Abstract

Individuals with autism spectrum disorder (ASD) can have difficulty recognizing emotional expressions. Here we asked whether the underlying perceptual coding of expression is disrupted. Typical individuals code expression relative to a perceptual (average) norm that is continuously updated by experience. This adaptability of face coding mechanisms has been linked to performance on various face tasks. We used an adaptation aftereffect paradigm to characterize expression coding in children and adolescents with autism. We asked whether face expression coding is less adaptable in autism and whether there is any fundamental disruption of norm-based coding. If expression coding is norm-based, then the face aftereffects should increase with adaptor expression strength (distance from the average expression). We observed this pattern in both autistic and typically developing participants, suggesting that norm-based coding is fundamentally intact in autism. Critically, however, expression aftereffects were reduced in the autism group, indicating that expression-coding mechanisms are less readily tuned by experience. Reduced adaptability has also been reported for coding of face identity and gaze direction. Thus there appears to be a pervasive lack of adaptability in face-coding mechanisms in autism, which could contribute to face processing and broader social difficulties in the disorder.

Introduction

A central feature of autism spectrum disorder (ASD) is difficulty with affective processing and reciprocal social interactions (American Psychiatric Association, 2013; Kanner, 1943). Several theorists have suggested that atypical face processing mechanisms may contribute to these social difficulties (Dawson et al., 2005; Schultz, 2005). Consistent with this view, atypical gaze patterns and brain activity have been reported during the visual processing of facial expressions (for a review, see Harms, Martin, & Wallace, 2010). Moreover, the recognition and interpretation of facial expressions is often impaired in individuals with ASD (Nuske, Vivanti, & Dissanayake, 2013), with a recent large meta-analysis (48 studies involving 78 comparisons, 63 of which used face tasks) estimating a substantial effect size for the deficit of 0.41 after correction for publication bias (Uljarevic & Hamilton, 2013).

Here we seek to better understand affective processing in autism, by examining the underlying visual coding of facial expressions. In typical populations, facial expressions appear to be adaptively coded as deviations from a norm or average expression in a multi-dimensional face space (Figure 1) (Burton, Jeffery, Skinner, Benton, & Rhodes, 2013; Rhodes et al., 2017; Skinner & Benton, 2010, 2012). Norm-based coding can be neurally implemented by opponent coding, with pairs of neural populations, tuned to opposite extremes, coding each expression-related dimension in face space. The norm is signaled implicitly by equal activation in the two populations and is continuously updated (adapted) by experience. This adaptive updating is indexed by aftereffects, whereby adaptation to an expression biases us to perceive an expression with opposite visual properties (Figure 1) (e.g., Skinner & Benton, 2010).

INSERT FIGURE ONE ABOUT HERE

In typically developing individuals, adaptation appears to play a functional role in face perception (for reviews, see Rhodes & Leopold, 2011; Webster & MacLeod, 2011). Typical adults who adapt more to facial expressions, as indexed by larger expression aftereffects, show better expression recognition (Palermo et al., 2017; Rhodes et al., 2015). Similarly, typical adults who adapt more to face identity show better identity recognition (Dennett, McKone, Edwards & Susilo, 2012; Rhodes, Jeffery, Taylor, Hayward, & Ewing, 2014; Rhodes et al., 2015). Moreover, at an individual level, those autistic children and adolescents who adapt less to face identity show poorer identity recognition (Rhodes, Ewing, Jeffery, Avard, & Taylor, 2014) and those autistic individuals who adapt less to gaze direction show poorer gaze categorization (Pellicano, Rhodes, & Calder, 2013). Therefore, any reduction in expression adaptation could potentially contribute to expression processing difficulties in ASD.

Two previous studies have examined expression aftereffects in high-functioning adults with autism (Cook, Brewer, Shah, & Bird, 2014; Rutherford, Troubridge, & Walsh, 2012). Rutherford et al. examined the effects of adapting to expressions (happy, sad, fear, anger, disgust, surprise) on the perceived expression of neutral test faces. Compared with controls, responses in the ASD group were less consistent and showed atypical patterns. For example, whereas adaptation to negative expressions biased typical participants to see positive expressions, as expected, it biased ASD participants to see negative expressions. Cook et al. found no reduction in the size of expression aftereffects in autistic adults. However, their procedure may have underestimated these aftereffects in the typical adults. Their participants adapted to faces showing either disgust or anger and then had to respond “disgust” or “anger” to test faces from a disgust-anger continuum. However, Rutherford et al. showed that adaptation to both these expressions biased typical, but not autistic, participants to see a happy expression, a response option that was not available to Cook et al.'s participants. Thus, the expression aftereffects of typical participants are likely to have been underestimated, which could mask any group difference.

In the present study we assessed whether expression adaptation is reduced in ASD using a procedure that should be optimally sensitive to expression adaptation: an experimental approach that directly assesses the expected bias to perceive *opposite* visual properties (Cook, Matei, & Johnston, 2011). We also examined whether there is any more fundamental disruption of norm-based, opponent coding of expression in autism. If coding is norm-based, then expression aftereffects should get larger as adaptors get more extreme (i.e., further from the norm) (Figure 1). This increase reflects the greater activation of channels (which are tuned to extreme values) by more extreme adaptors, resulting in greater reductions in responsiveness and therefore larger aftereffects (McKone, Jeffery, Boeing, Clifford, & Rhodes, 2014, 2015; Rhodes et al., 2017). This pattern has been reported for expression aftereffects in typically developing children (Burton et al., 2013) and adults (Skinner & Benton, 2010, 2012) and holds across the full natural range of possible faces (Rhodes et al., 2017). We used a size change between adapt and test faces and allowed free eye movements, both of which should reduce the contribution of low-level (retinotopic) adaptation to the observed aftereffects. This procedure is widely used to ensure that aftereffects tap higher-level face-coding mechanisms (e.g., Ewing, Pellicano & Rhodes, 2012; Rhodes et al., 2011; Rhodes et al., 2017).

