Visual orientation processing in autism spectrum disorder: No sign of enhanced early cortical function

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It has been suggested that enhanced perceptual processing underlies some of the social difficulties associated with autism spectrum disorder (ASD). While a variety of visual tasks have been reported in which individuals with ASD outperform neurotypical individuals in control groups, the precise origin of such effects within the visual pathway remains unclear. It has recently been established that visual acuity is intact yet unremarkable in ASD. This suggests that the earliest levels of retinal processing are an unlikely candidate as the source of differences. The next potential levels for divergent visual processing are those involved in processing simple aspects of visual stimuli, such as orientation and spatial frequency, considered to be functions of early visual cortex. Here we focused on the basic processing of orientation. In three experiments, we assessed three basic aspects of orientation processing—discrimination, veridical perception, and detection—in participants with ASD in comparison to age-, gender-, and IQ-matched adults without ASD. Each experiment allowed for both qualitative and quantitative comparisons between the two groups. These provided a dense array of data indicating that participants with ASD perceive orientation of low-level stimuli in a qualitatively (as well as quantitatively) similar manner to participants without ASD in control groups, with no evidence of superior processing in detection, precision, or accuracy aspects of orientation perception. These results suggest that the source for altered perceptual abilities should be sought elsewhere, possibly in specific subgroups of people with ASD, other aspects of low-level vision such as spatial frequency, or subsequent levels of visual processing.

Introduction

A wealth of evidence has accumulated in favor of the view that people with autism spectrum disorder (ASD) may have a detail-oriented or feature-based visual-processing bias in perceptual tasks that may be associated with superior perceptual abilities (Caron, Mottron, Berthiaume, & Dawson, 2006; Dakin & Frith, 2005; Iarocci, Burack, Shore, Mottron, & Enns, 2006; Mottron, Dawson, Soulieres, Hubert, & Burack, 2006; for a recent meta-analysis, see Van der Hallen, Evers, Brewaeys, Van den Noortgate, & Wagemans, 2015). For example, in the domain of vision, individuals with ASD have been found to outperform neurotypical individuals in control groups at various tasks, such as stimulus discrimination (Plaisted, O'Riordan, & Baron-Cohen, 1998a; Plaisted, Saksida, Alcantara, &

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Weisblatt, 2003), search (O'Riordan, Plaisted, Driver, & Baron-Cohen, 2001; Plaisted et al., 1998b; Plaisted, Swettenham, & Rees, 1999), and locating simple shapes embedded in complex figures (Happe, 1999; Jolliffe & Baron-Cohen, 1997; Shah & Frith, 1983).

Despite a broad range of examples indicating some form of enhanced visual functioning, it has been challenging to pinpoint the neural level at which this superior visual processing emerges. Claims so far have pointed to potential origins as low as the retina, with one study initially suggesting that individuals with ASD have markedly superior levels of visual acuity (Ashwin, Ashwin, Rhydderch, Howells, & Baron-Cohen, 2009) suggestive of hypernormal photoreceptor density (Applegate, 2000; Falkmer et al., 2011). However, this effect was later shown to be an artifact of methodological issues that prevented correct assessment of acuity (Tavassoli, Latham, Bach, Dakin, & Baron-Cohen, 2011). This latter study conclusively showed visual acuity in individuals with ASD to be comparable to visual acuity in neurotypical individuals in control groups, consistent with other reports of unremarkable visual acuity in individuals with ASD (Falkmer et al., 2011; Keita, Mottron, & Bertone, 2010). These results render this lowest level of the visual-processing hierarchy—i.e., retinal-cone density and superior visual acuity—an unlikely candidate as the source of the enhanced performance seen in various visual tasks.

Alternatively, enhanced visual functioning may emerge at stages of visual processing upstream from the retina, including basic cortical processing of image properties such as orientation and spatial frequency, and progressively higher levels encompassing recognition, identification, and memory for visual patterns. A role for early cortical processing in enhanced perception in ASD has been considered by several studies (Caron et al., 2006; Keita, Guy, Berthiaume, Mottron, & Bertone, 2014; Latham, Chung, Allen, Tavassoli, & Baron-Cohen, 2013). For example, Caron et al. (2006) suggested that superior processing at the earliest stages of the visual pathway may be a reflection of V1 overfunctioning, based on the findings of enhanced performance with stimuli involving "simple visual material." Yet two important issues need to be clarified before more specific hypotheses can be considered regarding neurobiological origins of superior processing: (a) the true complexity of the stimuli and (b) the tasks used in experiments in practice with respect to the attributed stage of visual processing. What constitutes a "simple" visual stimulus as far as early cortical processing is concerned? What visual tasks can be confidently isolated to the functioning of V1 or V2 or other visual areas upstream from these?

Although it is widely accepted that individuals with ASD show superior performance in "low-level" perceptual processing, the bulk of the evidence that supports this assertion is based on relatively complex tasks or not-so-simple visual stimuli (though not all; see Bertone, Mottron, Jelenic, & Faubert, 2005; Keita et al., 2014). In fact, the degree to which a visual stimulus can be considered simple must inevitably be based on an underlying model for a representational space relevant to the early stages of neural visual processing rather than a colloquial sense of the word "simple." For example, square chips that make up a Block Design test stimulus, or colored geometric shapes, may appear simple enough within the context of naturalistic stimuli. Yet from an image-processing standpoint (digital as well as neurobiological), these stimuli are often broadband in spatial frequency, contain many orientations and possibly color information. Hence these are not necessarily optimal stimulus choices to probe V1 functionality, which is considered to involve a basic decomposition into spatial-frequency and orientation components (De Valois, Yund, & Hepler, 1982; Hubel & Wiesel, 1968; Hubel, Wiesel, & Stryker, 1977; Tootell, Silverman, & De Valois, 1981). Therefore, it is possible that, for the most part, the evidence for superior visual processing reflects intermediate to higher level stages of visual perception upstream from V1.

Present study

In the present study we have limited our investigation to *visual orientation*—one of the most prominent selectivities known to be associated with V1 organization (De Valois et al., 1982). We have chosen a Gabor pattern as our stimulus. Gabor patches have long been the stimulus of choice in studies of low-level spatial vision, for their localization in both spatial-frequency and spatial domains and their assumed resemblance to visual receptive fields at this level. We have also limited ourselves to the simplest possible tasks involving purely visual judgments, requiring no verbal labeling or explicit categorization of stimuli.

