

Kent Academic Repository

Full text document (pdf)

Citation for published version

Ulrich, Philip I. N. and Wilkinson, David T. and Ferguson, Heather J. and Smith, Laura and Bindemann, Markus and Johnston, Robert A. and Schmalzl, Laura (2016) Perceptual and Memorial Contributions to Developmental Prosopagnosia. *Quarterly Journal of Experimental Psychology* . ISSN 1747-0218.

DOI

<https://doi.org/10.1080/17470218.2016.1177101>

Link to record in KAR

<http://kar.kent.ac.uk/54995/>

Document Version

Author's Accepted Manuscript

Copyright & reuse

Content in the Kent Academic Repository is made available for research purposes. Unless otherwise stated all content is protected by copyright and in the absence of an open licence (eg Creative Commons), permissions for further reuse of content should be sought from the publisher, author or other copyright holder.

Versions of research

The version in the Kent Academic Repository may differ from the final published version.

Users are advised to check <http://kar.kent.ac.uk> for the status of the paper. **Users should always cite the published version of record.**

Enquiries

For any further enquiries regarding the licence status of this document, please contact:

researchsupport@kent.ac.uk

If you believe this document infringes copyright then please contact the KAR admin team with the take-down information provided at <http://kar.kent.ac.uk/contact.html>



Perceptual and Memorial Contributions to Developmental Prosopagnosia

Philip I N Ulrich, David T Wilkinson, Heather J Ferguson, Laura Smith, Markus Bindemann, Robert A Johnston & Laura Schmalzl

To cite this article: Philip I N Ulrich, David T Wilkinson, Heather J Ferguson, Laura Smith, Markus Bindemann, Robert A Johnston & Laura Schmalzl (2016): Perceptual and Memorial Contributions to Developmental Prosopagnosia, *The Quarterly Journal of Experimental Psychology*, DOI: [10.1080/17470218.2016.1177101](https://doi.org/10.1080/17470218.2016.1177101)

To link to this article: <http://dx.doi.org/10.1080/17470218.2016.1177101>



Accepted author version posted online: 15 Apr 2016.



[Submit your article to this journal](#)



[View related articles](#)



[View Crossmark data](#)

Publisher: Taylor & Francis & The Experimental Psychology Society

Journal: *The Quarterly Journal of Experimental Psychology*

DOI: 10.1080/17470218.2016.1177101

Perceptual and Memorial Contributions to Developmental Prosopagnosia

Philip I N Ulrich¹, David T Wilkinson¹, Heather J Ferguson¹, Laura Smith¹, Markus
Bindemann¹, Robert A Johnston¹, and Laura Schmalzl²

¹ University of Kent, England, UK

² Department of Family Medicine and Public Health, University of California San Diego, CA,
USA

Correspondence concerning this article should be addressed to:

Philip I N Ulrich, School of Psychology, Keynes College, University of Kent, Canterbury,
Kent, CT2 7NP, United Kingdom.

Telephone: +44 (0) 1227 827427

Fax: +44 (0) 1227 827030

Email: pinu5@kent.ac.uk

This work was partly supported by British Academy Grant SG102500 awarded to D.T.W.
and H.J.F.

Word count (excluding abstract, references and figure captions): 8,050

Abstract

Developmental prosopagnosia (DP) is commonly associated with the failure to properly perceive individuating facial properties, notably those conveying configural or holistic content. While this may indicate that the primary impairment is perceptual, it is conceivable that some cases of DP are instead caused by a memory impairment, with any perceptual complaint merely allied rather than causal. To investigate this possibility, we administered a battery of face perception tasks to 11 individuals who reported that their face recognition difficulties disrupt daily activity and who also performed poorly on two formal tests of face recognition. Group statistics identified, relative to age- and gender-matched controls, difficulties in apprehending global-local relations and the holistic properties of faces, and in matching across viewpoints, but these were mild in nature and were not consistently evident at the level of individual participants. Six of the 11 individuals failed to show any evidence of perceptual impairment. In the remaining five individuals, no single perceptual deficit, or combination of deficits, was necessary or sufficient for poor recognition performance. These data suggest that some cases of DP are better explained by a memorial rather than perceptual deficit, and highlight the relevance of the apperceptive/associative distinction more commonly applied to the allied syndrome of acquired prosopagnosia.

Keywords: face blindness, perception, memory, individual differences

Perceptual and Memorial Contributions to Developmental Prosopagnosia

Prosopagnosia is characterised by a difficulty in recognising people by their facial appearance in the absence of visual, sensory or general intellectual impairment (see Bate, 2012). Initial case reports featured individuals whose symptoms could be attributed to an acquired brain injury, often involving occipital-temporal cortex (Barton, 2008; Barton & Cherkasova, 2003; Barton, Press, Kennan, & O'Connor, 2002; Damasio, Tranel, & Damasio, 1990; Davies-Thompson, Pancaroglu, & Barton, 2014; Gainotto & Marra, 2011). Since the 1970s there have been increasing reports of cases that appear to be developmental in origin, showing no structural lesion (though see Garrido et al., 2009 for evidence of subtle changes in grey matter volume) and seemingly evident from the early years of life (e.g., Temple, 1992; Kracke, 1994; Ariel & Sadeh, 1996; Bentin, Deouell, & Soroker, 1999; Grueter et al., 2007; Avidan, Tanzer, & Behrmann, 2011; Rivolta, Palermo, Schmalzl, & Coltheart, 2012). Both acquired and developmental prosopagnosia (DP) show a relatively high co-occurrence with difficulties in object identification (Behrmann, Avidan, Marotta, & Kimchi, 2005; Gauthier, Behrmann, & Tarr, 1999) and poor navigational skill (De Haan & Campbell, 1991; Duchaine, Parker, & Nakayama, 2003; Jones & Tranel, 2001). However, while there is evidence to suggest that the symptoms of acquired prosopagnosia can stem primarily from an apperceptive deficit, which refers to a difficulty in integrating physical characteristics to form a face percept, or an associative deficit, which is a post-perceptual difficulty in linking the face percept to relevant semantic information (Dalrymple et al., 2011; De Renzi, 1986; De Renzi, Faglioni, Grossi, & Nichelli, 1991; Tippett, Miller, & Farah, 2000), the distinction is not always clear. This is even less so in DP as most reported cases are accompanied by some type of perceptual impairment. Here we report the results of a group study in which no single perceptual deficit was either necessary or sufficient for DP to occur. In the majority of cases,

no perceptual deficit was apparent at all. These observations support the idea that there is an isolable memorial component in DP.

Most studies of DP report allied perceptual impairment. A deficit is most commonly identified in recovering configural or holistic information. This is typically inferred by an unusual inversion effect, which normally reflects an advantage for identifying faces that are upright rather than upside-down, or a composite effect, which reflects an advantage for identifying the top half of a face when this is horizontally offset with the bottom half of another face than when the two are aligned. Both advantages are frequently absent in prosopagnosia (Avidan et al., 2011; Behrmann et al., 2005; Lee, Duchaine, Wilson, & Nakayama, 2009; Le Grand et al., 2006; Nunn, Postma, & Pearson, 2001; Palermo et al., 2011; Schmalzl, Palermo, & Coltheart, 2008). Lower-level deficits associated with the recovery of first-order relations, such as those capturing the familiar configuration of the eyes, nose and mouth (Garrido, Duchaine, & Nakayama, 2008), and the apprehension of global-local hierarchical levels (as tested with Navon compound letters; Navon, 1977) (Avidan et al., 2011; Behrmann et al., 2005; Schmalzl et al., 2008) have also been reported.

Perhaps unsurprisingly, more general tests of face perception, such as the Cambridge Face Perception Test (Avidan et al., 2011; Chatterjee & Nakayama, 2012; Dingle, Duchaine, & Nakayama, 2005; Duchaine, Germine, & Nakayama, 2007), face matching paradigms (Ariel & Sadeh, 1996; Behrmann et al., 2005; Humphreys, Avidan, & Behrmann, 2007; Lee et al., 2009; Nunn et al., 2001) and matching across viewpoint (Behrmann et al., 2005; Duchaine, 2000; Duchaine et al., 2006; Lee et al., 2009; Schmalzl et al., 2008), that are not designed to isolate a particular type of processing (such as the recovery of first- or second-order relations), also unveil impairment. These perceptual deficits are sometimes accompanied by problems apprehending emotional expression (Ariel & Sadeh, 1996; De Haan & Campbell, 1991; Duchaine et al., 2006; Garrido et al., 2009; Kracke, 1994;

Minnebusch, Suchan, Ramon, & Daum, 2007), age (Ariel & Sadeh, 1996; De Haan & Campbell, 1991; Kracke, 1994), gender (Ariel & Sadeh, 1996, De Haan & Campbell, 1991, Duchaine et al., 2006), and attractiveness (Duchaine et al., 2006; Le Grand et al., 2006), although it is unclear whether these latter problems are purely perceptual in nature.

At first glance, these findings might be taken as evidence that DP is perceptual in origin, with impaired recall arising because faces are not adequately encoded at the level of the structural description. However, close examination of the published data indicates that there is considerable variability in the perceptual deficits reported (Avidan et al., 2011; Stollhoff et al., 2011). For example, despite frequent reports of a deficit in configural processing, this is not always present (Duchaine, 2000; Le Grand et al., 2006). Even family members with congenital prosopagnosia do not show consistent patterns of perceptual deficits (Schmalzl et al., 2008). This raises the question as to whether, on one hand, DP has multiple perceptual origins or, on the other hand, some (or all) of the perceptual deficits co-occur with a memory impairment but do not cause difficulties in face recognition *per se*. Given the relatively small number of individuals with DP who have been investigated with this aim and the lack of uniform assessment, it is still difficult to decide between these alternatives.

