Reduced adaptability, but no fundamental disruption, of norm-based face-coding mechanisms in cognitively able children and adolescents with autism

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Running head: face coding in autism

Keywords: autism, face recognition, face identity aftereffects, adaptive coding, norm-based coding

Abstract

Faces are adaptively coded relative to visual norms that are updated by experience. This coding is compromised in autism and the broader autism phenotype, suggesting that atypical adaptive coding of faces may be an endophenotype for autism. Here we investigate the nature of this atypicality, asking whether adaptive face-coding mechanisms are fundamentally altered, or simply less responsive to experience, in autism. We measured adaptive coding, using face identity aftereffects, in cognitively able children and adolescents with autism and neurotypical age- and ability-matched participants. We asked whether these aftereffects increase with adaptor identity strength as in neurotypical populations, or whether they show a different pattern indicating a more fundamental alteration in face-coding mechanisms. As expected, face identity aftereffects were reduced in the autism group, but they nevertheless increased with adaptor strength, like those of our neurotypical participants, consistent with norm-based coding of face identity. Moreover, their aftereffects correlated positively with face recognition ability, consistent with an intact functional role for adaptive coding in face recognition ability. We conclude that adaptive norm-based face-coding mechanisms are basically intact in autism, but are less readily calibrated by experience.

1.0 Introduction

Adaptive, norm-based coding mechanisms play an important role in our ability to recognize faces (for reviews, see Rhodes & Leopold, 2011; Webster & MacLeod, 2011). These mechanisms code faces relative to norms that are continuously updated by experience. Their operation can be seen in identity aftereffects, in which exposure to a face (e.g., antiDan) shifts the average towards that face, selectively biasing us to see the opposite identity (e.g., Dan) in face space (Figure 1) (e.g., Leopold, O'Toole, Vetter, & Blanz, 2001; Rhodes & Jeffery, 2006). These face identity aftereffects tap higher-level face-coding mechanisms, as indicated by findings that they are larger for upright than inverted faces (Rhodes, Evangelista, & Jeffery, 2009). Moreover, the selectivity of the bias for the opposite identity, with smaller aftereffects observed for equally perceptually dissimilar but non-opposite adapt-test face pairs, suggests that the average face functions as a perceptual norm for coding identity (Rhodes & Jeffery, 2006).

Norm-based coding is an efficient way to represent the distinctive information that allows us to recognize faces. In addition, the adaptation of face norms by experience calibrates face coding mechanisms to our diet of faces, which can enhance face discrimination and recognition (Armann, Jeffery, Calder, Bühlhoff, & Rhodes, 2011; Wilson, Loffler, & Wilkinson, 2002) (although this is not always found, Nishimura, Doyle, Humphreys, & Behrmann, 2010; Rhodes, Maloney, Turner, & Ewing, 2007). Moreover, individuals with more adaptable face-coding mechanisms, as indicated by larger identity-related face aftereffects, have better face recognition (Dennett, McKone, Edwards, & Susilo, 2012; Rhodes, Jeffery, Taylor, Hayward, & Ewing, 2014). Taken together, these findings support a functional role for adaptive norm-based coding in face recognition ability.

Figure 1. A simplified (2 dimensional) face space with two faces, Dan and Jim, an Average face (created by morphing 20 male, Caucasian faces) and two antifaces, antiDan and antiJim. An antiface is made by morphing a face towards, and beyond, the Average, and has opposite properties to that face. Reduced-identity-strength versions of Dan and Jim, created by morphing those identities towards the Average, are also shown. Identity aftereffects occur when exposure to a face biases subsequent perception towards a face with opposite properties. For example, after viewing antiDan for a few seconds, we are biased (briefly) to see Dan.