We have specified three basic tasks aimed at assessing primary processing of visual orientation. These are (a) discrimination, (b) veridical perception, and (c) detection of orientation. It has been well known since the late 1800s that orientation processing is superior at cardinal angles (horizontal and vertical) compared to oblique angles (e.g., diagonal; Appelle, 1972). Termed the *oblique effect*, this phenomenon has been shown for a variety of aspects of orientation processing (Camisa, Blake, & Lema, 1977; Campbell, Kulikowski, & Levinson, 1966; Emsley, 1925; Essock, 1980; Westheimer & Beard, 1998). In three experiments, we systematically examined three facets of visual orientation processing in participants with ASD as well as participants without ASD in a control group across a range of base orientations. In each experiment, this manipulation allowed us to conduct two types of comparisons between the performance of participants with and without ASD. In order to compare the groups qualitatively, we assessed the participants via systematic measurement of performance across a range of base orientations, thus enabling us to examine the status of the oblique effect in the group with ASD. This comparison between the overall shapes of the performance curves and the characteristic profiles of the oblique effect allowed us to check for *qualitative* deviations from normal visual function. On the other hand, differences in the level of performance between the two groups allowed us to examine *quantitative* deviations, such as enhanced or impaired processing. Across these three experiments we tested two main hypotheses: (a) Individuals with ASD are quantitatively distinct from individuals without ASD and show superior orientation perception, and (b) individuals with ASD are qualitatively distinct from individuals without ASD and exhibit an altered pattern that deviates from the oblique effect.

Preview

In three experiments, we refute both hypotheses and show that adults with ASD do not differ from adults without ASD, either qualitatively or quantitatively, at the most basic levels of orientation processing, encompassing discrimination, veridical perception, and detection.

General methods

Two groups of adults participated in this study: 29 adults each with and without ASD. All 29 participants in each group completed Experiment 1; 18 of those participants from each group completed Experiment 2; and 15 from each group who participated in Experiment 2 also completed Experiment 3. The protocol was approved by the ethics review boards of the University of British Columbia, Simon Fraser University, and Vancouver General Hospital. Informed consent was obtained in accordance with the Declaration of Helsinki. All participants were unaware of the purposes of the experiment.

All participants had verbal and nonverbal intelligence assessed using the Wechsler Abbreviated Scale for Intelligence (WASI-II; Wechsler, 2011). A Full Scale IQ score of less than 75 was used as an exclusion criterion for participation in the study. Given that we were assessing visual performance, we chose to match the two groups on nonverbal IQ, age, and gender for each individual experiment (Burack, Iarocci, Flanagan, & Bowler, 2004). The two groups were not matched on verbal IQ; the group with ASD had significantly lower scores than the group without ($p = 0.02$) in Experiment 1, but this difference was not significant in either Experiment 2 ($p = 0.18$) or Experiment 3 ($p = 0.09$).

All participants had normal or corrected-to-normal visual acuity confirmed by an optometrist. Normal visual acuity was defined as 20/30 or better (i.e., 20/24 at the intermediate distance). The optometric screening was accomplished via an eye exam that consisted of auto-refraction, manual refraction if necessary, visual acuity at far distance (20 ft), and visual acuity at intermediate distance (67 cm). Participants' own corrective glasses were measured using a lensometer to confirm appropriate correction. When a participant's corrective lenses were deemed insufficient, the participant used trial lenses in order to participate with the correct refraction.

All participants completed the Autism Spectrum Quotient (AQ) questionnaire (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). The AQ is a 50-item self-report measure of ASD symptoms that can be used as a screening measure. The range of possible scores is 0–50, and the cutoff recommended for referring a participant for an assessment for ASD is 32. Our exclusion criterion for participants in the control group was an AQ score above 20, chosen as the point of greatest separation between adults with and without ASD while allowing for higher scoring individuals such as those in the mathematics and sciences (Baron-Cohen et al., 2001).

The participants with ASD ($N = 29$) were previously diagnosed by a clinician using the criteria from the text revision of the *Diagnostic and Statistical Manual of Mental Disorders, Fourth Edition* (American Psychiatric Association, 2000). Diagnostic reports were obtained to verify the diagnoses. The Autism Diagnostic Observation Schedule (Lord, Rutter, DiLavore, & Risi, 1999) was administered by trained researchers in the Autism and Developmental Disorders Lab to confirm diagnoses for the majority of participants ($N = 23$). Comorbid psychiatric disorders reported for the larger sample of 29 participants with ASD were epilepsy/seizures (2), depression (1), attention-deficit/hyperactivity disorder (1), posttraumatic stress disorder (1), and obsessive-compulsive disorder (1). The two participants with seizures reported that they were taking seizure medication.

Experiment 1: Orientation discrimination

Orientation-discrimination thresholds were measured as a function of base orientation spanning a 180°

range starting from the horizontal position. Discrimination thresholds allow us to infer the precision of orientation perception around various base orientations. We expected to observe the oblique effect, which predicts higher precision (i.e., lower thresholds) around cardinal angles (vertical and horizontal) compared to oblique orientations.

Methods

Participants

Twenty-nine adult participants with ASD (eight women, 21 men, age = 23.2 ± 7.1 years) and 29 without ASD (nine women, 20 men, age = 26.3 ± 7.8 years) took part in this experiment. WASI-II Full Scale IQ scores for the group with ASD ranged from 76 to 134 ($M = 100.21 \pm 14.99$), and scores for the control group ranged from 77 to 134 ($M = 108.72 \pm 12.81$); the means of both groups were in the "Average" range. In addition, the two groups were matched on nonverbal IQ ($p = 0.16$), age ($p = 0.11$), and gender.

Experimental setup

The experiments were implemented using a computer equipped with a Cambridge Research Systems (CRS; Rochester, UK) VSG 2/3 graphics card and Sony Trinitron 17-in. monitor (model Multiscan17seII). Gamma correction was carried out using a CRS OptiCAL photometer (model OP200-E) and software provided by CRS. The mean luminance of the display was 17.4 cd/m^2. The experiment was programmed in MATLAB (MathWorks, Inc., Natick, MA; www.mathworks.com) using tools from the CRS VSG Toolbox for MATLAB and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Participants were seated at a distance of 70 cm from the screen.

