Neuroscience

RESEARCH ARTICLE

A. J. Herringshaw et al./Neuroscience 395 (2018) 49–59



Neural Correlates of Social Perception in Children with Autism: Local versus Global Preferences

Abbey J. Herringshaw, Sandhya L. Kumar, Kaitlyn Noel Rody and Rajesh K. Kana*

Department of Psychology, University of Alabama at Birmingham, Birmingham, AL, USA

Abstract—The Weak Central Coherence account of autism spectrum disorders posits that individuals with ASD utilize a detail-oriented information processing bias. While this local bias is helpful in visual search tasks. ASD individuals falter in social cognition tasks where coherence is advantageous. The present study examined the neural correlates of Weak Central Coherence in ASD during visual and social processing. Fifteen ASD and sixteen typically developing children/adolescents completed a social/visual information processing task in an fMRI scanner. The stimuli consisted of human characters, composed of geometrical shapes, displaying different emotions. In the locally oriented Shape condition, participants indicated whether a given shape was present in a figure. In the Emotion condition, participants identified the emotion conveyed by the character in the figure at the global level. Whole-brain within- and between-group activation and seed-to-voxel functional connectivity analyses were conducted in SPM12 and the CONN toolbox. The ASD group was significantly faster in shape identification, but less accurate in emotion identification. The TD group showed significantly increased areas of activity over the ASD group in the Shape task in regions associated with executive control, such as the medial prefrontal cortex and middle frontal gyrus, suggesting increased interference from the global/social information. During the Emotion condition, the ASD group showed decreased connectivity between frontal and posterior regions and between body perception and motor networks, suggesting a possible difference in mirroring. The findings suggest that social cognitive factors, not visual processing biases, underlie the observed behavioral differences. © 2018 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: autism, central coherence, perception, social cognition, fMRI.

INTRODUCTION

A recent report estimates that 1 in 59 children in the United States today are affected by an autism spectrum disorder (ASD) (Center for Disease Control and Prevention, 2018). Deficits in social interaction have long been considered the core symptom of ASD across all levels of functioning. Individuals on the spectrum have documented deficits in emotion recognition (e.g., Lerner et al., 2012), recognition of familiar faces (Weigelt et al., 2011), recognition of biological motion (Blake et al., 2003), and empathy (Sucksmith et al., 2013). Theory-of-

mind (ToM), which describes the ability to explain and predict the behavior of others by attributing to them specific mental states, such as their intentions, beliefs, desires, or emotions, is also consistently found to be impaired in this group (Baron-Cohen et al., 1985; Castelli et al., 2002; Senju, 2012; Kana et al., 2015). Further, children on the spectrum tend to attend less to social stimuli (Pierce et al., 2011), show decreased neural activity following social reward (Delmonte et al., 2012), and initiate social interactions less often than typically developing children (Hauck et al., 1995).

The neural bases of these social difficulties have also been extensively investigated. Studies of the "social brain" in ASD have found abnormalities in the structure and function of core areas of social cognition, including the amygdala, inferior frontal gyrus (IFG), superior temporal sulcus (STS), temporo-parietal junction (TPJ), anterior cingulate cortex (ACC), and medial prefrontal cortex (MPFC) (Bauman and Kemper, 1994; Baron-Cohen et al., 1999; Critchley et al., 2000; Castelli et al., 2002; Dichter et al., 2009; Carter et al., 2012; Murdaugh et al., 2014; Patriquin et al., 2016; Kana et al., 2017). Further, in typically developing (TD) individuals, specialized neural areas for viewing human faces (the fusiform face

E-mail address: rkana@uab.edu (R. K. Kana).

Abbreviations: ACC, anterior cingulate cortex; ASD, autism spectrum disorder; DMN, default mode network; EBA, extrastriate body area; FBA, fusiform body area; fMRI, functional MRI; GLM, general linear model; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; ITG, inferior temporal gyri; MFG, middle frontal gyri; MPFC, medial prefrontal cortex; pSTS, posterior superior temporal sulcus; SFG, superior frontal gyri; SMA, supplementary motor area; SPL, superior parietal lobule; STS, superior temporal sulcus; TD, typically developing; VIQ, Verbal IQ.

^{*}Corresponding author. Address: Department of Psychology, University of Alabama, Birmingham, CIRC 235G, 1719 6th Ave South, Birmingham, AL 35294-0021, USA. Fax: +1-(205)-975-6330.

area, FFA), human bodies (the extrastriate body area, EBA, and fusiform body area, FBA), and biological motion (the posterior superior temporal sulcus, pSTS) have also been identified (Puce et al., 1996; Downing et al., 2001; Pelphrey et al., 2003). Studies investigating the social brain in individuals with ASD have found reduced specialization for faces in the FFA (Schultz et al., 2000) and dysfunctional pSTS activity in response to social stimuli (Pelphrey et al., 2005). Disrupted neural activity within social brain hubs, such as FFA and STS, has also been documented in unaffected siblings of individuals with ASD, leading to propositions of a potential ASD neuroendophenotype (Kaiser et al., 2010; Spencer et al., 2011). Moreover, functional connectivity differences among key regions of the social brain have also been reported in individuals with ASD (Kana et al., 2009, 2015; von dem Hagen et al., 2012; Libero et al., 2015).