Face identity aftereffects are reduced in children with autism (Ewing, Leach, Pellicano, Jeffery, & Rhodes, 2013; Pellicano, Jeffery, Burr, & Rhodes, 2007), in the relatives of individuals with autism (Fiorentini, Gray, Rhodes, Jeffery, & Pellicano, 2012) and in neurotypical men with high levels of autistic traits measured by Autism Quotient scores (Rhodes, Jeffery, Taylor, & Ewing, 2013). These results have led to the proposal that atypical adaptive coding of faces may be an endophenotype for autism (Fiorentini et al., 2012; Rhodes et al., 2013). Moreover, atypical adaptive coding of faces could potentially contribute to the face recognition difficulties often observed in autism (for reviews, see Dawson, Webb, & McPartland, 2005; Golarai, Grill-Spector, & Reiss, 2006; Sasson, 2006; Webb, Faja, & Dawson, 2011; Weigelt, Koldewyn, & Kanwisher, 2012).

Here we ask exactly how the adaptive coding of face identity is compromised in individuals with autism. One possibility is that their adaptive face-coding mechanisms are simply less responsive to face inputs than are those of neurotypical individuals. Alternatively, however, there could also be some more fundamental alteration in their face-coding mechanisms. For example, abstraction of prototypes (norms) is impaired in autism (Gastgeb, Dundas, Minshew, & Strauss, 2012; Gastgeb, Rump, Best, Minshew, & Strauss, 2009; Gastgeb, Wilkinson, Minshew, & Strauss, 2011; Klinger & Dawson, 2001), raising the possibility that face-coding mechanisms may not be norm-based.

To determine more precisely how adaptive face-coding mechanisms are compromised in autism, we examined how face identity aftereffects vary with adaptor identity strength in cognitively able children and adolescents with autism and a group of age- and ability-matched neurotypical participants. In neurotypical children and adults, identity aftereffects generally increase with adaptor strength (Jeffery, Read, &

Rhodes, 2013; Jeffery et al., 2011). This pattern is consistent with norm-based opponent coding of identity-related dimensions, where each face dimension is represented by activation in two neural populations, tuned to opposite ends of the dimension, with equal activation representing a neutral point or norm. More extreme adaptors shift the norm further, resulting in larger aftereffects (shifts in perception of average or low-identity-strength test faces), because they activate their preferred populations more strongly than less extreme adaptors. An alternative, non-norm-based model, is multichannel coding of identity, where each dimension is represented by activation in multiple populations (channels) tuned to distinct dimension values. With multichannel coding, aftereffects increase initially with adaptor identity strength, but then decrease, as adaptors become too extreme to affect the populations coding a given test stimulus (Blakemore & Sutton, 1969; Clifford, Wenderoth, & Spehar, 2000).

Studies of identity aftereffects in autism to date have not varied the identity strength of adaptors, but have instead used a single identity strength. With this design, the reduced aftereffects observed in autism could simply reflect weaker updating of norms by experience in an otherwise intact norm-based face-coding system. Alternatively, however, they could arise from a non-norm-based, multichannel coding system, in which strong-identity-strength adaptors have little effect on the channels coding (the weak-identity-strength) test faces. By examining how identity aftereffects change with increasing identity strength of adaptors, we should be able to distinguish between these possibilities. If face identity aftereffects increase with adaptor strength in our typically developing participants, but decrease with adaptor strength in our participants with autism, then we would conclude that face identity is not coded relative to perceptual norms in autism. Alternatively, an

increase in aftereffects with increasing adaptor strength in both groups would be consistent with norm-based coding of face identity in both groups. We included a size difference between the adapt and test faces to minimize the contribution of low-level retinotopic adaptation to our aftereffects, and a change detection task during adaptation to ensure good attention to the adapting faces (Ewing, Leach, et al., 2013; Rhodes et al., 2011).

We also examined whether individual differences in adaptive coding strength are related to face recognition ability in our participants. In neurotypical adults, identity-related face aftereffects correlate positively with face recognition ability, consistent with a functional role for adaptive face-coding mechanisms (Dennett et al., 2012; Rhodes et al., 2014). We asked whether this link is already present in younger neurotypical individuals and whether it is disrupted in autism. Given that adaptive face-coding mechanisms appear to be mature in young children, we expected to see this link in our neurotypical participants (Jeffery et al., 2010; Jeffery et al., 2013). It was an open question, however, whether this link would also be seen in our participants with autism. Although face identity aftereffects are reduced in autism, they are not eliminated, and so adaptability might remain linked to face recognition ability. Alternatively, there might be some more fundamental dissociation between adaptability and recognition. We used an individual differences approach to assess the link between face adaptation and face recognition ability in each group. Specifically, we examined correlations between face identity aftereffects and face recognition ability, controlling for non-face (car) recognition ability.

