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ORIGINAL PAPER

The Influences of Face Inversion and Facial Expression on Sensitivity to Eye Contact in High-Functioning Adults with Autism Spectrum Disorders

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Abstract We examined the influences of face inversion and facial expression on sensitivity to eye contact in high-functioning adults with and without an autism spectrum disorder (ASD). Participants judged the direction of gaze of angry, fearful, and neutral faces. In the typical group only, the range of directions of gaze leading to the perception of eye contact (the cone of gaze) was narrower for upright than inverted faces. In both groups, the cone of gaze was wider for angry faces than for fearful or neutral faces. These results suggest that in high-functioning adults with ASD, the perception of eye contact is not tuned to be finer for upright than inverted faces, but that information is nevertheless integrated across expression and gaze direction.

Keywords Autism · Gaze · Eye contact · Cone of gaze · Facial expression · Face inversion

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Introduction

Eye contact is central to human social interaction. The direction of people's gaze provides a cue to the focus of their attention, which can in turn support inferences about their interests and intentions (Argyle and Cook 1976; Kendon 1967). In typical adults, judgments of gaze are impaired by face inversion (Jenkins and Langton 2003; Schwaninger et al. 2005), a result suggesting that sensitivity to the direction of gaze could be tuned by experience to be specialized for upright faces. In addition, facial expression modulates typical adults' judgments of eye contact (Ewbank et al. 2009; Rhodes et al. 2012), a result suggesting that typical adults may integrate information from expression and gaze cues when making judgments of eye contact.

Adults with autism spectrum disorders (ASD) show deficits in some aspects of gaze processing, including understanding of the social meaning of gaze (e.g., Baron-Cohen et al. 2001), and discriminating small differences between direct and averted gaze in upright faces (e.g., Dratsch et al. 2013). Here, we investigated whether the influences of face inversion and facial expression on sensitivity to eye contact are typical in adults with ASD by having high-functioning adults with and without ASD judge whether gaze was direct or averted to the left or right in photographed faces that varied in facial expression and orientation.

Sensitivity to Eye Contact in Typical Adults

Typical adults can detect differences of 1–2° in the direction of someone else's gaze toward objects in the environment (Bock et al. 2008; Symons et al. 2004; Vida and Maurer 2012a). However, the range of directions of gaze over which adults judge that an observer is looking directly at them (called the "cone of gaze") is much larger, at approximately 5.5° in width (Gibson and Pick 1963; Lord and Haith 1974; Vida and Maurer 2012b) and 7° in height (Vida and Maurer 2012b). Failure to attribute eye contact when a someone else's gaze is directed toward oneself could result in social costs (e.g., missed opportunities to interact with others). Typical adults' tendency to attribute eye contact over a relatively large range of directions of gaze could serve to minimize these costs.

In typical adults, face inversion impairs sensitivity to the direction of gaze, as indicated by higher thresholds for discriminating between leftward and rightward gaze for inverted faces than for upright faces (Jenkins and Langton 2003; Schwaninger et al. 2005). This effect appears to be driven primarily by the inversion of the eyes. When the orientation of the eye region (including eyebrows, eyelids, and part of the bridge of the nose) and that of the outer face context are manipulated independently, inversion of the eye region impairs sensitivity to the direction of gaze to a similar extent whether the face context is upright or inverted (Jenkins and Langton 2003). Also, typical adults' ability to discriminate small differences in the direction of gaze is equal for full faces and for eyes isolated by occluding all but the visible surface of the eyeball (the palpebral fissure) and the lower eyelid, and is equally impaired when these stimuli are inverted (Schwaninger et al. 2005). These results suggest the importance of visual cues in and around the palpebral fissure, as viewed in an upright orientation.

In typical adults, the perception of eye contact interacts reciprocally with that of facial expression. Several studies have demonstrated that the direction of gaze affects processing of facial expression (see Graham and LaBar 2012, for review). Some of these studies indicate that eye contact facilitates the perception of facial expressions associated with approach (e.g., anger) and that it impairs the perception of those associated with avoidance (e.g., fear) (e.g., Adams and Kleck 2003; Milders et al. 2011). However, others report that eye contact generally facilitates expression perception (e.g., Bindemann et al. 2008). There is also evidence that facial expression affects the perception of eye contact. The cone of gaze is wider for angry than for fearful or neutral faces, with no difference between the latter two (Ewbank et al. 2009; Rhodes et al. 2012). As suggested in Ewbank et al. (2009), the observed effect of facial expression on judgments of eye contact may indicate that typical adults possess an adaptive bias to interpret hostile signals as self-directed. Taken together, these results suggest that typical adults combine information from gaze and expression when judging either gaze or facial expression. This ability may be adaptive, as it may allow individuals to respond selectively to combinations of expression and gaze cues that are important for survival. For example, an angry face with direct gaze may be interpreted as a stronger signal of threat than an angry face with averted gaze (e.g., Adams and Kleck 2005) because the former indicates that the threat is directed toward the viewer.

Sensitivity to Eye Contact in Autism

Abnormal eye contact during face-to-face social interactions is a characteristic of autism (American Psychiatric Association 2000). Individuals with autism are known to have impairments in their ability to perceive mental state information from the direction of gaze (Baron-Cohen and Goodhart 1994; Baron-Cohen 1995; Baron-Cohen et al. 1995, 1997, 2001), show autonomic hyper-arousal to eye contact (Kaartinen et al. 2012; Kyläiinen and Hietanen 2006, but also see Joseph et al. 2008), and, at least under some circumstances, spend less time than controls fixating the eye region when viewing faces (e.g., Dalton et al. 2005; Jones et al. 2008; Klin et al. 2002; Pelphrey et al. 2002; Spezio et al. 2007, but also see Falck-Ytter and von Hofsten 2011).

Given sufficient differences between direct and averted gaze and a long duration of exposure to the stimulus, individuals with ASD can make accurate judgments of eye contact (Ashwin et al. 2009; Senju et al. 2008). For example, high-functioning adults with ASD are as accurate as typical adults in discriminating between direct gaze and gaze averted 30° to the left or right (Ashwin et al. 2009). However, both children and adults with ASD are less accurate than controls in discriminating small differences between direct and averted gaze (Campbell et al. 2006; Dratsch et al. 2013; Gepner et al. 1996; Howard et al. 2000; Webster and Potter 2008, 2011). Even when differences between direct and averted gaze are large, high-functioning adults with ASD are less accurate and slower than controls when the duration of exposure is short (Wallace et al. 2006). These results suggest that the ability to discriminate between direct and averted gaze is impaired in individuals with ASD compared to that in typical individuals.