Evidence for the idea that memory deficits can occur independently of perceptual impairments is limited to only a few studies. Two of these (Dalrymple, Garrido, & Duchaine, 2014; McKone et al., 2011) reported a memory impairment with intact face perception. Dalrymple and colleagues showed this dissociation in five of sixteen adult participants while McKone and colleagues showed it in four of the six tested. However, face perception was only assessed via the Cambridge Face Perception Test (CFPT; Duchaine, Germine, & Nakayama, 2007) which, despite its widespread use (Bowles et al., 2009), may not fully capture and differentiate subtle but relevant perceptual deficits (see e.g., Chatterjee &

Nakayama, 2012; and DPs F30a and M29 in Garrido, Duchaine, & Nakayama, 2008). More compelling evidence was reported by Lee et al. (2009), who administered a test battery to three family members classified as DP. The father showed characteristically low scores on the most widely used tests for prosopagnosia, the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006) and a famous faces recognition task, both of which are predominantly memory based. However, he showed normal performance on all five perception tests, including the CFPT (Duchaine, Germine, & Nakayama, 2007), face detection, emotional expression recognition (from eyes alone), and matching across viewpoint. Although suggestive of a memory impairment, the study did not report, except in in one experiment (the face detection task), whether his normal accuracy scores were accompanied by normal reaction times. This is problematic because some cases of prosopagnosia are better characterised by slowed rather than inaccurate responding (Delvenne, Seron, Coyette, & Rossion, 2004; Gauthier, Behrmann, & Tarr, 1999).

The aim of the present study was to cast further light on the role of perceptual and memory factors in DP. Specifically, we wanted to investigate whether some cases of DP are more likely memorial than perceptual in origin. Of course, the value of any such investigation rests on the detail and diversity of the test battery administered. To assess face memory, we utilised the two most commonly used tests: (1) the CFMT which probes the ability to learn new faces, and (2) a famous faces task to assess longer-term memory. We also administered the commonly used CFPT, which probes the ability to make fine-grained perceptual distinctions between unfamiliar faces. We supplemented these measures with the comprehensive battery devised by Schmalzl et al. (2008), which has proven sensitivity to the main types of perceptual deficit reported in this population. The battery comprises tasks that together estimate the ability to both detect and individuate faces, including measures that are sensitive to the detection of first- and second-order spatial relations, global/local processing,

holistic processing, the detection of feature and contour changes, viewpoint matching, and judgements of facial expression. Note that the Famous Faces task (Exp. 1) and the CFMT (Exp. 2) are reported first, as these were employed to classify DP, followed by the CFPT (Exp. 3) and the test battery (Exp. 4 to 10). However, during data collection, these tasks were administered in a different order (Exp. 4 to 10, Exp. 3, Exp. 2, and Exp. 1). Below we describe the ability of 11 individuals with face recognition difficulties to perform these tests, relative to a group of age- and gender-matched controls.

General Method

Participants

All participants reported normal or corrected-to-normal vision and no documented history of brain injury. To eliminate influence of the own-race recognition bias (see Brigham & Malpass, 1985), participants were all Caucasian and had lived in the UK for the last three years. Ethical approval for this study was granted by the School of Psychology Ethics Board at the University of Kent, and written informed consent was obtained from each participant at enrolment.

Developmental prosopagnosics. Thirty individuals responded to adverts placed in the local newspaper and on the University departmental website which encouraged people to get in touch if they experienced face recognition difficulties. Both advertisements referred to “face blindness” rather than “developmental prosopagnosia” and featured the following statements, “Do you have difficulty recognising friends when not expecting to see them?” and “Do you have difficulty keeping up with characters in a film?”. These questions were not intended to confirm the presence of prosopagnosia, but to confirm a degree of face recognition difficulty that was worthy of further assessment. An interview with each self-referred participant was subsequently conducted in our research laboratory. This lasted

approximately one hour and sought confirmation that the recognition difficulties were symptomatic of DP. To be considered for study, each individual had to (1) answer “yes” to all eight questions about their activities of daily living (ADL) using a DP questionnaire devised by DeGutis, DeNicola, Zink, McGlinchey and Milberg (2011), (2) confirm that the recognition problem had been evident since childhood, (3) confirm that the difficulty had not followed from a traumatic or other prominent neurological event, and (4) confirm that it was not accompanied by a developmental (e.g., autism or Asperger’s syndrome) or psychiatric disorder. Unprompted, many individuals also mentioned the presence of similar symptoms in a family relative. To confirm that a participant has prosopagnosia, each individual then had to score below two standard deviations of the control group’s accuracy on the Famous Faces Task and below the established 58.4% cut-off (i.e., an overall score of 42 or below; see e.g., Bennetts, Butcher, Lander, Udale, & Bate, 2015; Duchaine & Nakayama, 2006) on the Cambridge Face Memory Task (see Experiments 1 and 2 below). Of the 30 self-referred individuals, 11 (3 male, 2 left-handed) aged 25-62 years (mean = 46.1, SD = 14.8) met all of these criteria and were therefore deemed eligible for enrolment.

Control group. Eleven (4 male, 2 left-handed) participants aged 25-62 years old (mean = 46.2, SD = 14.4) were recruited to closely match the age, gender, and handedness of the DP group. Typically the difference in age between each control and their corresponding DP was less than one year, but up to two years maximum. All confirmed that they were unaware of a problem recognising faces, answered no to all questions on the ADL questionnaire, and did not report a significant neurological or psychiatric history.

General Procedure

Testing was conducted in a psychology laboratory at the University of Kent. The computerised tasks were administered on a Microsoft Windows® computer and stimuli were

presented on a 20.1 inch Dell™ monitor at a resolution of 1024 × 768 pixels. Participants were seated at a distance of 1 meter from the computer screen, with their eyes level with the top of the monitor. Responses were given using a Dell™ USB keyboard. All participants took part in all experiments described below.

Statistical Approach

The responses of each group to the various experimental manipulations were analysed using either univariate or mixed-effects ANCOVAs (with significant interactions explored using Bonferroni-corrected pairwise comparisons). For those tasks that required a speeded response, inferential analyses were only performed on mean correct reaction times that fell within two standard deviations of each participant's mean and that had been log transformed to base power 10. MANCOVAs were also performed on the accuracy and RT data to determine whether a linear combination of perceptual sub-test scores, accounting for age, was more associated with the DP than control group. To provide a handle on individual variability within the DP group, individual test scores were also compared to the control group using Crawford and Howell's (1998) modified *t*-tests, which are less vulnerable to the inflated Type 1 error rate that can occur when *z*-scores are calculated from relatively small control group samples. To increase the likelihood of uncovering perceptual impairment (and thereby refute our prediction that some cases of DP are more memorial than perceptual in nature), these *t*-tests were initially uncorrected for multiple comparisons ($\alpha = 0.05$). As can be seen in Figure 2, this liberal criterion served us well given that the prevalence of perceptual impairment turned-out to be low. Cronbach's alpha was calculated (based on the 22 control and DP participants) for all experiments in which performance in both groups was below ceiling, except the CFMT and CFPT for which internal consistency reliability has been widely reported (Bowles et al., 2009).

Although the controls and DPs were closely age-matched, the range was relatively large (37 years). Given evidence that age can affect performance on key measures such as the CFMT and CFPT (Bowles et al., 2009), we therefore included age as a co-variate in all statistical tests that follow. As described below, there were only two instances (in the configural and holistic tasks) in which experimental performance deteriorated as age increased but importantly these effects did not interact with Group and only influenced variables that are widely seen as less diagnostic of face perception impairment than other variables measured here. Mindful of the finding by Bowles et al. (2009) that age-related norms become especially important in studies that recruit prosopagnosics over the age of 50, we performed an additional statistical procedure in which age was added as a binomial variable (< 50 years [n=12] vs. > 50 years [n=10]) to each experimental analysis. This factor again failed to reach significance in any of the experiments ($\alpha = 0.05$) except in several sub-conditions of the Composite task but here it neither interacted with Group nor with the inversion effect (i.e. the outcome of most interest). Given the modest and limited nature of the age effects that emerge when age is treated as a binomial variable, no further mention is made of them in this report.

Experiment 1: Famous Faces Task

To assess long-term retention and retrieval of faces, participants were presented with pictures of well-known celebrities to name. Face images were gathered from the internet and all depicted a frontal view with minimal hair occlusion and no visible accessories such as hats and earrings (though glasses were permissible if usually worn). Images were cropped to include only the face and external features (hair, ears, jaw line) and presented on a black background (see Figure 1). Cropped stimuli that were less than 320 pixels high were rejected, and faces were proportionally resized to subtend no more than $3.9^\circ \times 5.3^\circ$ of visual angle

with a resolution of 72 pixels per inch. Seventy-seven images were presented in a random order, with each trial beginning with a central fixation cross for 500ms, ending with a blank screen for 500ms. The face remained on-screen until an unspeeded response was made. Participants were asked to name out loud the celebrity or, if the name did not come to mind but they knew the identity of the person, to provide a distinguishing semantic fact. Either response was marked as “correct” if the individual was identified. Task duration was approximately eight minutes.

(Figure 1 about here)

Internal consistency, as assessed using Cronbach’s alpha, was .970. A univariate ANCOVA showed that the DP group (accuracy = 40.7%, SD = 15.1) performed the task less accurately than the control group (accuracy = 82.3%, SD = 9.9), $F(1,19) = 59.85$, $p < .001$. There was no main effect of Age, $F(1,19) = 1.56$, $p = .08$. The individual test scores of the DPs were compared to the controls using Crawford and Howell’s (1998) modified *t*-distribution and, as with all other experiments, are presented in Figure 2.