Stimuli and procedure

A 3-cpd Gabor patch at a fixed Michelson contrast of 0.5 was used across base orientations ranging between 0° and 180°. Trials were blocked by base (reference) orientation, resulting in eight experimental blocks (22.5°, 45°, 67.5°, 90°, 112.5°, 135°, 157.5°, 180°) completed in a random order by each participant. Each block was preceded by a brief warm-up of 10 trials, to allow participants to acclimate to the new reference orientation being tested. Performance on the warm-up trials indicated that all participants understood the task instructions. A psychophysical staircase controlled the orientation increment presented at each trial using two randomly interleaved staircases that lasted 40 trials each. Staircases were implemented using the QUEST procedure (Watson & Pelli, 1983) in Psychophysics Toolbox.

Each trial began with an abrupt presentation of a 150-ms fixation cross, followed by the reference-orientation stimulus for 150 ms, another 150-ms fixation screen, then the test-screen stimulus for 150 ms, and finally a blank screen that remained until the participant entered a response by pressing either 1 or 2 on the number pad of a computer keyboard. Participants were asked to indicate whether the test orientation was to the left (counterclockwise, 1) or the right (clockwise, 2) compared to the reference orientation (see Figure 1A for an illustration of the procedure).

Blocks in which threshold estimates were determined to vary too greatly from one another (defined as one value being more than twice the other) were discarded and repeated until reliable threshold estimates could be established. No differences between the group with ASD and the control group were observed regarding the need to repeat blocks.

Participants were given auditory feedback for correct answers in the form of a single click; incorrect answers resulted in two clicks.

Data analysis

Each block used two randomly interleaved staircases to estimate orientation-discrimination thresholds at a criterion accuracy of 82%. The estimates were averaged to produce one overall threshold estimate for each of the eight tested reference orientations.

Results and discussion

Figure 2 shows orientation-discrimination thresholds as a function of reference orientation for the group with ASD (red curve) and the control group (black curve). Thresholds were submitted to a repeated-measures ANOVA with reference orientation as the within-subject factor and group (ASD, control) as the between-subjects factor. We found a significant main effect of reference orientation, $F(7, 392) = 23.22$, $p \ll 0.001$. Post hoc comparisons showed that thresholds at all oblique orientations differed significantly from those at both the vertical and the horizontal orientations (Tukey–Kramer comparisons test, all ps < 0.05), while there were no differences for thresholds at oblique orientations or between vertical and horizontal (all ps > 0.05)—consistent with the oblique effect. These results replicate prior findings of the oblique effect in orientation discrimination (e.g., Westheimer & Beard, 1998).

No main effect of group was found, $F(1, 56) = 0.00$, $p = 0.97$, nor a significant interaction between group and reference orientation, $F(7, 392) = 0.41$, $p = 0.90$. The

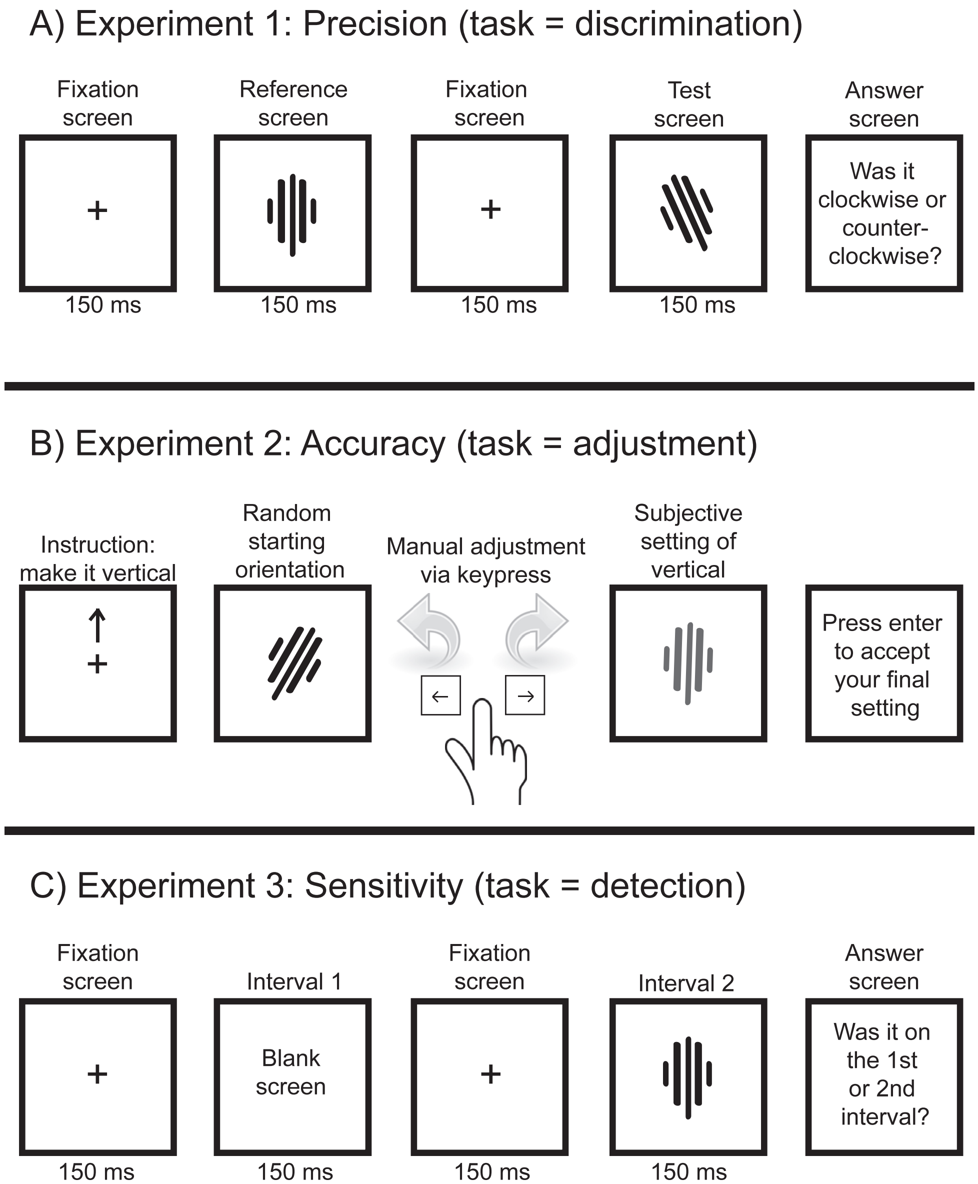

Figure 1. Schematic illustration of a typical trial in Experiments 1, 2, and 3. (A) Experiment 1: protocol for measuring precision of orientation perception using an orientation-discrimination task. Participants were shown a reference orientation followed by a test orientation. They were then asked to say whether the test orientation was clockwise or counterclockwise compared to the reference orientation. Discrimination thresholds were measured for eight reference orientations (22.5°, 45°, 67.5°, 90°, 112.5°, 135°, 157.5°, and 180°). (B) Experiment 2: protocol for measuring accuracy of perceived orientation using an adjustment task. Participants were required to manually (via key press) adjust a randomly oriented Gabor to a specified target orientation (vertical, 90°; horizontal, 180°; or oblique, 45°). (C) Experiment 3: protocol for measuring orientation sensitivity using a detection task. Participants were shown a Gabor stimulus (in one of four orientations: vertical, 90°; horizontal, 180°; oblique, 45° and 135°) in one interval and a blank screen in the other and asked to indicate which interval contained the stimulus. The contrast of the Gabor stimulus was controlled via a psychophysical staircase, allowing estimation of detection contrast thresholds at each orientation.