2.0 Method

2.1 Participants

Twelve cognitively able children and adolescents with autism (11 boys) aged 9 years 2 months to 14 years 8 months, were recruited from local schools and the West Australian Register for Autism Spectrum Disorders (See Table 1). All had received independent diagnoses of either Autistic Disorder ($n = 7$), Asperger's Syndrome ($n = 4$) or Pervasive Developmental Disorder Not Otherwise Specified ($n = 1$) by a multidisciplinary team (see Glasson et al., 2011, for details) following DSM-IV criteria (American Psychiatric Association, 2013). They also completed Module 3 of the Autism Diagnostic Observation Schedule – 2 (ADOS-2) (Lord et al., 2012) and all met the ADOS-2 criterion for autism spectrum disorder (cutoff score of 7). Moreover, all parents rated their child above the cut-off level for clinically-significant levels of autistic symptomatology on the Lifetime version of the Social Communication Questionnaire (SCQ) (Rutter, Bailey, & Lord, 2003).

Twelve typically developing children and adolescents (11 boys), who were well matched to our autism sample on chronological age ($p = .70$), non-verbal IQ ($p = .99$) and verbal IQ ($p = .51$), also participated (Table 1). They were selected from a larger sample of 48 typical participants (30 male; $M = 12$ years, 0 month, $SD = 2$ years, 3 months; range = 8 years, 7 months to 16 years, 2 months), who provided reliability data for the measures used.

Table 1. Descriptive statistics for Chronological Age, Cognitive Ability (PIQ, VIQ), Lifetime SCQ and ADOS-2 scores.

Measure	Group				
	Autism (n = 12)		Typical (n = 12)		
	Mean (SD)	Range	Mean	Range	
Chronological Age (yrs:mths)	12:2 (1:8)	9:2,14:8	12:5 (1:10)	8:8,14:6	$t(22) = -0.40, p = .70$
NVIQ ^a	110.9 (14.7)	84-129	110.0 (11.8)	96-141	$t(22) = -0.02, p = .99$
VIQ ^a	98.3 (9.6)	86-117	100.3 (3.9)	96-106	$t(14.5) = -0.67, p = .51$
SCQ ^{b,c}	25.7 (7.1)	12-34	2.1 (2.7)	0-9	$t(14.6) = 10.65, p < .001$
ADOS-2 ^b	10.5 (2.9)	7-15			

Notes. ^a Non-Verbal (NV) and Verbal (V) IQ were each measured with two subtests of the WASI (Wechsler, 1999): NVIQ = Matrix Reasoning and Block Design, VIQ = Similarities and Vocabulary.

^b Higher scores on both the Social Communication Questionnaire (SCQ, Rutter et al., 2003) and ADOS-2 (Autism Diagnostic Observation Schedule – 2, Lord et al., 2012) indicate increased symptoms. ADOS-2 score reported = Communication + Social Interaction algorithm total (cutoffs: autism = 10, autism spectrum = 7). ^c n=12 for the ASD sample, n=10 for the typical sample. Degrees of freedom adjusted for unequal variances where appropriate.

2.2 Tasks and Measures

2.2.1 Face Identity Aftereffect Task. This task was adapted from an identity aftereffect task used previously with children and adults (Ewing, Leach, et al., 2013; Jeffery et al., 2013). Reliability was good, with a mean Spearman-Brown corrected split-half reliability of .69 (calculated over 50 random splits of the data from our 48 typical children and adolescents). Briefly, the task is presented as a game in which robbers (adapting faces) are caught by police officers (test faces). Participants must watch the robber closely to prevent them escaping and then indicate which of two

officers caught them. To ensure attention to the adapting face, the robbers' eyes or lips brighten slightly at one point during adaptation, and participants must indicate which feature changed.

