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ORIGINAL PAPER

Investigating the Influence of Autism Spectrum Traits on Face Processing Mechanisms in Developmental Prosopagnosia

Regan Fry[1,2] · Xian Li[4] · Travis C. Evans[1,3] · Michael Esterman[1,3,6] · James Tanaka[5] · Joseph DeGutis[1,2]

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Abstract

Autism traits are common exclusionary criteria in developmental prosopagnosia (DP) studies. We investigated whether autism traits produce qualitatively different face processing in 43 DPs with high vs. low autism quotient (AQ) scores. Compared to controls (n = 27), face memory and perception were similarly deficient in the high- and low-AQ DPs, with the high-AQ DP group additionally showing deficient face emotion recognition. Task-based fMRI revealed reduced occipito-temporal face selectivity in both groups, with high-AQ DPs additionally demonstrating decreased posterior superior temporal sulcus selectivity. Resting-state fMRI showed similar reduced face-selective network connectivity in both DP groups compared with controls. Together, this demonstrates that high- and low-AQ DP groups have very similar face processing deficits, with additional facial emotion deficits in high-AQ DPs.

Keywords Developmental prosopagnosia · Autism quotient · Face memory · Holistic processing · Emotion recognition

Introduction

Developmental prosopagnosia (DP), or severe lifelong face recognition[1] impairment in the absence of brain injury or significant visual problems (Behrmann & Avidan, 2005; Duchaine et al., 2006; Susilo & Duchaine, 2013), has a general population prevalence rate of approximately 2% (Kennerknecht et al., 2006). Though individuals with DP typically exhibit normal social-emotional functioning apart from face recognition difficulties (Duchaine et al., 2009), there is evidence that DP is associated with an increased rate of autism spectrum disorder (ASD; Minio-Paluello et al., 2020), defined in the DSM-5 as a group of developmental disabilities affecting communication and social behavior. Likewise, it has been reported that those with ASD have a substantially higher rate of DP (up to 36%,[2] Minio-Paluello et al., 2020) than the general population prevalence rate of 2% (Kennerknecht et al., 2006). However, the nature and causes of the co-occurrence between autism traits and DP are poorly characterized (Cygan et al., 2018). As a field, DP researchers have generally assumed that individuals with comorbid DP and either an ASD diagnosis or higher autism traits have a different type of prosopagnosia and have routinely excluded this sizeable group of DPs from their studies (Bate et al., 2019; Corrow et al., 2016; Dalrymple & Palermo, 2016; Shah et al., 2015a, 2015b). For example, it could be that face recognition deficits in those with higher

✉ Joseph DeGutis
degutis@hms.harvard.edu

1 Boston Attention and Learning Laboratory, VA Boston Healthcare System, 150 S. Huntington Ave., 182JP, Boston, MA 02130, USA

2 Department of Psychiatry, Harvard Medical School, Boston, MA, USA

3 Department of Psychiatry, Boston University School of Medicine, Boston, MA, USA

4 Psychological and Brain Science Department, Johns Hopkins University, Baltimore, MD, USA

5 Department of Psychology, University of Victoria, Victoria, BC, Canada

6 National Center for PTSD, VA Boston Healthcare System, Boston, MA, USA

[1] Though the term 'face recognition' has been used to describe both face memory and face perception (e.g., Benton Face Recognition Test), in the present study we use the term to refer to face memory.

[2] Although labeled 'developmental prosopagnosics', the diagnostic criteria were less strict than typically used in prosopagnosia studies and included individuals who did not self-report face recognition difficulties. Including individuals who had z-scores < -2 on the CFMT and who self-reported face recognition deficits on the PI20 would result in 12% of their sample having DP, which is still far greater than expected in the general population.

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ASD traits may be due more to social aversion and lack of interest rather than more fundamental deficits in face perception or memory (see below). The goal of the present study was to examine whether individuals with developmental prosopagnosia (DPs) who have higher levels of autism traits (i.e., broader autism phenotype or BAP, Landry & Chouinard, 2016; Wheelwright et al., 2010) differ from DPs with lower levels of autism traits across a broad battery of assessments including face memory, face perception, holistic face processing, eye and mouth processing, emotion recognition, and in their neural selectivity and connectivity of face processing regions measured by fMRI.

Developmental prosopagnosia is considered to be a disorder that is selective to face perception and memory, with a subset of DPs potentially showing concurrent deficits in object recognition (Geskin & Behrmann, 2017; though see Fry et al., 2020). In contrast, ASD encompasses a much broader set of impairments that affect domains of social interaction and communication, which can include symptoms similar to those of DP such as face memory impairments and increased social anxiety (Ozonoff et al., 2008; Davis et al., 2011; DSM-5). Although there is evidence that the deficits related to autism traits and DP are dissociable (e.g., Duchaine et al., 2009), other results indicate that the impairments of the two disorders can overlap. In particular, Minio-Paluello and colleagues (2020) recently showed that over a third of their sample of 80 adults with autism had significant face memory impairments on the Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006) that could not be explained by variance in general intelligence. However, the extent to which the presence of autism traits alters the neural and behavioral manifestation of DP has yet to be described in detail.

When occurring in isolation, individuals with DP and ASD both demonstrate face memory deficits, though the mechanisms underlying these deficits may differ. Compared with typically developing controls, individuals with ASD demonstrate less interest in faces, worse face memory, and worse facial emotion recognition (Dwyer et al., 2018; Grelotti et al., 2002; Weigelt et al., 2013), largely thought to be due to avoidance of the eye region of the face and an aversion to social stimuli (Dalton et al., 2005; Madipakkam et al., 2017; Tanaka & Sung, 2016; Weigelt et al., 2012). These characteristics contrast with findings from non-ASD DP studies showing that, despite severe face recognition deficits, the majority of DPs have intact emotion recognition ability (Duchaine et al., 2003; Humphreys et al., 2007) or show more modest deficits in emotion recognition (Biotti & Cook, 2016; Kress & Daum, 2003). DPs notably demonstrate a wide range of face processing deficits, many of which can also be found in ASD, such as impairments in face memory and decreased attention to the eyes (Bobak et al., 2016), as well as other impairments not usually associated with ASD, such as poor face matching ability (Mishra et al., 2021; White et al., 2017) and holistic face processing deficits (DeGutis et al., 2012; Avidan et al., 2011; Palermo et al., 2011; though see Biotti et al., 2017). DPs' impairments in face recognition can also occur in the absence of impaired social-emotional communication impairment (e.g., reading social cues, body language, etc., though some show increased social anxiety; see Davis et al., 2011) or motivational impairment (Duchaine et al., 2009). This contrasts with the face processing pattern seen in ASD, wherein several studies have found intact holistic processing (using the Part-whole task, composite task, and the Thatcher illusion–see Weigelt et al., 2012 for a review) with only isolated studies finding reduced holistic processing abilities (e.g., O'Brien et al., 2014, using upright and inverted animated faces). The lack of consistent holistic face processing impairments in individuals with ASD further suggests face recognition impairments in the general autism population are not driven by impairments in face perception per se but are instead the result of atypical gaze patterns and/or reduced attention to the internal features of the face. In contrast, DP studies have demonstrated a consistent pattern of holistic processing deficits using the part-whole task (DeGutis et al., 2012), face inversion tasks (Klargaard et al., 2018), and less consistently, the composite face task (Avidan et al., 2011; Palermo et al., 2011; see Biotti et al., 2017 for an exception).

On a neural level, ASD has typically been associated with more widespread network deficits than DP (Uddin et al., 2013). In particular, individuals with ASD have shown reduced resting-state functional connectivity between the posterior superior temporal sulcus (pSTS), a brain region involved in understanding social motivations and actions, and fronto-parietal regions in the 'action observation' network (Alaerts et al., 2014). Additionally, fMRI studies have found reduced activation of the temporal parietal junction in autism, proposed to support 'theory of mind', while viewing socially awkward stimuli (Pantelis et al., 2015). ASD studies examining brain activation in face-selective regions such as the fusiform face area (FFA) and occipital face area (OFA) have found conflicting results. While some studies found reduced FFA and OFA activation in response to faces (Grelotti et al., 2005; Humphreys et al., 2008; Pierce et al., 2001; Schultz et al., 2003), others have reported activation similar to typically developing controls (Jiang et al., 2013). These conflicting findings may be linked to the heterogeneity of ASD individuals. In contrast to individuals with ASD, DPs frequently demonstrate reduced face selectivity in core (OFA, FFA, pSTS) and extended (anterior temporal) face-selective regions during localizer tasks (Gerlach et al., 2019; Jiahui et al., 2018) as well as reduced FFA face adaptation (Furl et al., 2011) and reduced resting-state connectivity amongst face-selective regions (Song et al., 2015,

but see Behrmann et al., 2005 for an exception). Overall, ASD commonly implicates brain regions/networks involved in social-emotional communication and social utilization of face information (e.g., pSTS), while DP is often associated with ventral occipito-temporal and anterior temporal regions more involved in face perception and identification (e.g., OFA, FFA, anterior temporal face area).

The established co-morbidity of and similarities between the two disorders raise the question of whether cases of comorbid ASD and DP are the result of autism spectrum disorder causing face recognition impairments (e.g., the strong interaction model, see below for further description), or whether the two are simply distinct but co-occurring disorders (e.g., the independent co-occurrence model, see below). Prior studies investigating the relationship between autism traits and face recognition ability as well as impairments in these domains have shown both overlapping (Halliday et al., 2014) and distinct mechanisms (Barton et al., 2004; Minio-Paluello et al., 2020). In a typically developing population, Halliday and colleagues (2014) investigated the reciprocal relationship between face recognition and ASD trait levels using separate hierarchical multiple regressions to determine which factors best predicted face recognition and Autism Quotient scores (AQ, Baron-Cohen et al., 2001a, 2001b; Wheelwright et al., 2010) on a continuous level. They found that the two factors exhibited a bi-directional relationship: AQ scores reliably predicted face recognition scores, and face recognition performance uniquely contributed to scores on the AQ independently from gender, university major, and performance on an object memory task. This study suggests that, within a healthy control sample, there is a reciprocal relationship where either autism traits may lead to a decrement in face processing ability, or face recognition impairments may heighten autism traits related to social-emotional communication.

Other studies have directly examined the link between face recognition and social abilities. Barton and colleagues (2004) compared the face recognition performance of 24 adults with social developmental disorder[3] (SDD) with a typically developed control group and a group of 12 prosopagnosics (9 acquired, 3 developmental) to determine the severity of face recognition deficits, if present. They found that while two-thirds of the SDD participants had face recognition impairments (*d*' ranging from 0.75 to 2.25, M = 1.59, on a Famous Faces Test, compared with a *d*' M = 2.77 in the control sample and M = 0.37 in the prosopagnosic sample), this subset with face recognition impairments did not differ from the remainder of the SDD group on the Social Skills Inventory (Riggio, 1992), indicating that severity of face processing impairments did not affect severity of social-emotional impairments in the group with SDD. This finding suggests that, while face processing deficits often co-occur with social developmental disorders, face processing deficits are not an inevitable result of social developmental disorders, nor are they necessarily modulated by the severity of the disorder. Another study by Minio-Paluello and colleagues (2020) measured face recognition impairments in a sample of 80 adults with autism and found that the subset of 29 individuals with both ASD and z-scores < -2 on the CFMT (indicating impaired face memory) did not differ from those who had autism in the absence of impaired face memory on any measures of autism symptom severity, including the Autism Diagnostic Observation Schedule (Gotham et al., 2009) and the AQ, nor did they differ on the Reading the Mind in the Eyes (RMET; Baron-Cohen et al., 2001a, 2001b) and the Wechsler adult intelligence scale (Wechsler, 2008). This further suggests that face recognition impairments in adults with autism are largely unrelated to the severity of social-emotional communication impairments. Taken together, these studies suggest the interesting possibility that face recognition and social-emotional communication may be related in the typically developing population but may not be as closely linked once a certain level of impairment is reached in either ASD or face recognition ability.