Aside from the aforementioned social-cognitive symptoms of ASD, atypical perceptual processing is being increasingly studied, with perhaps the most robust evidence coming from studies of visual processing (see Simmons et al., 2009, for a review). In particular, individuals with ASD are often described as "not seeing the forest for the trees," in a seeming violation of the global precedence characteristic of visual processing seen in TD individuals (Navon, 1977). Previous literature suggests that the global processing bias seen in TD individuals may be altered in individuals with ASD, coupled with an advantage in tasks requiring detail-oriented visual abilities. For example, participants with ASD have shorter reaction time and greater accuracy in completing Embedded Figures Tests (Shah and Frith, 1983; Pellicano et al., 2006), complex pattern construction (Plaisted et al., 1998), and visual search tasks (O'Riordan et al., 2001). A deficit in holistic processing in ASD has also been observed, such as in gestalt-type perception tasks (Bolte et al., 2007). Further, eye-tracking studies have found that during naturalistic scene viewing, individuals with ASD show increased attention to pixel-level details while finding categorical information less salient (Wang et al., 2015). At the neural level, brain activity during locally directed visual tasks in ASD has been linked to IFG and superior and inferior parietal areas (SPL and IPL) (Manjaly et al., 2003). Studies have also implicated an over-reliance on relatively posterior, basic visual processing areas (Ring et al., 1999; Samson et al., 2012; Kana et al., 2013) and decreased functional connectivity between frontal and relatively posterior neural regions (Liu et al., 2011).

Some models of ASD have posited that locally oriented visual processing is part of a larger locally oriented cognitive processing bias. The Weak Central Coherence model of ASD (WCC; Frith, 1989; Happé and Frith (2006)), for example, proposes that an inability to "see the big picture" is a core deficit of ASD. WCC finds support for this claim from studies showing that individuals with ASD struggle to process information in context across sensory modalities and cognitive processes, including correctly pronouncing homographs based on context (Frith and Snowling, 1983) and providing more details and fewer "big picture" components when telling

a story (Barnes and Baron-Cohen, 2012). Similarly, the Enhanced Perceptual Functioning (EPF) model proposes a general enhancement in low-level perceptual abilities in ASD, resulting in increased reliance on posterior, primary perception areas and their associative sensory cortices across many types of information processing (Mottron et al., 2006). Both models suggest that this processing bias could lead to atypical social interactions, which often require integrating many different elements (i.e., facial expression, voice and prosody, body language, environment and context) in order to function efficiently.

However, it is a matter of debate whether local processing strengths must necessarily come at the cost of global processing deficits and whether social difficulties exist entirely independently of atypical perceptual processing in a more "fractionable" manner (Happé et al., 2006; Pellicano et al., 2006; Wang et al., 2015). This functional MRI (fMRI) study seeks to elucidate the relationship between visual processing biases and social difficulties in ASD using a task that targets local visual search and social cognition in tandem. Specifically, we aim to: (1) to examine local processing bias in performance in a task that targets visual and social skills in tandem, and further to determine the relation of mentalizing abilities and visual processing bias to task performance; and (2) to examine the neural mechanisms underlying visuospatial advantage and global processing deficits in children with ASD. We hypothesize that individuals with ASD, relative to TD, will show faster reaction time and higher accuracy while performing the local, non-social task, and slower reaction time and lower accuracy while performing the global, social task. Second, we hypothesize that across both tasks, participants with ASD will show reduced activity in the social brain network; increased activity in posterior, basic visuospatial processing areas; reduced frontal-parietal connectivity; and reduced connectivity within the social brain network. This study will provide novel insights into the neural circuitry underlying visual processing strengths and weaknesses in ASD and provide a potential link between altered perceptual processing patterns and social cognition abilities.