The test identities were gray-scale photographs of two male identities (Ted and Bob¹). Reduced identity strength versions were made by morphing each identity towards an average face (made from 20 male faces) using FantaMorph 5.3.2 in varying increments, to produce 40%, 60% and 80% versions. The 40% and 60% versions were used only in training and the 80% and average (0%) were used as test stimuli in the main task. Test and training faces were $3.8^\circ \times 3.5^\circ$, at a viewing distance of approximately 50cm. For each target identity, three adapting antifaes (robbers) were created by caricaturing the average face away from the target identity by 60%, 100% and 140% using FantaMorph. Adapting faces were $5.1^\circ \times 5.1^\circ$. The size difference between adapt and test stimuli was intended to minimize the contribution of low-level adaptation. The texture of the average face was applied to all stimuli. We used the brush tool in Photoshop to slightly brighten the lips or irises of the adapting faces (by adjusting the opacity level of a white area placed over the iris and lips: 25% for eyes, 15% for lips) for use in the change detection task (Figure 2). To minimize non-facial cues, an oval mask covered the hairline.

Participants began with training in recognizing the test faces (Ted, Bob), introduced as team captains, and familiarization with lower strength versions of the test faces, introduced as the captain's brothers. They were told to respond with the captain's name whenever they saw him or one of his brothers, using labelled keyboard keys. Auditory feedback (raindrop sound for correct, quack for incorrect) was given to indicate correct and incorrect responses during training. Participants

¹ This face is named "Rob" in Jeffery et al., (2013)

were then introduced to the change detection task. They were told to indicate which feature changed in the robber's face, by saying, "eyes" or "lips", as soon as they saw the change. Their responses were entered by the experimenter.

Figure 2. Example of an adapting stimulus identity, Anti-Bob, at three intensity levels: 60%, 100%, 140% (left column). The eye- and lip-change versions of these stimuli that appeared during the change-detection task are also shown (right columns).

Participants then completed the adaptation task. On each trial an adapting face appeared for five 1000 ms exposures, with 100 ms ISIs. During either the second or third 1000 ms exposure the lips or eyes brightened. Participants had to say, “eyes” or “lip”, when they saw the change. After the adapting sequence there was a 200 ms ISI followed by the test face for 400ms. A blue frame surrounded the test face to clearly distinguish it from the adaptor faces. A response screen then prompted participants to identify the test face using labelled keyboard keys. The experimenter discretely recorded their change-detection response using a mouse click. Participants initiated each trial by pressing the space bar.

Each of the 6 adaptors (2 identities x 3 strengths) appeared in 14 trials: 10 trials with the average test face and 4 with an 80% test face (two for each target face). The 80% test faces were included as easy trials to help maintain motivation, and were not used to calculate aftereffects. These 84 trials were randomly divided into four testing blocks. The first block began with four practice trials using 80% test faces. Each subsequent block began with a reminder of how to identify the target identities, with each 100% identity shown on screen and participants asked to identify them. Participants took short breaks between blocks. Half-way through each block there was an additional trial in which robber ‘escaped’ with a precious item (e.g., a sports car, iPad) to keep participants engaged. The task took 20-30 minutes to complete.

2.2.2 Cambridge Face Memory Test for Children (CFMT-C). This task was adapted from the widely-used adult CFMT (Duchaine & Nakayama, 2006), which has good reliability (Cronbach's $\alpha = .89$, Bowles et al., 2009). The child version used here follows the same design, except that the study set size is reduced (5 rather than 6 to-be-remembered items) and there are fewer test foils (2AFC rather than 3AFC) (Pellicano, Pimperton, & Duchaine, 2014). The CFMT-C has good

reliability, with a mean Spearman-Brown corrected split-half reliability of .85 (calculated over 50 random splits, from the data of our 48 typical child and adolescent participants).

2.2.3 Cambridge Car Memory Test for Children (CCMT-C). We adapted this task from the adult CCMT, which is analogous to the CFMT, but uses cars instead of faces (for details see Dennett et al., 2011). The adult version has good reliability (Cronbach's alpha = .83, Dennett et al., 2011). Our child version follows the same design as the CFMT-C, described above. Reliability was good, with a mean Spearman-Brown corrected split-half reliability of .79 (calculated over 50 random splits, from the data of our 48 typical child and adolescent participants).