Although these studies provide insight into the reciprocal relationship between face recognition and autism traits, less is known about the manner in which autism traits affect the expression of face recognition impairments when DP is the primary disorder (though Barton et al., 2004 used a small sample of prosopagnosics as an impaired control group to measure face performance in their SDD group, they were not assessed for SDD using the Social Skills Inventory). Because DP is typically diagnosed using face memory performance and self-report questionnaires rather than face perception assessments (Bowles et al., 2009; Shah et al., 2015a, 2015b), individuals with very high levels of social impairment may reach the cut-off for prosopagnosia based on poor face memory alone, though their impairment may be due to social aversion and lack of visual input rather than face processing-specific deficits. Given this, one possible model of the relationship between DP and autism traits is that the expression of face impairment in DP is related to AQ score (as seen in the typically developing population; Halliday et al., 2014) and thus follows different behavioral patterns when accompanied by high levels of autism traits (i.e., strong interaction model). This might reflect, as some researchers suggest (Dalton et al., 2005; Riby et al., 2009), that face recognition impairments in conjunction with high levels of autism traits are more associated with external factors such as diminished gaze fixation rather than fundamental deficits in face perception or memory. If this is the case,

[3] SDD in this study encompasses autism, Asperger's, and pervasive developmental disorder—not otherwise specified. As of 2013, according to the DSM-5, these disorders are included under the diagnosis of autism spectrum disorder.

we would expect to see similarly impaired face memory performance (e.g., Cambridge Face Memory Test, Duchaine & Nakayama, 2006; measures of recollection, Stumps et al., 2020) in DPs with high and low levels of autism traits, while seeing less impaired face perception (e.g., Cambridge Face Perception Task, computerized Benton Face Recognition Task) in the DPs with higher levels of autism traits. In contrast, we would predict similar eye discrimination deficits in high and low AQ DPs on measures of feature discrimination ability such as the Part-whole and Georges tasks, but that these deficits would be driven by different mechanisms (e.g., eye contact aversion vs. perceptual deficits, respectively).

A second possibility is that when the population is strongly impaired in one domain (in this case, faces) ASD traits and DP more independently co-occur, and the level of autism traits does not impact either the severity or manner of face recognition impairments (independent co-occurrence model). This would align more closely with Barton and colleagues' (2004) finding that adults with SDD and co-occurring facial recognition impairments did not differ on a social skills measure from those without face recognition impairments. If this is the case, in the current study we would predict that DPs with high levels of autism traits would show a behavioral face recognition profile similar to that of DPs with lower levels of autism traits in tests of both face memory (Cambridge Face Memory Test, Old/New, recollection/familiarity) as well as face perception (Cambridge Face Perception Test, Same/Different Face Matching Task, computerized Benton Face Recognition Task, Part-Whole, Georges Task, University of Southern California Face Perception Task).

In the current study, our goal was to investigate how the presence of autism traits relates to the manifestation of DP in adults. We recruited 43 developmental prosopagnosics and 27 typically developing control subjects. DPs were categorized into low or high autism trait levels based on their AQ score. While not a diagnostic label, the broader autism phenotype (BAP) describes a subclinical set of characteristics that are qualitatively similar to features of autism and was initially developed to study family members of individuals with autism (Landry & Chouinard, 2016). Common characteristics of the BAP include mild impairments in social and communication skills that resemble those seen in autism spectrum disorder (Gerdts & Bernier, 2011), and occurrences of mild face recognition impairment have been found in parents of children with ASD (Wilson et al., 2010). To more effectively measure face processing impairments in the two groups, we collected data across a range of domains including face memory, face perception, holistic processing, facial feature discrimination, facial emotion recognition, fMRI localizer scans of face-, body-, object- and scene-selective regions, and resting-state fMRI. This was done to create a more complete profile of the deficits seen across groups. Because the reliability of individual measures of face processing can be limited (e.g., Ross et al., 2015), when possible, we incorporated multiple tasks within a domain in our MANOVA and multivariate regressions models to provide more robust evidence of similarities and differences between the two groups. While many of the tasks provided direct insights into our hypothesized outcomes (e.g., face memory and holistic processing), others were more exploratory in nature (e.g., object memory, body- and scene-selectivity) to examine potential group differences in other domains.

If the two disorders present themselves independently, we would expect to see a similar behavioral profile between the high AQ and low AQ DPs, reflecting that DPs' facial recognition impairments are not modulated by the presence of autism traits. Also, because ASD may particularly affect the social utilization of face information, we predicted that we would see differences between high and low AQ DPs in regions of the brain involved in social-emotional communication and emotion interpretation, such as the pSTS, while showing similar face selectivity in the OFA and FFA. Conversely, if DPs with high levels of autism traits demonstrate a different type of facial processing deficit than DPs with low autism traits, then we would expect to find variations in behavioral performance between the groups. Specifically, we would expect to see better holistic processing abilities in the high AQ group (Ventura et al., 2017; Weigelt et al., 2013), along with impaired face memory and perceptual sensitivity to the eyes compared to typically developing controls (Madipakkam et al., 2017; Tanaka & Sung, 2016). Across both the strong interaction and independent co-occurrence models, we would expect to see worse emotion recognition in the higher AQ group (Bolte & Poustka, 2003; Celani et al., 1999; Smith et al., 2010). By comparing these groups on a large battery of face perception, memory, and fMRI tasks, we can better characterize the impact that autism traits have on the behavioral and neural outcomes of DP.

Methods

Participants

Participants were 43 developmental prosopagnosics and 27 typically developed controls between the ages of 18 and 70 years old ($M_{DP} = 38.1$, $SD_{DP} = 13.9$, $M_{TD} = 42.4$, $SD_{TD} = 10.3$). Developmental prosopagnosics were recruited from our database of previous DP participants in the Boston area, references from other research labs (Dr. Matthew Peterson, Massachusetts Institute of Technology; Dr. Brad Duchaine, Dartmouth College, www.faceblind.org), and individuals who responded to our advertisement on the Massachusetts Bay Transportation Authority subway system.

Control subjects were recruited and tested at the Harvard Decision Science Laboratory in Cambridge, Massachusetts.

Developmental prosopagnosics reported lifelong face recognition deficits (all but one scored > 60 on the PI20) in the absence of significant neurological disorders or moderate/severe traumatic brain injury (TBI) or mild TBI in the past 6 months. All DPs had normal performance on the Wechsler Test of Adult Reading (M = 46.6, SD = 2.5; Wechsler, 2001), indicating normal full-scale IQ (the tests correlate at r = 0.73; Spreen & Strauss, 2006). Aside from face recognition impairment, the DPs were otherwise high functioning and able to complete an intensive 3-h testing battery. The majority of the DPs scored 44 or below (z-score < -2) on the original CFMT (see supplementary materials; Duchaine & Nakayama, 2006), indicating severe objective face recognition deficits. We also included six participants that we consider to be mild DPs who scored between 44 and 48 on the CFMT (-2 < z-score < -1.5), since the rest of their profiles were consistent with prosopagnosia (e.g., PI20 > 60, famous faces < 0.65). Notably, removing these participants had no appreciable effects on the key analyses. Typically developing controls did not report any face recognition deficits and all scored 45 or above on the CFMT. Participants were also pre-screened and excluded if they had musculoskeletal impairments that would hinder performance on computer tasks, a lack of English proficiency, any current psychiatric disorders, intellectual impairments, or current alcohol or substance dependence. All participants had normal or corrected-to-normal vision and scored within the normal range on the Leuven Perceptual Organization Screening Test (L-POST; Torfs et al., 2014) to rule out other causes of poor face recognition.

Informed consent was obtained for all participants prior to data collection according to the Declaration of Helsinki. Participants were compensated for their time at a rate of $10 per hour. The study was approved by the VA Boston Healthcare System and Harvard Medical School Institutional Review Boards, and all study tasks were completed at the VA Boston Healthcare System in Jamaica Plain, Massachusetts or the Harvard Decision Science Lab in Cambridge, Massachusetts.

Autism Traits

Our measure of autism traits in the population was the widely used, validated Autism Quotient questionnaire (AQ; Baron-Cohen et al., 2001a, 2001b). The AQ is a 50-item self-report questionnaire designed to identify symptoms of autism spectrum disorder in adults. Participants are instructed to respond either "definitely agree," "slightly agree," "slightly disagree," or "definitely disagree" to each item, with approximately half of the items designed to evoke an "agree" response from a neurotypical adult. The questionnaire covers the domains of social skills, communication, imagination, attention to detail, and attention switching and for the purposes of the current study, the total score was used (Baron-Cohen et al., 2001a, 2001b).

Categorization of low vs. high AQ was based on the broader autism phenotype (BAP; Wheelwright et al., 2010). Based on Wheelwright and colleagues' 2010 study, a score of 23 or above on the AQ is > 1 SD above the normative mean and thus constitutes the broader autism phenotype. Using this criterion, in the current study a score of 23 or above was classified as an "AQ+ DP" (N = 15) while a score of below 23 was classified as an "AQ- DP" (N = 28). This cut-off allowed us to examine the relevant features typical of autism spectrum disorder while retaining large enough group sizes for meaningful group-level comparisons.

Memory Measures

Cambridge Face Memory Test

The Cambridge Face Memory Test (Duchaine & Nakayama, 2006) is a highly validated and widely used face memory task. During the learning phase, participants are shown each target face from three different viewpoints for three seconds each and are then asked to select which face they just viewed from a selection of three faces using the number keys. This learning trial repeats for each of the six target faces. After the learning phase, participants are shown all six target faces again for a total of 20 s. They are then given 30 forced-choice trials where they must select from among three faces which one was one of the six target faces they just learned. After these 30 test trials, participants again are shown all six faces for another 20 s, and the final 24 trials include Gaussian noise intended to obscure the internal facial features. The dependent variable is the total correct trials out of 72.

Old/New Face Recognition Task

During the study phase of the Old/New task, participants are shown 60 cropped and grayscale faces and are instructed to study the faces for a later memory test (Stumps et al., 2020). Faces were presented in the center of the screen for 1.5 s each, and each face repeated a second time in the same order. All subjects received the same order of faces. Immediately after the study phase, participants were presented with the 60 target and 60 lure faces randomly intermixed, and on each trial were asked to rate on a scale of 1–6 their level of confidence in classifying each face as "old" or "new" (1–Confident Old, 2–Somewhat Sure Old, 3–Guessing Old, 4–Guessing New, 5–Somewhat Sure New, 6–Confident New). Confidence ratings appeared directly below each face. Participants were instructed to try and use all confidence ratings when responding. Recollection and familiarity

parameters were calculated using the Matlab ROC toolbox (see Stumps et al., 2020). "Recollection" is reflective of a participant's ability to specifically recall a face as seen previously with context specific to its prior viewing. "Familiarity," on the other hand, reflects a participant's belief that they saw a face before without recalling the specific instance in which they viewed the face. DPs have been shown to rely more strongly on familiarity and present with deficits in face recollection (Stumps et al., 2020).