EXPERIMENTAL PROCEDURES

Participants

Seventeen high-functioning children with ASD and seventeen age-and-IQ-matched TD control children initially completed the study. IQ was assessed via the WASI (Wechsler, 1999). Three participants were excluded from further analyses due to excessive head motion during the fMRI scan (>20% of images above 2 mm movement threshold), resulting in a final sample of fifteen participants in the ASD group and sixteen in the TD group. Although the sample as originally recruited was matched on age and IQ (both Verbal and Performance), the final sample had significant group differences in age (ASD mean = 13.18 years; TD mean = 11.86 years, t(29) = 2.27, p < .05), and Verbal IQ (VIQ) differences approached significance (ASD mean = 101.00, TD mean = 112.31, t(29) = 1.96, p = .06). However,

neither age nor VIQ showed a significant relationship to performance (RT or accuracy) in either condition (r's range .06 to .32, all N.S.). Additionally, no significant correlations were found between either age or VIQ and overall head motion (r's .055 and -.211, respectively, both N. S.), suggesting that the differential characteristics of the groups after removing the subjects were due to chance; accordingly, it was deemed appropriate to include both age and VIQ as covariates in the activation model to further rule out any possible confounding effects. Groups did not differ on Performance or Full Scale IQ (FSIQ). Participant characteristics can be found in Table 1. Due to sex differences in the prevalence of ASD, participants were primarily male (Females: ASD = 1, TD = 2). Participants ranged in age from 9 to 14 years old and were part of a larger study including structural and functional neuroimaging. Participants were recruited from the University of Alabama at Birmingham (UAB) Civitan-Sparks clinics, doctor referrals, Autism Society of Alabama, parent support groups, and local autism events in the Birmingham, AL area. Due to the neuroimaging component of this study, the following exclusion criteria were applied: history of major surgery, presence of non-removable metal in body, claustrophobia, being left-handed, IQ < 75, extreme difficulty laying still for 45 min, and extreme sensitivity to noise. Grouping was based on self-report of a previous clinical diagnosis, and was not determined by random assignment. ASD symptom severity in the sample was characterized with the Social Responsiveness Scale (SRS) (Constantino and Gruber, 2012) to confirm group differences in autistic trait levels.

Experimental paradigm

The stimuli consisted of human figures made up of a series of geometrical shapes (see Fig. 1). The experimental task included three conditions: global/emotion processing, local/shape processing, and a fixation baseline. In the global/Emotion condition, participants were asked to identify the emotion/mood portrayed by the posture of the character in the figure. Two answer choices were presented simultaneously

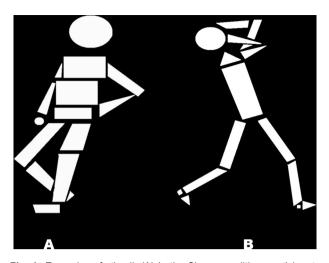


Fig. 1. Examples of stimuli: (A) In the Shape condition, participants detected the presence of a rectangle in the figure; (B) In the Emotion condition, participants judged the emotion of the character (in this case, "upset").

with the figure (e.g., "sad" or "scared"), and participants made their selection via button press. In the local/shape condition, participants were asked to indicate "ves" or "no", via button press, whether a given shape was present in the figure (e.g., whether the figure contains a triangle). The fixation condition consisted of a small cross centered on the presentation screen. Each participant viewed 12 global/emotional, 12 local/shape stimuli, and 7 fixation periods that are 24 s long. Stimuli were randomized and presented in an event related design. Each stimulus was presented for 6 s. with an inter-stimulus-interval of 5 s. The fixations were presented at the beginning and at the end of the experiment and after every 4 stimuli presentations throughout. All stimuli were presented via a reflected screen while participants were being scanned.

Assessment measures

Reading the Mind in the Eyes - child (RME). Adapted from the widely used adult version, the child version of

Table 1. Participant characteristics

	Ν	M	SD	Min	Max	t-value	df	p-value
Age								
ASD	15	13.81	1.84	9.90	17.10	2.27	29	.03*
TD	16	11.86	1.40	10.29	13.81			
Full Scale IQ								
ASD	15	102.93	14.03	75.00	126.00	-1.38	29	.18
TD	16	110.31	15.59	87.00	139.00			
VIQ								
ASD	15	101.00	13.98	74.00	128.00	-1.96	29	.06
TD	16	112.31	17.80	83.00	145.00			
PIQ								
ASD	15	104.20	16.58	74.00	132.00	42	29	.68
TD	16	106.37	12.47	93.00	137.00			
SRS Total								
ASD	15	107.80	26.56	51.00	148.00	8.94	29	.00***
TD	16	21.60	26.25	4.00	87.00			

this task (Baron-Cohen et al., 2001) includes 28 photographs of the eye region of human faces. Children are presented with four words and asked to choose which word best describes what the person is thinking or feeling. Position of the words is randomized and vocabulary is appropriate for the age of children in the study. RME is an advanced test of emotion recognition and also taps mental state attribution abilities, which is an early step in mentalizing. Scores on the RME can range from 0 to 28; higher scores represent improved accuracy, with any score greater than 9 indicating above chance-level accuracy.