(Figure 2 about here)

Experiment 2: Cambridge Face Memory Test (CFMT)

The CFMT was administered to assess participants’ ability to learn and retrieve the identities of new faces. In contrast to the other face perception tests described below which rely only on detection or matching, the CFMT incorporates both a perceptual and memorial component (for details see Duchaine & Nakayama, 2006). In short, participants are first asked to learn six faces, each from three viewpoints. The recall phase is then divided into

three blocks. In Block 1 (introduction) participants are briefly shown a target face and then immediately shown 3 more faces and asked which one they just saw. Given that the study and test images are the same, the task can be correctly performed using image matching alone. In Block 2 (novel images), participants are first shown all six target faces in frontal view and given 20 seconds to review them. Across 30 trials, they are then required to pick out each of these faces from a three-face line-up consisting of a new image of the target identity and two foils. Block 3 (noise) is a 24 trial variation of Block 2 (including the same 20-second review screen) but with Gaussian noise added to the stimuli to keep performance below ceiling and place greater reliance on mechanisms believed central to face recognition. Responses were unspeeded and task duration was approximately eight minutes.

Accuracy was, as is typical, highest for the introduction condition (mean = 90.4%, SD = 17.2), followed by the novel images condition (mean = 64.4%, SD = 21.4) and lowest for the noise condition (mean = 50.9%, SD = 21.4). A one-way ANCOVA revealed a main effect of Group, $F(1,19) = 77.84, p < .001$, indicating that controls (mean = 81.8%, SD = 8.9) were more accurate than the DPs (mean = 51.0%, SD = 6.9). There was no main effect of Age ($F(1,19) = 0.01, p = .91$). Individual performance is described in Figure 2.

Experiment 3: Cambridge Face Perception Test (CFPT)

The CFPT was administered to assess the perception of facial similarity (for details of the original task see Duchaine, Germine, & Nakayama, 2007). In short, participants are given 60 seconds to arrange six frontal facial images according to their similarity to a $\frac{3}{4}$ view target face that appears directly above (see Figure 3). Eight different upright arrangements are then duplicated, inverted, and intermixed to create 16 pseudorandomised trials. Scores reflect how many deviations the participants' order of the faces falls from the correct order. Task duration was approximately 18 minutes.

(Figure 3 about here)

The mean correct responses for all participants are shown in Table 1. A 2 (Group) \times 2 (Orientation) ANCOVA failed to find significant effects involving Orientation (all $F_s(1,19) \leq 3.66$, $p_s \geq .07$), Group or Age (both $F_s(1,19) \leq 2.48$, $p_s \geq .13$). An inversion index was calculated using the formula: (upright - inverted) / (upright + inverted) (see Wilkinson, Ko, Wiriadjaja, Kilduff, McGlinchey, & Milberg, 2009). A normal inversion effect (negative index value) was demonstrated for each group and when interrogated with ANCOVA was found to be comparable across Group and Age (all $F_s(1,19) \leq 2.31$, $p_s \geq .15$). Individual analysis indicated that only one of the 11 DPs demonstrated significant impairment on the CFPT in comparison with the control group. This impairment was only evident in the upright CFPT condition but did not eliminate the inversion effect.

(Table 1 about here)

Experiment 4: Basic Configural Processing

A global-local Navon task (Navon, 1977) was administered to assess basic configural processing, that is the perception of both global/local structure and global precedence. This task does not utilise face stimuli and it remains unclear whether it relates to DP (Duchaine, Yovel, & Nakayama, 2007). However, it has been used repeatedly as an analogue to assess the bias for processing faces holistically compared to on an individual featural level (Behrmann et al., 2005; Bentin, DeGutis, D'Esposito, & Robertson, 2007; Macrae & Lewis, 2002; Perfect, Weston, Dennis, & Snell, 2008; Weston & Perfect, 2005). Stimuli consisted of the outline of either a circle or square (global shapes), which was made up from either small

circles or small squares (local shapes) (see Figure 4). Stimuli subtended $6.8^\circ \times 6.8^\circ$ of visual angle. On congruent trials, local and global elements matched (i.e. the big square was composed of small squares), while on inconsistent trials they had a different appearance (i.e. the big square was composed of small circles). The first block consisted of 40 randomised trials (20 congruent and 20 incongruent) with each trial beginning with a central fixation cross for 500 milliseconds (ms), followed by the stimulus which remained on screen until a response was made, ending with a blank screen for 500ms. Participants were asked to identify the large shape by pressing “c” or “s” on a standard computer keyboard quickly and accurately (as was the case for all tests described below, the mapping between response button and stimulus selection was counterbalanced across participants). The second block was identical to the first but participants were asked to identify the smaller shape. Task duration was approximately four minutes.

(Figure 4 about here)

The responses of three DPs were removed prior to analysis because they confused the response key mappings. Cronbach’s alpha for the RT data was .839 but was not calculated for the accuracy data as the mean accuracy for both groups was near ceiling (98%). The mean correct responses and reaction times for all other participants are shown in Table 1. The correct responses were then subjected to a 2 (Group) \times 2 (Global Target/Local Target) \times 2 (Consistent/Inconsistent) repeated-measures ANCOVA controlling for age as a covariate. Local judgements were more accurate than global judgments, $F(1,16) = 5.62, p < .05$, and were moderated by age, $F(1,16) = 4.66, p < .05$, such that they became easier as age decreased. Neither the main effect of Consistency nor the Consistency \times Target interaction term reached significance (both $F_s(1,16) \leq 0.93, p_s \geq .35$), though this may have arisen

because of the observed ceiling effects in mean accuracy. A three way interaction of Group, Target and Consistency was also observed, $F(1,16) = 7.55, p < .05$, and was driven by more accurate responses to local targets in the control group when they were consistent (mean = 100.0, SD = 0.0) compared to inconsistent (mean = 96.8, SD = 4.0) with the global target ($p < .01$). The main effects of Group and Age were not reliable (both $F_s(1,16) < 0.27, p_s \geq .61$).

The same ANCOVA was applied to the RT data and indicated that reaction times were shorter for consistent versus inconsistent trials, $F(1,16) = 4.94, p < .05$. The main effect of Target was not significant, $F(1,16) = 1.18, p = .30$, but a significant Target \times Consistency interaction emerged, $F(1,16) = 5.60, p < .05$, which was driven by an effect of Consistency only at the Local level ($p < .001$). However, this interaction effect reduced as age increased, $F(1,16) = 5.01, p < .05$. There was no main effect of Age, $F(1,16) = 1.11, p = .31$, and no main effect, $F(1,16) = 1.11, p = .31$, or interactions involving the factor Group (all $F_s(1,16) \leq 3.43, p_s \geq .08$). Finally, performance was once again assessed at the level of the individual (see Figure 2). Only one (DP 2) of the 11 DPs demonstrated significant impairment in the Configural task, showing slower RTs than the controls.

Experiment 5: Face detection

The Mooney task (Mooney, 1957, 1960) was administered to assess the detection of first-order relations (e.g., the basic configuration of a pair of eyes above a nose and mouth), which are believed to be important for recognising a face as a face. Stimuli consisted of degraded facial images in which all colour was transformed to black or white. Individual pixels of contrasting luminance were removed to form smooth blocks of colour so that shadows and highlights were made salient. These stimuli were then duplicated and individually rearranged to form images with no discernible form, thus creating the non-face images. Stimuli subtended $6.9^\circ \times 6.9^\circ$ of visual angle. The task consisted of 40 trials, each

containing a pair of stimuli comprising one face and one non-face (see Figure 5). Trials began with a central fixation for 500 ms, followed by the stimulus which remained on screen until a response was made, ending with a blank screen for 500 ms. Participants were instructed to choose quickly and accurately which image depicted a face by pressing “1” or “2”. Task duration was approximately two minutes.

(Figure 5 about here)

Cronbach’s alpha for the RT data was .864 but was again not calculated for the accuracy data as the mean accuracy for both groups was near ceiling (98%). The mean correct responses and reaction times are shown in Table 1. Accuracy and reaction times were analysed in separate univariate ANCOVAs as a function of Group and Age and produced no statistically significant differences (Age in accuracy $F(1,19) = 2.86, p = .11$; Group in RTs $F(1,19) = 3.88, p = .06$; all other $F_s(1,19) \leq 0.47, p_s \geq .50$). Individual analysis indicated that none of the 11 DPs demonstrated impairment in this task (see Figure 2).

Experiment 6: Holistic processing

Holistic processing refers to the simultaneous encoding of multiple features and their integration into a coherent whole. This capacity is taken as a core requirement for normal face processing (see Rossion, 2008). The most widely recognised measure of holistic face processing is the Composite Faces Task (Le Grand, Mondloch, Maurer, & Brent, 2004). Participants are presented with pairs of faces in which the tops and bottoms of each face are either aligned or misaligned (see Figure 6). While the bottom halves of the faces are always different, the top halves can match and participants are asked to determine as quickly and accurately as possible whether the top halves of the faces are the same or different. In the

current experiment, responses were registered by pressing “s” or “d” on the keyboard. The composite face effect relies on the assumption that misaligned faces disrupt holistic processing and force recognition to be based on features instead. This should therefore lead to better featural discrimination performance, of the top halves of the faces, in the misaligned compared to the aligned condition (Maurer et al., 2002).

The first block (aligned) consisted of 48 randomised trials evenly divided into “same” or “different” conditions. In the second block (misaligned), the bottom half of the face stimuli was shifted half-way to the right. Each trial began with a central fixation cross for 500 ms, followed by the stimulus which remained on screen until a response was made, ending with a blank screen for 500 ms. Aligned face stimuli subtended $6.6^\circ \times 9.8^\circ$ of visual angle and misaligned face stimuli subtended $9.8^\circ \times 9.8^\circ$ of visual angle. Task duration was approximately six minutes.

(Figure 6 about here)

Cronbach’s alpha was .794 for the accuracy data and .958 for the RT data. The mean correct responses and reaction times are shown in Table 1. A 2 (Group) \times 2 (Alignment) ANCOVA (with age again entered as a covariate) of the accuracy scores revealed a main effect of Age, $F(1,19) = 9.22$, $p < .01$, whereby accuracy reduced as age increased, but importantly this did not interact with Group. Analysis of the RT data showed that the control group generated shorter reactions overall, $F(1,19) = 4.87$, $p < .05$, but no other effects reached significance (all $F_s(1,19) \leq 1.70$, $p_s \geq .21$).