2.3 Procedure

Participants completed these tasks in two 90-120 minute sessions held on separate days. Tasks were completed in the following order: CFMT-C (first session), CCMT-C (second session), face identity aftereffect (second session). Each session contained one other task that was unrelated to the present study. Participants were tested individually in a quiet room in their home or school or at the University of Western Australia. The experimenter sat beside the child during all tasks to monitor engagement and provide verbal encouragement. Participants received a certificate, a movie ticket and a small toy or chocolate for their participation. The study was approved by the Human Research Ethics Committee at the University of Western Australia and all participants and their parents provided written consent prior to their participation.

3.0 Results

3.1 Face identity aftereffects

Identity aftereffects were measured as the proportion of trials on which the average test face was identified as the identity opposite the adapting antiface.

Significant aftereffects (greater than 0.5) were observed at all three adaptor levels for both the autism group (60% $t(11) = 2.93$, $p = .014$, Cohen's $d = 0.84$; 100% $t(11) = 3.66$, $p = .004$, Cohen's $d = 1.06$; 140% $t(11) = 5.58$, $p < .0001$, Cohen's $d = 1.61$) and the typical group (60% $t(11) = 3.22$, $p = .008$, Cohen's $d = 0.93$; 100% $t(11) = 7.13$, $p < .0001$, Cohen's $d = 2.06$; 140% $t(11) = 12.72$, $p < .0001$, Cohen's $d = 3.67$) (Figure 3).

Figure 3. Mean identity aftereffects for each adaptor strength and participant group.

Individual data points are also shown for all participants. SEM bars are shown.

Inspection of Figure 3 shows that aftereffects were generally lower for the autism group relative to the typical group, except at the weakest adaptor strength (60% adaptors), indicating reduced identity adaptation. However, aftereffects increased with adaptor strength for both groups, consistent with norm-based coding of identity in participants with autism as well as typical participants. Neither group showed a decrease at higher adaptor strengths that would indicate multichannel coding. Thus, there was no evidence of any qualitative difference in coding mechanisms between the groups.

These observations were confirmed by a two-way repeated measures ANOVA conducted with group (autism, typical) as a between-participants factor and adaptor strength (60%, 100%, 140% antiface) as a repeated measures factor. Planned t-tests were used to test for differences between groups and adaptor strengths. There were significant effects of group, $F(1,22) = 4.66$, $p = .042$, $\eta_p^2 = .175$, and adaptor strength, $F(2,44) = 19.81$, $p < .001$, $\eta_p^2 = .474$, and a significant interaction, $F(2,44) = 3.43$, $p = .041$, $\eta_p^2 = .135$ (Figure 3).² Aftereffects were significantly smaller in the autism group than the typical group for the two strongest adaptor strengths, $t(22) = 3.05$, $p = .003$, 1-tailed, Cohen's $d = 1.30$ (140% adaptors), $t(22) = 1.97$, $p = .031$, 1-tailed, Cohen's $d = 0.84$ (100% adaptors), but not for the weakest (60%) adaptor strength, $t(22) = 0.09$, $p = .933$, Cohen's $d = 0.04$. For the typical group, aftereffects increased significantly from 60 to 100 adaptors, $t(11) = 3.13$, $p = .01$, Cohen's $d = 1.89$, and from 100 to 140 adaptors, $t(11) = 2.33$, $p = .040$, Cohen's $d = 1.40$. For the autism

² Although groups were matched on PVIQ, the lowest and highest scores were nevertheless lower for the autism group than the typical group. When centred PVIQ was used as a covariate, all effects remained significant, except for the interaction between adaptor strength and group, which was marginally significant, $F(2,1501) = 3.316$, $p = .062$, $\eta_p^2 = .136$, thus providing even clearer evidence that the group difference is quantitative rather than qualitative.

group, there was a significant increase from 60% to 140%, $t(11) = 3.29, p = .007$, Cohen's $d = 1.98$, but no significant increase from 60% to 100%, $t(11) = 1.37, p = .198$, Cohen's $d = 0.83$, or from 100% to 140% adaptors, $t(11) = 1.65, p = .128$, Cohen's $d = 0.99$.