Global and Local Processing Speed. Global and local processing speed in non-social stimuli was also measured in each participant. In a separate experiment utilizing the same study participants, children with and without ASD were presented with larger geometric figures (global level) made up of smaller geometric shapes (local level; for example, a group of small triangles might be arranged to form a large square). Participants were instructed to identify either the globalor local-level shape via button press. Reaction time was measured with E-Prime software. Utilizing only correct trials, participants' global vs. local processing bias was calculated by subtracting their average global speed from their average local speed. Thus, a more negative score on this index indicates a stronger local bias, whereas a more positive score suggests a stronger global bias.

Data acquisition

Images were acquired on the 3T Siemens Allegra Scanner at the UAB Civitan International Research Center (CIRC) functional neuroimaging center. For structural imaging, initial high-resolution T1-weighted scans were acquired using a 160-slice 3D MPRAGE volume scan with TR = 200 ms, TE = 3.34 ms, flip angle = 7 degrees, FOV = 25.6 cm, $256 \times 256 \text{ matrix}$ size, and 1-mm slice thickness. For functional imaging, single-shot gradient-recalled echo-planar pulse sequence that offers the advantage of rapid image acquisition [Repetition Time (TR) = 1000 ms, Echo Time (TE) = 30 ms, flip = 60 degrees, Field of View (FOV) = 24 cm, matrix 64×64] was used. This sequence covers most of the cortex (17 5-mm thick slices with a 1-mm gap acquired in an oblique-axial orientation) in a single cycle of scanning (1 TR) with an in-plane resolution of $3.75 \times 3.75 \times 5$ mm.

Data analyses: preprocessing

Functional images were preprocessed with the default functional imaging preprocessing pipeline in the SPM12 CONN functional connectivity toolbox, version 15.h (Whitfield-Gabrieli and Nieto-Castanon, 2012). This consists of the following steps: resampling to $2\times2\times2$ -mm voxels and unwarping, centering, slice time correction, normalization to the Montreal Neurological Institute (MNI) template, outlier detection (ART-based scrubbing), and smoothing to an 8-mm Gaussian kernel. Motion parameters were entered as multiple regressors and

images with motion over 2.0 mm were regressed entirely out of the time course. Any participants with more than 20% of their images removed due to motion were dropped from the analyses to ensure data quality (3 total participants). There were no significant differences in head motion between the two groups, as defined by the each participants' root mean square of displacement (t(30) = .68, N.S.).

Data analyses: statistical analyses

Reaction time (RT) and accuracy, as measured by E-Prime, were analyzed for each participant in SPSS v. 24. Only trials answered correctly were included in the calculation of average RT for each participant; all other variables and neuroimaging analyses included both correct and incorrect trials. Four separate independentsample T-tests (ASD and Control) (Emotion RT, Emotion accuracy, Shape RT, and Shape accuracy) were conducted to identify ASD and TD group differences. Any statistically significant group differences on task performance measures were entered as dependent variables in a hierarchical linear regression model where group was entered as the first prediction step, followed by global/local processing speed bias and RME scores in step 2. All continuous independent variables were mean-centered. Activation-based general linear model (GLM) analyses were performed in SPM12. Within-group and between-group contrasts performed Shape > Fixation, for the were Emotion > Fixation, Shape > Emotion, Emotion > Shape contrasts. Age and VIQ were entered as nuisance regressors into the model for activation analysis. Monte Carlo simulation analyses were conducted to determine voxel-count thresholds (iterations = 10,000; p = .05 FWE corrected). All withingroup results were corrected to a cluster-level threshold of p = .001 (32 voxels) and all between-group analyses were conducted with a Monte-Carlo correction value of p = .005 (62 voxels).

Data analysis: functional connectivity

Seed-to-seed weighted GLM functional connectivity analyses were performed in the CONN v.h toolbox of SPM12 (Whitfield-Gabrieli and Nieto-Castanon, 2012). Nine seed regions were chosen a priori as most theoretically relevant to our hypotheses, based on previous literature. These included: three areas key to visual processing of the human body, the posterior superior temporal sulcus (pSTS) (Allison et al., 2000), extrastriate body area (EBA) (Downing et al., 2001), and fusiform body area (FBA) (Peelen and Downing, 2005); three regions associated with global versus locally oriented attention, the inferior parietal lobule (IPL) (Fink et al., 1996), superior parietal lobule (SPL) (Corbetta et al., 1995), and inferior frontal gyrus (IFG) (Manjaly et al., 2005); the MPFC, which is important in attentional control, higher order thought, and social cognition (Gilbert et al., 2010; Frith and Frith, 2007); the inferior, middle, and superior occipital gyri, which are key to basic visual processing (e.g., Wandell et al., 2005); and the precentral

gyrus, which plays an important role in mirroring aspects of action understanding (Hari et al., 1998).