lack of a group effect indicates that there are no quantitative differences (i.e., the group with ASD did not perform better or worse than the control group), and the lack of interaction effect indicates that there are no qualitative differences (i.e., the group with ASD showed the characteristic oblique effect, as did the control group).

Experiment 2: Veridical perception

In Experiment 1 we measured participants' discrimination ability around various reference orientations. This measure indicates sensitivity to perturbations—i.e., fine-grain orientation deviations—from those

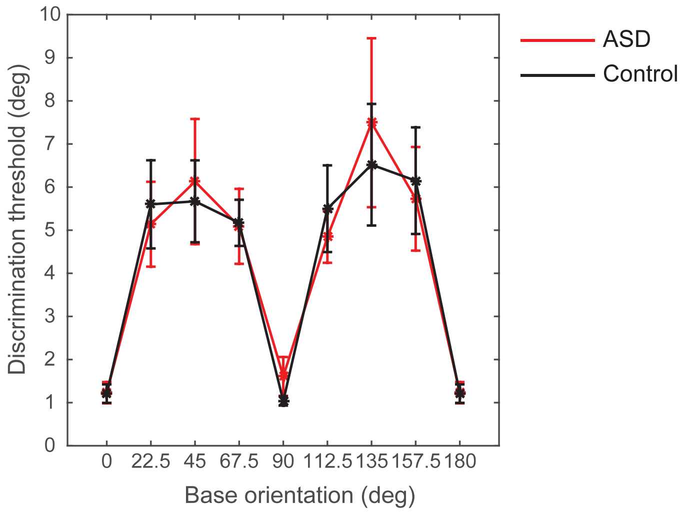

Figure 2. Results of Experiment 1. Orientation-discrimination thresholds are plotted as a function of base (reference) orientation for the group with ASD (red curve) and the neurotypical control group (black curve). As expected, precision was higher at cardinal orientations (shown by lower discrimination thresholds) compared to oblique angles (where thresholds were significantly higher). No differences in performance were observed between the two groups.

reference orientations but not whether perceived orientation at those base angles was veridical. To address this, we asked participants to manually adjust the orientation of a Gabor stimulus to a target orientation. The central tendency of repeated settings to a given target orientation across trials allowed us to infer the accuracy of orientation perception at those orientations and estimate any systematic biases away from veridical perception. Variability of the settings across trials allowed us to infer precision of perception at that orientation.

Methods

Participants

All 29 adults with ASD who participated in Experiment 1 were invited to participate in Experiment 2; of these, 16 responded to our call. Sixteen adult participants with ASD (four women, 12 men, age = 24.9 ± 8.7 years) and 16 without ASD (five women, 11 men, age = 24.9 ± 4.5 years) participated in this experiment (all had also participated in Experiment 1). WASI-II Full Scale IQ scores for the group with ASD ranged from 79 to 129 ($M = 100.88 \pm 14.20$) and for the control group ranged from 85 to 123 ($M = 108.81 \pm 10.99$). The two groups were matched on nonverbal IQ ($p = 0.2$), age ($p = 0.98$), and gender.

Experimental setup

This experiment utilized a Dell laptop computer (model 3750) equipped with a 17-in. antiglare LED screen. The experiment was programmed in SuperLab version 5.0 (www.superlab.com).

Stimuli and procedure

Sine-phase Gabor patches at a fixed Michelson contrast of 0.8 were presented on a uniform gray background of 33 cd/m^2 luminance at a viewing distance ranging from 50 to 70 cm, depending on participant comfort. At these viewing distances, the spatial frequency of the Gabor patches was in the range from 3 to 4 cpd.

We used a method-of-adjustment paradigm in which participants were asked to manually adjust (via key press) the orientation of a Gabor to a specified target angle (vertical, 90°; horizontal, 180°; oblique, 45°). Each trial began with a fixation cross, followed by a Gabor at a randomly chosen starting orientation. Trials were blocked by target orientation, and each block lasted 40 trials. Participants were asked to press 1 to rotate the stimulus in a counterclockwise direction or 2 to rotate it clockwise. They were instructed to indicate via key press when they had finished adjusting the setting for the Gabor to the desired target orientation. Performance indicated that all participants understood the task instructions. See Figure 1B for an illustration of this procedure.

Data analysis

Error at each trial was computed as the difference between the participant's final setting and the target orientation. Absolute error, for each target orientation, was computed as the absolute value of the average error across the 40 trials in the respective block. The sample standard deviation of error across 40 trials of each block was also computed. These two measures, absolute mean error and standard deviation of error, allowed assessment of veridicality of perception and precision for each target orientation.

Results and discussion

Figure 3A shows bias, or absolute error, in participants' settings as a function of the target orientation. Veridical perception is characterized by settings that are centered on the target orientation. Net biases in settings indicate departures from veridicality, computed as absolute mean error for each individual as a function of target orientation. As seen in Figure 3A, both groups of participants were near veridical in their perception of the two cardinal

