2008, suggests that they may make more saccades directly to specific facial features).

In contrast to the mouth results, DPs as a group consistently showed deficient holistic processing of the eye region, and their levels of holistic processing of the eye region had no relationship to their face recognition abilities. This fits well with two recent case studies of the part–whole task in APs, who similarly demonstrate a lack of holistic advantage for the eye region (Busigny et al., 2010; Ramon et al., 2010). Because the eye region has been shown to be the most diagnostic for face recognition in neurotypical individuals (Butler et al., 2010; Caldara et al., 2005; Schyns et al., 2002; Vinette et al., 2004) and because DPs demonstrate a consistent lack of holistic processing of the eye region, the current results suggest that disrupted holistic processing of the eye region may be fundamental to face recognition deficits in prosopagnosia. Considering the evidence supporting that DPs roughly attend to the entire target face in the current task, how would a lack of a holistic advantage for the eye region arise? One possibility is that when shown the target face at the beginning of the trial, DPs attempt to apply their limited holistic processing resources to the eyes, nose, and mouth. They are successful with the mouth, and possibly the nose, but because DPs are perhaps overwhelmed with the number of elements in the eye region and their configural relations (e.g., sclera/iris, eye shape, eyebrows, eye/eyebrow spacing, intraocular spacing, intraeyebrow spacing, position of eyes/eyebrows on face), they are unable to perceptually integrate this information with the rest of the face (Rossion, Kaiser, Bub, & Tanaka, 2009). Thus, when the target face disappears, DPs are left with the eye region represented in more of a non-holistic, part-based manner. This part-based representation may prevent them from receiving any benefit from seeing the eyes within the original whole face context at test.

In addition to DPs' deficient holistic advantage for the eyes, DPs consistently performed worse than controls on both eye and mouth part trials (it is challenging to interpret the nose results because both DPs and controls were so close to chance on these trials). It is notable that DPs' poor performance on mouth part trials contrasts their intact holistic advantage for the mouth. One explanation of these results, in line with a previous DP study (Yovel & Duchaine, 2006), is that DPs have a basic deficit in processing the shapes of facial features and that this deficit dissociates from their holistic processing deficits. An alternative explanation is that DPs' holistic and part deficits in the current task reflect a similar mechanism. In particular, DPs' limited holistic processing abilities compared to controls may result in a smaller perceptual field, the spatial window across which DPs are able to integrate information (see more on this below). Because of this, to encode all the features, DPs may have to shift attention between facial features in the target face more than do controls, which could reduce the time they spend encoding each facial feature and result in less detailed feature representations. Reduced mouth part trial accuracy may co-occur with an intact holistic mouth advantage because holistic processing may rely more on less detailed, lower frequency information that is distinct from the more detailed information used in part processing.

The current results and our interpretations are consistent with the theory from the AP literature that prosopagnosia is accompanied by a reduced perceptual field and, as a consequence, an inability to extract diagnostic contextual information from the eye region (Ramon & Rossion, 2010; Rossion, 2009). According to Rossion (2009), a perceptual field refers to "the area of vision where the observer can extract diagnostic visual information for the task . . . related terms could be the functional visual field or the perceptual spatial window" (p. 305). In particular, Ramon and Rossion (2010) suggest that acquired prosopagnosia is accompanied by a reduction in the spatial extent of the perceptual field during face individuation that makes it so that, in contrast to controls, they are unable to process information outside the focus of attention. Regarding the current results, it could be that DPs' spatially smaller perceptual window causes them to shift their attention to attempt to build a representation of the whole face. Perhaps because of the multiple elements in the eye region, there is not enough time for DPs to holistically process the eye region before they shift their attention to the mouth. The mouth, which is relatively less complex than the eye region, may take DPs less time to process holistically, and the time they spend attending to the mouth is sufficient to produce a holistic advantage. An alternative idea to this spatially smaller perceptual field in prosopagnosia is that there is a reduced integration capacity in a normal-sized perceptual field (i.e., across the entire face). Potentially spared whole-face integration abilities in prosopagnosics may allow them to process less complicated features (e.g., nose and mouth) in a holistic manner. This interpretation could explain why even directly cueing acquired prosopagnosics to attend to vertical spacing changes in the eye region only marginally improves their ability to perform this task (Ramon & Rossion, 2010). Thus, even with the help of directed spatial attention, the perceptual system in prosopagnosics may be unable to fully grasp the information in the eye region.