Performance on the change detection task was excellent for both groups (autism $M = 93.9\%$, $SD = 5.3\%$; typical $M = 96.4\%$, $SD = 3.3\%$), with no significant difference between groups, $t(22) = 1.37, p = .184$, Cohen's $d = .58$. Thus, there was no evidence that participants with autism attended less to adapting faces than typical participants. Nor were there any significant group differences when detection of eye and lip changes were examined separately, both $ts < 1.41, ps > .17$, Cohen's $ds < .60$ (eye changes: autism $M = 97.4\%$, $SD = 3.1\%$; typical $M = 98.0\%$, $SD = 3.2\%$; lip changes: autism $M = 90.5\%$, $SD = 9.4\%$; typical $M = 94.8\%$, $SD = 5.3\%$).

Identification of the 80% test faces was also very good, indicating that participants remained engaged during testing and did not forget the target identities. Performance was marginally better for typical ($M = 94.1\%$, $SD = 6.5\%$) than autistic ($M = 87.9\%$, $SD = 9.6\%$) participants, $t(22) = 1.86, p = .076$, Cohen's $d = .79$.

3.2 Face and Car Recognition

As expected, autistic participants performed more poorly on the face recognition test than typical participants (Table 2), although this difference was not significant, $t(22) = 1.54, p = .14$, Cohen's $d = 0.66$. However, one typical participant performed very poorly (see also Figure 4). When they were removed, the group difference was significant, $t(21) = 2.46, p = .023$, Cohen's $d = 1.07$. There was no significant group difference for car recognition whether this participant was included, $t(22) = 0.86, p = .40$, Cohen's $d = 0.37$, or not, $t(21) = 0.87, p = .40$, Cohen's $d = 0.38$.

Table 2. Descriptive statistics for face and non-face recognition performance (percent correct).

Measure	Group			
	Autism (N = 12)		Typical (N = 12)	
	Mean (SD)	Range	Mean	Range
CFMT-C	77.9 (8.6)	67 – 92	84.9 (13.0)	57 – 100
CCMT-C	82.1 (10.9)	60 – 100	85.4 (7.9)	68 – 95

Notes. CFMT-C Cambridge Face Memory Test - Child, CCMT-C Cambridge Car Memory Test - Child.

3.3 Relationship between face adaptation and face recognition ability

For each participant group, we examined whether face adaptation (identity aftereffects collapsed across adaptor strength) is linked to face recognition ability (CFMT-C scores) and to face-selective recognition ability, measured by residuals from a regression predicting face recognition (CFMT-C) scores from car recognition (CCMT-C) scores (see DeGutis, Wilmer, Mercado, & Cohan, 2013). Given the small sample size, we focus on effect sizes rather than significance levels (Cohen, 1988). Aftereffects correlated strongly with both face recognition and face-selective recognition in the typical group (Table 3, Figure 4).³ For the autism group, there was a strong correlation with face recognition and a moderate correlation with face-selective recognition.

³ The scatterplot shows a possible outlier in the typical group (Figure 4). However, the correlations remained substantial, $r(9) = .418$, $p = .201$, partial $r(8) = .301$, $p = .398$ (controlling car recognition), when this participant was removed.

Table 3. Pearson product-moment correlations of face identity aftereffects (AEs) with face recognition ability (CFMT-C), non-face (car) recognition ability (CCMT-C) and face-selective recognition ability, for the typical and autism groups.

Participant Group			CFMT-C	CCMT-C	Face-Selective Recognition ^a
Autism N = 12	Face identity	r	.601	.487	.383
	AE	p	.039	.108	.219
Typical (Matched) N = 12	Face identity	r	.708	.320	.657
	AE	p	.010	.311	.020

^a Residuals from regression with CCMT-C predicting CFMT-C scores.