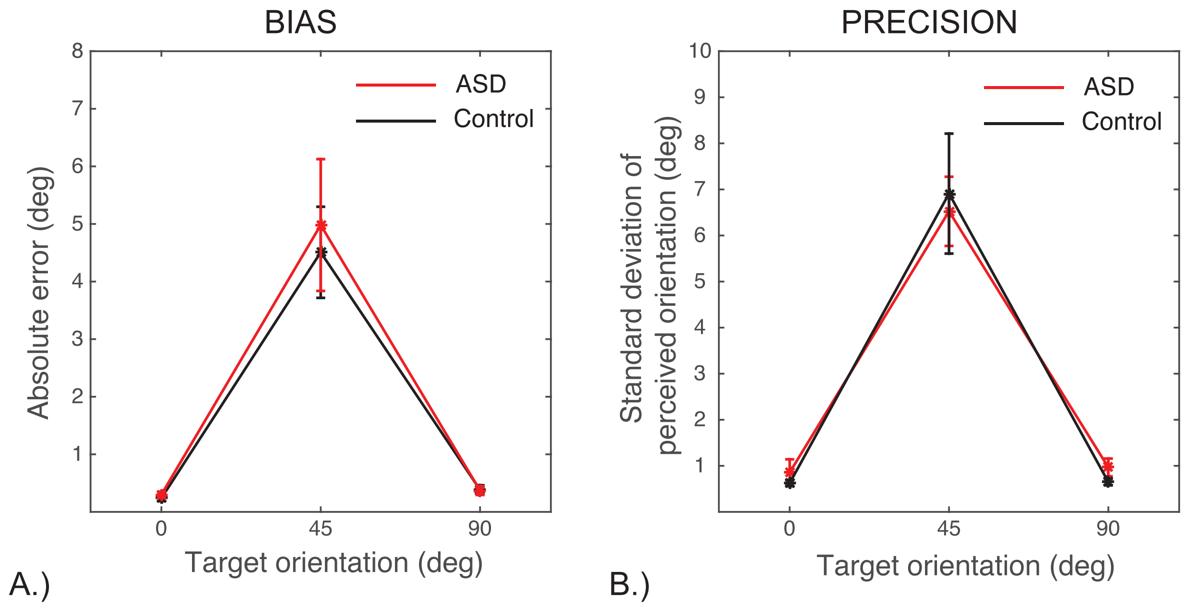

Figure 3. Results of Experiment 2. (A) Group averages of absolute mean error are plotted as a function of target orientation for the group with ASD (red curve) and the control group (black curve). While orientation perception was found to be near veridical for the cardinal orientations, significant biases were seen for the oblique orientation. No differences were observed between the groups with and without ASD. (B) Group averages of standard deviation of orientation settings are plotted as a function of target orientation for the group with ASD (red curve) and the control group (black curve). Precision of orientation perception, inversely related to the standard deviation of settings, was high for the cardinal orientations yet was significantly decreased for the oblique orientation, as expected. No differences were observed between the two groups.

orientations, horizontal and vertical, but showed substantial biases, or departures from veridicality, at the diagonal orientation, consistent with the oblique effect. Absolute mean error was submitted to a repeated-measures ANOVA, with target orientation (0°, 45°, 90°) as a within-subject factor and group (ASD, control) as a between-subjects factor. We found a significant main effect of target orientation, $F(2, 60) = 40.49$, $p \ll 0.001$, but no main effect for group, $F(1, 30) = 0.14$, $p = 0.71$, and no interaction between group and target orientation, $F(2, 60) = 0.11$, $p = 0.90$. Post hoc comparisons revealed that absolute error at the 45° orientation ($M = 4.75$) was significantly greater than those at 0° ($M = 0.27$) and 90° ($M = 0.38$) orientations (Tukey–Kramer, both ps < 0.05), whereas the cardinal-orientation conditions did not differ from one another (Tukey–Kramer, $p > 0.05$).

Whereas veridicality is related to the central tendency of a participant's settings, precision is based on the variability of settings around the central tendency. Thus, it is possible to have veridical but imprecise perception or vice versa. Although measurements of discrimination thresholds are the gold standard for assessing precision, as in Experiment 1, the variability of orientation settings in the present experiment provides a second, independent estimate of precision and an opportunity to obtain a verification of our results in Experiment 1. Figure 3B shows the standard deviation—which is inversely related to the precision—of each individual's settings averaged across participants as a function of target orientation. Consistent with Experiment 1 as well as the literature, we find that precision was high for horizontal and vertical target orientations and lower for the diagonal target orientation: the hallmark pattern of the classical oblique effect (Westheimer & Beard, 1998). Figure 3B shows that both groups of observers demonstrate the oblique effect, with no signs of qualitative or quantitative differences between the group with ASD and the control group. To statistically verify these observations, standard deviations of orientation settings were submitted to a repeated-measures ANOVA, with target orientation (0°, 45°, 90°) as a within-subject factor and group (ASD, control) as a between-subjects factor. We found a significant main effect of orientation, $F(2, 60) = 68.27$, $p \ll 0.001$, but no main effect of group, $F(1, 30) = 0.01$, $p = 0.93$, and no interaction between the two, $F(2, 60) = 0.21$, $p = 0.81$. Post hoc comparisons revealed that the standard deviation of settings at the 45° orientation ($M = 6.72$) was significantly greater those that at 0° ($M = 0.74$) and 90° ($M = 0.81$) orientations (Tukey–Kramer, both ps $<$ 0.05), while the cardinal-orientation conditions did not differ from one another (Tukey–Kramer, $p >$ 0.05).

Neither quantitative nor qualitative differences between the group with ASD and the control group were found, as suggested by the lack of a group main effect and the lack of an interaction in both measures of bias and precision.

Experiment 3: Contrast detection

Contrast thresholds for detecting a Gabor patch were measured as a function of stimulus orientation. Detection thresholds allowed us to infer differential sensitivity to varying orientations. We expected to replicate the oblique effect, which predicts higher sensitivity (i.e., lower thresholds) around cardinal orientations (vertical and horizontal) compared to oblique orientations. In this experiment, we chose to use a high-spatial-frequency Gabor stimulus because the magnitude of the oblique effect in detection contrast thresholds is known to be more pronounced at higher spatial frequencies (Berkley, Kitterle, & Watkins, 1975; Campbell et al., 1966; Essock & Lehmkuhle, 1982; Lennie, 1974; Mitchell, Freeman, & Westheimer, 1967).

Methods

Participants

All adults with ASD who had participated in Experiment 1 were invited to participate in Experiment 3; of these, 13 responded to our call. Thirteen adult participants with ASD (four women, nine men, age = 24.1 ± 7.2 years) and 13 without (five women, eight men, age = 23.6 ± 3.1 years), all of whom had participated in Experiment 1, took part in this experiment. WASI-II Full Scale IQ scores for the group with ASD ranged from 79 to 119 ($M = 99.00 \pm 13.25$), whereas the control group's IQ scores ranged from 98 to 123 ($M = 109.92 \pm 8.46$). The two groups were matched on nonverbal IQ ($p = 0.11$), age ($p = 0.83$), and gender.