One previous study suggests that the effects of face inversion on gaze processing are atypical in children with ASD (Senju et al. 2008). In this study, 9- to 15-year-old children with and without ASD viewed arrays of five or nine faces and judged whether a face with a particular direction of gaze (direct, averted left or averted right) was present in the array. When faces were presented in an upright orientation, typically developing children showed more efficient visual search (i.e., a smaller difference in response time between smaller and larger arrays) for detection of direct gaze than for detection of averted gaze. This effect was not present for inverted faces. In contrast, children with ASD showed more efficient search for direct gaze in both orientations (Senju et al. 2008). This result suggests that the perceptual mechanism underlying sensitivity to eye contact may not be specialized for upright faces in ASD.

Previous research suggests that the effects of the direction of gaze on processing of facial expression may be atypical in children with ASD. In one study, typically developing 9- to 14-year-old children were faster to recognize fearful and angry faces when they were paired with a motivationally congruent direction of gaze (e.g., anger with direct gaze, fear with averted gaze) than when gaze and expression were incongruent. This effect was absent in children with ASD (Akechi et al. 2009). In a second study, typically developing 9- to 14-year-old children showed greater amplitude in the N170 ERP component for congruent combinations of expression and gaze than for incongruent combinations. This result may reflect more extensive cortical processing of expressions presented with a congruent direction of gaze. This effect was also absent in children with ASD (Akechi et al. 2010). In sum, children with ASD do not show evidence of typical interactions between perceptions of expression and gaze, when measured by either behavioural or neural indices.

In sum, previous research indicates that the influence of face inversion on gaze processing (Senju et al. 2008), and the influence of the direction of gaze on the perception of facial expression (e.g., Akechi et al. 2009, 2010), are atypical in children with ASD. Previous studies have not examined the influences of face inversion or facial expression on sensitivity to eye contact in adults with ASD, and have not provided precise estimates of the width of the cone of gaze in this population. That was the purpose of the current study. Specifically, we examined the influences of face inversion and facial expression on sensitivity to eye contact in high-functioning adults with ASD. In addition, we measured for the first time the precise width of the cone of gaze in this population. Participants with and without ASD viewed photographs of angry, fearful, and neutral faces. Gaze was either direct or averted, varying in a series of small steps to the left and right. In separate blocks of trials, participants viewed each face in an upright and inverted orientation. For each face, participants pressed one of three buttons to indicate whether the model's gaze was direct or averted to the left or right. For each participant, we estimated the width of the cone of gaze for each expression and orientation. The results of this investigation provide the first information on whether individuals with ASD combine information from expression and gaze cues when making judgments of eye contact. The results also provide the first information on whether the atypical interactions between perceptions of expression and gaze (Akechi et al. 2009, 2010) and the atypical effect of inversion on gaze processing (Senju et al. 2008) observed in children with ASD persist into adulthood, or whether these aspects of sensitivity normalize by adulthood, an outcome that could reflect a developmental delay.

Table 1 Age and IQ scores of participants; standard deviations are shown in parentheses

Group	Age (years)	Verbal IQ	Performance IQ	Full-scale IQ
ASD	27.6 (6.5)	97.6 (14.7)	101.9 (14.8)	99.5 (12.6)
Control	26.3 (6.4)	97.8 (12.3)	100.6 (13.7)	99.5 (12.8)
	$t(32) = .56$, $p > .55$	$t(32) = .05$, $p > .95$	$t(32) = .25$, $p > .80$	$t(32) = .01$, $p > .95$

Method

Participants

The ASD group consisted of 17 adults (12 male, M age = 27.6 years, age range = 18–42 years) with autism spectrum disorders. The age- and IQ- (Wechsler Adult Intelligence Scale, Version 3) matched control group consisted of 17 adults (14 male, M age = 26.3 years, age range = 20–44 years) without any developmental disorders (see Table 1 for demographic information). All participants in the ASD group had previously received clinical diagnoses of autism, Asperger syndrome, or pervasive developmental disorder not otherwise specified. One of the authors (MDR) confirmed their diagnoses with the Autism Diagnostic Observation Schedule (ADOS-G) Module 4 (Lord et al. 2000, see Table 2 for diagnostic information). All participants had normal or corrected-to-normal letter acuity. Four additional participants with ASD were replaced because they failed to meet our criterion for performance on practice trials (see Procedure section for details) ($n = 1$), or because their response curves were too broad to allow confident estimation of the width of the cone of gaze (see Curve Fitting section for description of this

Table 2 ADOS scores for the ASD group: mean, standard deviation in parentheses, and range

Communication	Social	Repetitive
4.2 (2.5)	8.5 (3.2)	.3 (.6)
2–9	3–16	0–2

measure) from their data for at least one expression and orientation ($n = 3$).

Stimuli

The stimuli came from the set used in Ewbank et al. (2009), which is comprised of images from the NimStim Face Stimulus Set (Tottenham et al. 2009) and the Karolinska Directed Emotional Faces image set (Lundqvist and Litton 1998). The stimuli consisted of grayscale digital photographs of four adult males posing angry, fearful, and neutral expressions.

As in the only previous study of the influence of facial expression on sensitivity to eye contact (Ewbank et al. 2009), the stimuli were confined to male faces, the gender for which angry expressions might be expected to have a stronger effect. We note that male and female faces have been shown to differentially influence recognition of angry expressions (see Becker et al. 2007) and hence our results cannot be generalized to female faces.

The direction of gaze in each male face was either direct or digitally manipulated in small steps (2, 3, 4, 5, 7, or 9 pixels to the left and right) (see Fig. 1 for examples). We added the nine pixel images to the original stimuli because the seven pixel images were not sufficient to define the boundaries of the cone of gaze for several participants in Ewbank et al. (2009). The method of manipulating the direction of gaze in pixels in the current study does not allow direct quantitative comparisons to previous studies in which sensitivity to eye contact was measured in visual degrees of eye rotation (e.g., Dratsch et al. 2013; Gamer and Hecht 2007; Gamer et al. 2011; Vida and Maurer 2012b). However, both methods provide a realistic and fine-grained manipulation of the direction of gaze, and therefore allow the assessment of relative differences in sensitivity to eye contact across expressions, orientations, and groups (e.g., differences between adults with and without ASD).