Figure 4. Scatterplots showing positive associations between face identity aftereffects and face recognition ability in autistic participants (left) and in age- and ability-matched typical (right) participants.

We also conducted multiple regression analyses with face recognition (CFMT-C) as the outcome variable and face identity aftereffects, age and full-scale IQ as predictors, for each group. Face identity aftereffects were the only predictor to approach significance for the typical group ($\beta = .64$, $B = 107.38$, $p = .054$, 95% CI = -2.51, 217.27) and the only significant predictor for the autism group ($\beta = .88$, $B = 64.52$, $p = .038$, 95% CI = 4.59, 124.45). We then added car recognition (CCMT-C) as a predictor, to test whether face identity aftereffects predicted face-selective recognition ability. They did for the typical group ($\beta = .80$, $B = 134.93$, $p = .038$, 95% CI = 9.75, 260.11), but not for the autism group ($\beta = .53$, $B = 38.83$, $p = .214$, 95% CI = -28.40, 106.06), although the β indicates a moderate effect size.

These correlation and regression results indicate a clear link between face aftereffects and face recognition ability in both groups that is independent of age and cognitive ability. This link is also selective for face recognition ability in both groups, although it only reached significance in the typical group.

4.0 Discussion

Our results point to a quantitative, but not a qualitative, difference between the adaptive face-coding mechanisms of autistic and typical children and adolescents. Face identity aftereffects were generally smaller for individuals with autism, replicating previous findings (Ewing, Leach, et al., 2013; Pellicano et al., 2007), but there was no evidence of any more profound qualitative difference. Identity aftereffects increased with adaptor strength for both groups, consistent with norm-based coding of face identity. Neither group showed any decrease that would indicate non-norm-based, multichannel coding. Therefore, we suggest that norm-based coding

is used to represent face identity in autism, but that face norms are less readily calibrated by experience.

Reduced adaptability in our participants with autism cannot readily be attributed to poor attention to the adapting faces. They performed well on the change detection task that was designed to focus attention on the adapting faces. Furthermore, their aftereffects did not differ from those of typical participants for the weakest identity-strength adaptors (with significant aftereffects for both groups). Rather, reduced adaptability emerged for higher adaptor strengths. This interaction has also been reported for relatives of individuals with autism (Fiorentini et al., 2012). It might indicate weaker sensitivity to increases in facial distinctiveness, perhaps reflecting shallower tuning of underlying opponent neural populations to dimension extremes (e.g., Fig 3, Dennett et al., 2012). Alternatively, it might reflect a contribution of floor effects for the weakest adaptor level, because several participants in each group showed no aftereffect (see Figure 3, where 50% = no aftereffect).

Nor can reduced adaptability in participants with autism be readily attributed to differences in the face features attended by the two groups. Compared with typical individuals, individuals with autism may look less at the eyes and more at the mouth (Klin, Jones, Schultz, Volkmar, & Cohen, 2002; Neumann, Spezio, Piven, & Adolphs, 2006; but see Senju & Johnson, 2009). However, our change detection task required attention to both the eyes and the mouth, which should minimize any effects of such differences. We also note that, although we only used a single pair of identities, reduced identity aftereffects have been reported in participants with autism using other pairs of identities (Ewing, Leach, et al., 2013; Pellicano et al., 2007). Therefore, the results are unlikely to reflect any idiosyncracies of the test pair used here.

The pattern of aftereffects we obtained was consistent with norm-based opponent coding, but not (non-norm-based) narrowband multichannel coding, of identity by both our autistic and typically developing participants. These are the two models that have received most attention in the literature on adaptive face-coding mechanisms (Jeffery et al., 2010; Jeffery et al., 2013; Jeffery et al., 2011; McKone, Jeffery, Boeing, Clifford, & Rhodes, 2014; Susilo, McKone, & Edwards, 2010; Zhao, Seriès, Hancock, & Bednar, 2011). Nevertheless, there may be other models that could produce the pattern observed here. For example, recent quantitative modelling of identity aftereffects over a wider range of adaptor identity strengths than used here (and extending beyond the natural range of faces) in neurotypical adults, has raised the possibility of a third channel tuned explicitly to the norm (McKone et al., 2014). Therefore, we cannot rule out more subtle differences in the identity coding mechanisms of autistic and typically developing participants.