Novel Object Memory Test

The Novel Object Memory Test (NOMT) mirrors the structure of the CFMT using novel objects (Ziggerins) instead of faces (Richler et al., 2017), and omitting the noise trials in the latter half of the test to better equate scores between the two tasks. This task is a useful measure of domain-general object memory separate from face recognition ability. Similar to the CFMT, the dependent variable is the total correct trials out of 72.

Perceptual Measures

Part-Whole Task

In the part-whole task (from Tanaka et al., 2004, used with permission of Jim Tanaka, University of Victoria), target faces were designed using a single Caucasian male face and inserting different features (eyes, nose, mouth) to create six unique target faces. During whole trials, foil faces were created by switching one of the features (eyes, nose, or mouth) with a feature from a different target face. When only a single feature was shown during the test phase (part trials), foil stimuli were an isolated facial feature (eyes, nose, or mouth) from a different target face. During the study phase, one of the six target faces is presented in the center of the screen for 1,000 ms following a 500 ms fixation cross. Next, a scrambled face mask is displayed for 500 ms. During the test phase, participants are presented with a pair of images side by side, either whole faces (whole trials) or isolated features (part trials). One of the images matches the target they just viewed, and the other is a foil image. Stimuli remain on the screen until participants select either '1' to indicate that the left image is the target image, or '2' to indicate that the right image is the target. For whole trials, subjects must choose between the whole target face and a whole foil face. For part trials, subjects must choose between a single feature from the target face (eyes, nose, or mouth) and the same feature from one of the foil faces. Subjects did not know which feature they would be tested on during each trial. There were 72 trials (36 parts trials and 36 whole trials), with 24 trials for each feature category. We calculated the holistic advantage by first regressing the part trial 'control condition' from the whole trial 'condition of interest' (using the regression equation in the control sample, e.g., see DeGutis et al., 2013), and then applying this equation to calculate residuals for DPs and controls.

Cambridge Face Perception Test

The Cambridge Face Perception Test (CFPT) is a computerized sorting task in which participants arrange six front-view faces according to their similarity to a three-quarter view target face (Duchaine et al., 2007). Participants completed eight upright sorting trials and eight inverted sorting trials. The dependent variable is the sum of the deviations from the correct order across all sorting trials. We calculated the holistic advantage by first regressing the inverted trial 'control condition' from the upright trial 'condition of interest' (using the regression equation in the control sample, e.g., see DeGutis et al., 2013), and then applying this equation to calculate residuals for DPs and controls.

Georges Task

The Georges task provides a measure of internal and external facial feature discrimination ability (Malcolm et al., 2004). On a single trial, participants are presented with frontal views of three same-identity unfamiliar faces in a triangular arrangement for two seconds, with the lower two faces slightly offset horizontally. Two faces are identical and one has a single feature manipulation. There were six possible manipulations spanning three categories: internal feature position, feature size, and external contour. Feature position was manipulated with either a decrease in interocular distance or elevation of the mouth. Feature size was modified by increasing the vertical width of both eyes or increase in the vertical width of the mouth. External contour was modified by elevating the hairline or narrowing the chin. Participants indicated which of the three faces differed from the other two using the left, right, and up arrow keys. There were 108 trials, with six different face identities. Dependent variables were the percentage correct for each feature.

Computerized Benton Face Recognition Task

In this computerized version of the original Benton Face Recognition Task (Benton & Van Allen, 1968; Rossion & Michael, 2018), six grayscale photographs of unfamiliar faces (3×3.5 cm) are presented with the majority of external features cropped out. The target face is presented at the top of the screen with the six test faces below, in two rows of three. During the first six trials participants must select the face that matches the target exactly, and in the next 16 trials they are instructed to select which three faces are the same identity as the target face. During this portion of the

test the six test faces have either lighting changes or viewpoint changes. Lighting and viewpoint change trials are intermixed, and the stimuli are displayed until the participant completes their responses. Participants are instructed to make their responses as quickly as possible without losing accuracy. There are 54 trials, and the dependent variable is the total number of correct matches.

University of Southern California Face Perception Test

The University of Southern California Face Perception Test (USCFPT) is a perceptual face-matching task that uses synthetic grayscale computer-generated faces. The face stimuli were generated using Facegen software and were provided by Irving Biederman (Yue et al., 2012). The faces include no external cues such as hair or clothing. Each trial displayed a single target face (3.2×4.2 cm) at the top of a screen, and two test faces below it for a total of 5 s. The participant must then select which of the two test faces matches the top target face using either the left or right arrow key. Responses were recorded even after the faces disappeared. There was a total of 96 trials.

Same/Different Face Matching Task

The Same/Different Face Matching Task (SDFMT; Berger et al., 2022) is a simultaneous matching task where the participant must indicate whether two faces are the same identity or different identities from among different viewpoints (front view vs. 3/4 view) or changes in lighting (fully lit vs. lighting from the side). Face images are greyscale and cropped to remove external features such as hair or clothing. During each trial, a pair of faces is presented simultaneously for 3 s each and participants are instructed to respond '1' if the faces are the same identity and '0' if the faces are different identities. Foils were selected to have matching verbal descriptions (e.g., dark hair, thin nose, large eyes). There are seven different trial types: (1) Same identity from front view, (2) same identity with lighting change, (3) same identity with viewpoint change, (4) different identity from front view, (5) different identity with lighting change, (6) different identity with viewpoint change, (7) same identity on a different day, (8) same identity and same day but cropped differently. There are 210 total trials, with 30 trials per trial type.

Emotion/Self-Report Measures

Social Interaction Anxiety Scale

The Social Interaction Anxiety Scale (SIAS; Mattick & Clarke, 1998) is a self-report scale designed to measure the amount of distress an individual experiences during social interactions with others. There are 20 items, each measured on a five-point Likert scale. Each item includes a statement about social interaction (e.g., "I am tense mixing in a group"). Individuals can respond whether they believe the characteristic is "not at all characteristic or true of me," "slightly characteristic or true of me," "moderately characteristic or true of me," "very characteristic or true of me," or "extremely characteristic or true of me." Three of the items are reverse-scored, and the points are then summed to create a total measure score. Only 22 DPs completed the SIAS.

Reading the Mind in the Eyes

The Reading the Mind in the Eyes Test (Baron-Cohen et al., 2001a, 2001b) was designed to test the ability to decipher the emotions of others by viewing only the eyes. In this test, an image showing only the eye region of the face (eyes, eyebrows, bridge of nose) is presented along with four mood descriptors. The participant must choose which of the four words best describes the emotion the eyes are showing. The dependent variable was the total correct out of 36 items. Thirty-one DPs and none of the control sample completed the RMET test.[4]

20-item Prosopagnosia Index

The 20-item Prosopagnosia Index (PI20) is a self-report questionnaire that assesses difficulty with face recognition (Shah et al., 2015a, 2015b). Items are measured on a five-point scale from "Strongly disagree" to "Strongly agree" and include statements such as "I feel like I frequently offend people by not recognizing who they are" and "I often mistake people I have met before for strangers." The dependent variable is the total score out of 100, with 100 being the most severe prosopagnosia symptoms.

Imaging Measures

fMRI Scanning Procedure

There were 33 DPs (six males, mean age 37.5 y) and 25 typically developing adults (11 males, mean age 33.6 y) that participated in the fMRI session, including 22 of the 28 AQ- DPs and 11 of the 15 AQ+ DPs. It should be noted that the resting-state and task-based fMRI results for overall DPs vs. controls were previously reported by Li et al. (2020) and for

[4] A 102-person age- and gender-matched control group collected after this study was completed had an average RMET score of 28.80 (SD = 3.57). This score was significantly higher than that of the AQ+ DP group ($p = .016$) but did not differ from the AQ- DP group ($p = .606$). Details describing this later control group are included in the supplementary materials.

the purposes of the current study, DPs were further broken up into AQ+ DP and AQ- DP groups.

Using a 3-Tesla Siemens Prisma and 32-channel head coil, we performed the following scans for each participant: (1) high-resolution 3D anatomical MPRAGE, (2) one 6-min resting-state fMRI scan, (3) four runs of dynamic localizer scans containing four visual categories (faces, scenes, bodies, and objects). Stimuli in the localizer were brief video clips of each category similar to those used in Jiahui et al. (2018). Each participant completed four runs, which comprised 18 s category blocks of video clips, which in total lasted 4 min (per run). Each visual category was displayed for 2 blocks in each run in a quasi-random order across scans, with an exception for faces (4 blocks in total, with 2 blocks of non-famous faces and 2 blocks of famous faces, which was composed of video clips of Barack Obama and Donald Trump). Stimuli were presented using PsychoPy v1.85.4 and displayed to the participant via at the rear of the scanner.

fMRI Processing and Analysis

To promote replicability, we adopted the default pipeline offered by fMRIPrep (see detailed description in supplementary material) to preprocess both the resting-state and the dynamic localizer task fMRI data. The fMRIPrep preprocessed dynamic localizer scans were then smoothed at a 6 mm kernel (see nilearn.image.smooth_img), and submitted to a GLM in SPM12 (welcome center human neuroimaging), with physiological noise regressors (i.e., CSF signal, white matter signal, head displacement, and six head-motion parameters [three rotations and three translations]) computed from fMRIPrep included. Contrasts between categories were subsequently added to examine the specialized tuning towards the face category at our regions of interest.

Category selectivity was used to measure how strongly tuned a cortical area was to a particular category. Using the dynamic localizer scans, selectivity for faces was defined as the contrast between the response to faces (the combination of famous and non-famous) and the response to scenes. Similar to previous studies (e.g., Ramot et al., 2019), we chose the face vs. scene contrast to maximize our ability to localize robust face selective regions (e.g., greater sensitivity to detect occipital face area, Schwarz et al., 2019), though it should be noted that very similar results were found when examining the face vs. object contrast. The bilateral fusiform face area (FFA), occipital face area (OFA), posterior superior temporal sulcus (pSTS), and anterior temporal lobe (ATL) were identified for each individual. Using a similar approach, we also individually identified scene- (occipital place area-OPA, parahippocampal place area-PPA, scenes vs. objects), body- (extrastriate body area-EBA, fusiform body area-FBA, bodies vs. objects), and object-selective regions (lateral-occipital cortex-LO, and the posterior fusiform sulcus-pFS, objects vs. faces/scenes/bodies).

The four runs from the localizer task were divided into the localization runs and the test run to carry out a "leave-one-out" analysis. In each of the leave-one-out combinations, three of the four runs for a participant were used to localize the regions of interest (ROIs) for faces. To avoid the double-dipping problem, the responses of the selected ROIs to each stimulus condition were then measured in the left-out run. All four combinations were analyzed and then averaged to produce the final result for each participant.