There are two commonly applied methods to calculate a face composite effect (that is, the illusion that the top halves of two faces are different when aligned with two different bottom halves of faces). The traditional measure is obtained by subtracting performance on

same-misaligned trials from that on same-aligned trials. Using this method, reliability was .56 for the accuracy data and .70 for the RT data (calculated using the subtraction method described by DeGutis, Wilmer, Mercado, & Cohan, 2013). Both groups generated negative face composite effect scores in accuracy and positive scores in RT, which is suggestive of holistic processing. Allied univariate ANCOVAs revealed no effect of Group or Age in either the accuracy or RT data (Age in accuracy $F(1,19) = 4.07, p = .06$; all other $F_s(1,19) \leq 0.47, p_s \geq .50$). The second method of assessing the composite effect is to calculate an inversion index (misaligned - aligned) / (misaligned + aligned) (see Avidan et al., 2011). Again, both groups showed positive indices in accuracy and negative indices in RT, indicative of holistic processing. The ANCOVAs showed no significant Group or Age differences (all $F_s(1,19) \leq 0.92, p_s \geq .35$). No individual DPs showed impairment in this task (see Figure 2).

Experiments 7 & 8: Detection of spacing, feature and contour changes

In Experiment 7, the Jane Task (Le Grand Mondloch, Maurer, & Brent, 2001) was used to estimate participants' sensitivity to subtle changes in either the identity or spacing of individual features. Several reports exist of impairment in this task in DP (Schmalz et al., 2008; Le Grand et al., 2006; Rivolta et al., 2012), justifying its inclusion here. All stimuli were derived from just one face (Jane's) that had been altered from the original in one of three ways; (1) in the spacing condition the eyes were moved in/out (see Figure 7) or the eyes and mouth were moved up/down, (2) in the feature condition, the eyes and mouth were replaced with those from another face, and (3) in the contour condition, the internal part of the face was combined with the contour from another face. Each of the three conditions consisted of 30 randomised pairs of faces (presented alongside each other), with one of the faces altered on 50% of the trials. Each face stimulus subtended $6.6^\circ \times 9.8^\circ$ of visual angle. Each trial began with a central fixation cross for 500ms, followed by the stimulus until a

response was made, and ending with a blank screen for 500ms. Participants were asked to indicate quickly and accurately whether the two faces presented were the same or different by pressing “s” or “d”.

In Experiment 8, the entire procedure was repeated but with the faces inverted. Sensitivity to second-order relations is strongly affected by inversion (Freire, Lee, & Symons, 2000; Leder & Bruce, 2000) so individuals who normally make use of this information to identify faces should be adversely affected by the manipulation. Task duration was approximately 11 minutes for each of the two experiments.

(Figure 7 about here)

Cronbach’s alpha in Experiment 7 was .794 for the accuracy data and .976 for the RT data, and in Experiment 8 was .881 for the accuracy data and .979 for the RT data. The mean correct responses and reaction times are shown in Table 1. In Experiment 7, a 2 (Group) \times 3 (Feature change) ANCOVA indicated that the controls were generally more accurate than the DPs, $F(1,19) = 5.87, p < .05$. Group also interacted with Feature change, $F(2,38) = 3.72, p < .05$; while DPs were more accurate at detecting feature compared to contour changes, the controls showed no such sensitivity ($p < .001$). There was no main effect or interaction involving Age (both $F_s \leq 0.15, p_s \geq .78$). Despite the higher group accuracy for controls, none of the individual DPs showed evidence of impairment (see Figure 2).

The RT analysis indicated that controls were generally faster to respond than the DPs, $F(1,19) = 4.77, p < .05$, and that, together, differences in features (mean = 3.275, SD = 0.13) were more quickly detected than differences in spacing (mean = 3.421, SD = 0.22) or contour (mean = 3.373, SD = 0.18) ($F(2,38) = 3.32, p < .05$) (pairwise p -values $< .005$). Group and Feature did not interact with each other, $F(2,38) = 1.33, p = .28$. There was no main effect or

interaction involving Age (both $F_s \leq 0.69$, $ps \geq .51$). Again, however, the overall impairment in the DPs was not robust at an individual level, with only two participants (DP 2 and DP 10) showing significantly slower RTs to the controls (see Figure 2).

The effect of inversion in the two groups was explored by subtracting the performance in the inverted experiment from that in the upright experiment. This was calculated separately for the accuracy and RT data. Reliability was .31 for the accuracy data and .94 for the RT data (DeGutis et al., 2013). Both groups showed normal inversion effects, producing accuracy and RT inversion effect scores that were above and below zero respectively for all Feature conditions except the spacing change condition in which the DP group did not show a negative RT inversion effect score. A 2 (Group) \times 3 (Feature change) ANCOVA was conducted separately on the inversion effect scores of correct responses and reaction times. No main effects or interaction terms reached significance in the accuracy inversion analysis (Feature change $F(2,38) = 2.08$, $p = .14$; Feature \times Age $F(2,38) = 2.49$, $p = .10$; all other $F_s \leq 0.90$, $ps \geq .35$), but in the RT data controls (mean = $-.102$, SD = 0.11) produced a more negative inversion effect score than the DPs (mean = $.007$, SD = 0.15) ($F(1,19) = 4.27$, $p = .05$). The Group \times Feature change interaction was also significant, $F(2,38) = 3.62$, $p < .05$, and was driven by a lower (i.e. negative) inversion effect score in the spacing change condition in the controls vs. DPs ($p < .01$). There was no main effect or interaction involving Age (both $F_s \leq 1.37$, $ps \geq .27$). At the individual level, and when collapsing across spacing and contour conditions (inversion effects are not expected in feature change detection; reliability rises to .49 and .94 for accuracy and RT respectively [DeGutis et al., 2013]), only DP 2, DP 3 and DP 9 produced a smaller inversion effect score (RT data only) than the control group (see Figure 2). An alternative inversion index calculated again using the formula: (upright - inverted) / (upright + inverted) (see Wilkinson,

Ko, Wiriadjaja, Kilduff, McGlinchey, & Milberg, 2009) yielded the same pattern of statistically significant and non-significant effects.

Experiment 9: Viewpoint matching

To assess the ability to form viewpoint-independent representations of faces, participants were asked to quickly and accurately match unfamiliar faces presented at different horizontal viewpoints, which were full frontal, 45-degree mid-profile, and 90-degree side profile view. Each trial consisted of a full frontal view of an unfamiliar face simultaneously presented above three other faces, one of which was the same person and the remaining two were foils. All three were presented at either the same or a different viewpoint to the target. Participants had to indicate, via button press, which of the three test faces was the same person depicted above in full frontal view (see Figure 8). Each face subtended, on average, $3.5^\circ \times 7.9^\circ$ of visual angle and was positioned within a frame subtending $16.3^\circ \times 12.3^\circ$ of visual angle. Of the 60 trials, 20 showed front views of the three faces, in another 20 trials the faces were at 45° (10 left, 10 right), and in the remaining 20 the faces were at 90° (10 left, 10 right). All trials were randomised and began with a central fixation cross for 500ms, followed by the stimulus which remained on screen until a response was made, ending with a blank screen for 500ms. Task duration was approximately five minutes.

(Figure 8 about here)

Cronbach's alpha was .426 for the accuracy data and .937 for the RT data. The low Cronbach's alpha for the accuracy data is due to highly consistent participant performance. Mean accuracy across the three conditions was 93.3% (SD = 3.3) for controls and 88.9% (SD = 4.4) for the DP group. As expected, accuracy in both groups was highest when the 3 test

faces were full-frontal (control mean = 99.1%, SD = 2.0; DP mean = 98.6%, SD = 2.3) followed by the 45 degree side views (control mean = 95.5%, SD = 4.7; DP mean = 89.5%, SD = 6.1), and then the 90 degree profiles (control mean = 85.5%, SD = 7.9; DP mean = 78.6%, SD = 7.4).

A 2 (Group) \times 2 (Angle) ANCOVA conducted on the accuracy data revealed a main effect of Angle (Front > 45 > 90), $F(2,38) = 4.06$, $p < .05$, and a significant main effect of Group, $F(1,19) = 6.72$, $p < .05$, which reflected higher accuracy for the control group (though note that accuracy was still high in the DP group). No other main effect or interaction terms reached significance (Group \times Angle interaction $F = 2.66$, $p = .08$; all other $F_s \leq 0.40$, $p_s \geq .54$). However, despite the higher control group accuracy only two individuals (DP 7 and DP 10) showed evidence of significant impairment (see Figure 2).

The same ANCOVA conducted on the RT data also showed a main effect of Angle, $F(2,38) = 23.11$, $p < .001$. The main effect of Group, $F(1,19) = 4.31$, $p = .052$, and the Group by Angle interaction did not reach significance, $F(2,38) = 2.96$, $p = .06$ (all other $F_s \leq 1.56$, $p_s \geq .22$). At the individual level, only one participant (DP 10) performed significantly below the group mean.

Experiment 10: Judgments of emotional expression

Judgements of emotional expression are generally spared in prosopagnosia (Humphreys et al., 2007; Nunn et al., 2001) but have been shown in some cases of DP (De Haan & Campbell, 1991; Duchaine et al., 2006; Minnebusch et al., 2007). Consequently, emotion recognition was also assessed here. Stimuli were made up of 48 faces depicting the six emotions of happiness, sadness, anger, fear, surprise or disgust (Ekman & Friesen, 1976) (see Figure 9), each subtending $5.8^\circ \times 8.8^\circ$ of visual angle. Each trial began with a central fixation cross for 500 ms, followed by a face stimulus, which remained on screen until a

response was made, and ending with a blank screen for 500 ms. Participants were asked to quickly and accurately judge the emotional expression of the face by pressing one of six buttons (a reference key showing which button should be pressed for each emotion was placed below the monitor during the experiment). Task duration was approximately 5 minutes.