Seeds were generated using the WFU PickAtlas toolbox (Maldjian et al., 2003) within SPM 12. The IFG, IPL, SPL, MPFC, and precentral gyrus seeds were created using their respective anatomical definition in the standard atlas provided in the program. Inferior, middle, and superior occipital avri, again as defined by the PickAtlas standard atlas, were collapsed into a single occipital seed given their proximity and conceptual relevance to the project. The EBA, FBA, and pSTS, which were not part of the standard PickAtlas atlas, were defined by creating a spherical region around peak MNI coordinate values for each region, as established in previous literature examining the three respective regions in participants at a similar developmental level and considering their respective spatial extent (Ross et al., 2014; Kana and Travers, 2012). Specific coordinates and radii for each ROI mask can be found in . Due to data indicating that there are hemispheric differences in global/local attention in TD individuals (Weissman and Woldorff, 2005), as well as in functional organization more generally in ASD (e.g., Cardinale et al., 2013), left and right hemisphere seeds were processed separately, with the exception of the MPFC (a midline structure). This resulted in a total of 17 seed regions. Group differences in connectivity were examined at significance thresholds FDR-corrected to p < .05 at the individual seed level.

RESULTS

Task performance

Results of four separate independent-sample t-tests revealed significant group differences in RT for the Shape condition [t(29) = -2.94, p < .01], such that the group was significantly faster mean = 2778 ms, TD mean = 3370 ms); and accuracy scores for Emotion condition (t(29) = -2.13, p < .05). such that the ASD group was significantly less accurate (ASD mean = 88.63%, TD mean = 95.31%) (Table 2). No significant group differences were found for Shape accuracy (ASD mean = 85.55%, TD mean = 90.10%) **Emotion** RT (ASD $mean = 2599 \, ms,$ mean = 2980 ms). Of note, the group difference in Emotion accuracy also fell above an adjusted significance threshold (95% likelihood adjusted p value = .0167) following a step-down sequential correction for multiple comparisons (Holm, 1979), and further interpretation should proceed with this limitation in mind. The results of follow-up regression analyses indicated that group was a significant predictor of Shape RT at step 1 (F(1,29) = 8.64, p < .01) and accounted for 20.3% of RT variance. The addition of RME and global/local bias at step 2 accounted for a significant increase in variance (change in $R^2 = .16$, F(2,27)= 3.49, p < .05), where RME was a significant predictor $(\beta = .41, p < .05)$, but global/local bias $(\beta = .03, N.S.)$ was not. The full model accounted for 32% of Shape RT variance (F(3,27) = 5.70, p < .01). In predicting Emotion accuracy, group was again a significant predictor at step 1 (F(1,29) = 4.43, p < .05), accounting for 10.3% of variance. However, the addition of RME and global/local bias at step 2 did not account for a significant increase in variance (change in $R^2=.08$, F(2,27)=1.36, N.S.) and rendered the full model non-significant (F(3,27)=2.42, N.S.). Neither RME ($\beta=.28$) or global/local bias ($\beta=.08$) were significant predictors of Emotion accuracy.

Within-group neural activity

Within-group analysis showed largely overlapping patterns of neural activity across both ASD and TD groups and both the Shape > Fixation and Emotion > Fixation contrasts (see Fig. 2). In these contrasts, both groups showed significant areas of activation bilaterally across the occipital lobe, in IPL, SPL, middle and inferior temporal regions, calcarine, lingual, and fusiform gyri, thalamus, hippocampus, IFG, precentral gyri, and supplementary motor area (SMA).

In comparing the tasks to each other, the ASD group showed significant activity for Shape > Emotion in: bilateral middle occipital gyri, SPL, IPL, cuneus, and precuneus; and parahippocampal, lingual, precentral gyri. The TD group showed significant activity for Shape > Emotion in: bilateral inferior, middle, and superior occipital avri, inferior temporal avri (ITG). middle frontal gyri (MFG), superior frontal gyri (SFG), precuneus, fusiform gyrus, and SMA; left MPFC and SPL and IPL; and right IFG, cingulate, lingual gyrus, putamen, and insula (see Fig. 3 and Table 3). No areas of significant activation survived statistical correction for the Emotion > Shape contrast in the ASD group. The showed increased group activity Emotion > Shape in left IFG, left calcarine gyrus, and right precuneus (see Fig. 3 and Table 3).

Between-group neural activity

In comparing the groups directly, no areas of significantly different neural activity were found Shape > Fixation contrast (p = .005, k = 62 voxels). However, in the Emotion > Fixation contrast, the ASD group showed greater activity, relative participants, in five distinct clusters (see Fig. 4 and Table 3): (1) bilateral precuneus extending to parts of the posterior cingulate and cuneus; (2) left SFG and MFG; (3) right lingual gyrus, extending to parts parahippocampus and hippocampal formation; (4) left IPL, including angular gyrus and supramarginal gyrus and (5) right ITG. The Shape > Emotion contrast showed significant TD > ASD activation in three distinct clusters: (1) a cluster spanning across right ACC, MPFC, SFG, and MFG; (2) left SFG; and (3) left IPL, including postcentral gyrus.