To avoid rater bias, each category selective ROI was individually defined with an automated pipeline. Specifically, using the Harvard–Oxford Atlas, an anatomical mask was created as a structural confinement for each ROI within each category. For example, for the right FFA, in each subject, the four runs' face vs. scene contrast map was first mapped to retain only the positive-valued voxels, i.e., voxels that were selectively responsive to faces in contrast to scenes. Then, the anatomical confinement for the right FFA was applied to each of the four runs' (face vs. scene) contrast map to retain the positive values only in the right ventral occiptal-temporal region (i.e., the anatomical area that contains the functional area of right FFA, regardless of individual variation). We then identified the largest most activated cluster within this region (see nilearn.plotting.find_xyz_cut_coords) for each run's contrast map. The center of mass for the identified cluster was computed for each run. The coordinates computed from the localization runs were averaged, over which a 6 mm radius sphere was created from the left-out run's contrast map. The beta values within this sphere were averaged to index each individual's right FFA specialized tuning towards faces (i.e., face selectivity) in the current left-out run. This process was looped through the four leave-one-out combinations. Finally, we used the average of the four runs to estimate selectivity in each stimulus-selective region in each participant.

Resting State fMRI

First-level models Following the preprocessing steps outlined above, resting-state data were analyzed at the single subject level using general linear models (GLMs). Within first-level models, we modeled nuisance regressors including 6 rigid body motion regressors, framewise displacement between volumes, mean time series extracted from white matter and cerebrospinal fluid, and a linear trend to account for slow drift throughout the scan session. To further minimize motion-related confounds, we censored TRs that exceeded 0.3 mm framewise displacement as well as the previous TR. Within these first-level models, data were bandpass filtered (0.01–0.10 Hz) to remove additional noise

associated with physiological processes of non-interest (e.g., respiration).

Whole-brain model Using the residual outputs from first-level models, we extracted the cleaned time series for the left and right pSTS ROI defined by the face localizer task. For the left and right pSTS ROIs, we averaged and combined the time series to form a single bilateral ROI time series. We characterized group differences in voxel-wise connectivity across the brain using AFNI's 3dMVM program (Cox, 1996). Given our primary research aims, we focused on contrasting voxel-wise connectivity between the AQ+ and AQ- DP groups. To control family-wise error (FWE) in these exploratory analyses, we used a combined voxel-wise and cluster threshold approach. To determine the necessary cluster threshold at a nominal threshold of $p = 0.01$, we submitted the observed smoothness of the residual outputs to AFNI's more stringent non-parametric 3dClustSim function. Using a voxel-wise threshold of $p = 0.01$, a cluster threshold of 48 voxels controlled for FWE at $p < 0.05$. For clusters that survived whole-brain correction for the AQ+ vs. AQ- DP group contrast, we extracted beta coefficients to characterize the pattern of group differences.

Statistical Approach

First, we ran a multivariate analysis of variance (MANOVA) to test for any group differences within the broader domains of face memory, face matching, holistic processing, and feature processing. Including multiple tasks measuring these broader face recognition processes provides converging evidence and ensures that we can characterize an overall pattern of either similarities or differences between the two groups that are not subject to variation in a single task, as well as allows us to measure different aspects of these constructs by varying elements such as presentation time, number of faces presented, and recall delay. To further ensure that our MANOVAs did not miss significant differences within a subdomain (e.g., eye processing), we performed Bayesian null hypothesis testing as well as performed t-tests on individual measures, FDR-corrected for the number of tests in that domain (see Table 2). For converging evidence using a continuous measure of autism traits, we next ran multivariate multiple regressions to determine whether measures of face processing were significantly predicted by continuous AQ scores. Next, we calculated bivariate Pearson correlations between the AQ scores and each of the behavioral measures within the entire DP sample (FDR-corrected for multiple comparisons) to examine potential relationships between the level of autism traits and different aspects of face recognition. We also ran formal outlier analyses ($> 1.5 \times$ interquartile range added to the third quartile, SPSS version 25) and re-ran the key analyses excluding the outliers from the relevant tasks (CFPT, USCFPT, Part-whole, inversion effect, and Georges). Removing the outliers yielded identical results, and these analyses can be found in the supplementary materials.[5]

For the task-based fMRI analyses, we focused on face selectivity and first conducted a 2 (DP/TD) × 4 (region) × 2 (hemisphere) ANOVA comparing category selectivity between the DP and TD groups to determine if there were general DP differences. We next performed a 3 (AQ+/AQ-DP/Control) × 4 region × 2 (hemisphere) ANOVA to determine whether any of the groups differed in their face selectivity. We next examined selectivity to categories beyond faces. We tested whether DPs and Controls showed selectivity differences in body-, scene-, and object-selective regions using a 2 (DP/control) × 6 (region) × 2 (hemisphere) ANOVA and finally, examined AQ+ and AQ- DP differences by performing a group × 6 (region) × 2 (hemisphere) ANOVA.

To analyze resting state functional connectivity within the face network, we conducted a 2 (DP/TD) × 4 (region) × 2 (hemisphere) ANOVA between the DP and TD groups to determine whether the groups differed in their network connectivity for each node in the face network. We then conducted a 2 (AQ+/AQ- DP) × 2 (hemisphere) ANOVA of the pSTS, followed by a 2 (group) × 3 (region) × 2 (hemisphere) with the remaining face regions to determine if there were any differences between the AQ+ and AQ- DP groups. Finally, for the expoloratory whole-brain analyses that used a bilateral pSTS ROI time series, we compared the connectivity of AQ+ and AQ- DPs for each of the regions that survived whole-brain correction using independent-samples *t*-tests.

Sample Size Justification

Our sample size was guided by previous studies comparing face recognition between DPs and controls (N = 76, 38 DP, DeGutis et al., 2012; N = 60, 30 DP, Fry et al., 2020; Barton et al., 2004; Jiahui et al., 2018). To test for individual differences, we used a sample similar in size to studies that have found significant individual differences between feature sensitivity, holistic processing, and face recognition (N = 38, Richler et al., 2017; N = 43, DeGutis et al., 2013). Further, studies of the broader autism phenotype have previously characterized group-level behavioral differences between controls and individuals with the BAP in a sample size of 50 when

[5] Because 11 of the DPs in the AQ+ group had AQ scores below the standard clinical cut-off of 32 (Woodbury-Smith et al., 2005) suggestive of mild ASD traits, we also ran exploratory analyses on a smaller group of DPs with AQ scores equal to or above 32 (N = 4), comparing them with the AQ- group measures to evaluate if there were any behavioral differences in the group that fell above the clinical cut-off. These analyses showed very similar results and can be found in the supplementary materials.

Table 1 Group demographic means, standard deviations, and ANOVA results comparing all three groups

	AQ+ DP		AQ− DP		TD		ANOVA
	M	SD	M	SD	M	SD	p-values
Age	39.87	11.38	37.11	15.20	42.37	10.29	.313
Gender (F:M)	9:5	–	24:4	–	14:13	–	.024*
Education	17.20	3.10	17.81	2.04	15.63	4.06	.043*
AQ	28.33	5.38	14.50	4.84	19.33	6.36	< .001***
PI20	80.80	10.81	82.71	7.56	36.89	7.06	< .001***
CFMT	40.40	3.77	39.64	4.71	58.78	7.92	< .001***

*Statistically significant at $p < 0.05$

***Statistically significant at $p < .001$

investigating speed of orientation to social cues in the eye region (Cohen's *d* ranging from 0.85 to 0.93; 25 controls, 25 BAP; Scheeren & Stauder, 2008). Though the previous literature does not provide an indication of the sizes of effects that we would expect to see, we included a sample size of participants similar to other studies comparing face processing between DPs and controls and describing significant individual differences. In particular, Barton and colleagues (2004) compared 12 individuals with prosopagnosia, 24 adults with SDD, and 12–15 healthy controls and were able to identify distinct differences (Cohen's *d* ranging from 2.79 to 3.45) in performance on face recognition between the healthy controls, prosopagnosics, and a subgroup of the adults with SDD. Thus, based on these previous studies, we included a sample size of 43 DPs and 27 typically developed controls.

For the neuroimaging analyses, previous studies have found significant DP vs. Control differences in face-selective regions (Cohen's d = 0.69) using sample sizes of 22 DPs and 27 Controls (e.g., Jiahui et al., 2018). Further, studies have found significant differences in face-selective regions between ASD adults and Controls (Cohen's d = 1.13) when using sample sizes of 13 ASD and 15 Controls (e.g., Humphreys et al., 2008). Thus, our sample size of 33 DPs and 25 Controls should provide sufficient power to detect both DP vs. Control and autism-trait related differences in DPs.

Results

Participants

The AQ+ DP group (n = 15) did not differ from the AQ- DP group (n = 28) in age [$t(41) = -0.62$, $p = 0.542$], education [$t(40) = 0.78$, $p = 0.443$], or gender ($p = 0.116$), see Table 1. The average AQ of the AQ+ group was significantly higher than that of the AQ- group ($t_{41} = 8.59$, $p < 0.001$). Similarly, the DP group did not differ from the typically developed control group in age, however, the TD group had a higher proportion of males than the AQ- group as well as a lower overall education level. Education has shown not to predict additional variance in general memory performance outside of age (West et al., 1992), and face recognition abilities have shown to be independent of both education and IQ (Wilmer, 2017). Further, the gender imbalance between the groups would, if anything, decrease the DP/TD group differences in face recognition performance, as females have shown slightly better face recognition performance than males (Mishra et al., 2019; Rennels & Cummings, 2013). The AQ scores of the AQ + group were significantly higher than those of the TD group ($t_{40} = 4.63$, $p < 0.001$), and the average AQ score of the AQ- group was significantly lower than the TD group ($t_{53} = 3.18$, $p = 0.002$).

Face and Object Memory

We first compared AQ+ and AQ- group performance on our battery of face memory tasks (CFMT, famous faces memory test, Old/New, recollection, familiarity) using a MANOVA, expecting that AQ + DPs would show similar levels of memory impairments to AQ- DPs, as all DPs were selected for poor face memory. The overall memory model was not significant ($F(5,35) = 1.48$, $p = 0.223$, $\eta_p^2 = 0.174$). Results from follow-up *t*-tests for each measure also showed non-significant group differences (see Table 2).

We next performed Bayesian null hypothesis testing and found that comparing scores between the two DP groups yielded a Bayes Factor (BF_{01}, in support of the null hypothesis) of 3.77 for the CFMT, 3.59 for the NOMT, and 1.57 for the FFMT. Comparing performance on the Old/New Face Recognition task between groups resulted in a BF_{01} of 2.68 for overall score, 4.14 for recollection, and 3.63 for familiarity, all indicating anecdotal (1–3) to substantial (3–10) evidence in favor of the null hypothesis (Jarosz & Wiley, 2014).