We measured expression aftereffects in children and adolescents, because autism is a developmental disorder, and any atypicalities may be particularly apparent in this group. We tested cognitively-able children and adolescents with autism and a group of age- and cognitive ability-matched neurotypical participants. We asked whether expression aftereffects are reduced in the ASD group and whether expression coding is norm-based in this group. We also measured expression recognition, using a developmentally appropriate task (adapted from Gao & Maurer, 2009 Experiment 1), to see whether any atypicalities observed in adaptability of expression coding mechanisms could be linked directly to expression recognition performance.

Method

Participants

Nineteen cognitively able children and adolescents with ASD (17 male, sex ratio determined by availability) aged 9 years 2 months to 16 years 3 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* = 13), Asperger's Syndrome (*n* = 5) or Pervasive Developmental Disorder Not Otherwise Specified (*n* = 1) by a multidisciplinary team following DSM-IV criteria (American Psychiatric Association, 2013). These participants completed the current tasks as part of a larger testing battery, which ran across multiple testing sessions and included tasks that have published elsewhere (e.g., Rhodes et al., 2014; Rhodes, Neumann, Ewing & Palermo, 2014). They also completed Module 3 of the Autism Diagnostic Observation Schedule – 2 (ADOS-2) and 12 met the ADOS-2 criterion for autism spectrum disorder (cutoff score of 7) (Lord et al., 2012). All parents rated their child at or above the cutoff (score of 12) for clinically-relevant levels of autistic symptomatology on the Social Communication Questionnaire (SCQ) (Corsello et al., 2007).

We selected typically developing comparison individuals (N = 19, 14 male) from a larger sample of 48 typically developing children and adolescents (30 male; M = 12 years, 0 months, SD = 2 years, 3 months; range = 8 years, 7 months to 16 years, 2 months), who had been tested to provide reliability data for a larger battery of measures reported elsewhere. The selection was constrained to provide the best match to our autism sample on chronological age (*p* = .98), non-verbal IQ (*p* = .56) and verbal IQ (*p* = .67) (and completed prior to any examination of the measures under investigation in the present study) (Table 1).

Sample size was determined by availability and resembles that of other studies reporting reduced face adaptation in autism (e.g., Pellicano, Jeffery, Burr, & Rhodes, 2007; Rhodes, Ewing, et al., 2014).

Adaptation Task

The task was adapted from one previously used to measure face identity aftereffects in typically developing children (Burton et al., 2013). It was programmed in SuperLab 4.0. In each trial of the task, participants viewed an adaptor, which had to be monitored for eye or lip changes (brightness adjustment) to ensure attention to the adapting faces. They then saw a test face, and made a judgment about which expression they saw. The task was presented as a developmentally appropriate game, in which participants took the role of adventurers who had to free a kingdom from an evil queen by identifying the expressions of villagers trapped in paintings. The adaptor stimuli were guard ‘statues’ that could be caught by identifying small movements: the eye and lip changes.

Stimuli. The test stimuli were average expression faces (a morph of happy, sad, angry, fearful, surprised, disgusted and neutral expression morphs) as well as 80% versions of the happy and sad expressions (created by morphing together 25 male and 25 female faces showing each expression), taken from Skinner and Benton (2010). The adaptors were 60%, 100% and 140% anti-expressions, created by morphing each (100%) target expression along a trajectory passing through the average expression and beyond. We used the average expression, consistent with previous research investigating norm-based coding of expression (e.g., Burton et al., 2013; Skinner & Benton, 2010). These anti-expressions are visual opposites of the corresponding target expressions, so that, for instance, the upturned lips of a happy expression became downturned lips in anti-happy images. They may not correspond to familiar, nameable expressions. Versions of the adapting stimuli were created with either brightened lips or irises (achieved by placing a white layer over the feature at 20% opacity) for use in the attention control task during adaptation. Adaptors subtended a visual angle of approximately 4.7° x 6.4° when viewed from a distance of 50cm. Test stimuli were presented at 75% of the size of the adaptors (approximate visual angle of 3.6° x 4.8°) and free eye movements were allowed, to minimize low-level adaptation. All stimuli were presented in greyscale on a grey background.

Training. Prior to the adaptation trials, participants learned to identify the happy and sad target expressions at 100% strength, using labeled keyboard keys. They were given unlimited time to identify these expressions in a sequence of eight trials (two expressions x four repetitions), with auditory feedback (a “correct” or “incorrect” sound effect) after each response. When all eight expressions in the sequence were identified correctly, participants completed the same training with 40%, 60% and 100% expressions in a sequence of twelve trials (two expressions x three strengths x two repetitions). When they scored 75% correct or better with these unlimited exposure trials, they repeated the training with 400 ms exposures and without auditory feedback (as in the main task). When they scored at least 75% correct under these conditions, participants were introduced to the change detection task. They began with more extreme eye and lips changes than those used in the adaptation task, presented in a sequence of 12 adaptors: 6 anti-sad and 6 anti-happy, each shown for 1000 ms with 100 ms interstimulus intervals (ISIs). For each anti-expression there was one exposure with an eye change and one with a lip change, giving four changes in total across the sequence. Participants watched the sequence and responded verbally when they saw a change. If they missed more than one change, they repeated this task. They then repeated this training with eye and lip changes at the brightness levels used in the main task.