Functional connectivity analyses

The ASD participants, compared to TD participants, showed decreased functional connectivity for the Emotion condition (See Table 4). Specifically, significant decreases in connectivity were seen between: (1) left precentral gyrus and right pSTS; (2) left precentral gyrus and right occipital gyri; (3) left precentral gyrus

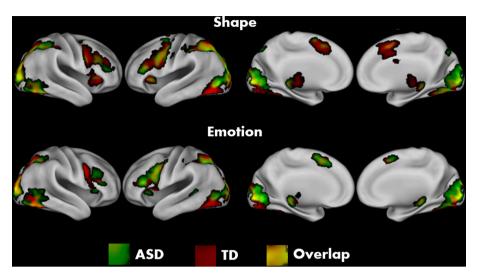


Fig. 2. Statistically significant within-group activation maps for the Shape (top panel) and Emotion (bottom panel) conditions, for ASD and TD participants, in contrast with fixation baseline.

and left occipital gyri; (4) left IFG and left FBA; and (5) right occipital gyri and right FBA. There were no statistically significant between-group differences in functional connectivity in the Shape condition.

DISCUSSION

This study sought to examine the neural mechanism of possible local visual search advantage and global/social perceptual weaknesses in children with ASD. Behaviorally, local search advantage and global emotion perception deficits were found. However, these differences did not relate to our measure of individual global/local processing style. Further, neural activation and functional connectivity revealed group differences in brain regions related largely to social cognitive processes.

Slower reaction times. decreased accuracy, and many areas increased neural of were noted within processing for the Shape each group condition (as compared to the Emotion condition), suggesting more difficulty with this task overall. The idea that the ASD group had more difficulty identifying local shapes than global emotions is contrary to the notion of a local processing bias advantage for these participants. However. when directly comparing the groups, the ASD group performed the Shape task significantly faster than the TD group did. Taken together, this pattern of performance might be better interpreted as a specific TD disadvantage. such that the

Shape task was more difficult for both groups, but that the ASD group may have addressed this challenge more efficiently. Follow-up regression analyses indicated that in our sample, mentalizing abilities better accounted for these group differences than did global vs. local processing abilities. This suggests that the ASD group may have experienced reduced interference from the salient social information being portrayed by the global human figure, contributing to their quicker completion times.

While processing shapes, relative to emotions, the ASD group recruited extensively from the occipital regions, which are important for basic visual processing. Conversely, the TD group showed increased activation in prefrontal cortex areas during shape processing

Table 2. Task performance

	Ν	М	SD	Min	Max	<i>t</i> -value	df	<i>p</i> -value
RMIE								
ASD	15	18.07	3.37	11.00	22.00	-1.49	29	.15
TD	16	19.56	2.13	15.00	22.00			
LG Bias								
ASD	15	216.73	428.80	-467.19	1282.09	0.81	29	.43
TD	16	108.42	315.56	-257.45	789.75			
RT Shape								
ASD	15	2778.41	673.49	1001.60	3578.67	-2.94	29	.006**
TD	16	3369.81	427.61	2456.91	3938.64			
RT Emotion								
ASD	15	2599.16	751.86	1415.71	4207.13	-1.71	29	.10
TD	16	2980.43	465.88	2181.25	3538.18			
Acc Shape								
ASD	15	85.56	14.93	41.67	100.00	-1.12	29	.27
TD	16	90.10	6.25	75.00	100.00			
Acc Emotion								
ASD	15	88.63	10.93	62.72	100.00	-2.13	29	.04*
TD	16	95.31	6.06	83.33	100.00			

Note: * significant at p < .05. ** significant at p < .05. ** significant at p < .01. RMIE = Reading Mind in the Eyes, LG Bias = global or local processing speed bias, RT Shape = Reaction Time for the Shape condition (ms), RT Emotion = Reaction Time for the emotion Emotion Condition (ms), Acc Shape = Accuracy for the Shape condition, Acc Emotion = Accuracy for the Shape condition

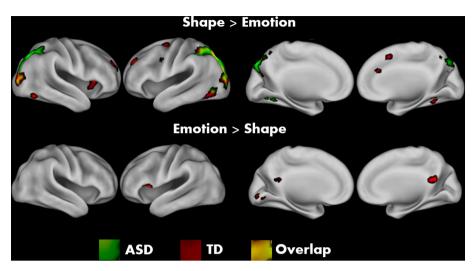


Fig. 3. Statistically significant within-group activation maps for the Shape > Emotion and Emotion > Shape contrasts for ASD and TD participants.