(Figure 9 about here)

Cronbach's alpha was .535 and the following results should consequently be interpreted with caution. Mean accuracy was 85.0% for the controls (SD = 5.3) and 83.3% for the DP group (SD = 8.5). A univariate ANCOVA failed to find reliable differences involving Group or Age (both $F_s(1,19) \leq 0.83$, $ps \geq .37$). One individual (DP 7) produced a mean score that was significantly below the control group mean (see Figure 2). Given the need to select one of six possible response buttons, RTs were not analysed.

MANCOVA Results

Four separate MANCOVAs were performed on the accuracy and reaction time data to assess whether a more general perceptual difference existed between the DP and control group, as characterised by performance across multiple tests rather than on any one test in particular. Age was controlled for as a covariate and Group was the fixed factor.

(1) MANCOVA of Accuracy data:

The following 16 dependent variables were included: the upright and inversion index scores from Experiment 3, the four conditions and face composite effect scores from Experiment 6,

the three conditions from Experiment 7, the spacing and contour inversion effect scores from Experiments 7 and 8, the three conditions from Experiment 9, and the overall score from Experiment 10. Note that 'total' summary scores were not included because of their interdependence with the condition-specific scores from which they were derived. Due to collinearity ($r > .8$), scores in the upright condition from Experiment 3 and the intact-same condition from Experiment 6 were also removed. The MANCOVA failed to reach statistical significance, $F(14,6) = 2.77$, $p = .11$, Wilk's $\Lambda = 0.134$, partial $\eta^2 = .87$, and Age was not a significant factor, $F(14,6) = 2.5$, $p = .14$.

(2) MANCOVA of RT data:

The following 14 dependent variables were included: the overall score from Experiment 5, the four conditions and face composite effect scores from Experiment 6, the three conditions from Experiment 7, the spacing and contour inversion effect scores from Experiments 7 and 8, and the three conditions from Experiment 9. Due to collinearity, data from the intact-diff condition from Experiment 6, the spacing condition from Experiment 7, and the 45 degree condition from Experiment 9 were removed. The MANCOVA failed to reach statistical significance, $F(10, 10) = 1.78$, $p = .19$, Wilk's $\Lambda = 0.360$, partial $\eta^2 = .64$, and Age was not a significant factor, $F(10,10) = 0.8$, $p = .67$.

(3) MANCOVA of RT and Accuracy data combined:

All accuracy and RT variables described in the above MANCOVAs were included but again failed to produce a reliable effect, $F(19,1) = 3.81$, $p = .39$, Wilk's $\Lambda = 0.014$, partial $\eta^2 = .99$. Age was not a significant factor, $F(19,1) = 0.50$, $p = .83$.

(4) MANCOVA of those six measures that might be considered most sensitive to face perception deficits; the face composite effect accuracy, viewpoint total accuracy, CFPT accuracy, face detection RT, face composite effect RT, and the Jane inversion effect RT.

Again, the test did not reach significance, $F(6,14) = 2.55$, $p = .07$, Wilk's $\Lambda = 0.478$, partial $\eta^2 = .52$) and Age was not a significant factor, $F(6,14) = 0.81$, $p = .58$.

Discussion

We present data from 11 individuals with DP as defined by self-reported difficulties in face recognition and relative impairment on the famous faces test (DP group mean = 41%; control group mean = 82%), and the CFMT (DP group mean = 51%; control group mean = 82%). Group analysis revealed some evidence of perceptual impairment compared to the controls; accuracy was lower for one of the experimental conditions sensitive to global-local interference (Experiment 4), for detecting Jane Upright changes (Experiment 7) and viewpoint matching (Experiment 9), while RTs were slightly longer on subtests of the Jane Upright (Experiment 7) and composite processing tasks (Experiment 6), and there was a reduced inversion effect in one condition of the Jane task (Experiment 7 & 8). However, when set against the severe recognition failure shown by the DPs on the Famous Faces Test and the CFMT, these perceptual impairments were subtle; accuracy was always well above chance, less than 15% of the corresponding control mean, and accompanied by normal inversion effects. Additionally, unlike other instances of prosopagnosia (e.g., Avidan et al., 2011; Wilkinson et al., 2009), the observed reaction time differences only ever differed from the control means by milliseconds rather than seconds making it difficult to see how these could explain the profound identification problems. The failure to clearly distinguish between the perceptual capacities of the DPs and controls could not be easily attributed to differences in age. Compellingly, the patterns observed at the group level were also not evident at the individual level: six of the 11 DPs showed no evidence of perceptual impairment, while the remainder showed heterogeneous impairment profiles. In line with this, the MANCOVAs failed to identify a combination of perceptual test scores that differentiated the DPs from the

controls. Together, these data suggest that no single perceptual impairment, or combination of perceptual impairments, is necessary or sufficient for face recognition failure (as defined by the ADL scale, Famous Faces Test and CFPT) to occur in DP.

Examination of individual performance in Figure 2 shows that the most prevalent perceptual impairments were observed on the Jane Upright RT, Jane RT inversion effect, and the viewpoint matching task. For each of these tasks, two or more individuals performed significantly worse than the control group mean. The fact that so few participants encountered difficulty with the viewpoint task is noteworthy because, along with the CFPT, Mooney test, and composite inversion effect, this task is seen as particularly sensitive to face identification impairment (by contrast, the configural task does not involve faces, the emotional expression task does not involve face identification and the Jane Upright task may lack sensitivity to DP – see Yovell and Duchaine, 2006). Given that performance was so much more impaired on the memory compared to perceptual tests, we suggest it unlikely that the identification problems were perceptual in origin, and propose that many of the isolated perceptual deficits were merely co-morbid to DP. That is, they were simply allied rather than directly causal. This alludes to the idea that DP, like its acquired counterpart, has a dissociable memorial element (Barton, 2008; Damasio, Tranel, & Damasio, 1990; De Renzi et al., 1991). If true then perhaps some of the perceptual deficits seen in DP are motivational in origin and reflect a reluctance to maximise perceptual face processing during laboratory testing. For example, if the individual knows that he/she is unable to retain facial information then the attentional focus during visual processing may move to non-defining facial attributes or other aspects of appearance such as voice, body shape or posture. Alternatively, and admittedly speculatively, it remains possible that a higher-level memory impairment compromises lower-level perceptual processing via disruptive back-propagated messages.

The non-uniform profile of perceptual impairment seen in the current sample is similar to that reported by Schmalzl et al. (2008) who administered the same battery to members of one family, of whom seven were categorised as DP. All showed a different combination of perceptual impairments but, unlike in the present sample, six of those individuals also failed to show a face inversion effect on the Jane task. Interestingly, one of the seven individuals who showed evidence of DP at screening (i.e. reported that they could not identify photographs of family members), showed no evidence of impairment on any of the perceptual tests. This led the authors to conclude that although a subtle perceptual deficit could not be ruled out, the individual's impairment "seems to lie in the ability to associate a visual percept of a face with an individual identity" (p.113). The current data suggest that the divergent pattern seen in this family member may not be uncommon.

For future research, we suggest the need for additional, larger group studies (as opposed to the single-case or small-group approaches that currently predominate) that are more amenable to robust inferential statistical procedures and that provide a better measure of individual heterogeneity that, as was the case here, belies averaged group effects. While the sample size recruited in the present study is larger than that in most other developmental prosopagnosia studies, it is most likely still too small to speak to the behaviour of the wider population. And although the conjoint administration of the CFMT and Famous Faces Test allows one to separately probe, on one hand, the learning and short-term retention of unfamiliar faces and, on the other, the recollection of faces that have been seen many times over, neither is sensitive to other important determinants of memory ability. A related concern is that while some measures, such as the CFMT, seem able to detect individual differences in performance, others may not have such sensitivity and, accordingly, the profile of individual data reported here must be seen as more suggestive than definitive. This problem of measurement is compounded by the fact that no experimental test of DP has

received diagnostic validation. Consequently, it remains unclear what percentage change in these tests constitutes a minimal clinically important difference.

Finally, we note from a more applied perspective that in cases where a memory encoding deficit predominates, transcranial neuro-modulatory techniques such as tDCS or vestibular stimulation may, by virtue of their capacity to promote cortical excitability and long-term potentiation (see Utz, Dimova, Oppenländer, & Kerkhoff, 2010), afford therapeutic value (see Bate & Bennetts, 2014; Wilkinson, Ko, Kilduff, McGlinchey, & Milberg, 2005; Wilkinson, Ferguson, & Worley, 2012).

References

- Ariel, R., & Sadeh, M. (1996). Congenital visual agnosia and prosopagnosia in a child: A case report. *Cortex*, 32(2), 221-240. doi:10.1016/S0010-9452(96)80048-7
- Avidan, G., Tanzer, M., & Behrmann, M. (2011). Impaired holistic processing in congenital prosopagnosia. *Neuropsychologia*, 49(9), 2541-2552.
doi:10.1016/j.neuropsychologia.2011.05.002
- Barton, J. J. S. (2008). Structure and function in acquired prosopagnosia: Lessons from a series of 10 patients with brain damage. *Journal of Neuropsychology*, 2(1), 197-225.
doi:10.1348/174866407X214172
- Barton, J. J. S., & Cherkasova, M. (2003). Face imagery and its relation to perception and covert recognition in prosopagnosia. *Neurology*, 61(2), 220-225.
doi:10.1212/01.WNL.0000071229.11658.F8
- Barton, J. J. S., Press, D. Z., Keenan, J. P., & O'Connor, M. (2002). Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology*, 58(1), 71-78. doi:10.1212/WNL.58.1.71
- Bate, S. (2012). *Face Recognition and its Disorders*. Hampshire, UK: Palgrave Macmillan.