Adaptation trials. The trial sequence is illustrated in Figure 2. On each trial an anti-expression adaptor was presented for five 1000 ms exposures, with 100 ms ISIs, giving a total adaptation time of five seconds. On either the second or third exposure the eye or lip changed in brightness and participants responded vocally ("eyes" or "lips") as soon as they saw the change. The experimenter discretely recorded their responses using mouse clicks. After the last adapting exposure there was a 200 ms ISI, followed by a test face for 400 ms surrounded by a blue frame to clearly indicate that it was the test face. Participants then saw a response screen, which prompted them to use one of the marked keys to identify what expression (happy, sad) they had seen. They then pressed the spacebar to move on to the next trial.

INSERT FIGURE TWO ABOUT HERE

Each of the six adaptors (2 anti-expressions x 3 strengths) appeared in 14 trials: 10 trials with the average test face (used to calculate aftereffects) and 4 with 80% expression test faces (included to provide easy trials to maintain motivation and to ensure that participants were labelling the expressions correctly). These 84 trials were divided into four blocks, containing approximately equal numbers of each trial type. Trials were pseudo-randomised within each block so that the same adapting expression was not presented more than twice in a row. The first block began with four practice trials with 100% happy and sad test faces. The 100% happy and sad expressions were shown at the beginning of each block to remind participants what these expressions looked like. Half-way through each block there was an extra trial in which the test face did not appear, but instead, children were presented with an item that was 'stolen' by the evil queen (e.g. crowns, jewels). This was intended to keep participants engaged in the task. In addition, participants took short breaks between blocks. The task took approximately 20 minutes.

Expression Sensitivity Task

This task was adapted from Gao and Maurer (2009, Experiment 1). It is sensitive to developmental improvements in recognizing sadness and fear (but not happiness; anger not tested). We created four expression trajectories (2 male, 2 female) for each of happiness, anger, fear and sadness, by morphing between neutral and expressive faces (with the same identity) from the NimStim Face Stimulus Set (Tottenham et al., 2009) (see Gao & Maurer, 2009 for details). Each continuum contained eight intensity levels (0%, 10%, 20%, 30%, 40%, 60%, 80% or 100%) (Figure 3). The 128 images were split into two 64-trial blocks, each containing images for one male and one female identity. Block order was counterbalanced across participants. On each trial a face was presented for 1000 ms and participants had to categorize it as either neutral, fearful, sad, happy, or angry. Responses were made by selecting a cartoon face corresponding to each expression, eliminating the need for verbal labels (Figure 3). Trials were presented in random order. The task was presented as a game: “In this game you will be seeing people who are watching different movies that make them feel different things. Some of the movies are making them feel scared, sad, happy and angry and some of the movies are not making them feel anything at all. When you see each different face, it’s your job to say what they are feeling. Now sometimes people feel just a little bit sad, or just a little angry rather than a LOT of these feelings. That’s what makes this game tricky. When you see each face, just try and pick the cartoon that best matches the feeling the person is getting from the movie.” The task took approximately 10 minutes.

INSERT FIGURE THREE ABOUT HERE

General Procedure

Participants completed these tasks as part of a larger test battery administered over two 90-120 minute sessions held on separate days. The expression adaptation task and the first expression block was always completed during session one and the second expression block in session 2. Note – where participants completed an additional face adaptation task (relating to identity, as published in Rhodes et al., 2014) they did so during testing session 2. Thus there was no risk of those participants who completed sessions having any additional familiarity with adaptation procedures that could influence the current results. Participants were tested individually in a quiet room in their home or school or at the University of Western Australia on 15" Macbook Pro laptop computers. The experimenter sat beside the child 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.

Results

Aftereffects

We calculated aftereffects as the proportion of responses to the average test face that matched the adapting anti-expression (e.g., proportion "happy" after anti-happy adaptors) minus the proportion that mismatched (e.g., proportion "happy" after anti-sad adaptors). Positive values indicate that perception has been biased away from the adapting expression towards the opposite expression, as expected. Zero indicates no effect of the adaptor on responses (i.e., the same number of happy and sad responses after either adaptor). A single typical participant identified by SPSS as a (low) outlier (1.5-3 interquartile ranges outside the interquartile range) on the aftereffect task was excluded from the analysis. This exclusion did not affect the matching of the groups.

The results are shown in Figure 4. For both groups, aftereffects increased with increasing adaptor strength, consistent with norm-based coding. A two-way repeated measures ANOVA, with adaptor strength as a repeated measures factor and group as a between-participants factor, yielded a significant main effect of adaptor strength, $F(2,70) = 9.14$, $p < .0001$, $\eta_p^2 = .207$, and no significant interaction with group, $F(2,70) = 0.24$, $p = .787$, $\eta_p^2 = .007$. Separate one-way ANOVAs confirmed that adaptor strength had a significant effect for both groups, $F(2,36) = 3.44$, $p = .043$, $\eta_p^2 = .160$ (ASD), $F(2,34) = 6.07$, $p = .006$, $\eta_p^2 = .263$ (typical). This significant effect of adaptor strength also held for the subset of participants who met the more stringent ADOS-2 criterion for ASD (N = 12), $F(2,22) = 4.90$, $p = .017$, $\eta_p^2 = .308$. These results strongly suggest that expression coding remains norm-based in autism.

Significant adaptation occurred at all adaptor strengths for both groups, with all aftereffects significantly above zero: all *t*s > 3.96, *p*s < .001 (ASD group), all *t*s > 4.27, *p*s < .001 (typical group). However, aftereffects were significantly reduced in the ASD group (M = 0.26, SE = 0.04) compared to the typical group (M = 0.38, SE = 0.04), $F(1,35) = 5.15$, $p = .03$, $\eta_p^2 = .128$. This result suggests that expression-coding mechanisms may be less readily adapted by experience in autism.