The results of current study help to clarify previous studies of holistic face processing in DPs. Studies examining the composite face effect in DPs have found both normal (Le Grand et al., 2006; Susilo et al., 2010) and reduced effects (Avidan et al., 2011; Palermo et al., 2011). According to the current findings, one explanation for the presence of significant composite effects in DPs (Le Grand et al., 2006; Susilo et al., 2010) is that they combine the to-be-ignored lower half of the face with the upper half and perceive the illusion of a different upper face because they holistically process the mouth and possibly the nose. Additionally, the current results shed light on studies showing reduced or absent composite effects in tasks that require DPs to match the upper half of the target and test face (Avidan et al., 2011; Palermo et al., 2011). It could be that because DPs have general difficulties in integrating information in the eye region, this makes them slower and less accurate on both aligned and misaligned trials. This could potentially produce a floor effect in performance and reduce DPs' composite effect compared to that of controls (see Palermo et al., 2011, and to a lesser extent Avidan et al., 2011).

In addition to providing accounts for the discrepant composite task results found in DPs, the current study also clarifies the source of DPs' consistently reported reduced (Le Grand et al., 2006) or absent (Duchaine et al., 2007) face inversion effects. In particular, the current results suggest that there may be two opposing effects at work: a lack of an inversion effect for the eye region and normal inversion effects for the mouth and potentially the nose. Which effect dominates probably depends on the nature of the stimulus changes, as well as to which facial features DPs attend. For example, when forced to discriminate faces based on vertical and horizontal eye spacing changes, DPs performed poorly on upright faces and show substantially reduced or absent inversion effects (Le Grand et al., 2006; Schmalzl et al., 2008). In contrast, for tasks in which the eyes, mouth, or nose can be used to discriminate faces such as on the CFPT, as a group DPs show more of a range of inversion effects from present to completely absent (Garrido, Duchaine, & Nakayama, 2008; Russell, Duchaine, & Nakayama, 2009). It may be that DPs who attend more to the mouth region show larger inversion effects whereas those who attend to the eye region show smaller or absent inversion effects.

As well as helping to clarify the DP holistic face processing literature, the current results also help to differentiate DP from autism spectrum disorders (ASDs), another group of developmental disorders demonstrating significant face recognition deficits. Though there is still some debate whether individuals with ASDs demonstrate holistic face processing deficits, a recent comprehensive review of the literature suggests that they *do not*, and that other mechanisms such as the representation of faces in "face space" are more consistently impaired (Weigelt, Koldewyn, & Kanwisher, 2012). In contrast to this literature review of ASDs, the current results suggest that DPs have a basic deficit in holistic face processing. For example, in the part−whole task, our finding of a complete lack of a holistic advantage for the eyes contrasts with either equivalent or greater than normal holistic advantage for the eye region found in individuals with ASDs (Faja, Webb, Merkle, Aylward, & Dawson, 2009; Joseph & Tanaka, 2003). Additionally, though anecdotal and empirical reports suggest that, unlike neurotypical individuals, both individuals with ASDs and DPs do not prefer attending to the eye region, the current results suggest that this may be for different reasons. DPs may attend more to the mouth to extract recognition-related information whereas individuals with ASDs may attend more to the mouth because they find direct eye gaze aversive (Dalton et al., 2005). Thus, though both DPs and individuals with ASDs have severe face recognition impairments, the current results suggest that they come from distinct causes.

Together, the current results shed new light on developmental prosopagnosia by using a classic holistic processing task with a large group of DPs and separately analysing the eye region, nose, and mouth. We find compelling evidence that DPs attempt to holistically process faces and, while largely successful for the mouth, are unsuccessful for the eye region. These findings are consistent with Ramon and Rossion's (2010) perceptual field model of prosopagnosia and suggest that DPs have either a spatially reduced perceptual field or a reduced perceptual integration capacity across a normal-sized perceptual field. These results also explain many of the somewhat discrepant findings in the holistic processing in prosopagnosia literature and open up new potential avenues of research.

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