Face images subtended a visual angle of approximately 12° × 8° from a distance of 50 cm. The images were displayed on a Sony SDM-M81 18-inch LCD monitor set to a resolution of 1,152 × 870 and a refresh rate of 75 Hz. The experiment was run in Matlab 7.6.0 (R2008a) (MathWorks, Natick, MA, USA) with the Psychophysics Toolbox extensions (Brainard 1997) on an Apple Mac mini computer.

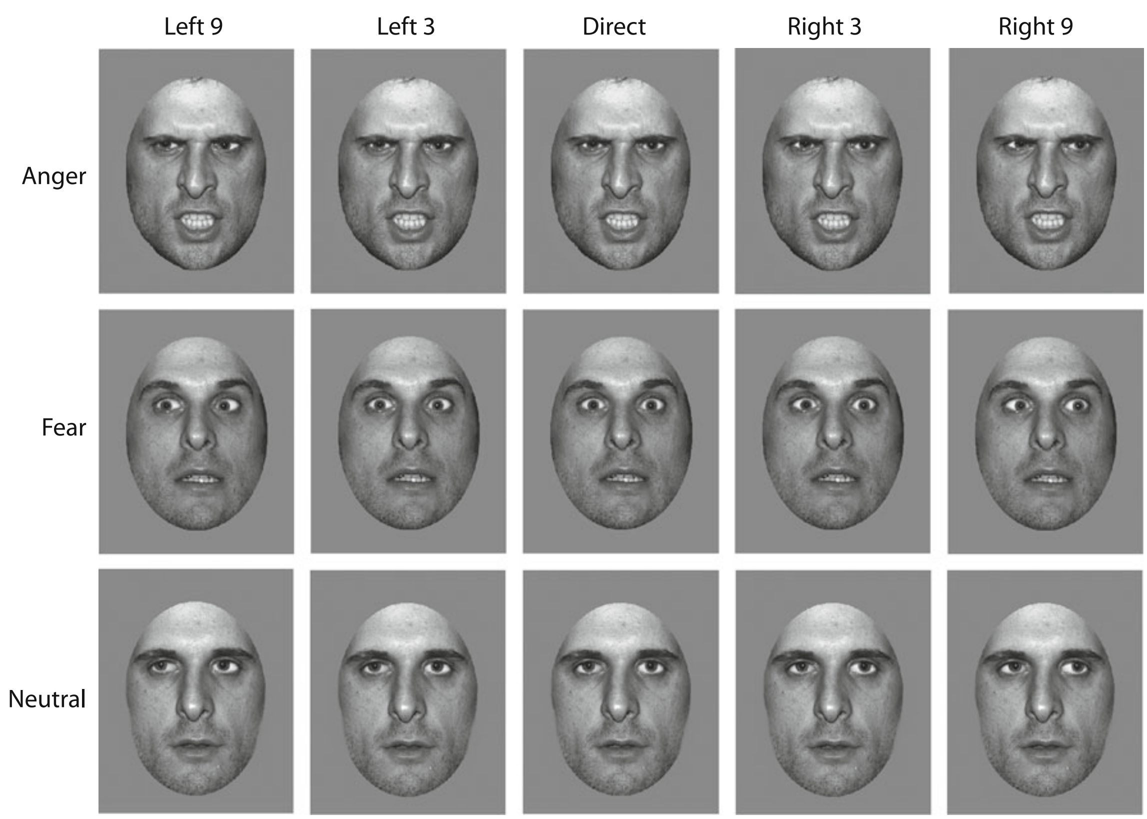

Fig. 1 Examples of stimuli. Each model displayed angry, fearful and neutral expressions. One model posing each of the three expressions is shown for five of the directions of gaze used in the current experiment: 9 pixels left, 3 pixels left, direct gaze, 3 pixels right, and 9 pixels right

Apparatus

Participants were positioned 50 cm in front of the computer monitor. Participants entered responses on a computer keyboard placed on a table directly in front of them. The experiment used four keys on the keyboard. Participants used the F key with a leftward-pointing arrow taped over the top to indicate left responses, the H key with a rightward-pointing arrow taped over the top to indicate right responses, and the G key with a blue circle taped over the top to indicate direct responses. Participants pressed the spacebar to begin each trial.

Design

Each participant completed two blocks of test trials, one including only upright faces and the other including only inverted faces. The order of blocks was counterbalanced across participants. Before the test blocks, each participant received a practice block.

The practice block consisted of 12 trials in which each of the four models was presented with a neutral expression. On each trial, gaze was either direct or averted to the farthest positions (nine pixels) to the left or right. During practice trials, participants received feedback indicating whether their responses were correct or not (a cartoon image of a happy face with a 1,000 Hz tone for correct responses and a cartoon image of a sad face with a 400 Hz tone for incorrect responses). Participants were allowed to repeat each practice block up to two times to reach a criterion of 75 % accuracy. Sixteen participants in the ASD group and 15 participants in the typical group met this criterion on the first attempt, for both the upright and inverted blocks. Two participants in the typical group required a second attempt to reach criterion in the inverted block. One participant in the ASD group was replaced for failure to reach this criterion within three attempts.

In each of the two test blocks (upright and inverted), the participant viewed each of the three expressions, four models and 13 directions of gaze twice, for a total of 312 trials per block. Trials were presented in a pseudo-randomized order, with the constraint that the same direction of gaze and expression were presented on no more than two consecutive trials. During test trials, participants received general encouragement but no trial-specific feedback.