(relative to emotion processing). In directly comparing the groups on the Shape > Emotion contrast, increased TD activity was observed in right ACC, MPFC, and superior/middle frontal areas; left SFG; and left IPL. These regions are implicated in previous studies of attentional selection and response inhibition, particularly in the face of competing emotional stimuli (e.g., Kaping et al., 2011; Cai et al., 2014), as well as in holistic or coherence processing (Ciaramelli et al., 2007). This may reflect a greater degree of cognitive control needed to direct one's attention away from the emotional stimuli of the human figure to the non-social shape stimuli by the control group.

Presumably, ASD participants with lower mentalizing abilities did not have this same difficulty directing their attention away from the social stimuli, allowing them to complete the task more quickly. Thus, the TD group automatically processed the salient social information even when it was disadvantageous to do so, whereas the ASD group was able to ignore the social stimuli more easily in order to focus on the Shape task. The reduced automatic salience of social stimuli in children

with ASD could have important implications for ongoing experience-dependent learning (Klin et al., 2009, 2015). As these authors argue, several atypical visual attention mechanisms may cause individuals with ASD to systematically attend to social stimuli less often than TD individuals. Over the course of development. this visual attention pattern leaves individuals with ASD with a greatly reduced set of experiences from which to draw social knowledge. which may contribute to the atvoical social communication that is characteristic of the condition.

The ASD group also had significantly lower accuracy than the TD group for emotion processing, which was not predicted by either mentalizing

abilities or global/local processing bias. Despite this, the group differences in neural activation and connectivity seen in this condition were largely in regions associated with social processing. This may indicate that the RME test may not be capturing all aspects of social and emotional processing and the emotion recognition difficulties in our participants with ASD may be driven by other factors, such as a mirroring or simulation approach to mind reading (Goldman, 1998). A selfreferential processing approach to reading emotions in our task is possibly implicated by three different findings: the pattern of increased activity in ASD participants (relative to TD) during emotion processing (Emotion > Fixation); the areas of significantly increased activity during emotion processing (rather than shape) within the TD participants; and the regions showing reduced functional connectivity found in ASD participants during emotion processing.

Increased activity in ASD participants (ASD > TD) during emotion processing in regions including parts of the default mode network (DMN) (precuneus, PCC,

Table 3. Peaks of significant group differences in task-related brain activity

Group Condition	Cluster volume (mm ³)	Brain regions with local activation peaks	Hemisphere	Coordinates of peak activation		Peak <i>T</i> value	
				X	Y Z		
ASD > TD	68	Inferior Temporal Gyrus	Right	54	-60	-16	4.93
Emotion >	738	Precuneus	Left	-10	-56	16	4.43
Fixation		Precuneus	Right	6	-52	14	4.37
	263	Superior Frontal Gyrus	Left	-20	28	46	4.17
	85	Lingual Gyrus	Right	18	-40	-2	4.06
	65	Angular Gyrus	Left	-54	-54	34	3.29
ASD < TD	653	Anterior Cingulate	Right	12	42	18	4.64
Shape >		Medial Prefrontal Cortex	Right	8	48	44	3.81
Emotion		Superior Frontal Gyrus	Right	18	60	20	3.70
		Middle Frontal Gyrus	Right	22	44	30	2.97
	72	Superior Frontal Gyrus	Left	-20	58	18	3.94
	67	Inferior Parietal Lobule	Left	-50	-26	46	3.31

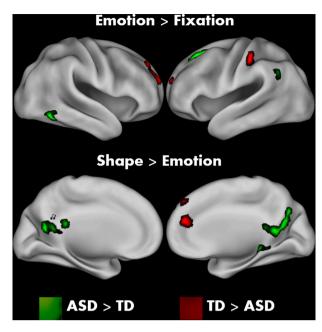


Fig. 4. Areas of statistically significant group differences in activation for the Emotion (top panel) and Shape (bottom panel) tasks contrasted with fixation and emotion respectively.

SMA and angular gyrus) (Andrews-Hanna et al., 2010) may suggest self-referential or mirroring processes. The participants with ASD also showed increased activation in the hippocampal formation and SFG; these regions have been associated with self-referential processing via autobiographical memory retrieval and channeling the DMN toward goal-based action in relevant tasks, respectively (Buckner et al., 2008; Vatansever et al., 2015). However, it is notable that self-referential activity was only seen in the Emotion > Fixation contrast and not the Emotion > Shape within-group contrast, as was seen in the TD group. Rather, the ASD group did not show any activation unique to the emotion recognition condition, possibly indicating a similar approach to both the Shape and Emotion tasks and perhaps a failure to modulate visual processing strategies with changing task demands. Moreover, while the increased ASD > TD activity in the DMN and mirroring network in the Emotion > Fixation contrast indicates at least some engagement of this system for emotion recognition, it is possible that this result is being driven, at least in part, by decreased DMN activity by the ASD group during the

Fixation condition, which is consistent with previous literature (e.g., Murdaugh et al., 2012).