- Bate, S., & Bennetts, R. J. (2014). The rehabilitation of face recognition impairments: a critical review and future directions. *Frontiers in Human Neuroscience*, 8(491), 1-17. doi:10.3389/fnhum.2014.00491
- 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. doi:10.1162/0898929054475154
- Bentin, S., DeGutis, J. M., D'Esposito, M., & Robertson, L. C. (2007). Too many trees to see the forest: Performance, event-related potential, and functional Magnetic Resonance Imaging manifestations of integrative congenital prosopagnosia. *Journal of Cognitive Neuroscience*, 19(1), 132-149. doi:10.1162/jocn.2007.19.1.132
- Bentin, S., Deouell, L. Y., & Soroker, N. (1999). Selective visual streaming in face recognition: Evidence from developmental prosopagnosia. *NeuroReport*, 10, 823-827.
- Bennetts, R. J., Butcher, N., Lander, K., Udale, R., & Bate, S. (2015). Movement cues aid face recognition in developmental prosopagnosia. *Neuropsychology*, 29(6), 855-860. doi:10.1037/neu0000187
- Bowles, D. C., McKone, E., Dawel, A., Duchaine, B., Palermo, R., Schmalzl, L., . . . Yovel, G. (2009). Diagnosing prosopagnosia: Effects of ageing, sex, and participant-stimulus ethnic match on the Cambridge Face Memory Test and Cambridge Face Perception Test. *Cognitive Neuropsychology*, 26(5), 423-455. doi:10.1080/02643290903343149
- Brigham, J. C., & Malpass, R. S. (1985). The role of experience and contact in the recognition of faces of own- and other-race persons. *Journal of Social Issues*, 41(3), 139-155. doi:10.1111/j.1540-4560.1985.tb01133.x
- Chatterjee, G., & Nakayama, K. (2012). Normal facial age and gender perception in developmental prosopagnosia. *Cognitive Neuropsychology*, 29(5-6), 482-502. doi:10.1080/02643294.2012.756809

Crawford, J. R., & Howell, D. C. (1998). Comparing an individual's test score against norms derived from small samples. *The Clinical Neuropsychologist*, *12*(4), 482-486.

doi:10.1076/clin.12.4.482.7241

Dalrymple, K. A., Garrido, L., & Duchaine, B. (2014). Dissociation between face perception and face memory in adults, but not children, with developmental prosopagnosia.

Developmental Cognitive Neuroscience, *10*, 10-20. doi:10.1016/j.dcn.2014.07.003

Dalrymple, K. A., Oruç, I., Duchaine, B., Pancaroglu, R., Fox, C. J., Iaria, G., . . . Barton, J. J. S. (2011). The anatomic basis of the right face-selective N170 in acquired prosopagnosia: A combined ERP/fMRI study. *Neuropsychologia*, *49*(9), 2553-2563.

doi:10.1016/j.neuropsychologia.2011.05.003

Damasio, A. R., Tranel, D., Damasio, H. (1990). Face agnosia and the neural substrates of memory. *Annual Review of Neuroscience*, *13*, 89-109.

doi:10.1146/annurev.ne.13.030190.000513

Davies-Thompson, J., Pancaroglu, R., & Barton, J. (2014). Acquired prosopagnosia: structural basis and processing impairments. *Frontiers in Bioscience, Elite*, *6*, 159-174. doi:10.2741/E699

De Haan, E. H. F., & Campbell, R. (1991). A fifteen year follow-up of a case of developmental prosopagnosia. *Cortex*, *27*(4), 489-509. doi:10.1016/S0010-9452(13)80001-9

De Renzi, E. (1986). Current issues on prosopagnosia. In H. D. Ellis (Ed.), *Aspects of Face Processing* (pp. 243-252). Dordrecht, Netherlands: Nijhoff.

De Renzi, E., Faglioni, P., Grossi, D., & Nichelli, P. (1991). Apperceptive and associative forms of prosopagnosia. *Cortex*, *27*(2), 213-221. doi:10.1016/S0010-9452(13)80125-6

DeGutis, J., DeNicola, C., Zink, T., McGlinchey, R., & Milberg, W. (2011). Training with own-race faces can improve processing of other-race faces: Evidence from

developmental prosopagnosia. *Neuropsychologia*, 49(9), 2505-2513.

doi:10.1016/j.neuropsychologia.2011.04.031

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, 87-100. doi:10.1016/j.cognition.2012.09.004

Delvenne, J.-F., Seron, X., Coyette, F., & Rossion, B. (2004). Evidence for perceptual

deficits in associative visual (prosop)agnosia: a single-case study. *Neuropsychologia*,

42(5), 597-612. doi:10.1016/j.neuropsychologia.2003.10.008

Dingle, K. J., Duchaine, B. C., & Nakayama, K. (2005). A new test for face perception.

Journal of Vision, 5(8), 40. doi:10.1167/5.8.40

Duchaine, B., & Nakayama, K. (2006). The Cambridge Face Memory Test: Results for

neurologically intact individuals and an investigation of its validity using inverted

face stimuli and prosopagnosic participants. *Neuropsychologia*, 44(4), 576-585.

doi:10.1016/j.neuropsychologia.2005.07.001

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. doi:10.1080/02643290701380491

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. doi:10.1093/scan/nsm003

Duchaine, B. C. (2000). Developmental prosopagnosia with normal configural processing.

Cognitive Neuroscience and Neuropsychology, 11(1), 79-83. doi:10.1097/00001756-

200001170-00016

Duchaine, B. C., Parker, H., & Nakayama, K. (2003). Normal recognition of emotion in a

Prosopagnosic. *Perception*, 32, 827-838. doi:10.1068/p5067

Duchaine, B. C., Yovel, G., Butterworth, E. J., & 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.

doi:10.1080/02643290500441296

Ekman, P., & Friesen, W. V. (1976). *Pictures of facial affect*. Palo Alto, CA: Consulting Psychology Press.

Freire, A., Lee, K., & Symons, L. A. (2000). The face-inversion effect as a deficit in the encoding of configural information: Direct evidence. *Perception*, *29*, 159-170.

doi:10.1068/p3012

Gainotti, G., & Marra, C. (2011). Differential contribution of right and left temporo-occipital and anterior temporal lesions to face recognition disorders. *Frontiers in Human Neuroscience*, *5*(55), 1-11. doi:10.3389/fnhum.2011.00055

Garrido, L., Duchaine, B., Nakayama, K. (2008). Face detection in normal and prosopagnosic individuals. *Journal of Neuropsychology*, *2*(1), 119-140.

doi:10.1348/174866407X246843

Garrido, L., Furl, N., Draganski, B., Weiskopf, N., Stevens, N., Tan, G. C.-Y., . . . Duchaine, B. (2009). Voxel-based morphometry reveals reduced grey matter volume in the temporal cortex of developmental prosopagnosics. *Brain*, *132*(12), 3443-3455.

doi:10.1093/brain/awp271

Gauthier, I., Behrmann, M., & Tarr, M. J. (1999). Can face recognition really be dissociated from object recognition? *Journal of Cognitive Neuroscience*, *11*(4), 349-370.

doi:10.1162/089892999563472

Grueter, M., Grueter, T., Bell, V., Horst, J., Laskowski, W., Sperling, K., . . . Kennerknecht, I. (2007). Hereditary prosopagnosia: The first case series. *Cortex*, *43*(6), 734-749.

doi:10.1016/S0010 9452(08)70502-1

Hole, G. J. (1994). Configurational factors in the perception of unfamiliar faces. *Perception*, 23(1), 65-74. doi:10.1068/p230065

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. doi:10.1007/s00221-006-0621-5

Jaeschke, R., Singer, J., & Guyatt, G. H. (1989). Measurement of health status: Ascertaining the minimal clinically important difference. *Controlled Clinical Trials*, 10(4), 407-415. doi:10.1016/0197-2456(89)90005-6

Jones, R. D., & Tranel, D. (2001). Severe developmental prosopagnosia in a child with superior intellect. *Journal of Clinical and Experimental Neuropsychology*, 23(3), 265-273. doi:10.1076/jcen.23.3.265.1183

Kracke, I. (1994). Developmental prosopagnosia in Asperger syndrome: Presentation and discussion of an individual case. *Developmental Medicine and Child Neurology*, 36, 873-886. doi: 10.1111/j.1469-8749.1994.tb11778.x

Le Grand, R., Cooper, P. A., Mondloch, C. J., Lewis, T. L., Sagiv, N., de Gelder, B., & Maurer, D. (2006). What aspects of face processing are impaired in developmental prosopagnosia? *Brain and Cognition*, 61(2), 139-158. doi:10.1016/j.bandc.2005.11.005

Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2001). Neuroperception: Early visual experience and face processing. *Nature*, 410, 890. doi:10.1038/35073749

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. doi:10.1111/j.0956-7976.2004.00753.x

- Leder, H., & Bruce, V. (2000). When inverted faces are recognized: The role of configural information in face recognition. *The Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology*, 53(2), 513-536. doi:10.1080/713755889
- Lee, Y., Duchaine, B., Wilson, H. R., & Nakayama, K. (2009). Three cases of developmental prosopagnosia from one family: Detailed neuropsychological and psychophysical investigation of face processing. *Cortex*, 46(8), 949-964.
doi:10.1016/j.cortex.2009.07.012
- Macrae, C. N., & Lewis, L. L. (2002). Do I know you? Processing orientation and face recognition. *Psychological Science*, 13(2), 194-196. doi:10.1111/1467-9280.00436
- Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences*, 6(6), 255-260. doi:10.1016/S1364-6613(02)01903-4
- McKone, E., Hall, A., Pidcock, M., Palermo, R., Wilkinson, R. B., Rivolta, D., . . . O'Connor, K. B. (2011). Face ethnicity and measurement reliability affect face recognition performance in developmental prosopagnosia: Evidence from the Cambridge Face Memory Test–Australian. *Cognitive Neuropsychology*, 28(2), 109-146.
doi:10.1080/02643294.2011.616880
- Minnebusch, D. A., Suchan, B., Ramon, M., & Daum, I. (2007). Event-related potentials reflect heterogeneity of developmental prosopagnosia. *European Journal of Neuroscience*, 25(7), 2234-2247. doi:10.1111/j.1460-9568.2007.05451.x
- Mooney, C. M. (1957). Age in the development of closure ability in children. *Canadian Journal of Psychology*, 11(4), 219-226. doi:10.1037/h0083717
- Mooney, C. M. (1960). Recognition of ambiguous and unambiguous visual configurations with short and longer exposures. *British Journal of Psychology*, 51(2), 119-125.
doi:10.1111/j.2044-8295.1960.tb00732.x

Navon, D. (1977). Forest before trees: The precedence of global features in visual perception.