Both groups performed very well on the attention control task, correctly identifying most of the lip (M = 0.85, SE = .03, ASD; M = 0.89, SE = .03, typical) and eye (M = 0.97, SE = .01, ASD; M = 0.98, SE = .01, typical) changes. Crucially, there was no significant group difference for either, $t(35) = 0.72$ $p = .47$ (lip changes), $t(28) = 1.33$, $p = .193$ (eye changes, df corrected for unequal variances), which could have signaled systematic differences in attention paid to the adapting faces.

INSERT FIGURE FOUR ABOUT HERE

Expression Task

Not surprisingly, recognition performance increased with intensity of expression on all the expression continua, for both groups (Figure 5). To assess performance, we averaged proportion correct across morph levels 10-100 (0% morphs did not contain any of the target expression) for each expression continuum[1]. Two ASD participants identified as SPSS outliers (one high, one low) were dropped from the analysis. A two-way repeated measures ANOVA, with expression continuum as a repeated measures factor and group as a between-participants factor, yielded a significant effect of expression continuum, $F(3,102) = 33.58$, $p < .0001$, $\eta_p^2 = .497$. Accuracy was highest for happy (M = 0.71, SE = .01) and lowest for sad (M = 0.49, SE = .02), with intermediate performance on anger (M = 0.58, SE = .01) and fear (M = 0.59, SE = .02) (all differences significant, *p*s < .0001, except between anger and fear, $p = .46$). Importantly, there was no significant effect of group, $F(1,34) = 1.02$, $p = .319$, $\eta_p^2 = .029$ (M = 0.58, SE = .01, ASD; M = 0.60, SE = .01, typical) and no interaction between group and expression, $F(3,102) = 0.32$, $p = .811$, $\eta_p^2 = .009$. Performance was well above chance (0.2) for both autistic (M = .58, SE = .01, 95%CI = .56-.61) and typical participants (M = .60, SE = .01, 95%CI = .58-.63). The same results were obtained if we restricted the ASD sample to participants who met ADOS criteria (N = 12, but one identified as an SPSS outlier and dropped, leaving N = 11).

INSERT FIGURE FIVE ABOUT HERE

Correlations

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[1] We had also intended to use the means of fitted Gaussians as threshold measures of performance and the standard deviations of the fitted Gaussians as measures of the precision with which expressions are detected. However, fits were poor ($R^2 < .6$) for 10 participants (5 ASD, 5 typical), reducing power considerably. Therefore, we do not report those results in detail, although we note that they did not yield any group differences.

Given the small samples, we focus on effect sizes rather than significance levels (Cohen, 1988). In the typical group there was a small-to-moderate, non-significant, correlation between expression aftereffects (averaged across adaptor levels) and expression recognition (averaged across expression), $r = .217$, $p = .387$, $N = 18$. The size of the correlation is consistent with the modest (but significant) association found in much larger adult samples, which suggests a functional role for adaptation (Palermo et al., 2017; Palermo et al., 2013; Rhodes et al., 2015). Interestingly, there was no positive association in the ASD group, $r = -.111$, $p = .652$, $N = 19$. This result could arise because variation in the (reduced) adaptation in this group has no functional consequences. Alternatively, it could reflect atypical visual coding of expression in the expression recognition task (e.g., more verbal mediation, Harms et al., 2010). We note, however, that the correlations did not differ significantly between the groups, $z = -.92$, $p = .358$, and suggest that they be viewed with caution given the small samples.

There were no significant associations between symptom severity scores in the autism group (as measured by either the ADOS or SCQ) and expression recognition or expression aftereffect scores, all *r*s < .195, *p*s > .42.

Discussion

Facial expression coding mechanisms were less readily adapted by experience, as indicated by reduced expression aftereffects, in the ASD group. This reduced adaptability could potentially have negative consequences for expression processing, given the links between adaptation and performance on various face tasks in both typically developing (Dennett, et al., 2012; Palermo et al., 2017; Rhodes, Jeffery, et al., 2014; Rhodes et al., 2015) and autistic samples (Pellicano et al., 2013; Rhodes, Ewing, et al., 2014). These links strongly suggest a functional role for face adaptation, perhaps by calibrating coding mechanisms to the range of faces experienced (for discussion see Rhodes, 2017; Rhodes &

Leopold, 2011; Webster & MacLeod, 2011). Thus, reduced adaptability of expression coding mechanisms could potentially contribute to expression recognition problems and associated social interaction difficulties in children and adolescents with ASD.

That said, our autistic group showed no impairment on the expression recognition task used here. Of course, we used only one task and this result cannot be interpreted as evidence for intact expression recognition. However, many studies, including large ones, have also failed to find clear expression recognition deficits in ASD and there is substantial heterogeneity in effect sizes across studies (Uljarevic & Hamilton, 2013). Explaining this heterogeneity, which was unrelated to either mean age (range 6-41 years) or mean FSIQ (range 40-130) of the autism samples, remains a challenge for the field. One interesting possibility is that it may be related to differences in exposure to expression recognition training in intervention programs. Another possibility is that it could relate to differences n the extent to which tasks tap the face-selective component of expression recognition (Lewis, et al, 2016).

Although we found no expression recognition deficit, we did find reduced facial expression aftereffects in our ASD group. We have interpreted this result as evidence for reduced adaptability of the visual mechanisms that code facial expressions. However, there are other possibilities. If face space is organized differently in autism, as suggested by the atypical responses reported by Rutherford and colleagues (2011), then it is possible that we were not testing along the optimal (opposite) trajectories for our autistic participants (Cook et al., 2011). In this case, their aftereffects would naturally have been reduced relative to those of controls.