We found no evidence that the link between face adaptation and face recognition ability was disrupted in autism. There were substantial positive correlations between face adaptation and face recognition performance in both groups. Although these correlations must be interpreted with caution given our small samples, they are consistent with other evidence supporting links between adaptation and face processing ability. Specifically, the size of gaze aftereffects also correlates positively with the ability to categorize gaze direction in autistic, as well as typical, children (Pellicano, Rhodes, & Calder, 2013). Taken together, these results are consistent with a functional role for adaptation in face perception for children with autism, as well as for typical children.

An interesting question for future research is whether the reduced adaptation seen here for our autism group is selective for faces. Identity aftereffects have not

been assessed for non-face stimuli. However, closely related distortion aftereffects, which measure changes in what looks normal (i.e., in perceptual norms) in response to consistent changes in experience, have been assessed (Ewing, Pellicano, & Rhodes, 2013). Compared with age- and ability-matched neurotypical participants, children with autism showed reduced distortion aftereffects for faces, but not for cars or inverted faces. These results suggest that reduced updating of perceptual norms in autism could be relatively selective for faces.

All of our autistic participants had received clinical diagnoses of an autism spectrum disorder, which were confirmed by ADOS-2 scores, and parent ratings (SCQ scores) indicating a consistent history of autistic behaviour. However, they were all cognitively able and it is possible that a more profound, qualitative, disruption of adaptive face-coding mechanisms would occur in less cognitively able and/or more severely autistic participants, or in autistic individuals with more pronounced face recognition difficulties than in our current sample. Future studies with those populations will be needed to determine whether this is indeed the case.

In summary, we found that adaptive face-coding mechanisms in autism are less readily calibrated by experience. Importantly, however, coding remains norm-based, as indicated by the pattern of increasing face identity aftereffects with increasing adaptor identity strength. Therefore, the atypicality of adaptive face-coding mechanisms seen in cognitively able children and adolescents with autism is quantitative rather than qualitative in nature. We suggest that this quantitative atypicality may be part of a continuous distribution of reduced adaptability of face-coding mechanisms that extends into the general population (see Rhodes et al., 2013), consistent with it being an endophenotype for autism.

Acknowledgements

This research was supported by the Australian Research Council Centre of Excellence in Cognition and its Disorders (CE110001021), an ARC Professorial Fellowship to Rhodes (DP0877379) and an ARC Discovery Outstanding Researcher Award to Rhodes (DP130102300). We thank Mayu Nishimura and Daphne Maurer for co-creating the Robbers Game used in the Identity Aftereffects task, Ainsley Read for assistance designing testing protocols and assistance with testing, and Nichola Burton, Francis Caulfield and Samantha Bank for assistance with testing. Ethical approval was granted by the Human Research Ethics Committee of the University of Western Australia.

Figure Captions

Figure 1. A simplified (2 dimensional) face space with two faces, Dan and Jim, an Average face, created by morphing 20 male, Caucasian faces, and two antifaces, antiDan and antiJim. An antiface is made by morphing a face towards, and beyond, the Average, and has opposite properties to that face. Reduced-identity-strength versions of Dan and Jim, created by morphing those identities towards the Average, are also shown. Identity aftereffects occur when exposure to a face biases subsequent perception towards a face with opposite properties. For example, after viewing antiDan for a few seconds, we are biased (briefly) to see Dan.

Figure 2. Example of an adapting stimulus identity, Anti-Bob, at three intensity levels: 60%, 100%, 140% (left column). The eye- and lip-change versions of these stimuli that appeared during the change-detection task are also shown (right columns).

Figure 3. Mean identity aftereffects for each adaptor strength and participant group. Individual data points are also shown for all participants. SEM bars are shown.

Figure 4. Scatterplots showing link between face identity aftereffects and face recognition ability in autistic participants (left), age- and ability-matched typical (middle) participants, and in our larger group of typical participants (right).

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