Experimental setup

The experiment was implemented on a computer equipped with a CRS VSG 2/3 graphics card and a Sony Trinitron 17-in. monitor (model Multiscan17-seII). Gamma correction was carried out using a CRS OptiCAL photometer (model OP200-E) and software provided by CRS. The mean luminance of the display was 17.4 cd/m^2. The experiment was programmed in MATLAB using tools from the CRS VSG Toolbox for MATLAB and Psychophysics Toolbox. Participants were seated at a distance of 77 cm from the screen.

Stimuli and procedure

We used 22-cpd sine-phase Gabors at vertical (90°), horizontal (180°), and oblique (45° and 135°) orientations.

The task consisted of detecting a Gabor in a two-interval forced-choice paradigm. Each trial began with a 150-ms fixation cross, followed by Interval 1 for 150 ms, another 150-ms fixation screen, and then Interval 2 for 150 ms. Lastly, a blank screen remained until the participant entered a 1 or 2 response by key press to indicate the interval that contained the stimulus. An auditory beep signal marked each interval to prevent confusion between the two. Correct answers received feedback of a single click, whereas incorrect answers received two clicks. The next trial started immediately after a response was entered. Participants were instructed to maintain fixation throughout each trial. Eye movements were not monitored, but it was informally observed that participants did not have difficulty fixating the central cross. Performance on this task indicated that all participants understood the task instructions. See Figure 1C for a schematic illustration of this task.

The trials were blocked by orientation, and the four orientation blocks (vertical, 90°; horizontal, 180°; oblique, 45° and 135°) were completed in a random order after a brief warm-up. Two randomly interleaved staircases were utilized in each block to estimate contrast threshold for detection of the Gabor patch at the tested orientation. Staircases were implemented using the QUEST procedure in Psychophysics Toolbox.

Blocks in which threshold estimates were determined to vary too greatly from one another (defined as one value being more than twice the other) were discarded and repeated until reliable threshold estimates could be established. No differences between the group with ASD and the control group were observed regarding the need to repeat blocks.

Each staircase lasted 40 trials, for a total of 80 trials in each block.

Data analysis

Contrast thresholds were based on the average of the two estimates from the randomly interleaved staircases for each block, with an accuracy criterion of 82%.

Results and discussion

Figure 4 shows log-transformed contrast threshold values for detecting a Gabor stimulus as a function of orientation for the group with ASD (red curve) and the control group (black curve). Log contrast thresholds were submitted to a repeated-measures ANOVA, with

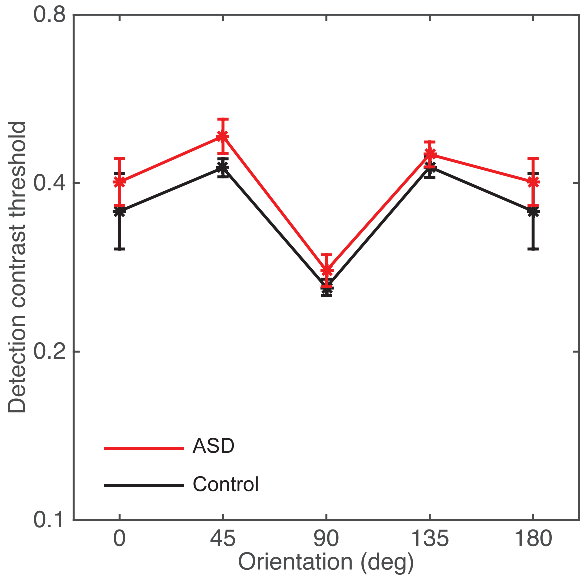

Figure 4. Results of Experiment 3. Detection contrast thresholds plotted as a function of orientation, where 90° and 180° designate vertical and horizontal, respectively (data at 0° represent horizontal and are identical to those plotted at 180°). Data for the group with ASD (red curve) show slightly less sensitive performance compared to the control group (black curve), but this difference did not reach significance.

orientation (0°, 45°, 90°, 135°) as a within-subject factor and group (ASD, control) as a between-subjects factor. This revealed a highly significant main effect of orientation, $F(3, 72) = 23.11$, $p \ll 0.001$. There was no main effect of group, $F(1, 24) = 1.70$, $p = 0.21$, and no interaction between group and orientation, $F(3, 72) = 0.15$, $p = 0.93$.

Both groups of participants qualitatively demonstrate the oblique effect—i.e., detection contrast thresholds were lower at cardinal compared to oblique orientations, revealing the characteristic sawtooth pattern observed here. The lack of an interaction between participant group and orientation supports the observation that the two groups did not differ qualitatively, demonstrating an intact oblique effect in the detection of orientation. Quantitatively, we did not find any evidence for superior performance in orientation detection by the group with ASD at any of the orientations. Instead, the group with ASD shows the opposite trend, with slightly lower sensitivity across all orientations.

Post hoc pair-wise comparisons between the four orientations showed that thresholds were significantly lower at the vertical orientation than all other orientations (Tukey–Kramer multiple-comparison test, all $ps < 0.05$). Although horizontal detection thresholds were also numerically lower than those at the oblique orientations, this difference did not reach significance.

Neither quantitative nor qualitative differences between the group with ASD and the control group were found, as suggested by the lack of a group effect and the lack of an interaction.

General discussion

Individuals with ASD reportedly accomplish a variety of tasks involving visual stimuli with superior competence (Gliga, Bedford, Charman, Johnson, & Team, 2015; Happe, 1999; Jolliffe & Baron-Cohen, 1997; Keita et al., 2014; Manning, Tibber, Charman, Dakin, & Pellicano, 2015; O'Riordan et al., 2001; Plaisted et al., 1998a, 1998b; Plaisted et al., 1999; Plaisted et al., 2003; Shah & Frith, 1983). A clear understanding of the source and nature of the altered neural function that brings about this superior performance would go a long way in characterizing the brain processes that collectively give rise to the complex symptomatology of ASD.