Cognitive Psychology, 9(3), 353-383. doi:10.1016/0010-0285(77)90012-3

Nunn, J. A., Postma, P., & Pearson, R. (2001). Developmental prosopagnosia: Should it be

taken at face value? *Neurocase*, 7(1), 15-27. doi:10.1093/neucas/7.1.15

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.

doi:10.1016/j.neuropsychologia.2011.02.021

Perfect, T. J., Weston, N. J., Dennis, I., Amelia, S. (2008). The effects of precedence on

Navon-induced processing bias in face recognition. *The Quarterly Journal of*

Experimental Psychology, 61(10), 1479-1486. doi:10.1080/17470210802034678

Rivolta, D., Palermo, R., Schmalzl, L., & Coltheart, M. (2012). Covert face recognition in

congenital prosopagnosia: A group study. *Cortex*, 48(3), 344-352.

doi:10.1016/j.cortex.2011.01.005

Rossion, B. (2008). Picture-plane inversion leads to qualitative changes of face perception.

Acta Psychologica, 128(2), 274-289. doi:10.1016/j.actpsy.2008.02.003

Schmalzl, L., Palermo, R., & Coltheart, M. (2008). Cognitive heterogeneity in genetically

based prosopagnosia: A family study. *Journal of Neuropsychology*, 2(1), 99-117.

doi:10.1348/174866407X256554

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. doi:10.1371/journal.pone.0015702

Temple, C. (1992). Developmental memory impairment: Faces and patterns. In R. Campbell

(Ed.), *Mental Lives: Case Studies in Cognition* (pp.199-215). London: Blackwell.

Tippett, L. J., Miller, L. A., & Farah, M. J. (2000). Prosopamnesia: A selective impairment in face learning. *Cognitive Neuropsychology*, *17*(1/2/3), 241-255.

doi:10.1080/026432900380599

Utz, K. S., Dimova, V., Oppenländer, K., & Kerkhoff, G. (2010). Electrified minds: Transcranial direct current stimulation (tDCS) and Galvanic Vestibular Stimulation (GVS) as methods of non-invasive brain stimulation in neuropsychology: A review of current data and future implications. *Neuropsychologia*, *48*(10), 2789-2810.

doi:10.1016/j.neuropsychologia.2010.06.002

Valentine, T. (1988). Upside-down faces: A review of the effect of inversion upon face recognition. *British Journal of Psychology*, *79*(4), 471-491. doi:10.1111/j.2044-8295.1988.tb02747.x

Weston, N. J., & Perfect, T. J. (2005). Effects of processing bias on the recognition of composite face halves. *Psychonomic Bulletin & Review*, *12*(6), 1038-1042.

doi:10.3758/BF03206440

Wilkinson, D. T., Ferguson, H. J., & Worley, A. (2012). Galvanic vestibular stimulation modulates the electrophysiological response during face processing. *Visual Neuroscience*, *29*(4-5), 255-262. doi:10.1017/S0952523812000235

Wilkinson, D., Ko, P., Kilduff, P., McGlinchey, R., & Milberg, W. (2005). Improvement of a face perception deficit via subsensory galvanic vestibular stimulation. *Journal of the International Neuropsychological Society*, *11*(7), 925-929.

doi:10.1017/S1355617705051076

Wilkinson, D., Ko, P., Wiriadjaja, A., Kilduff, P., McGlinchey, R., & Milberg, W. (2009).

Unilateral damage to the right cerebral hemisphere disrupts the apprehension of whole faces and their component parts. *Neuropsychologia*, *47*(7), 1701-1711.

doi:10.1016/j.neuropsychologia.2009.02.008

Yovel, G., & Duchaine, B. (2006). Specialized face perception mechanisms extract both part and spacing information: evidence from developmental prosopagnosia. *Journal of Cognitive Neuroscience*, 18(4), 580-593. doi:10.1162/jocn.2006.18.4.580

Figure Captions

Figure 1: Example stimuli from the FFT.

Figure 2: Mean accuracy scores and RTs for each DP (1 to 11) expressed as modified t-scores, derived by comparison to the control group mean and standard deviation. Scores that are significantly below the performance of the control group (i.e., > 2.23 , corresponding to $\alpha = 0.05$, $df = 10$) are shaded in black.

Figure 3: Example stimuli from the CFPT.

Figure 4: Example stimuli from the configural task.

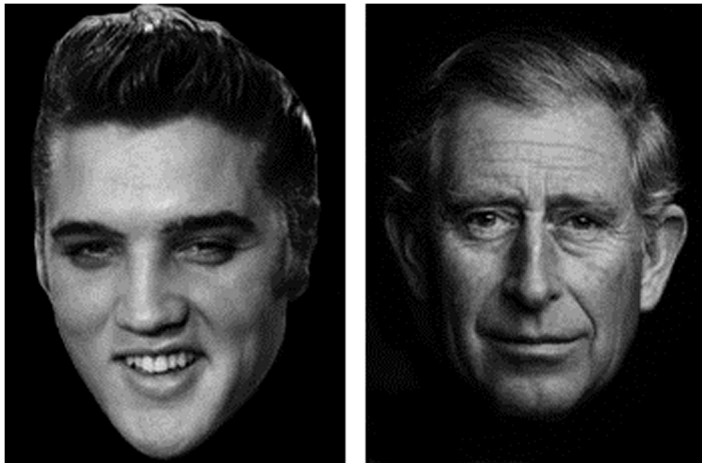
Figure 5: Example stimuli from the Mooney task.

Figure 6: Example stimuli ('different-misaligned' condition) from the composite task.

Figure 7: Example stimuli ('different' condition) from the Jane task.

Figure 8: Example stimuli presentation from the viewpoint task.

Figure 9: Example stimuli (surprise and happiness) from the emotional expression task.



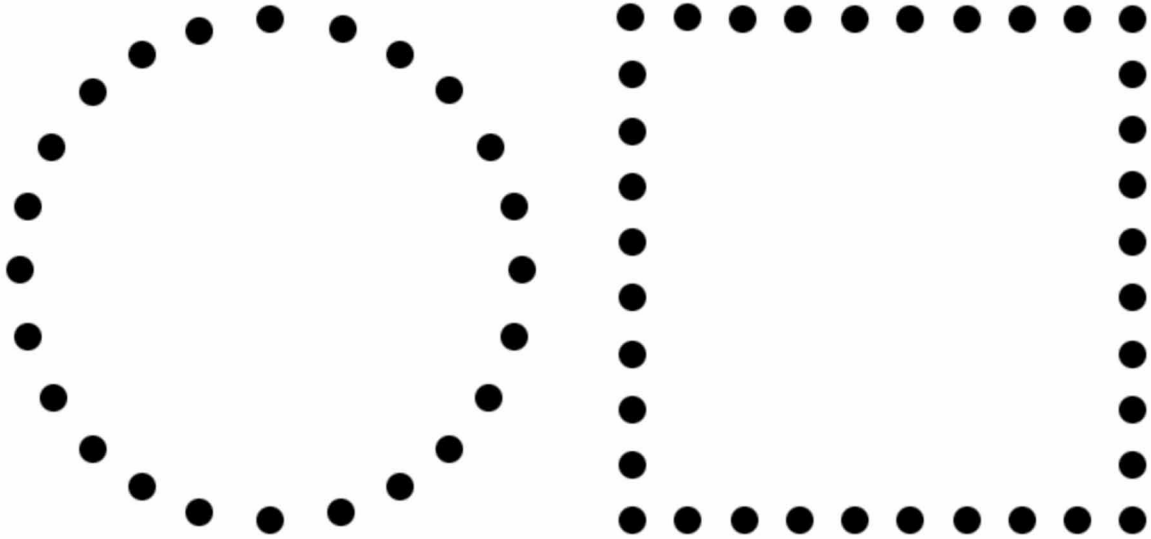
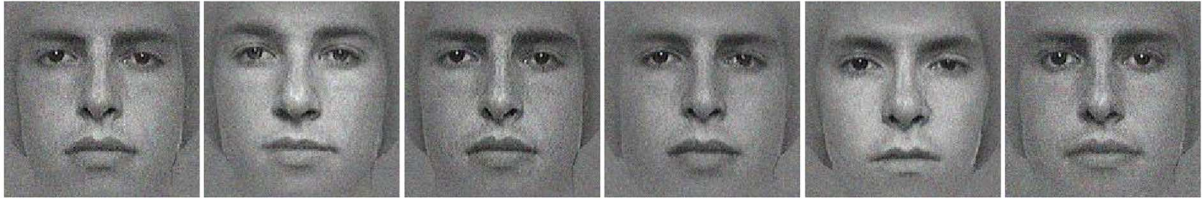
Accuracy