To determine if continuous AQ scores predicted overall face memory performance, we next performed a multivariate multiple regression in the DP group. The five face memory measures were not predicted by continuous AQ scores ($F(5,61) = 0.19$, $p = 0.966$, $\eta_p^2 = 0.015$). Examining Pearson correlations between the AQ and each of the memory measures demonstrated a very similar pattern of results–the AQ showed

Table 2 AQ- DP, AQ+ DP, and control behavioral task performance

Measure	AQ− DP	AQ+ DP	TD	*p*-values, *q*-values, and Cohen's *d*		
	N = 28	N = 15	N = 27	AQ+ vs. AQ-	AQ- vs. TD	AQ+ vs. TD
Cambridge Face Memory Test	39.64 ± 4.71	40.40 ± 3.77	58.78 ± 7.92	$p = .598$	$p < .001$***	$p < .001$***
				$q = .747$	$q < .001$***	$q < .001$***
				$d = .18$	$d = 2.94$	$d = 2.96$
Old/New Face Recognition Test	64.48% ± 5.75	62.62% ± 5.32	70.96% ± 10.82	$p = .310$	$p = .009$**	$p = .002$**
				$q = .775$	$q = .011$*	$q = .003$**
				$d = .34$	$d = .75$	$d = .98$
Recollection	.109 ± .095	.103 ± .095	.269 ± .236	$p = .819$	$p = .002$**	$p = .003$**
				$q = .819$	$q = .003$**	$q = .004$**
				$d = .06$	$d = .89$	$d = .92$
Familiarity	.594 ± .333	.532 ± .303	.835 ± .568	$p = .557$	$p = .064$	$p = .032$*
				$q = .928$	$q = .064$	$q = .032$*
				$d = .19$	$d = .52$	$d = .67$
Famous Faces Memory Test	32.47% ± 15.05	41.57% ± 13.44	73.82% ± 16.09	$p = .063$	$p < .001$***	$p < .001$***
				$q = .315$	$q < .001$***	$q < .001$***
				$d = .64$	$d = 2.65$	$d = 2.18$
USC Face Perception Test	74.52% ± 10.02	75.21% ± 9.02	78.63% ± 9.87	$p = .820$	$p = .132$	$p = .274$
				$q = .937$	$q = 162$	$q = .337$
				$d = .07$	$d = .41$	$d = .36$
Same/Different Face Matching Task	75.85% ± 5.09	74.10% ± 5.41	79.91% ± 6.58	$p = .298$	$p = .013$*	$p = .006$**
				$q = 1$	$q = .026$*	$q = .032$*
				$d = .33$	$d = .69$	$d = .96$
Part-whole Test	67.45% ± 4.97	66.39% ± 8.74	73.28% ± 15.79	$p = .614$	$p = .002$**	$p = .012$*
				$q = 1$	$q = .006$**	$q = .038$*
				$d = .15$	$d = .50$	$d = .54$
Whole eyes	74.26% ± 11.79	75.28% ± 15.79	85.49% ± 14.54	$p = .811$	$p = .003$**	$p = .041$*
				$q = .998$	$q = .008$**	$q = .094$
				$d = .07$	$d = .85$	$d = .67$
Part eyes	70.09% ± 11.06	70.56% ± 11.94	82.87% ± 12.03	$p = .899$	$p < .001$***	$p = .003$**
				$q = .959$	$q = .002$**	$q = .024$*
				$d = .04$	$d = 1.11$	$d = 1.03$
Whole mouth	77.53% ± 11.75	72.22% ± 14.32	79.63% ± 10.86	$p = .198$	$p = .495$	$p = .066$
				$q = 1$	$q = .528$	$q = .106$
				$d = .40$	$d = .19$	$d = .58$
Part mouth	65.63% ± 13.96	66.94% ± 10.74	65.28% ± 15.59	$p = .752$	$p = .931$	$p = .715$
				$q = 1$	$q = .931$	$q = .763$
				$d = .11$	$d = .02$	$d = .12$
Georges Task	52.31% ± 10.32	54.63% ± 8.88	55.34% ± 10.83	$p = .467$	$p = .298$	$p = .830$
				$q = 1$	$q = .341$	$q = .830$
				$d = .24$	$d = .29$	$d = .07$
Eye trials	50.40% ± 15.62	53.15% ± 18.06	57.80% ± 14.68	$p = .605$	$p = .079$	$p = .375$
				$q = 1$	$q = .115$	$q = .427$
				$d = .16$	$d = .49$	$d = .28$
Mouth trials	46.83% ± 10.87	48.70% ± 9.44	53.53% ± 11.77	$p = .576$	$p = .034$*	$p = .184$
				$q = 1$	$q = .054$	$q = .245$
				$d = .18$	$d = .59$	$d = .45$
Eye composite	61.28% ± 11.19	63.03% ± 12.63	71.09% ± 11.33	$p = .643$	$p = .002$**	$p = .042$*
				$q = 1$	$q = .008$**	$q = .084$
				$d = .15$	$d = .87$	$d = .67$

Table 2 (continued)

Measure	AQ− DP	AQ+DP	TD	*p*-values, *q*-values, and Cohen's *d*		
	N = 28	N = 15	N = 27	AQ+ vs. AQ-	AQ- vs. TD	AQ+ vs. TD
Mouth composite	59.25% ± 7.88	59.20% ± 7.00	63.44% ± 9.47	$p = .984$	$p = .079$	$p = .137$
				$q = .984$	$q = .105$	$q = .199$
				$d = .01$	$d = .48$	$d = .51$
Holistic processing						
Inversion Effect	− .1052 ± .080	− .093 ± .081	-.018 ± .128	$p = .644$	$p = .004$**	$p = .048$*
				$q = .937$	$q = .009$**	$q = .085$
				$d = .15$	$d = .82$	$d = .70$
Part-whole Effect	− .0411 ± .056	− .069 ± .072	.0002 ± .076	$p = .170$	$p = .026$*	$p = .007$**
				$q = 1$	$q = .046$*	$q = .028$*
				$d = .43$	$d = .62$	$d = .93$
Computerized Benton Face Recognition Test	40.96 ± 3.83	38.67 ± 3.96	45.65 ± 4.63	$p = .071$	$p < .001$***	$p < .001$***
				$q = 1$	$q < .001$***	$q = .002$**
				$d = .59$	$d = 1.10$	$d = 1.62$
Cambridge Face Perception Test	54.36 ± 15.28	51.87 ± 15.45	40.54 ± 14.47	$p = .617$	$p = .001$**	$p = .024$*
				$q = 1$	$q = .005$**	$q = .064$
				$d = .16$	$d = .93$	$d = .76$
PI20	82.71 ± 7.56	80.80 ± 10.81	36.89 ± 7.06	$p = .548$	$p < .001$***	$p < .001$***
				$d = .20$	$d = 6.26$	$d = 4.81$
Reading the Mind in the Eyes	29.18 ± 2.92	26.36 ± 3.98	–	$p = .028$*	–	–
				$d = .81$		
Social Interaction Anxiety Scale	19.77 ± 7.91	23.11 ± 11.48	21.04 ± 13.60	$p = .427$	$p = .758$	$p = .685$
				$d = .34$	$d = .11$	$d = .16$

Mean ± standard deviation. FFMT, USCFPT, SDFMT, Part-whole, Georges, eye and mouth composites, and Old New task scores represent percent correct, whereas the others represent the raw or total scores. Uncorrected *p*-values are derived from independent-samples t-tests comparing groups with low vs. high AQ test scores. q-values were calculated using a false discovery rate of .05

*Statistically significant at $p < 0.05$

**Statistically significant at $p < .01$

***Statistically significant at $p < .001$

little to no correlation with the CFMT, FFMT, Old/New face recognition task (accuracy, recollection, and familiarity), or the NOMT, indicating that the degree of autism traits was unrelated to severity of face memory impairment (see Fig. 1).

Face Matching, Holistic Processing, and Eye vs. Mouth Region Discrimination Performance

We next considered face perception performance, hypothesizing, based on studies of face processing in ASD (Ventura et al., 2017; Weigelt et al., 2012), that AQ+ DPs would have less impaired face perception and holistic processing abilities than AQ- DPs. To test this, we ran three MANOVAs comparing AQ+/AQ- DP performance on the different domains of face perception: Face matching (SDFMT, Benton-*c*, USCFPT, CFPT), Holistic processing (inversion effect, part-whole effect), and feature processing (Georges, Part-whole, eye composite, mouth composite). Interestingly, neither the face matching model ($F(4,38) = 1.24$, $p = 0.230$, $\eta_p^2 = 0.134$), the holistic processing model ($F(2,40) = 1.64$, $p = 0.208$, $\eta_p^2 = 0.076$), nor the feature processing model ($F(4,38) = 0.25$, $p = 0.909$, $\eta_p^2 = 0.026$) were significant. Results from post hoc *t*-tests comparing the individual measures between AQ+ and AQ- DPs showed a very similar pattern (see Table 2). Next, we performed Bayesian null hypothesis testing and found that comparing scores between the two DP groups yielded a BF_{01} of 3.88 for the inversion effect, 1.84 for the part-whole effect, 3.87 for the eye composite, and 4.26 for the mouth composite. Comparing performance on the individual tasks between groups resulted in a BF_{01} of 3.81 for the CFPT, 2.63 for the SDFMT, 3.80 for the Part-whole, 3.37 for the Georges, 0.99 for the Benton-*c*, and 4.17 for the USCFPT. Evidence in favor of the null hypothesis ranged from nonexistent (0–1) to substantial (3–10; Jarosz & Wiley, 2014).

Within the DP group, we next performed a multivariate multiple regression for each domain of face perception with AQ score as the predictor. We found that AQ scores did not

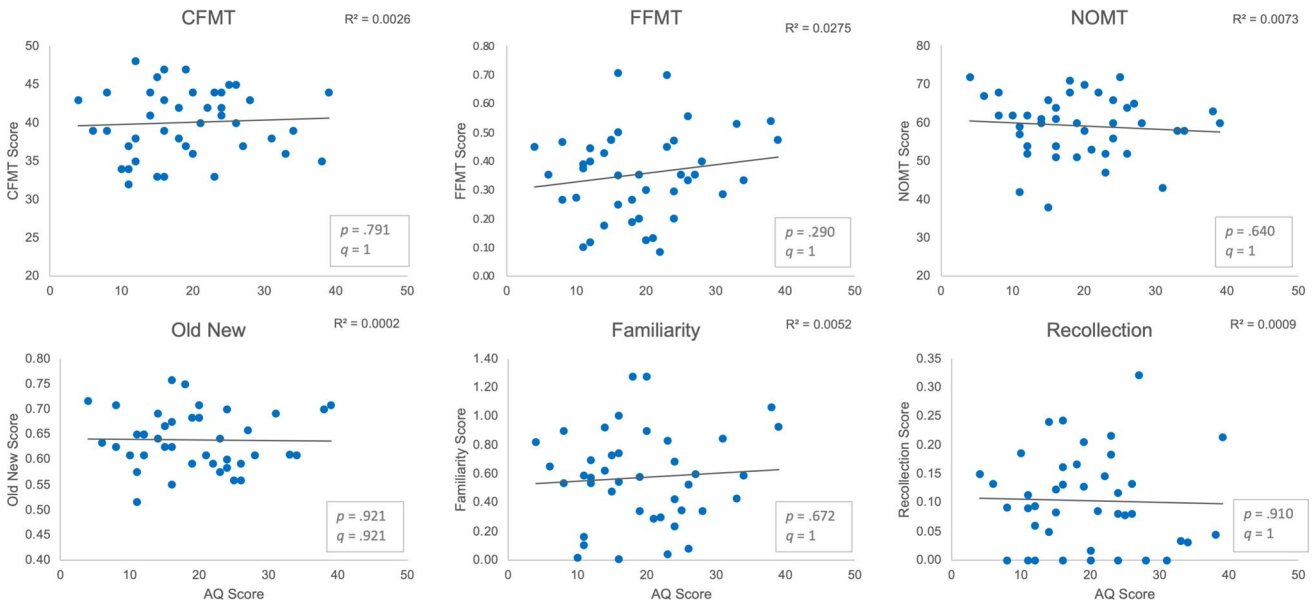

Fig. 1 Correlations between AQ scores and memory tasks in the entire DP population. *CFMT* Cambridge Face Memory Test, *NOMT* Novel Object Memory Test, *FFMT* Famous Faces Memory Test