Another possible reason for the reduced expression aftereffects observed could be reduced attention to the adapting faces. Individuals with ASD are likely less in interested in faces than typically developing participants, and reduced attention to adapting faces reduces face aftereffects (Rhodes et al., 2011). However, our use of a change detection task ensured good attention to the adapting faces, with autistic participants performing as well as typical participants. Therefore, differences in attention are unlikely to explain the reduced aftereffects (see also Ewing, Leach, Pellicano, Jeffery & Rhodes, 2013). Rather, we propose that they reflect a sluggish adaptive response to changes in facial expression. The same sluggish adaptive response has been observed for the coding of face identity in autism, with reduced identity aftereffects in the clinical population (Rhodes, Ewing, et al., 2014 – indeed, eleven of the twelve participants reported in that experiment were also in the present data set) and the broader phenotype (Fiorentini, Gray, Rhodes, Jeffery, & Pellicano, 2012; Rhodes, Jeffery, Taylor, & Ewing, 2013), and for the coding of gaze direction (Pellicano et al., 2013). Taken together, these results suggest a pervasive lack of adaptability in face-coding mechanisms. In the case of face identity coding, reduced adaptability may be part of the broader autism phenotype, as it extends to the relatives of individuals with autism (Fiorentini et al., 2012) and to the general population (see Rhodes et al., 2013). It will be interesting to determine whether reduced adaptability of expression coding is also part of the broader phenotype.

We found no evidence for any more fundamental disruption of norm-based coding in our ASD participants. Their expression aftereffects increased with adaptor strength, consistent with norm-based, opponent coding, as did those of the typical participants. These results parallel findings for face identity coding, which also remains norm-based in autism (Rhodes, Ewing, et al., 2014) and the broader phenotype (Fiorentini et al., 2012; Rhodes et al., 2013).

Given the heterogeneity of the disorder, and the small, cognitively able sample used here, we must consider the generality of our results. It seems likely that adaptability might be reduced further in more severely affected individuals. Another question is whether our findings would generalize to adults with autism. Cook and colleagues (2014) have suggested that reduced face adaptation might reflect a developmental delay that resolves by adulthood. In support of this claim, they found no deficit in expression aftereffects for high-functioning adults with autism. We argued earlier that their task likely underestimated expression aftereffects in typical adults, potentially masking any group deficit. An interesting future direction will be to see whether the aftereffect task used here reveals reduced adaptation in adults with autism. We note that an analogous identity aftereffect task that showed reduced adaptation in children and adults (Rhodes, Ewing, et al., 2014) failed to show a clear deficit in adults (Walsh et al., 2015), consistent with the developmental delay hypothesis.

In summary, although adaptive expression-coding mechanisms remain norm-based in children and adolescents with autism, they are less readily calibrated by experience. This reduced adaptability could potentially impair face expression processing in autism, although we note that no expression recognition deficit was found in our sample. Our results indicate that reduced autistic adaptability to faces extends beyond the coding of identity (Rhodes, Ewing, et al., 2014) and gaze direction (Pellicano et al., 2013), to include the coding of expression. This reduced adaptability in face-coding mechanisms may affect face-processing performance and contribute to associated social difficulties in autism.

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Table 1. Descriptive statistics for age, cognitive ability and autism symptomatology measures.

Measure	Group				
	ASD (n = 19)		Typical (n = 19)		
	M (SD)	Range	*M (SD)*	Range	
Age (Y;M)	12;3 (1;11)	9;2 – 16;2	12;3 (1;10)	8;10 -15;9	$t(36) = -.02$, $p = .98$
Nonverbal IQ[a]	112.5 (15.3)	84 – 134	110.4 (5.4)	96 - 118	$t(36) = .58$, $p = .56$
Verbal IQ[a]	101.9 (11.4)	86 – 126	103.1 (6.3)	88 - 114	$t(36) = -.42$, $p = .67$
Full Scale IQ[a]	107.3 (12.4)	90 – 134	107.8 (5.0)	98 – 116	$t(36) = -.15$, $p = .87$
SCQ[b]	23.9 (6.4)	12 - 34	1.9 (1.9)	0 - 7	$t(36) = 14.20$, $p < .001$
ADOS-2[b,c]	8.0 (4.5)	0 - 15			
CFMT-C[d]	79.1 (8.3)	66.7 – 93.3	85.2 (11.1)	56.7 - 100	$t(36) = -1.89$, $p = .03$[e]

[a] Nonverbal and verbal IQ were measured with the WASI (Wechsler, 1999): Matrix Reasoning and Block Design (nonverbal IQ) and Similarities and Vocabulary (verbal IQ). Full-scale IQ (FSIQ) was derived by standardizing the sum of both verbal and performance ability scores against age-based norms. [b] Higher scores on both the SCQ (Lifetime form, Rutter, Bailey, & Lord, 2003) and ADOS-2 (Lord et al., 2012) indicate a greater degree of autism symptomatology. [c] ADOS-2 score reported = Communication + Social Interaction algorithm total (cut-off = 7) [d] Accuracy (total percentage correct) on the Cambridge Face Memory Test - for Children (Croydon et al., 2014). [e] One-tailed independent samples t-test.

Figure Captions

Figure 1. A simplified (2 dimensional) face space showing an average (norm) expression, a happy expression and a sad expression (all from Skinner and Benton, 2011). Also shown are anti-expressions, made by morphing an expression towards, and beyond (to varying degrees), the average expression. An expression and its corresponding anti-expression have opposite visual characteristics. Aftereffects occur when exposure to an expression biases us to see an expression with opposite visual properties. For example, after viewing a strongly anti-sad face we are biased to see an average expression as sad.