	1	2	3	4	5	6	7	8	9	10	11
FFT	[REDACTED]										
CFMT	[REDACTED]										
CFPT Upright	- 0.12	[REDACTED]	1.91	1.73	0.81	- 0.67	1.18	0.07	2.10	1.55	- 0.86
CFPT Inversion Index	0.52	1.83	1.63	0.16	0.36	- 0.78	1.49	- 0.02	1.37	0.60	- 0.46
Configural	0.19	0.19	- 0.52	0.90	-	0.19	- 0.52	0.90	-	-	0.19
Mooney	0.56	- 0.81	- 0.81	0.56	0.56	0.56	- 0.81	0.56	- 0.12	0.56	0.56
Composite	0.44	0.29	1.63	0.59	1.63	- 0.31	- 0.01	0.44	- 1.06	- 0.16	1.18
Composite Effect	0.84	0.15	- 0.78	- 0.78	- 0.78	- 0.78	- 1.01	0.15	0.38	1.07	- 0.54
Jane Upright	- 1.26	- 1.01	- 0.63	0.00	- 0.50	- 0.50	- 1.77	- 0.25	- 1.51	- 0.50	- 1.14
Jane Inversion Effect	- 0.21	1.24	0.41	- 0.83	0.21	1.86	- 1.24	- 1.86	- 0.41	1.24	- 1.24
Viewpoint	- 1.44	- 0.48	- 1.44	- 0.48	- 0.96	- 0.48	[REDACTED]	0.00	- 1.91	[REDACTED]	0.00
Expressions	1.21	0.45	- 0.31	- 1.07	- 1.07	1.59	[REDACTED]	0.83	- 0.69	- 2.21	1.21

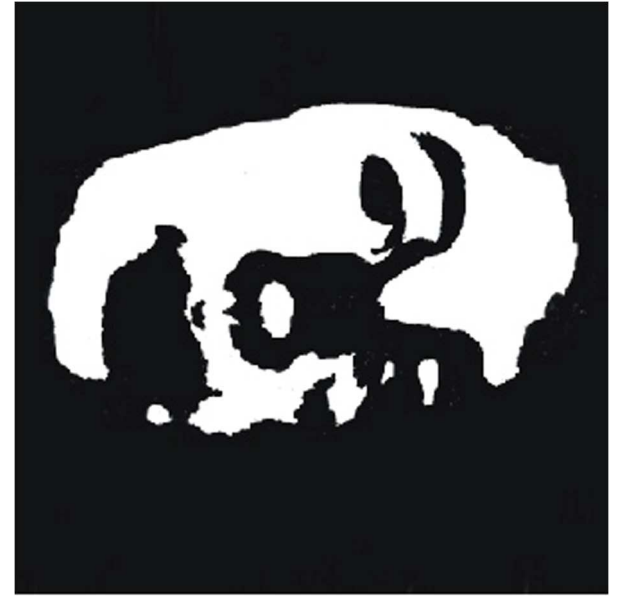
Response times

	1	2	3	4	5	6	7	8	9	10	11
Configural	0.23	[REDACTED]	1.1 3	- 0.35	-	1.81	- 0.16	- 1.19	-	-	- 0.43
Mooney	-	1.43	1.6	1.95	0.56	0.78	-	-	1.61	0.9	1.68

	1.15		6				0.10	0.29		6	
Composite	0.41	1.41	1.2 1	0.47	0.32	0.88	1.12	- 0.48	1.21	2.1 4	0.05
Composite Effect	- 0.13	- 0.19	1.2 5	- 1.02	- 0.85	- 0.41	0.14	0.01	- 0.01	0.5 5	- 0.28
Jane Upright	- 0.08		1.7 8	1.35	1.74	0.28	0.77	0.25	- 0.31		- 0.37
Jane Inversion Effect	0.74			0.61	1.73	1.52	0.45	- 1.78		0.1 7	0.67
Viewpoint	1.04	1.79	0.0 8	0.49	- 0.44	0.32	1.28	0.86	0.80		- 0.43



ACCEPTED



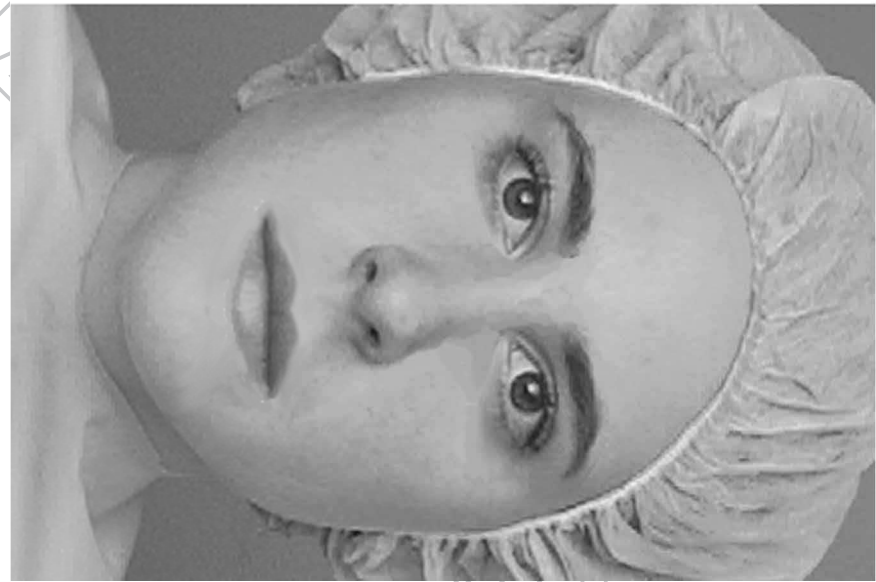
MUS

PT

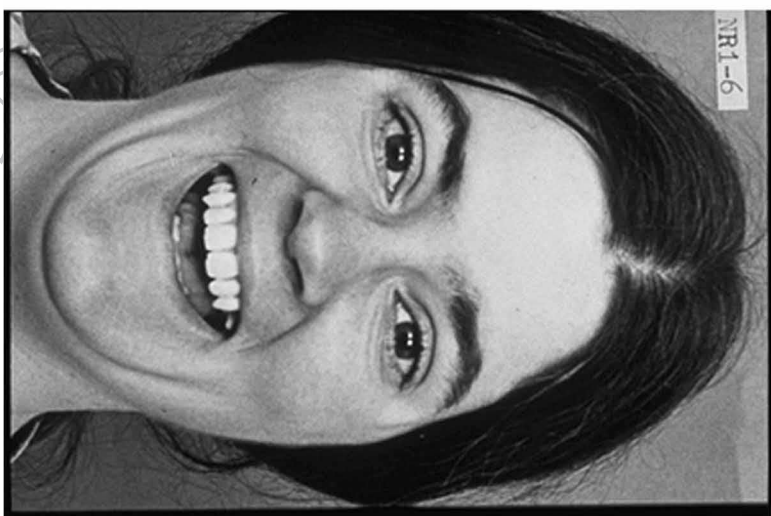
Ac



WV



FT



ACCEPTED MANUSCRIPT

Table 1

Means and standard deviations across participant group and task; CFE = Composite Face

Effect

Task	Condition	Accuracy				RT			
		Controls		DPs		Controls		DPs	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
FFT	Overall	0.82	0.10	0.41	0.15				
CFMT	Intro	0.99	0.02	0.82	0.21				
	Novel	0.83	0.10	0.46	0.11				
	Noise	0.68	0.16	0.34	0.09				
	Overall	0.82	0.09	0.51	0.07				
CFPT	Upright	4.41	1.30	5.73	1.68				
(Inaccuracy)	Inversion Index	-0.32	0.17	-0.21	0.15				
Configural	GlobalCon	0.99	0.02	0.99	0.02	2.74	0.06	2.82	0.14
	GlobalIncon	0.98	0.03	0.98	0.03	2.77	0.08	2.84	0.13
	LocalCon	1.00	0.00	0.99	0.02	2.79	0.11	2.80	0.12
	LocalIncon	0.97	0.04	1.00	0.00	2.81	0.10	2.85	0.13
	Overall	0.98	0.02	0.99	0.01	2.78	0.08	2.83	0.12
Mooney	Overall	0.98	0.04	0.98	0.02	2.92	0.07	2.98	0.07
Composite	IntactDiff	0.93	0.08	0.93	0.06	3.24	0.14	3.36	0.10
	IntactSame	0.81	0.18	0.87	0.12	3.30	0.17	3.39	0.08
	MisalignedDiff	0.86	0.16	0.89	0.10	3.20	0.11	3.31	0.10
	MisalignedSame	0.95	0.04	0.97	0.04	3.16	0.14	3.24	0.12
	Overall	0.89	0.07	0.92	0.06	3.22	0.12	3.32	0.09

CFE	Overall	0.14	0.17	0.11	0.13	-0.14	0.12	-0.15	0.08
Jane	Spacing	0.85	0.08	0.78	0.10	3.32	0.17	3.52	0.23
Upright	Feature	0.95	0.06	0.95	0.05	3.21	0.12	3.34	0.12
	Contour	0.83	0.15	0.69	0.13	3.32	0.15	3.43	0.20
	Overall	0.88	0.08	0.81	0.05	3.28	0.14	3.42	0.16
Jane	Spacing	0.16	0.14	0.18	0.13	-0.13	0.14	0.10	0.22
Inversion	Feature	0.07	0.10	0.05	0.08	-0.11	0.14	-0.05	0.13
Effect	Contour	0.14	0.13	0.11	0.13	-0.08	0.17	-0.01	0.17
	Overall	0.12	0.07	0.11	0.06	-0.10	0.11	0.01	0.15
Viewpoint	Front	0.99	0.02	0.99	0.02	3.26	0.11	3.33	0.14
	45 Degrees	0.95	0.05	0.90	0.06	3.40	0.14	3.51	0.11
	90 Degrees	0.85	0.08	0.79	0.07	3.49	0.14	3.63	0.11
	Overall	0.93	0.03	0.89	0.04	3.37	0.13	3.47	0.11
Expressions	Overall	0.85	0.05	0.83	0.09				

ACCEPTED