Procedure

Written consent was obtained after explaining the procedure. The experimenter introduced the task by explaining that the participant would see a series of faces on the screen, and that the participant's task would be to press one of the three buttons on the keyboard to indicate whether the model appeared to be looking at the participant, or away from the participant to the left or right. The participant then initiated practice trials. At the start of each trial, the words, "Press spacebar to continue." appeared at the centre of the screen. When the participant pressed the spacebar, an image of one of the faces appeared. After 500 ms, the image disappeared and was replaced by the words, "Where was that person looking?", which remained on the screen until the participant pressed one of the three response keys.[1] When the participant met the 75 % accuracy criterion on the practice block, the experimenter initiated test trials. Test trials had the same format as practice trials except for the absence of feedback. Participants typically completed each test block in approximately 10 min and completed the entire procedure in approximately 30 min.

Results

Curve Fitting

For each participant, we calculated the proportion of the eight trials at each direction of gaze on which the model was judged to be looking directly toward the participant, to the left, and to the right (see Fig. 2). To quantify sensitivity to eye contact, we fit logistic functions relating each participant's proportion of left and right responses to the directions of gaze. All fits were carried out using the glmfit routines from the Statistics Toolbox in Matlab (R2008a). The sum of the left and right fitted functions was then subtracted from 1 to define a third function fitting the proportion of direct responses. Goodness of fit was within acceptable parameters described in Vida and Maurer (2012b) for all fits (see Appendix 1 for details). Following Ewbank et al. (2009) and Vida and Maurer (2012b), we calculated the width of the cone of gaze as the difference (in pixels) between the points of intersection between the fitted ''direct'' function and the left and right functions. These points of intersection correspond to the directions of gaze where the participant was equally likely to judge that the model was making eye contact or looking away. The distance between the right and left points of intersection provides a measure of the width of the horizontal cone of gaze. Three individuals in the ASD group were replaced because their response curves were too broad to allow confident estimation of the width of the cone of gaze in at least one condition.

[1] In the previous study using a similar method, each face was presented for 200 ms (Ewbank et al. 2009). We were concerned that some lower-functioning participants would find it too difficult to perform the task with such a short duration of presentation. We extended the exposure time to 500 ms to make the task easier.

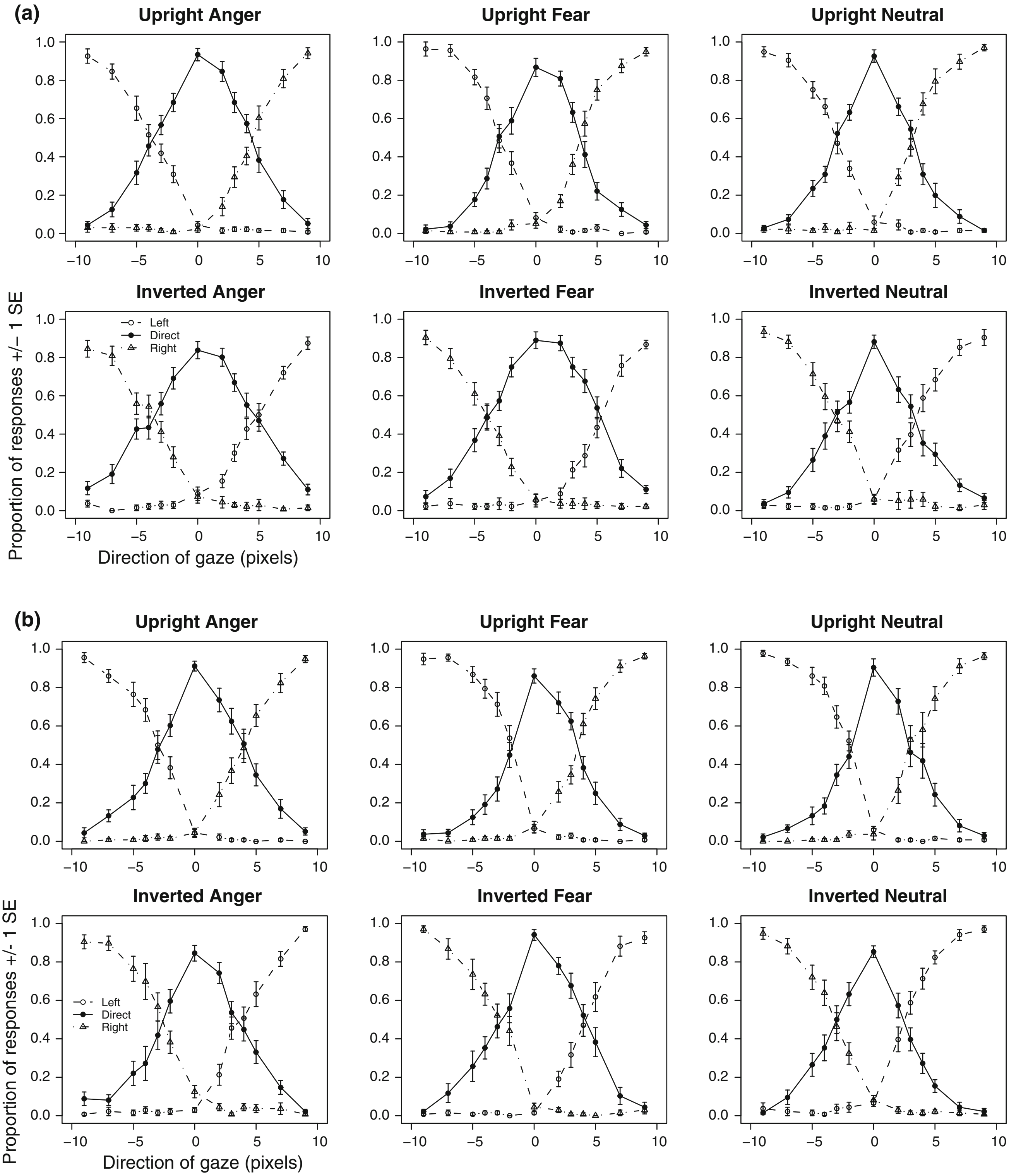

Fig. 2 **a** Mean proportion of each response type ±1 *SE* for typical participants, as a function of direction of gaze. Each plot displays the data for one expression and orientation. For the upright condition, *negative values* on the x axes represent gaze directed to the participant's left, and *positive values* represent gaze directed to the participant's right. For the inverted condition, *negative values* on the x axes represent gaze directed to the participant's right, and *positive values* represent gaze directed to the participant's left. The legend and axis labels supplied for the bottom left plot apply to all other plots in this panel. **b** Corresponding data for participants in the ASD group