Figure 2. Trial structure for the adaptation task. Participants adapt to an anti-expression (anti-happy or anti-sad) for 5 seconds and then see an average-expression test face for 400 ms. They must indicate whether the test face looks happy or sad. To ensure good attention to the adapting faces, participants must detect subtle changes in the colour of the eyes or lips.

Figure 3. Example expression continua for anger, fear, happiness and sadness in the expression sensitivity task. Each continuum contains morphed images that range from the average expression (0%) to the full strength expression (100%). Bottom row: The cartoon faces used to indicate responses.

Figure 4. Mean (*SEM*) expression aftereffects (proportion of responses to the average test face that matched the adapting anti-expression minus the proportion that mismatched) as a function of adaptor strength for participants with autism and typically developing controls. Individual participant scores are shown.

Figure 5. Mean proportion correct responses for each expression continuum for typical and ASD participants. SE bars are shown.

Figure One

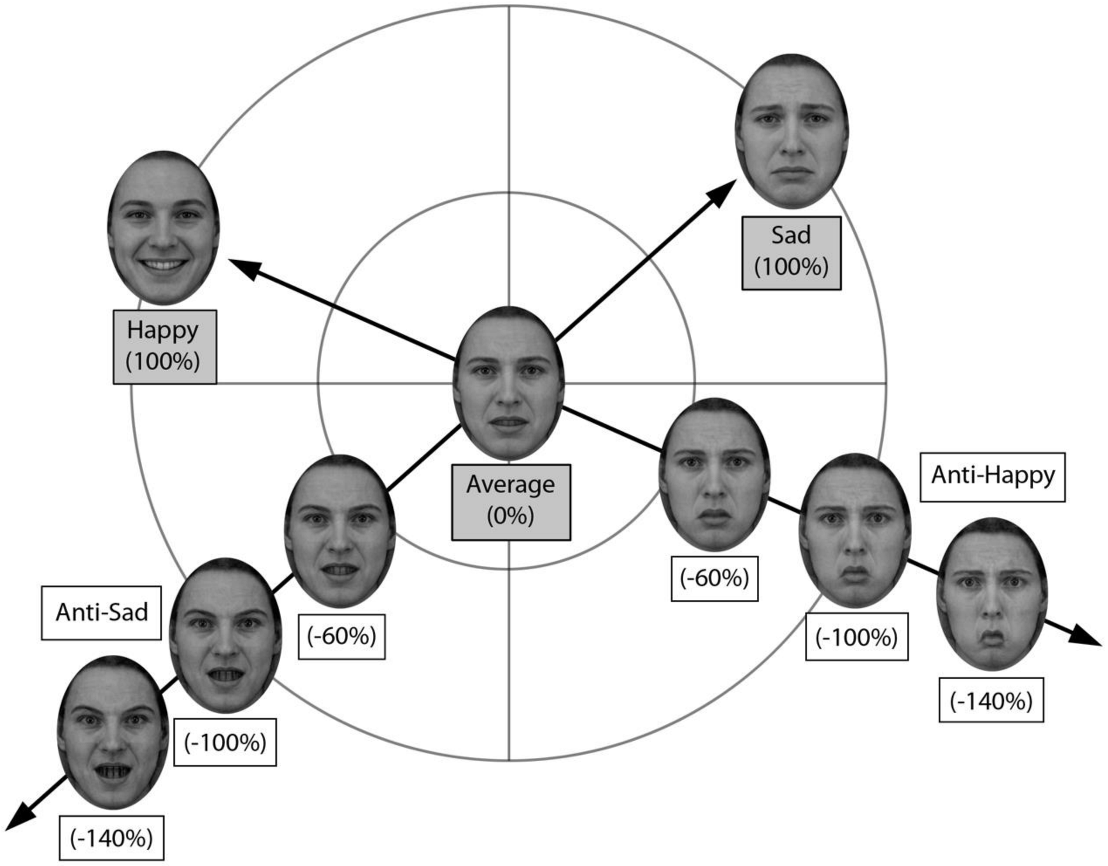