This study represents one leg of a systematic line of research aimed at conclusively clarifying whether the earliest stages of visual cortical processing, presumably attributable to V1, are enhanced for observers with ASD. In this study, we focused on the basic processing of orientation. Our approach incorporated several important methodological choices. First, we recruited a large number of participants to maximize generalizability and statistical power. Second, we included participants who were carefully characterized diagnostically; matched on age, gender, and IQ; and screened by an optometrist to ensure that all had normal or corrected-to-normal vision. Third, we chose simple stimuli (Gabor patches) and three basic visual tasks that are most likely representative of the earliest levels of cortical processing. Fourth, we ran all three tasks with the same subsets of participants in order to facilitate qualitative comparisons of the results across experiments. (Out of the 29 participants who completed Experiment 1, 16 also completed Experiment 2, and 13 also completed Experiment 3). Finally, instead of comparing the two groups at a single data point, we designed experiments to systematically measure performance across various base orientations. We took advantage of the classical oblique effect, which describes superior performance at cardinal base orientations compared to oblique ones. This allowed us to assess our data in light of predictions based on the literature, as well as enabling us to compare the performance of the group with ASD both qualitatively and quantitatively with the performance of our control group. Although the lack of statistically significant differences between the two groups does not necessarily imply equal performance, this dense array of data across three experiments provided a highly reliable context to evaluate the presence or absence of any such differences. Based on these data, we were able to test our two main hypotheses: (a) Individuals with ASD are quantitatively distinct from individuals without ASD and show superior orientation perception, and (b) individuals with ASD are qualitatively distinct from individuals without ASD and exhibit an altered pattern that deviates from the oblique effect. We confidently conclude that neither of these hypotheses is supported.

This conclusion is consistent with the findings of Brock, Xu, & Brooks (2011), who assessed orientation discrimination around a horizontal reference for a group of neurotypical individuals and found no correlation between discrimination thresholds and AQ scores, despite the fact that within the same group of observers, those with higher AQ scores were significantly faster in a search task involving the same discrimination stimuli as the target and distracters. In contrast, Dickinson, Jones, and Milne (2014) measured discrimination thresholds around the vertical and one oblique orientation for a large group of neurotypical individuals and found higher AQ scores to be associated with lower thresholds around the oblique orientation but not the vertical. They concluded that the lack of positive findings around cardinal axes represents a ceiling effect which minimized interparticipant variability. The results of this latter study are in direct contradiction with the results of our Experiment 1, in which we examined the same measure—orientation-discrimination threshold—using fairly similar methods. Despite the fact that we measured performance at six distinct oblique orientations as well as both cardinals, we did not find evidence for enhanced precision around any base orientation.

The reasons for the difference between the present results and those of Dickinson et al. are unclear, though methodological differences may play a role. First, Dickinson et al. used sinusoidal gratings as stimuli, whereas our present study, as well as that of Brock et al. (2011), used Gabor patches. Although a sine-wave grating theoretically contains power at a single spatial frequency (3 cpd for Dickinson et al.), this requires the stimulus to cover an infinite spatial extent. When in practice gratings are presented over limited apertures with sharp edges, as was the case for Dickinson et al., this inevitably introduces high spatial frequencies to the stimulus image. Based on several recent studies (e.g., Keita et al., 2014; Latham et al., 2013), it is possible that these high-spatial-frequency components were critical to enabling the enhanced performance found by Dickinson et al. A Gabor stimulus, by contrast, is localized in both spatial and spatial-frequency domains, and thus the spatial frequencies in our study and that of Brock et al. were tightly focused on 3 and 2 cpd, respectively, lacking any high-spatial-frequency components. Second, Dickinson et al. tested a sample of individuals outside a clinical context and utilized AQ scores as a measure of autistic traits, whereas our study compared a group of clinically diagnosed individuals with ASD to a control group without ASD and with AQ scores of 20 or less. One issue here is that the AQ, though closely associated with autistic traits, is nevertheless not a diagnostic tool to assess the presence or absence of ASD. Moreover, Dickinson et al. did not assess general intelligence in their sample.

Indeed, general intelligence characteristics of the group with ASD may play a critical role in whether enhanced processing is observed in this population (Caron et al., 2006). Bertone et al. (2005) used an orientation-identification task in which participants were presented with either a vertical or a horizontal sine-wave grating in noise and were asked to indicate the orientation of the stimuli. They found that their participants with ASD outperformed those without ASD in this task based on contrast thresholds for orientation identification. It is worthwhile to note that this study also used gratings as opposed to Gabors. In addition, the orientation-identification task is presumably a higher order visual task than all three basic orientation tasks used in our study. Perhaps the most important difference was the characteristics of the clinical group who participated in the study by Bertone et al., where 83% of the participants with ASD had a relative Block Design test peak (as indicated in Caron et al. 2006, pg. 1800). The Block Design test is one of the subtests of the Wechsler Intelligence Scale contributing to the calculation of nonverbal IQ; the test taker is required to manually rearrange blocks to reproduce a spatial pattern. Whereas conventionally a peak ability that is characterized by a profile of nonverbal IQ showing the highest score in the Block Design test (i.e., a BDT-peak) has been associated with autism, more recently, the actual incidence rate of a BDT-peak was shown to be 22% within a population of adults with autism with average intelligence (Siegel, Minshew, & Goldstein, 1996). In the present study, seven of our larger sample of 29 individuals with ASD showed a BDT-peak (as defined by having superior performance in the Block Design subtest relative to other subtests), corresponding to 24% of our sample, which is consistent with the general incidence rate of 22%.

To examine the possibility that superior low-level processing is related to exceptional performance in the Block Design test, we replotted our data from all three experiments, this time separating the groups with ASD into "BDT-peak" and "No BDT-peak" subgroups. As seen in Figure 5, two out of the three experiments do