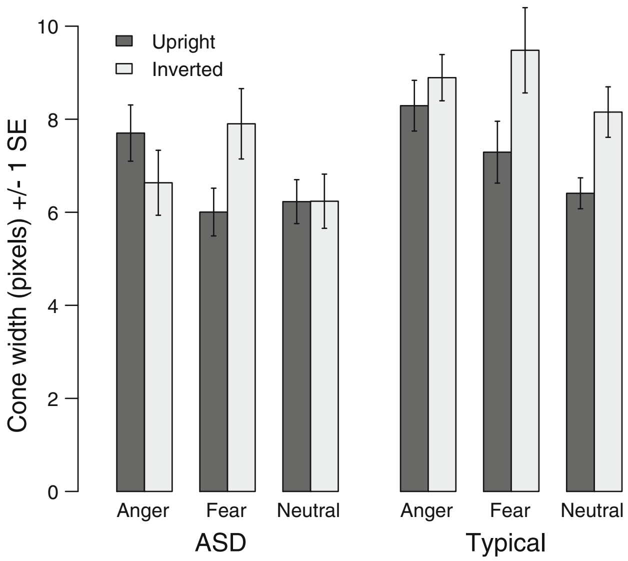

Fig. 3 Mean width of the cone of gaze (pixels) ±1 *SE* as a function of expression, orientation, and group

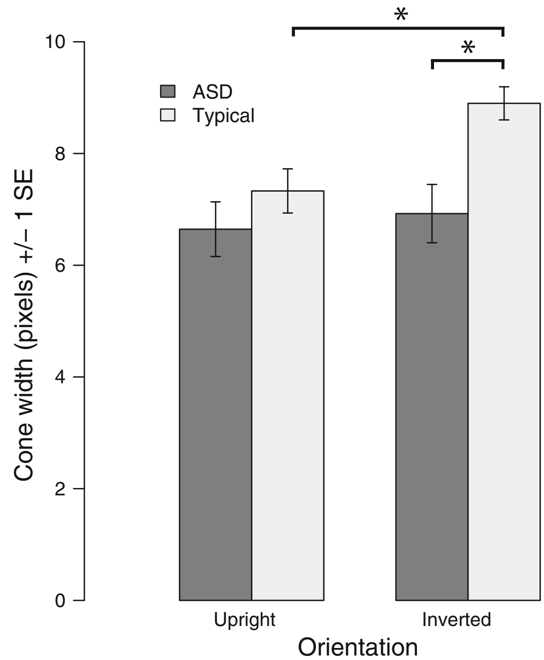

Fig. 4 Mean width of the cone of gaze (pixels) ±1 *SE* as a function of orientation and group. *indicates a significant difference, $p < .01$

Width of the Cone of Gaze

We carried out a mixed ANOVA with orientation (upright, inverted) and expression (anger, fear, neutral) as within-subject factors, group (ASD, typical) as a between-subject factor and the width of the cone of gaze as the dependent variable (see Fig. 3). There were significant main effects of orientation, $F(1, 32) = 13.13$, $p < .002$, $\eta_p^2 = .29$, expression, $F(2, 64) = 4.89$, $p < .02$, $\eta_p^2 = .13$, and group, $F(1, 32) = 4.55$, $p < .05$, $\eta_p^2 = .12$. There were also interactions between orientation and group, $F(1, 32) = 6.18$, $p < .02$, $\eta_p^2 = .16$, and between orientation and expression, $F(2, 64) = 10.55$, $p < .001$, $\eta_p^2 = .25$. There was no interaction between expression and group, or between orientation, expression, and group, *ps* > .45.

To follow up the interaction between orientation and group, we first asked whether face inversion affected the width of the cone of gaze in each group (see Fig. 4). We carried out paired-samples *t*-tests (one for each group, Bonferroni-corrected $\alpha = .025$) evaluating the null hypothesis that there was no difference in the width of the cone of gaze between upright and inverted faces. For the typical group, the cone of gaze was narrower in the upright condition ($M = 7.3$, $SD = 1.5$) than in the inverted condition ($M = 8.8$, $SD = 1.8$), $t(16) = 5.75$, $p < .001$, $d = .89$. For the ASD group, the width of the cone of gaze did not differ between the upright ($M = 6.6$, $SD = 2.0$) and inverted ($M = 6.9$, $SD = 2.1$) conditions, $p > .5$. In light of previous evidence that children with ASD make normal judgments of eye contact for upright faces, but do not show the distortion of judgments for inverted faces observed in typical children (Senju et al. 2008), we also investigated whether there was a group difference in the width of the cone of gaze for each face orientation. To examine this question, we carried out independent-samples *t*-tests (one for each orientation, Bonferroni-corrected $\alpha = .025$) evaluating the null hypothesis of no group difference in the width of the cone of gaze. For upright faces, there was no significant difference in the width of the cone of gaze between the ASD ($M = 6.6$, $SD = 2.0$) and typical ($M = 7.3$, $SD = 1.5$) groups, $p > .25$. For inverted faces, the cone of gaze was narrower in the ASD group ($M = 6.9$, $SD = 2.1$) than in the typical group ($M = 8.8$, $SD = 1.8$), $t(32) = 2.78$, $p < .01$, $d = .95$.

We followed up the expression by orientation interaction with repeated-measures ANOVAs (one for each orientation) evaluating the null hypothesis of no difference among the expression categories (see Fig. 5). For upright faces, there was a simple effect of expression, $F(2, 66) = 14.16$, $p < .001$, $\eta_p^2 = .30$. We followed up this effect with three paired-samples t-tests (Bonferroni-corrected $\alpha = .017$) comparing the width of the cone of gaze for upright faces between each possible pair of expressions. The cone of gaze was wider for anger ($M = 8.0$, $SD = 2.3$) than for fear ($M = 6.6$, $SD = 2.4$), $t(33) = 3.57$, $p < .002$, $d = .70$, and for neutral ($M = 6.3$, $SD = 1.6$), $t(33) = 6.32$, $p < .001$, $d = .80$. There was no difference between fear and neutral, $p > .5$. For inverted faces, there was a simple main effect of expression, $F(2, 66) = 3.95$, $p < .03$, $\eta_p^2 = .11$. We followed up this effect with paired-samples *t*-tests (Bonferroni-corrected $\alpha = .017$). There were no significant differences in the width of the cone of gaze