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FIGURE TWO

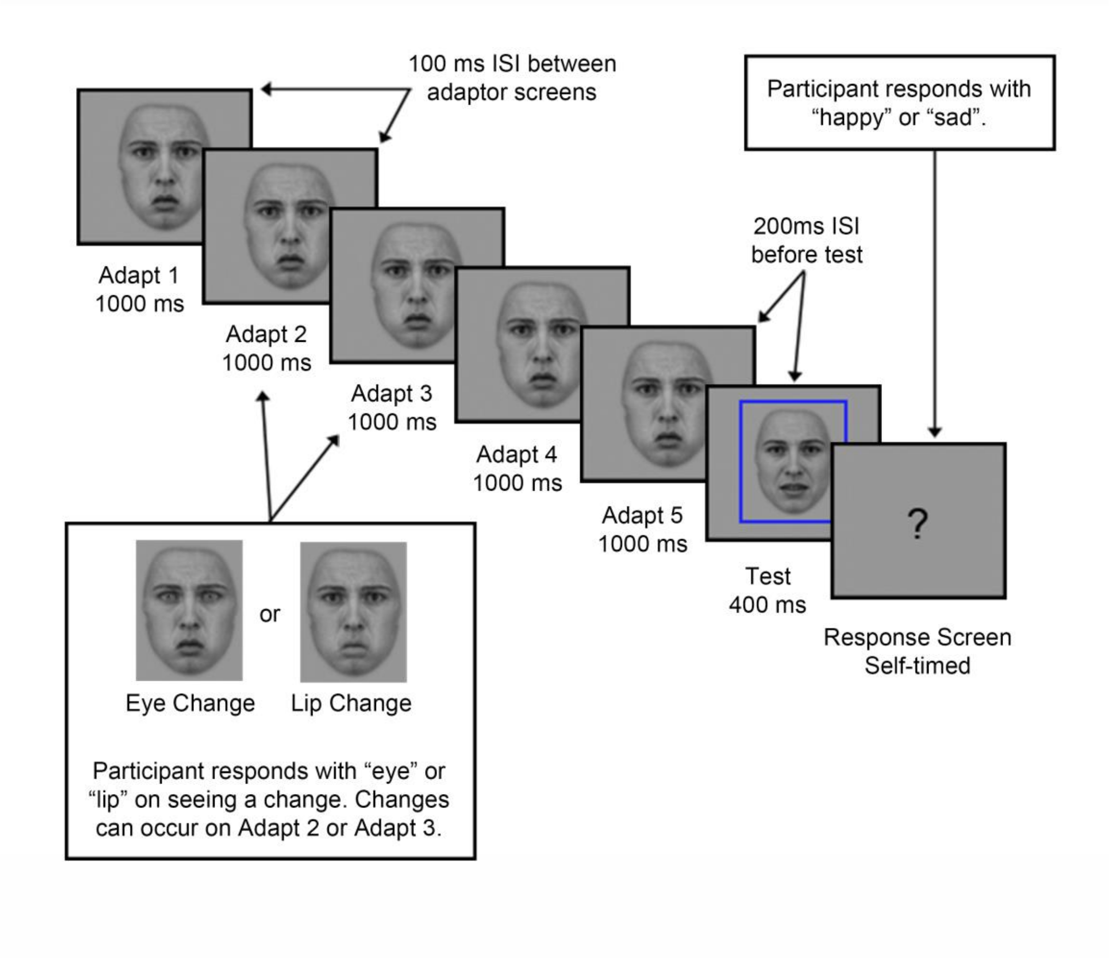

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FIGURE THREE

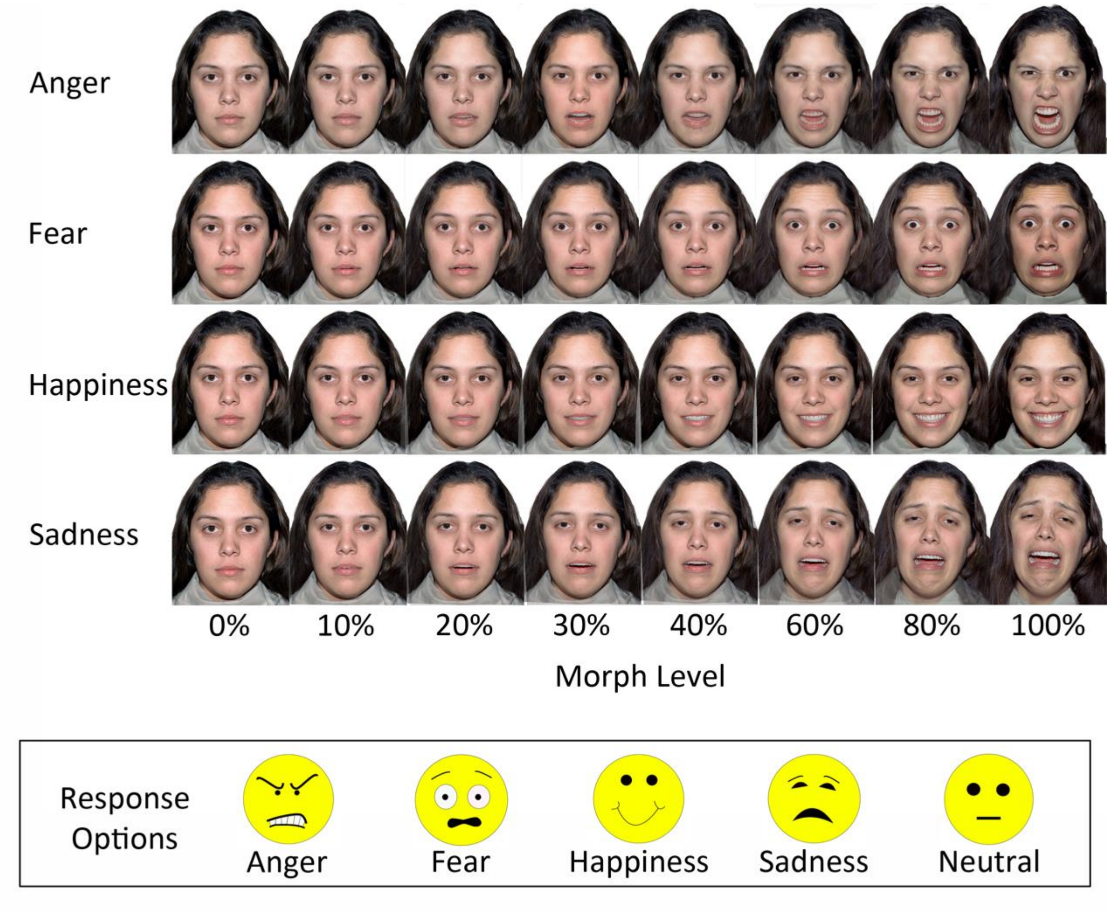

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FIGURE FOUR

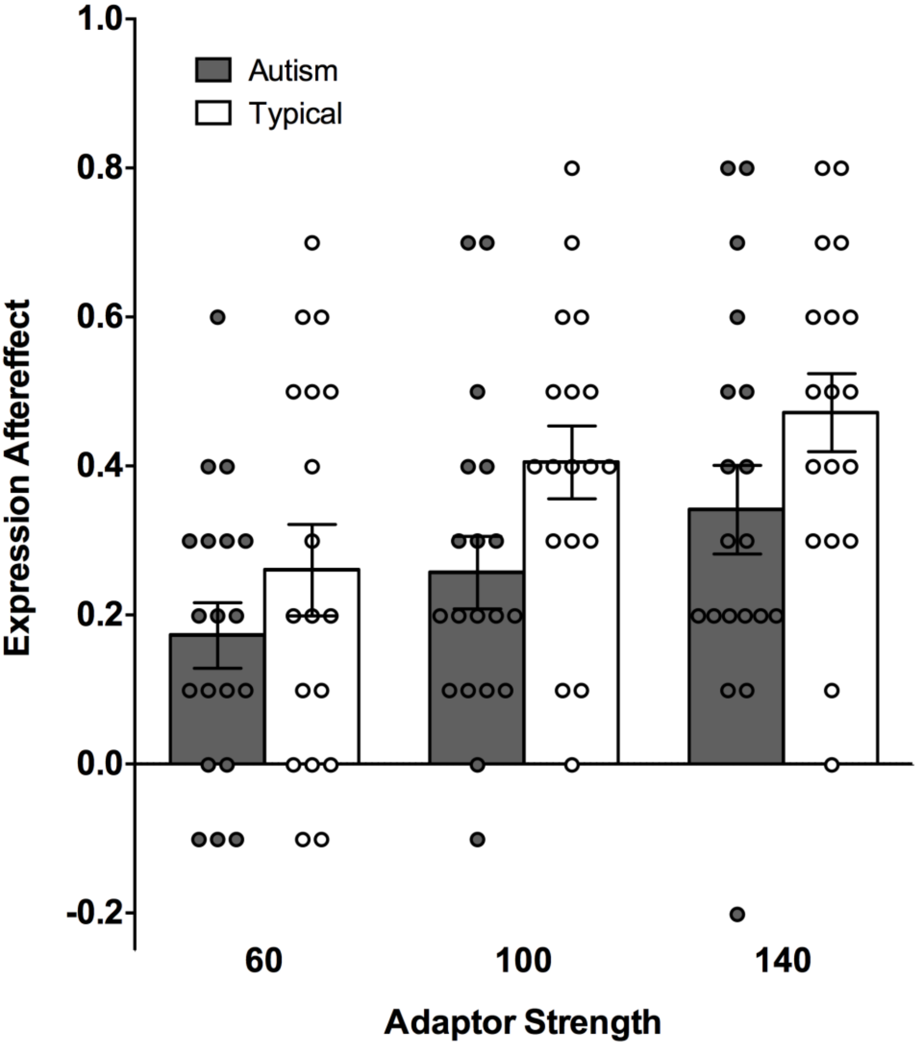

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FIGURE FIVE

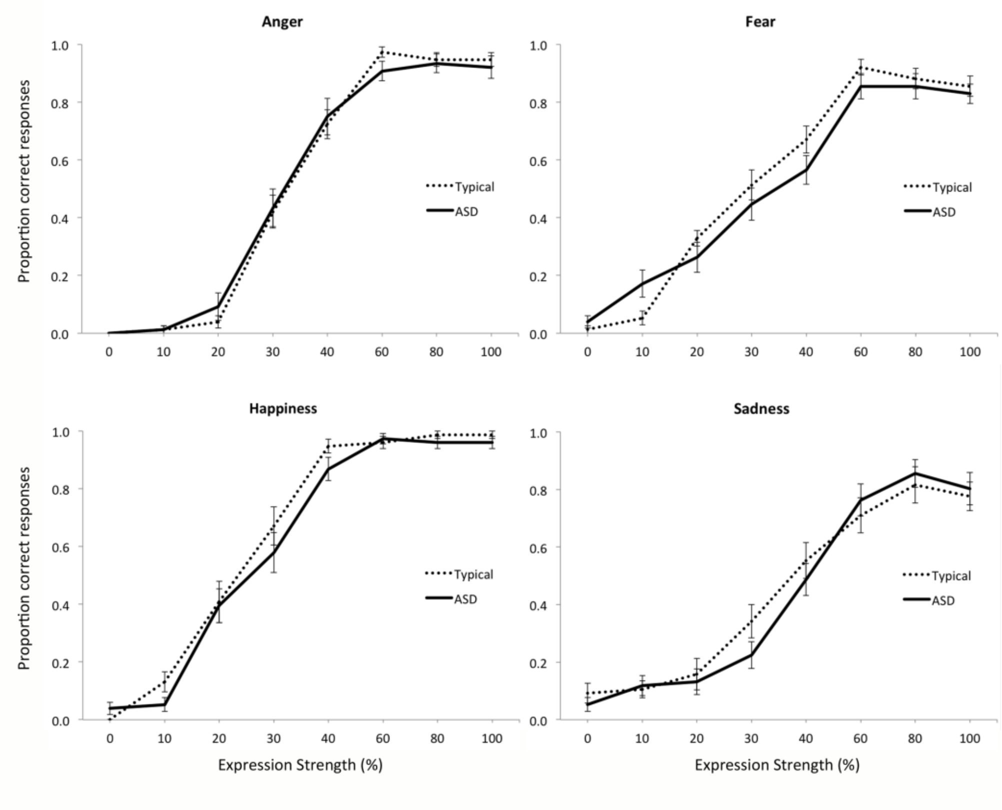

Figure 5. Mean proportion correct responses for each expression continuum for typical and ASD participants. SE bars are shown.