significantly predict overall performance on face matching tasks ($F(4,63) = 1.07$, $p = 0.378$, $\eta_p^2 = 0.064$), holistic processing measures ($F(2,67) = 0.72$, $p = 0.492$, $\eta_p^2 = 0.021$), or feature processing measures ($F(4,64) = 0.23$, $p = 0.919$, $\eta_p^2 = 0.014$). Likewise, correlations within the DP sample showed that continuous measures of the AQ showed little to no correlation with the perceptual measures (SDFMT, CFPT, BFRT-c, USCFPT, Georges Task), holistic processing (Part-whole, inversion effect), or relative attention to the eye or mouth regions (see Fig. 2). In the rare cases there was a modest directional trend, it was that DPs with *higher* AQ scores showed *worse* perceptual performance (e.g., Part-whole effect, r = -0.09; SDFMT, r = -0.20; the opposite result to that predicted by the strong interaction hypothesis). A summary of all the perceptual and memory differences between AQ+ DPs, AQ- DPs, and controls can be seen in Fig. 3.[6]

Emotion Recognition and Self-reported Social Functioning

We next compared performance on measures of emotion recognition ability and self-reported social functioning, predicting that the AQ+ group would demonstrate worse emotion recognition and increased social anxiety compared to the AQ- group (Spain et al., 2018). Note that 31 DPs completed the RMET, 22 DPs completed the SIAS, and no controls from the current study were given the RMET. As predicted, the AQ+ group scored significantly worse than the AQ- group on the RMET ($M_{AQ+} = 26.36$, $SD_{AQ+} = 3.98$, $M_{AQ-} = 29.18$, $SD_{AQ\_} = 2.92$; $p = 0.028$). However, the groups did not significantly differ in their SIAS scores ($M_{AQ+} = 23.11$, $SD_{AQ+} = 11.48$, $M_{AQ-} = 19.77$, $SD_{AQ-} = 7.91$; $p = 0.427$), and further, the DP groups were not significantly different from the control group's SIAS scores. The AQ+ group did not self-report worse face recognition impairments according to their PI20 scores ($M_{AQ+} = 80.80$, $SD_{AQ+} = 10.81$, $M_{AQ-} = 82.71$, $SD_{AQ-} = 7.56$; $p = 0.063$), and both groups scored higher (higher indicating worse impairment) than typically developing controls. Bayesian null hypothesis testing yielded a BF_{01} of 2.54 for the SIAS and 3.48 for the PI20 when comparing scores between the two DP groups, indicating anecdotal (1–3) to substantial (3–10) evidence in favor of the null hypothesis (Jarosz & Wiley, 2014).

Correlation analyses showed that, within DPs, the AQ was significantly negatively correlated with the RMET ($r = -0.516$, $p = 0.002$). However, the AQ did not significantly correlate with either social anxiety ($r = 0.261$, $p = 0.240$) nor self-reported face recognition difficulties ($r = -0.057$, $p = 0.716$; see Fig. 4).

fMRI Category Selectivity

Though the patterns of behavioral performance of AQ+ and AQ- DPs were very similar, it could be that the neural mechanisms underlying face processing differ between these groups. To test this possibility, we first examined face vs.

[6] Because our main control group was not given the RMET (see footnote 4) and z-scores were calculated using the main control group as the normative data, the RMET is excluded from this figure.

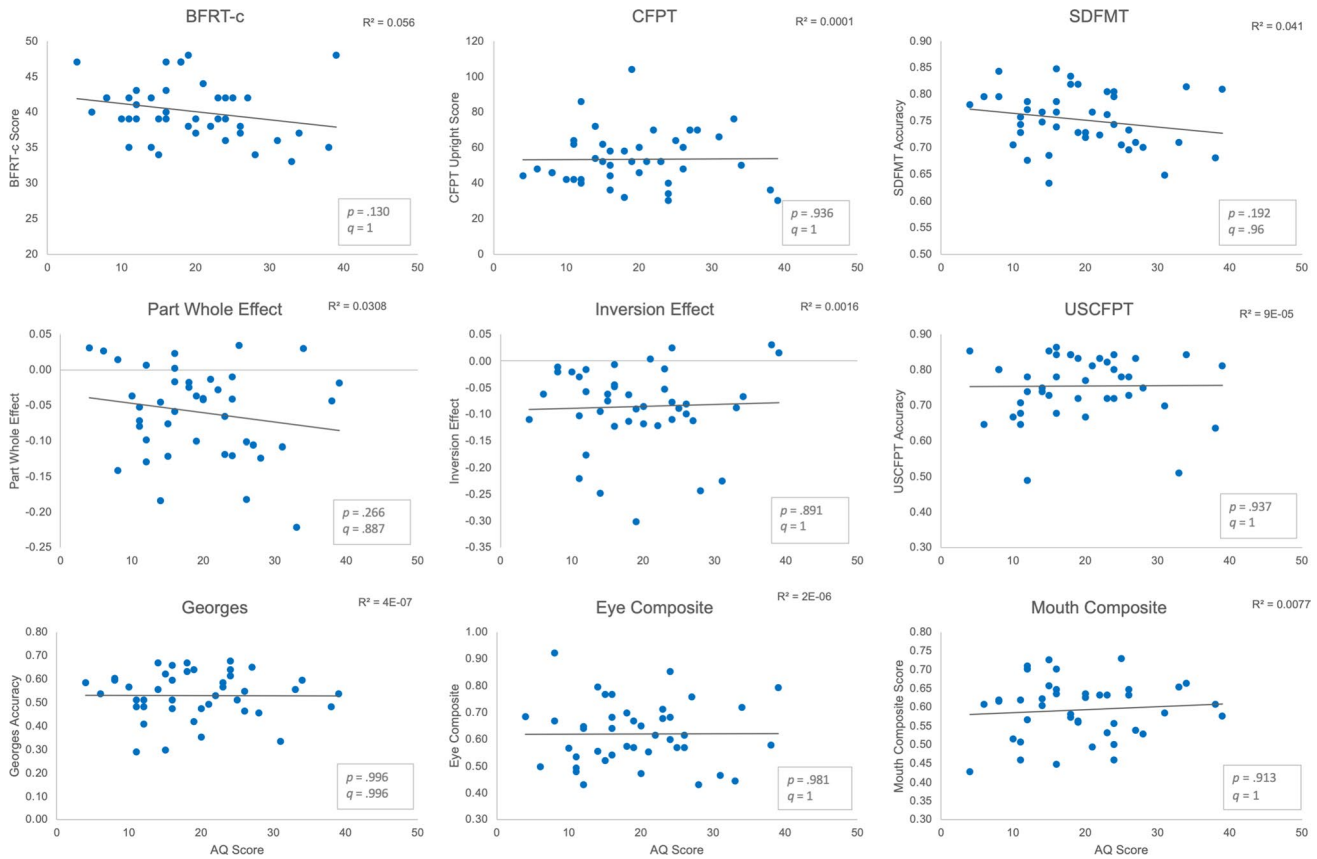

Fig. 2 Correlations between AQ scores and perceptual tasks in the entire DP population. *BFRT-c* Computerized Benton Face Recognition Test, *CFPT* Cambridge Face Perception Test, *SDFMT* Same/Different Face Matching Task, *USCFPT* University of Southern California Face Matching Task

scene selectivity during the fMRI localizer scans, focusing on individually defined face-selective regions (OFA, FFA, pSTS, anterior temporal face area—ATL). To identify significant DP/control differences, we performed a 2 (DP/control) × 4 (region) × 2 (hemisphere) ANOVA. We did not find a significant main effect of group ($F(1,55) = 1.11$, $p = 0.297$), but did find a significant group x hemisphere x region interaction ($F(3,165) = 2.74$, $p = 0.045$), driven by DPs demonstrating significantly reduced face selectivity compared to controls in the left OFA ($t(56) = 2.48$, $p = 0.016$, $q = 0.032$) and left FFA ($t(55) = 2.35$, $p = 0.022$, $q = 0.022$), while showing similar selectivity to controls in the other face-selective regions (see Fig. 5). We next performed a 3 (AQ+ DP/AQ- DP/control) × 4 (region) × 2 (hemisphere) ANOVA to see if overall differences exist between the groups and again found no main effect of group ($F(2,54) = 1.36$, $p = 0.265$) and though we did not find a significant group x region x hemisphere interaction ($F(6,162) = 2.06$, $p = 0.061$), we did observe a significant group x region interaction ($F(6,162) = 2.33$, $p = 0.034$). This was driven by the AQ- DP group having significantly reduced bilateral pSTS selectivity compared to the AQ+ DP group (average of left and right

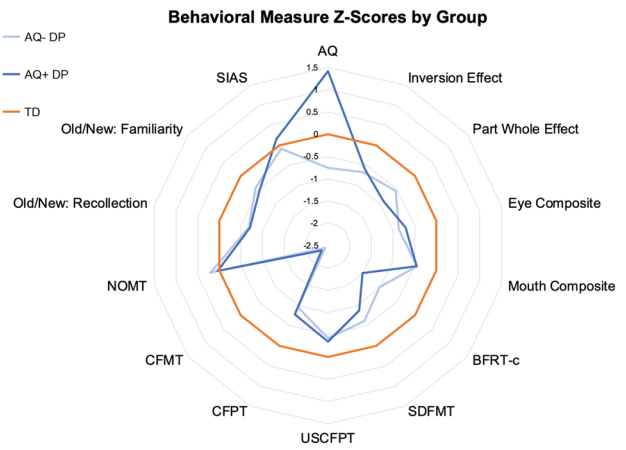

Fig. 3 Comparison of *z*-scores by group on behavioral task battery. *AQ* autism quotiet, *BFRT-c* computerized Benton Face Recognition Test, *SDFMT* Same/Different Face Matching Task, *USCFPT* University of Southern California Face Matching Task, *CFPT* Cambridge Face Perception Test, *CFMT* Cambridge Face Memory Test, *NOMT* Novel Object Memory Test, *SIAS* Social Interaction Anxiety Scale

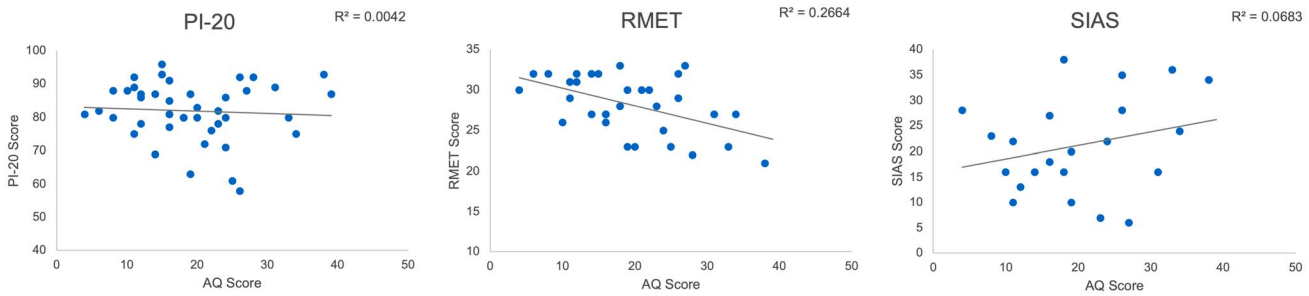

Fig. 4 Correlaions between AQ scores and self-reported face recognition as well as social and emotional measures in the entire DP population. *PI20* Prosopagnosia Index 20, *RMET* Reading the Mind in the Eyes Test, *SIAS* Social Interaction Anxiety Scale

pSTS t(56) = 2.64, $p = 0.009$), while showing similar selectivity in the other face-selective regions (see Fig. 5).