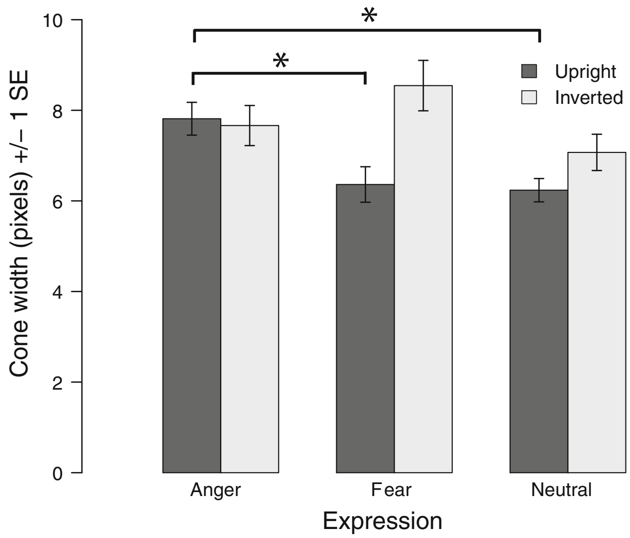

Fig. 5 Mean width of the cone of gaze (pixels) ±1 *SE* as a function of expression and orientation. *indicates a significant difference, $p < .01$

between anger ($M = 7.8$, $SD = 2.7$) and fear ($M = 8.7$, $SD = 3.4$), or between anger and neutral ($M = 7.1$, $SD = 2.4$), *ps* > .1. There was a trend in the direction of a wider cone of gaze for fear than neutral, but this did not reach the corrected statistical threshold, $t(33) = 2.46$, $p = .02$. Thus, although there was a significant simple main effect of expression for inverted faces, none of the pair-wise differences among expression categories were significant after correcting for multiple comparisons.

Individual Differences in the Effect of Face Inversion

Unlike typical adults in the current study and in previous studies (e.g., Jenkins and Langton 2003; Schwaninger et al. 2005), the ASD group in the current study displayed no effect of inversion on judgments of eye contact. However, it is possible that factors such as symptom severity or IQ modulated the magnitude of the effect of inversion within the ASD group. To investigate this possibility, we first calculated the size of the effect of inversion for each participant in the ASD group by subtracting the mean width of the cone of gaze for upright faces from that for inverted faces. We then carried out three Pearson correlations testing the association between measures of symptom severity (social, communication, repetitive) and the effect of inversion in the ASD group. There were no significant correlations, *r*s = −.09 to .03, *ps* > .45. We also carried out three Pearson correlations testing the association between measures of IQ (verbal, performance, full-scale) and the effect of inversion within the ASD group. There were no significant correlations, *r*s = .27–.35, *ps* > .15. Hence, in the current sample of 17 high-functioning adults with ASD, we found no evidence that symptom severity or IQ modulated the magnitude of the effect of inversion on the cone of gaze.

Ideal Observer Analysis

As shown in Fig. 1, the eyelids tend to be more closed in angry faces than in fearful or neutral faces. Hence, the wider cone of gaze observed for angry faces in the current study could reflect poorer visibility of parts of the palpebral fissure (e.g., the iris and sclera) that provide cues to the direction of gaze. To investigate this possibility, we carried out an ideal observer analysis. An ideal observer is a theoretical model that uses the optimal strategy for a given task (see Geisler 1989; Tjan et al. 1995, for details). The performance of our ideal observer was determined by the amount of variation in pixel luminance between images that was informative for discriminating the direction of gaze (see Appendix 2 for further details). In our task, shifts of gaze were generated by digitally manipulating the position of the iris within the palpebral fissure. Therefore, all low-level information available to perform the task was contained exclusively in the palpebral fissure. The dependent measure of our ideal observer analysis was the 75 % root mean square (RMS) contrast threshold, which represents the minimum stimulus visibility at which the ideal observer was able to achieve 75 % accuracy in discriminating between leftward and rightward gaze. A lower contrast threshold indicates that there is more information available for discriminating the direction of gaze.

We allowed the ideal observer only two choices (left or right) instead of the three choices (direct, left, or right) provided to human observers. This allowed us to specify the correct response for each trial, which in turn allowed us to vary the visibility of the stimulus according to the ideal observer's responses (see Appendix 1 for further details). The availability of low-level visual information will constrain human observers' sensitivity to the direction of gaze (e.g., Watt et al. 2007), whether two or three response alternatives are allowed. Hence, the current analysis allows inferences about the role of low-level visual information in the effects of facial expression on judgments of eye contact.

Inspection of Fig. 6 indicates that thresholds were lower for directions of gaze that diverged more from straight ahead. This result indicates that for larger shifts of gaze, there was more information available to discriminate between leftward and rightward gaze. This result is expected because, as shown in Fig. 1, a larger shift of gaze in a particular direction causes the eyes to appear less similar to eyes in which gaze is shifted in the opposite direction. Critically, Fig. 6 also indicates that angry and

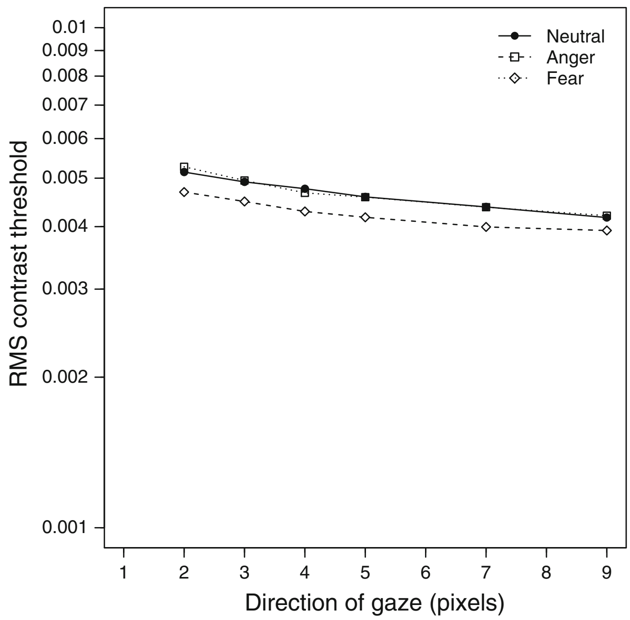

Fig. 6 Mean root mean square (RMS) contrast thresholds for the ideal observer ±1 *SE* as a function of the direction of gaze and expression type. In all cases, the standard error was so small that the error bar was occluded by the data point

neutral faces produced identical thresholds, whereas fearful faces produced lower thresholds. Note that this will be true whether the stimulus is upright or inverted. This result suggests that there is more information available to perform the task in fearful faces than in angry or neutral faces, with no difference between the latter two. This pattern is different from our finding that in both the typical and ASD groups, the cone of gaze was wider for angry faces than for fearful or neutral faces, with no difference between the latter two, and that the effect of expression was limited to upright faces. Hence, our ideal observer analysis suggests that the wider cone of gaze for upright angry faces does not arise from a lack of low-level visual information available for discriminating the direction of gaze.