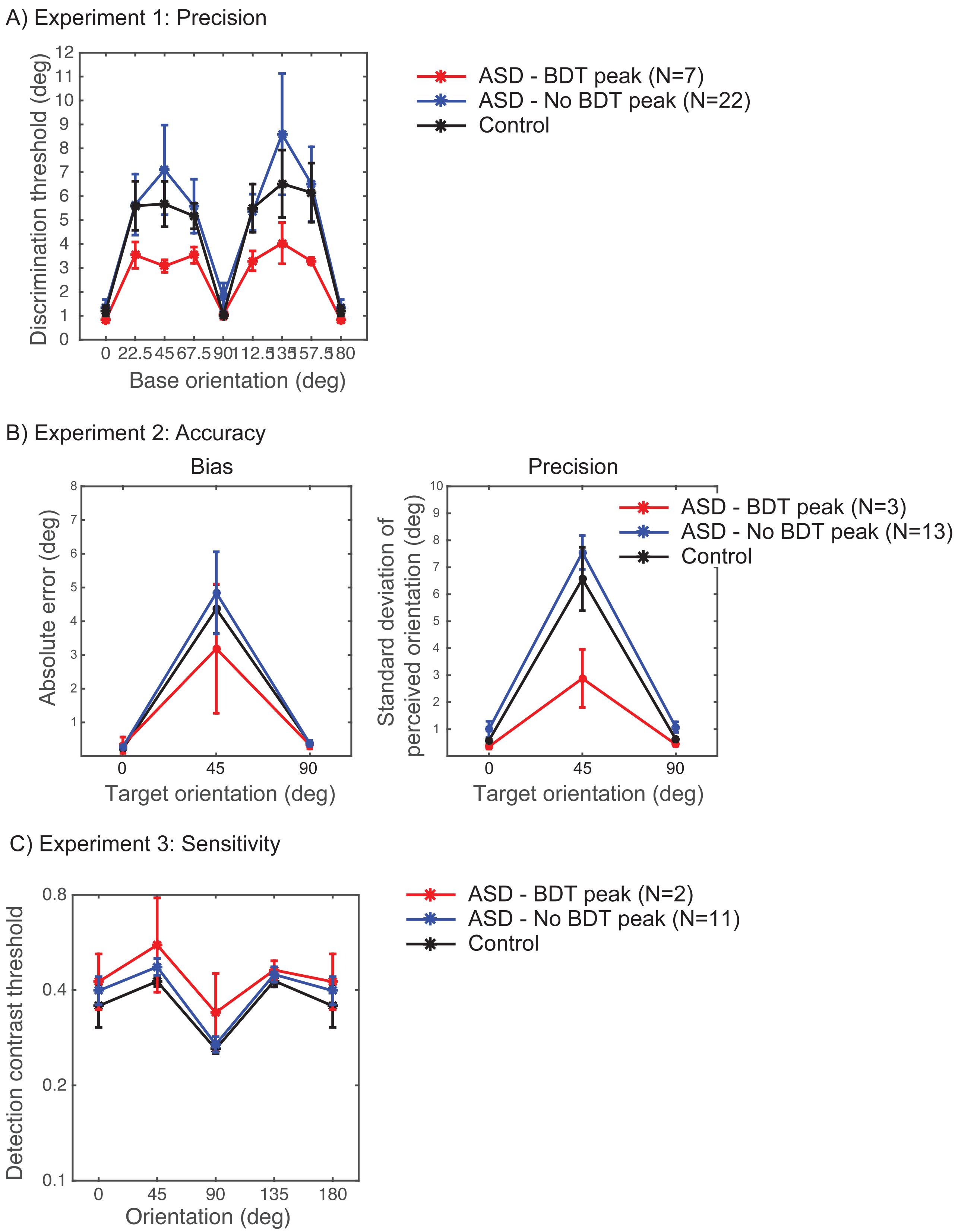

Figure 5. Data from participants with ASD who have a Block Design test peak. Data for all three experiments are replotted, this time separating the group with ASD into two subgroups based on whether they showed a BDT-peak (red curve) or not (blue curve). This post hoc observation hinted at the possibility that the presence of a BDT-peak may be a critical factor in whether enhanced perceptual processing is observed in individuals with ASD based on the results of Experiments 1 (A) and 2 (B), though this was not observed in Experiment 3 (C).

show indications for superior performance in the BDT-peak group, providing a potential explanation for the finding of enhanced orientation processing by Bertone et al. (2005). Since our study was not designed to specifically address BDT-peak within the population with ASD as a factor, we are not in a position to provide strong evidence, especially in light of the fact that Experiments 2 and 3 included only three and two BDT-peak individuals, respectively. It is important to note that the enhanced orientation-identification performance found by Bertone et al. was not replicated in a later study (Meilleur, Berthiaume, Bertone, & Mottron, 2014) using the same task with a different participant group. This lends further emphasis to the critical role of the specific makeup of the participant group with ASD. Thus, we can confidently say that given the 22% incidence of a BDT-peak in the adult population with ASD, investigations of enhanced perceptual processing within this population must assess measures of IQ and use true representative samples of both groups. The BDT-peak should be examined as a factor in future studies of perceptual processing in individuals with ASD.

The idea that enhanced perceptual functioning is limited to specific subgroups of individuals with ASD is not without precedent. A recent study by Bonnel et al. (2010) found that participants with autism showed superior pitch discrimination for simple tones but those with Asperger's syndrome did not. Indeed, the presence of a BDT-peak may be associated with speech delay in ASD (Ehlers et al., 1997). The present study does not provide any additional evidence on this point, and thus the relationship between speech delay, enhanced perceptual functioning, and Block Design performance needs to be investigated in future studies.

In the current study, the evidence does not support the hypothesis that in the overall population of people with ASD, enhanced perceptual processing involves the lowest levels of orientation processing, such as those considered to take place in V1. This result is consistent with recent fMRI studies. Schwarzkopf, Anderson, de Haas, White, and Rees (2014) examined response selectivity of the human visual cortex and found significantly larger population receptive fields in extrastriate regions in the participant group with ASD compared to a control group without. Importantly, no differences were found in V1. Similarly, a meta-analysis by Samson, Mottron, Soulieres, and Zeffiro (2012) found atypical fMRI response patterns in individuals with ASD to be most reliably clustered around regions associated with visual expertise. Altogether, these results suggest that the source for altered perceptual abilities should be sought elsewhere, possibly downstream from V1.

Amid significant controversy over nearly every aspect of visual processing in ASD (e.g., see Behrmann, Thomas, & Humphreys, 2006; Simmons et al., 2009), systematic studies painstakingly elaborating on intricate aspects of visual performance via rigorously designed psychophysical experiments with accurately characterized clinical populations are essential in decisively establishing what level of processing is unremarkable in ASD (regarding the status of visual attention in ASD, see, e.g., Grubb, Behrmann, Egan, Minshew, Carrasco, & Heeger, 2013; Grubb, Behrmann, Egan, Minshew, Heeger, & Carrasco, 2013). Our study contributes to this discussion, focusing on processing of visual orientation, and provides compelling evidence against the hypothesis that superior perceptual processing is a general characteristic of individuals with ASD that originates at the earliest levels of the visual-processing pathway. This result is consistent with recent interpretations of the Enhanced Perceptual Functioning model (Mottron et al., 2006). For example, Meilleur et al. (2014) showed perceptual atypicalities to be associated with an ASD-specific "p" factor that influences perceptual performance across levels of visual processing. More research is needed to explore whether enhanced perceptual processing is associated with a subgroup of individuals with ASD who show a BDT-peak.

Keywords: autism spectrum disorder, orientation perception, discrimination, detection, oblique effect, contrast sensitivity, enhanced perception

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