We also performed an exploratory comparison between DPs and controls in their scene-, object-, and body-selectivity, focusing on the occipital place area (OPA), the parahippocampal place area (PPA), the extrastriate body area (EBA), the fusiform body area (FBA), the lateral-occipital cortex (LO), and the posterior fusiform sulcus (pFS), using a 2 (DP/control) × 6 (region) × 2 (hemisphere) ANOVA. We did not find a significant main effect of group (F(1,55) = 0.01, p = 0.927), nor did we find a significant group x hemisphere x region interaction (F(5,275) = 0.87, p = 0.505). We then compared the AQ+ and AQ- DP groups using a 2 (AQ+ DP/AQ- DP) × 6 (region) × 2 (hemisphere) ANOVA, and similarly found no significant main effects of group (F(1,31) = 3.87, p = 0.058) or group x hemisphere x region (F(5,155) = 1.53, p = 0.185).

Resting-State Connectivity in the Face-selective Network

To examine overall levels of connectivity between each of the regions within the face network (FFA, OFA, ATL, pSTS), we first compared average functional connectivity between the DP and control groups. A 2 (DP/control) × 4 (region) × 2 (hemisphere) ANOVA showed a significant effect of group (F(1,54) = 8.99, $p = 0.004$) but no significant interactions between group, hemisphere, and region. As can be seen in Fig. 6, post hoc *t*-tests showed significantly lower functional connectivity in the DP group across all regions (all *p*'s < 0.05). To investigate whether there were differences between the AQ+ and AQ- DPs' pSTS connectivity, we first performed a 2 (AQ+ DP/AQ- DP) × 2 (hemisphere) ANOVA on the pSTS and found no significant group effects (F(1,30) = 0.26, $p = 0.612$). We next investigated whether there were any differences in connectivity between the AQ+ and AQ- DP groups within the remaining face regions using a 2 (AQ+ DP/AQ- DP) × 3 (region) × 2 (hemisphere) ANOVA and found no main effect of group (F(1,30) = 0.29, $p = 0.594$) or significant group interactions. A Bayesian independent sample test between the AQ+ and AQ- DP groups for each of the regions yielded BF_{01} ranging from 2.19 (left OFA) to 3.68 (left FFA), indicating anecdotal to substantial support in favor of the null hypothesis (Jarosz & Wiley, 2014).

Exploratory Functional Connectivity of the Superior Temporal Sulcus

Given the results of the task-based face selectivity analysis showing reduced pSTS selectivity in AQ+ compared to AQ- DPs, we next sought to examine if AQ+ vs. AQ- DPs showed any differences in connectivity between the bilateral pSTS and other regions outside of the face network. This could provide evidence that information in face processing regions may be processed differently in higher-level brain regions. When comparing the AQ+ and AQ- groups using whole-brain bilateral pSTS resting-state connectivity, we found that seven different regions survived whole-brain correction (corrected $p < 0.05$), including the left anterior middle temporal gyrus [$t(28) = 5.44$, uncorrected $p < 0.001$], the right inferior frontal gyrus [$t(11.5) = 3.58$, uncorrected $p = 0.001$], the right superior temporal gyrus [$t(28) = 5.32$, uncorrected $p < 0.001$], the right ventromedial prefrontal cortex [$t(28) = 5.63$, uncorrected $p < 0.001$], the right ventrolateral prefrontal cortex [$t(28) = 5.23$, $p < 0.001$], the left superior temporal gyrus [$t(28) = 5.51$, $p < 0.001$], and the left superior occipital gyrus [$t(28) = 4.38$, $p < 0.001$]. For all regions, the AQ+ group exhibited *greater* pSTS-ROI connectivity compared to the AQ- group with the exception of the left superior occipital gyrus, where the AQ+ group (M = -0.06, SD = 0.12) showed less connectivity than the AQ- group (M = 0.16, SD = 0.14). The RMET did not significantly correlate with any of the connectivity values of the above regions (all *p*s > 0.05).

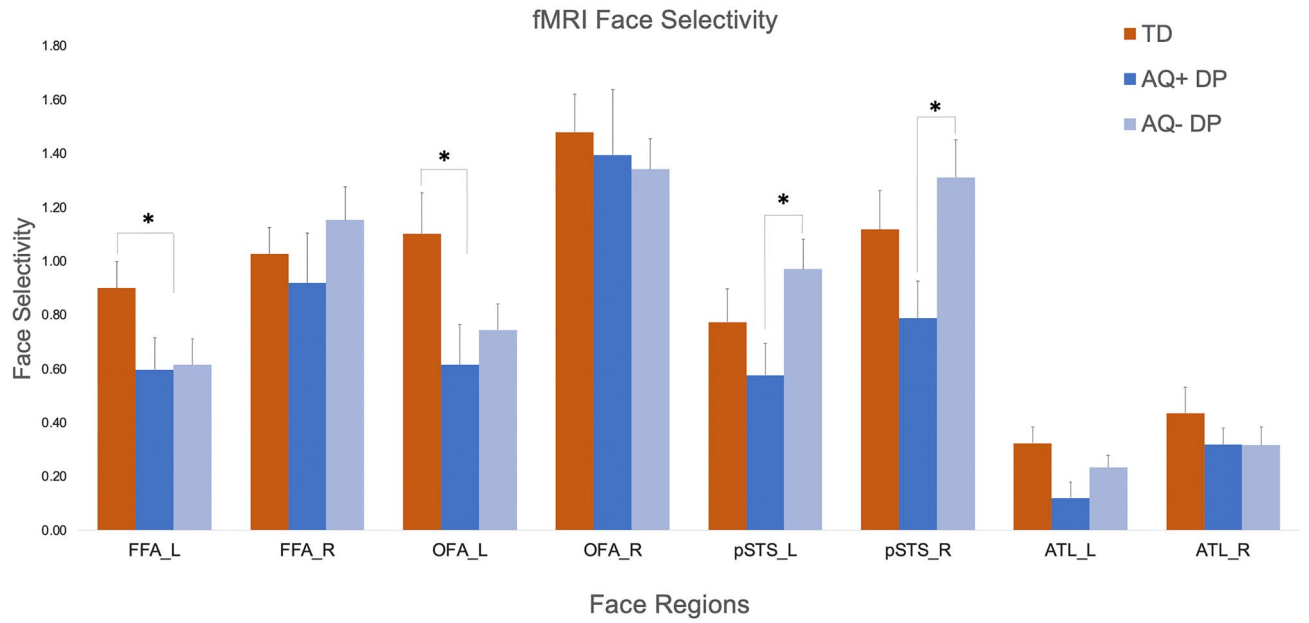

Fig. 5 Comparison of AQ-, AQ+, and TD face specificity in dynamic localizer fMRI task

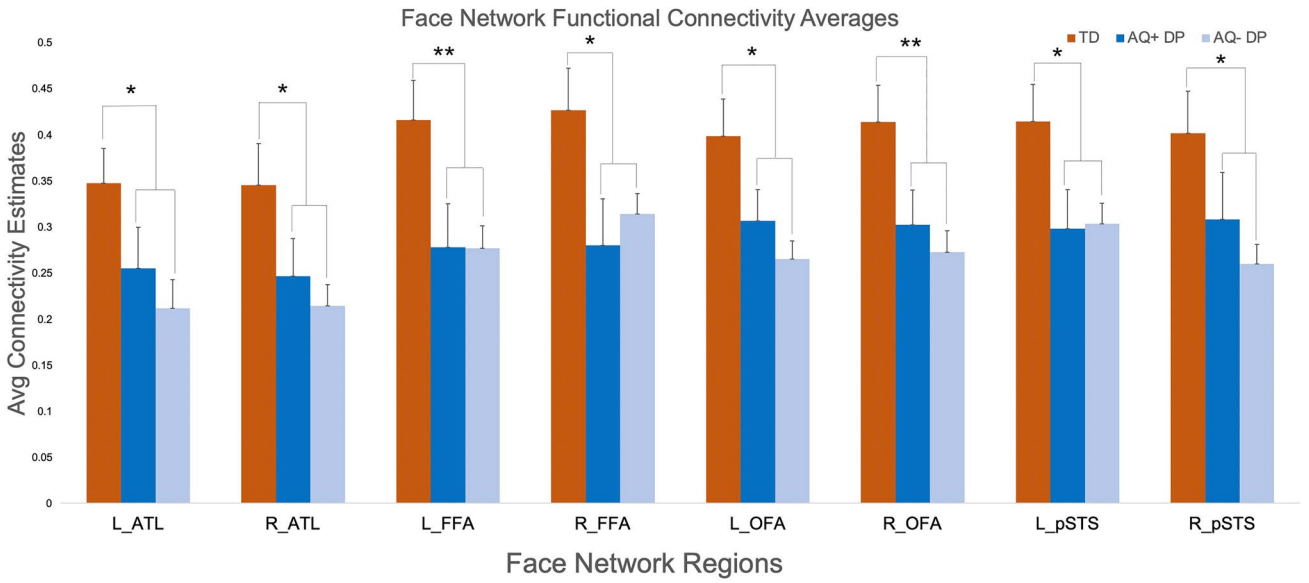

Fig. 6 Average functional connectivity of the face network across groups. *ATL* anterior temporal lobe face area, *FFA* fusiform face area, *OFA* occipital face area, *pSTS* posterior superior temporal sulcus, *TD* typically developed controls, *AQ+ DP* developmental prosopagnosics with higher autism traits, *AQ- DPs* developmental prosopagnosics with lower autism traits

Discussion

The goal of this study was to compare the mechanistic similarities and differences between DPs with higher (AQ+ DPs) and lower (AQ- DPs) levels of autism traits. To achieve this, we recruited a large sample of DPs (N = 43) with a range of autism traits and a group of matched controls (N = 27) and administered an extensive battery of face/object memory, face perception, facial emotion recognition, and self-reported face impairment and social functioning measures. We also had participants perform a face/scene/object/body localizer task and resting-state fMRI. Our findings demonstrated that the behavioral and neural face processing profiles of DPs with higher versus lower levels of autism traits were overall

quite similar across the domains of face memory, holistic processing, feature processing, and face matching. The main differences between the two groups were significantly poorer face emotion recognition and reduced pSTS face selectivity in an fMRI dynamic localizer task in the AQ+ compared to AQ- DP group. Both DP groups showed similarly reduced resting-state functional connectivity between regions of the face network when compared with controls. Interestingly, the AQ+ group showed significantly greater resting-state connectivity between the pSTS and several regions, including the inferior frontal gyrus, which has been implicated in face processing. The overall pattern of results we observed is inconsistent with the notion that the presence of autism traits fundamentally changes the mechanisms of DP but rather supports a more independent co-occurrence model of ASD traits and DP. These findings have important implications for the study and treatment of developmental prosopagnosia with accompanying autism traits.