Discussion

The current study provides the first information on the influences of face inversion and facial expression on sensitivity to eye contact in high-functioning adults with ASD, and provides the first precise estimates of the width of the cone of gaze in this population. The effect of inversion on the width of the cone of gaze differed between the groups. In the typical group, the cone of gaze was narrower for upright than inverted faces, a pattern suggesting that sensitivity to eye contact is specialized for upright faces. In the ASD group, the width of the cone of gaze was the same for upright and inverted faces. The cone of gaze for inverted faces was wider in the typical group than in the ASD group (i.e., for inverted faces, participants in the ASD group performed better than participants in the typical group), but there was no group difference in the width of the cone of gaze for upright faces. Although the effect of inversion on the width of the cone of gaze was atypical in the ASD group, the effects of expression on the cone of gaze were the same in each group. For upright faces, the cone of gaze was wider for angry faces than for fearful or neutral faces, with no difference between the latter two, a result suggesting that facial expression influences gaze perception similarly in the two groups. For inverted faces, there was no systematic effect of expression on the width of the cone of gaze in either group.

Sensitivity to Eye Contact in Upright and Inverted Faces

In the current study, the cone of gaze of typical adults was narrower for upright than inverted faces. This finding is consistent with previous evidence that typical adults are more accurate in judging the direction of gaze for upright faces than for inverted faces (e.g., Jenkins and Langton 2003; Schwaninger et al. 2005). These results suggest that the system for detecting eye contact could be tuned by experience with upright faces. This experience could also contribute to developmental changes in children's ability to discriminate small differences between direct and averted gaze (Vida and Maurer 2012b) and could influence tuning of cortical mechanisms for coding the direction of gaze (e.g., Calder et al. 2008).

When viewing upright faces, the ASD group made judgments of eye contact comparable to those of the control group, but did not show the widening of the cone of gaze for inverted faces observed in the typical group. This pattern is consistent with the results of a previous study that found differences when children with and without ASD viewed arrays of five or nine faces and judged whether a face with a particular direction of gaze (direct, averted left, or averted right) was present in the array. For upright faces, typically developing children showed more efficient visual search (i.e., a smaller difference in response time between smaller and larger arrays) for detection of direct gaze than for averted gaze. This effect was absent for inverted faces. In contrast, children with ASD showed more efficient search for direct gaze in both orientations (Senju et al. 2008). Our results indicate that the atypical effects of face inversion on judgments of eye contact observed in children with ASD (Senju et al. 2008) persist into adulthood. Together, our results and those of Senju et al. (2008) suggest that sensitivity to eye contact is not specialized for upright faces in children or adults with ASD.

The observed group difference in the influence of face inversion on sensitivity to eye contact could be a result of those with ASD having spent less time fixating the eye region of faces during early development (e.g., Jones et al. 2008). Differences in experience with the eye region could lead to differences in expertise in processing visual information within the eye region, which could contribute to differences in perceptual strategies. For example, normal expertise in processing information within the eye region could enable typical adults to base their estimates of the direction of gaze on relatively complex visual cues, at least some of which are likely to vary in appearance between upright and inverted faces (e.g., the appearance of the iris and sclera). This strategy could lead to lower sensitivity for inverted than upright faces. In contrast, lower expertise in processing information within the eye region could lead adults with ASD to adopt a perceptual strategy based on relatively simple visual cues, which may not vary significantly in appearance between upright and inverted faces (e.g., bilateral symmetry). This strategy could allow normal or near-normal sensitivity for upright faces, with no impairment for inverted faces. Alternatively, both groups might use the same visual cues, but greater specialization of face processing for upright faces in the typical group could make it more difficult for individuals in the typical group to process the cues in inverted faces.

An additional variable that could modulate sensitivity to eye contact in ASD is motion. The one previous study of the ability of adults with ASD to discriminate small differences between direct and averted gaze in a single face reported lower sensitivity in high-functioning adults with ASD than in typical adults (Dratsch et al. 2013). This result differs from our finding of no group difference in the width of the cone of gaze for upright faces. One key difference between our study and that of Dratsch et al. (2013) is that stimuli in the latter study were dynamic videos, whereas stimuli in the current study were static photographs. Since individuals with ASD show deficits in perception of complex non-biological and biological motion (e.g., Blake et al. 2003; Freitag et al. 2008), it is possible that a general impairment in processing of complex motion could contribute to abnormally low sensitivity to eye contact in live faces in ASD (Dratsch et al. 2013).

Although adults with ASD in the current study were able to make normal judgments of eye contact for upright faces, it should be noted that we replaced four participants with ASD because they did not reach criterion on practice trials ($n = 1$) or because their response curves were so broad that we were unable to confidently estimate the width of the cone of gaze ($n = 3$). Three of these participants scored well below the mean for the ASD group on at least one measure of IQ, and scored above the group mean on measures of the severity of social and communication symptoms, whereas one scored near the group mean on these measures. Hence, it is possible that sensitivity to eye contact is abnormally low in adults with ASD who are lower functioning and/or have more severe symptoms than the ASD group in the current study.

Effects of Facial Expression on Sensitivity to Eye Contact

Despite the fact that judgments of eye contact were not modulated by inversion in the ASD group, judgments were nevertheless modulated by expression. In both groups, the cone of gaze for upright faces was wider for angry faces than for fearful or neutral faces, with no difference between the latter two, and there was no systematic effect of expression for inverted faces. To our knowledge, this is the first evidence that facial expression influences judgments of eye contact in individuals with ASD. Our finding that inversion eliminated the effect of facial expression on the cone of gaze is consistent with previous research indicating that inversion disrupts recognition of facial expression in adults with and without ASD (see Weigelt et al. 2012, for review). Our results suggest that although sensitivity to eye contact may not be tuned normally to upright faces in adults with ASD, sensitivity to facial expression is nevertheless tuned to be finer for upright than inverted faces. However, we did not measure response times, and it is possible that facial expression modulates the speed of processing of the direction of gaze in a different way in adults with and without ASD.

Although the effects of expression in both the typical and ASD groups in the current study could reflect differences in the affective content of the facial expressions, they could instead reflect differences in lower-level visual information (e.g., the visibility of cues to the direction of gaze within the palpebral fissure). Two findings in the current study provide evidence against the latter possibility. First, as in Ewbank et al. (2009), face inversion eliminated the effects of expression on the cone of gaze. Since eye cues to the direction of gaze are equally visible in upright and inverted faces, it seems unlikely that the effects of expression in the current study were driven by differences in the visibility of these cues. Second, our ideal observer analysis revealed no differences between neutral and angry faces in the amount of low-level visual information available for discriminating the direction of gaze. Together, these results suggest that the wider cone of gaze for upright angry faces does not reflect differences in low-level visual cues.

As suggested in Ewbank et al. (2009), the wider cone of gaze for upright angry faces may reflect an adaptive bias to interpret hostile signals as self-directed. Our results suggest that this bias may be intact in adults with ASD. The current results are consistent with previous studies indicating that behavioural markers of threat detection are, to at least some degree, intact in individuals with ASD. Like typical adults, high-functioning adults with ASD are faster to detect angry faces than happy faces (Ashwin et al. 2006; Krysko and Rutherford 2009). Also, when viewing pairs of faces in which one face is that of a convicted murderer and the other is a layperson, high-functioning adults with ASD are as accurate as typical adults in choosing the more dangerous-looking face (Miyahara et al. 2010). The current results provide further evidence that behavioural markers of threat detection may be intact in ASD.

Although our results and those of previous studies suggest that behavioural markers of threat detection may be intact in ASD, it is possible that responses to threatening stimuli are mediated by an abnormal mechanism in ASD. It has been reported that when viewing facial expressions, individuals with ASD display both abnormally low (Ashwin et al. 2007; Baron-Cohen et al. 1999; Critchley et al. 2000) and high (e.g., Dalton et al. 2005; Kleinhans et al. 2009; Monk et al. 2010) activation in the amygdala, a brain region thought to be involved in alerting other brain areas involved in social perception and cognition to the emotional salience of stimuli (see Schultz 2005, for review). Hence, in the ASD group in the current study, the effect of expression on the width of the cone of gaze may have been mediated by an atypical neural response to the emotional salience of the facial expressions. Future studies could evaluate this possibility by measuring the neural correlates of the effects of facial expression on judgments of eye contact in ASD.

Previous studies have not examined the effects of expression on judgments of eye gaze in children or adults with ASD. However, previous research suggests that the opposite influence, of gaze direction on behavioural and neural indices of expression processing, is atypical in children with ASD (Akechi et al. 2009, 2010). Together, our results and those of previous studies could indicate that interactions between expression and gaze are developmentally delayed in ASD, such that these interactions are atypical in childhood, but normalize by adulthood. Alternatively, the results could indicate that interactions between gaze and expression are unidirectional in ASD, such that the influence of expression on the perception of gaze is normal, but the opposite influence is atypical. Future studies investigating the effect of expression on judgments of eye contact in children with ASD, and the effect of gaze on judgments of expression in adults with ASD, would allow evaluation of these possibilities.

Conclusions

This investigation has provided the first information on the influences of face inversion and facial expression on sensitivity to eye contact in high-functioning adults with ASD, and has provided the first precise estimates of the width of the cone of gaze in this population. The current results suggest that, like typical adults and children, high-functioning adults with ASD possess an adaptive bias to interpret hostile signals as self-directed. However, the lack of an inversion effect among adults with ASD suggests that their perception of eye contact may not rely on the same type of visual processing as in typical individuals.

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Appendix 1

We calculated the residual deviance for each logistic fit (see Dalgaard 2008; McCullagh and Nelder 1989). A larger residual deviance reflects greater discrepancy between the model and the data. The residual deviance and residual degrees of freedom for a fit correspond approximately to a χ^2 distribution (see Dalgaard 2008). A χ^2 probability of less than .05 is typically taken as an indicator of a poor fit. For the current design, the deviance residual corresponding with this probability is 19.65. The largest residual deviance observed in the current experiment was 5.44, which corresponds to a χ^2 probability of .91. Hence, there was no significant discrepancy between the data and the model for any of the fits in the current study.

Appendix 2

The ideal observer's task was as follows: on every trial, we presented a face from the main experiment with a particular direction of gaze (2, 3, 4, 5, 7, or 9 pixels, left or right), emotion (neutral, angry, fearful), identity, and root mean square (RMS) contrast. RMS contrast is defined as:

$$rms = \left[\frac{1}{n-1}\sum_{i=1}^{n}(x_i - \bar{x})^2\right]^{\frac{1}{2}}$$

where n is the number of pixels in the image, x_i is the intensity of pixel i (normalized so that $0 \leq x_i \leq 1$), and $\bar{x}$ is the mean normalized pixel intensity (Peli 1991). Using the optimal decision rule (Tjan et al. 1995), the ideal observer selected the most likely direction of gaze (left or right). Using QUEST, a Bayesian adaptive threshold estimator, the RMS contrast for the next trial was adjusted based on the correctness of the ideal observer's response, such that correct responses generally led to lower (less visible) contrast levels (Watson and Pelli 1983). Each contrast threshold was estimated based on 240 trials, and we estimated 25 thresholds per condition. Finally, note that in the absence of noise, the ideal observer will never respond incorrectly at any contrast level, so we added Gaussian white noise (RMS contrast = 0.28) to the stimulus on every trial. A new noise sample was generated for each trial, so that the appearance of the noise varied randomly across trials.

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