Diagnosed cases of autism have been described as having largely memory-based face recognition impairments, with intact face perception and holistic face processing and consistent patterns of eye avoidance (Tanaka & Sung, 2016). In our sample of DPs, we found that in addition to the expected poor face memory performance, the AQ+ and AQ- DP groups were similarly impaired in their face perception performance across a wide array of tasks. Both groups demonstrated deficits in face matching and holistic processing and showed a similar pattern of reduced feature sensitivity/discrimination compared to controls. This suggests that not only do AQ+ and AQ- DPs have an equivalent degree of face perception deficits but also that the likely sources of these deficits–poorer holistic processing and reduced feature processing (particularly of the eye region)–is comparable between the two groups. It also suggests that the relative levels of attention to the eye and mouth regions were similar between AQ+ and AQ- DPs, with both DP groups demonstrating more attention to the mouth and less attention to the eyes when compared with the control group. The attentional pattern of eye avoidance seen in the AQ+ DPs is similar to that of both non-DP ASD individuals (Madipakkam et al., 2017) and of typical DPs (Bobak et al., 2016), while their poor holistic processing is more similar to typical DP patterns (e.g., Avidan et al., 2011; DeGutis et al., 2012; Palermo et al., 2011) and is less consistent with prior findings in ASD populations (Ventura et al., 2017; Weigelt et al., 2012).

In addition to their similar behavioral profiles, we also found similarities between the AQ+ and AQ- DP groups in terms of fMRI task activation in face-, scene-, object-, and body-selective regions as well as in their resting-state functional connectivity. In particular, we found that during the face/scene/object/body localizer task, both AQ+ and AQ- DPs had similarly reduced selectivity in face-selective regions compared to controls, particularly in the left OFA and left FFA, components of the core face processing network (Haxby et al., 2002). This reduced face-selectivity is consistent with previous studies (Jiahui et al., 2018) and the left FFA reduction in selectivity is consistent with a recent DP study by Gerlach et al. (2019). However, both AQ+ and AQ- DPs had normal selectivity in body-, scene-, and object-selective regions. During resting-state scans, both AQ+ and AQ- DPs had similarly significantly reduced functional connectivity amongst all face-selective regions compared to controls and did not demonstrate AQ+ vs. AQ- differences in functional connectivity of any of the face-selective regions, including the pSTS. However, in an exploratory analysis, AQ+ DPs showed significantly stronger resting-state functional connectivity between the bilateral STS and several regions of the brain, including regions of the prefrontal cortex and temporal gyri, with the exception of the left superior occipital gyrus where they showed lower functional connectivity with the STS. These results demonstrate notable similarities between the functional connectivity of the face regions of AQ+ and AQ- DPs, apart from the region responsible for socio-communicative functions (pSTS).

Despite such similar face memory, face perception, and fMRI results, it is notable that AQ+ DPs showed poorer face emotion recognition on the RMET and reduced pSTS selectivity to faces compared to AQ- DPs. AQ+ DPs' impairment on the RMET is consistent with previous findings that individuals on the autism spectrum often have difficulty recognizing basic emotions (Griffiths et al., 2019). It is particularly notable that the AQ+ and AQ- DP groups did not differ in eye perception accuracy on the Part-whole or Georges tasks. This suggests that, in contrast to AQ+ DPs, AQ- DPs may be able to efficiently process eye-related information for highly overlearned categories such as emotions (though see Biotti & Cook, 2016), but have difficulty matching novel identities using the eyes in the Part-whole and Georges tasks. Additionally, the AQ+ DP group had numerically but not significantly higher self-reported levels of social anxiety. These results correspond with a meta-analysis that found links between social anxiety and autism (Spain et al., 2018), as well as previous studies linking poor face recognition with elevated social anxiety (Davis et al., 2011), and suggest that autism traits may relate to social anxiety in the AQ+ DP group while face recognition deficits relate to social anxiety in the AQ- DP group. The AQ+ DP group's scores on the RMET reflected the impaired emotion recognition that we might expect to find in populations with developmental disorders such as autism (Bolte & Poustka, 2003; Celani et al., 1999; Smith et al., 2010; Spain et al., 2018), which could reflect the AQ+ DPs' impairment in extracting social-emotional information from faces. These findings are further supported by our fMRI category selectivity results where, compared to the AQ- DPs, AQ+ DPs had significantly reduced face selectivity in the bilateral pSTS, a brain region

consistently implicated in processing dynamic aspects of faces (Pitcher et al, 2011) and processing facial expressions (Baseler et al., 2014).

The current results suggest that DPs with higher levels of autism traits do not demonstrate a different behavioral profile of holistic face processing, featural processing, or face memory deficits than DPs with lower levels of autism traits. In other words, the current results are inconsistent with a strong version of the autism phenotype x DP interaction model, where the presence of autism traits fundamentally changes the mechanisms and manifestation of DP. The current results provide support for a model where autism traits and DP are more independent and additive. This is consistent with a 2004 study demonstrating that participants with diagnosed social developmental disorders (including autism, Asperger's syndrome, and PDD-NOS, now classified under autism spectrum disorder) did not differ on their Social Skills Inventory based on either the presence or absence of co-occurring face recognition impairments (Barton et al., 2004), suggesting independence between face recognition impairments and social cognitive abilities (Minio-Paluello et al., 2020). Our study demonstrates the reciprocal finding, where participants with DP and co-occurring autism traits do not differ from those without co-occurring autism traits on a wide array of face processing tasks. Just as the presence or absence of face recognition impairments did not result in differing social impairments in participants with SDD, the presence or absence of autism traits did not result in differing face processing impairments in our participants with DP, aside from the expected emotion recognition deficits.

Taken together, our results, along with previous studies on face recognition and social development (Barton et al., 2004; Halliday et al., 2014; Minio-Paluello et al., 2020), provide converging evidence that the presence of autism traits may not necessarily strongly interact with prosopagnosia symptoms and likewise, that the presence of prosopagnosia may not necessarily interact with ASD traits. Still, this begs the question of why DP co-occurs at higher proportions in individuals with autism than in the general population. There are a few potential explanations, inspired by models proposed to explain high co-occurrence of ASD and ADHD (Leitner, 2014). One hypothesis is that there is a genetic basis for the co-occurrence, likely due to the heritable nature of both disorders as well as potential overlap of the genetic mechanisms. Their relative independence (e.g., cases where autism is present without DP, and vice versa) may be because DP affects face-selective regions involved in perception and memory, while ASD affects the more social cognitive regions such as the pSTS and temporal parietal junction. Face recognition abilities are highly heritable (correlation of 0.70 on face recognition scores in monozygotic twins) and have shown to be separate from general visual and verbal abilities (Wilmer et al., 2010). ASD similarly has a high estimated heritability (83%, Sandin et al., 2017). Further, the oxytocin receptor gene (OXTR) has been implicated in both DP (Bate et al., 2013; Cattaneo et al., 2016) and ASD (Jacob et al., 2007; Loparo & Waldman, 2014). Oxytocin plays an important role in social behaviors and bonding, and the administration of intranasal oxytocin has been shown to both improve face recognition in DPs (Bate et al., 2013) and increase eye contact in adult males with autism (Auyeung et al., 2015), suggesting a link between the disorders.

In addition to providing a better mechanistic understanding of DPs with ASD traits, the current results have important practical implications for including DPs with high autism traits in future studies. Even though between an estimated 15% and 35% of DPs in the general population have autism or high levels of autism traits (based on estimates that 1 in 54 has autism, CDC 2020, and 12–36% with autism have DP, Minio-Paluello et al., 2020), these individuals have been routinely excluded from DP studies (or have largely been studied separately from DP, see Murray et al., 2018; Corrow et al., 2016) under the assumption that DPs with high autism traits are mechanistically different from DPs with lower autism traits. The current findings suggest that high versus low AQ DPs are substantially more similar than they are different and future DP studies could benefit from including high AQ DP participants, both in terms of increasing overall study sample sizes as well as further testing the generalizability of findings between high and low AQ DPs. Another reason to include high AQ DPs is that it is possible that interventions that have been successful with low ASD trait DPs (e.g., DeGutis, Cohen, & Nakayama, 2014; Corrow et al., 2019) could help DPs with higher ASD traits as well.

Though the converging findings of the current study are compelling, there are limitations. First is the lack of ASD diagnosis in the AQ+ group. Though the current study focused on the broader autism phenotype, which demonstrates social and communicative impairments that are qualitatively similar to those seen in diagnosed ASD, a study using a sample of DPs with and without a diagnosis of ASD would provide a more conclusive picture of the interaction between the disorders. While we did compare the AQ- sample to the DPs that scored above 32 on the AQ (a widely used cut-off score correctly identifying 76% of patients in a clinical sample; Woodbury-Smith et al., 2005) and found similar results (see supplementary materials), this sample size was very small and may not be representative of the ASD population. Additionally, this study was performed in adults and therefore may not generalize to children. Symptoms of autism can change from childhood to adulthood (Marriage et al., 2009; Taylor & Seltzer, 2010), and it is therefore possible that the pattern of face recognition deficits differs between children with DP and low autism traits and children with DP and high autism traits. Furthermore, in the current study we could not differentiate attention to different

facial features from perceptual sensitivity and examining eye movements in future studies would be useful. Finally, the AQ+ vs. AQ- DP group sizes in the current study were on the smaller size, suggesting that there may be limitations in power to detect group differences. Though our approach of examining multiple converging measures within a domain, examining associations with a continuous measure of ASD traits, incorporating MANOVAs/multivariate regressions, and performing Bayes null hypothesis analyses mitigates this concern, it would be good to replicate these findings in larger samples of AQ+ vs. AQ- DPs.

These results have important implications for the future of studying combined DP and autism traits. The notable similarities between DPs with high and low levels of autism traits suggest that the presence of autism traits does not necessarily result in a different type of DP with regards to holistic face processing, featural processing, face memory abilities, and the neural mechanisms underlying these processes.

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Author Contributions JD and RF were responsible for study conceptualization, design, and participant recruitment. RF conducted the behavioral data analysis with supervision from JD. XL and TE conducted the fMRI analyses. JD and RF drafted the manuscript. XL, TE, ME, and JT provided critical feedback and edits to the manuscript. JD acquired funding for the study. All authors approved the final version of the manuscript.

Data Availability Upon acceptance of the manuscript, all data will made be publicly available on Dryad in accordance with NIH policy and with the approval of the VA Boston Healthcare System and Harvard Medical School IRBs.

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