Perhaps more importantly, the ASD group showed a pattern of decreased functional connectivity within the mirroring system during emotion recognition, as compared to the TD participants. Specifically, the ASD group showed decreased connectivity during the Emotion condition between IFG, which is a key part of the Mirror Neuron System (Rizzolatti et al., 2001), and FBA, a region specialized for viewing human bodies. The ASD group also showed several reduced functional connections involving the precentral gyrus, which is the location of the primary motor cortex; activation of the precentral avrus during action observation and understanding has been implicated as evidence for mirroring (Rizzolatti and Craighero, 2004). The ASD group had decreased connections between the left precentral gyrus and both the visual cortex (bilateral occipital regions) and the right pSTS, which specifically recognizes biological motion and human actions. These findings replicate those of previous studies indicating a role of mirroring recognition of emotional body postures (De Gelder et al., 2004; Kana and Travers, 2012; Libero et al., 2014) and suggest a disruption in the ASD group in a cognitive path linking visual cues of actions to emotional understanding via simulated action understanding. This may suggest the need for interventions encouraging perspective-taking and self-reflective approaches to social skill building in this population.

In addition to the aforementioned traditional social brain areas, the ASD group also showed increased activity in the right inferior temporal region, which is often implicated in common visual object recognition using feature-based strategies (e.g. Sigala, 2004). Previous literature has found that viewing other social stimuli (e.g., faces) elicited increased activation in right ITG in participants with ASD as compared to control subjects, who instead showed increased activation in the neighboring fusiform gyrus (Schultz et al., 2000). Further, the ASD group showed decreased functional connectivity to the FBA bilaterally. These findings may suggest altered recruitment of the FBA in the ASD group. This could serve as a point of convergence for the WCC and social brain theories, as the visual processing of bodies in the fusiform has been postulated to occur at a later stage of visual recognition than in the EBA (De Gelder et al., 2015). Further, while the EBA shows preferential activation for both body parts and whole bodies, FBA activity has shown

Table 4. Significant ASD < TD functional connectivity ROI pairs in the emotion condition

ROI pair	Beta		<i>t</i> -value (df = 29)	<i>p</i> -value	
	ASD TD				
L precentral: R pSTS	.03	.22	3.77	.012	
L precentral: R occipital	.14	.31	3.25	.024	
L precentral: L occipital	.11	.27	2.90	.037	
L IFG: L FBA	.11	.30	3.28	.044	
R FBA: R occipital	.03	.22	3.19	.027	

Note: p-values are FDR corrected at the seed level. L precentral = left precentral gyrus, R pSTS = right posterior superior temporal sulcus, R occipital = right inferior, middle, and superior occipital gyri, L IFG = left inferior frontal gyrus, L FBA = left fusiform body area, R FBA = right fusiform body area.

specificity to whole human bodies (Bauser and Suchan, 2015). Despite the greater attention that has been given to the fusiform gyrus, particularly the fusiform face area, in ASD, the function of this region in human body recognition in ASD has been minimally investigated. This may be an important area of future research.

There are several limitations of the present study that should be considered when evaluating its findings and implications. First, our participants' ASD diagnosis was obtained through records of previous diagnosis; we did not administer ADI and ADOS separately at our site. Regarding study design, the imaging protocol utilized a relatively short interstimulus interval with a fixed duration, which perhaps reduces the statistical precision of the experiment and could result in some true effects of participants' neural processing remaining undetected. Further, the study did not include conditions encompassing all possible combinations of processing level (global versus local) and stimulus type (shape vs. emotion), limiting the ability to state definitively which factor is driving observed behavioral differences. Finally, group differences in the Emotion condition reached significance only before correcting for multiple comparisons, likely related to a limited sample size.

CONCLUSIONS

The ASD group showed a local processing advantage. which was related to lower RME scores and reduced neural activity in areas implicated in attentional control, suggesting greater ease directing attention away from the social stimuli conveyed at the global level. Within the same perceptual experience, individuals with ASD did not modulate their perceptual style to activate an efficient neural network specialized for social information processing, particularly in terms of functional connectivity. Although the present study is limited in that the experimental design did not specifically disentangle the influence of perceptual vs. social cognitive factors, the neural regions involved and the lack of a relation to our global/local processing bias measure suggest greater support for the role of social cognition in explaining group differences in task performance.

ACKNOWLEDGMENTS

This work has been supported by the UAB College of Arts and Sciences Faculty Development Grant and the Department of Psychology Faculty Funds. The authors would like to thank Rishi Deshpande, Dr. Thomas DeRamus, and Dr. Lauren Libero for their help with this project at different stages. There are no conflicts of interest to report.

REFERENCES

- Allison T, Puce A, McCarthy G (2000) Social perception from visual cues: role of the STS region. Trends Cogn Sci 4(7):267–278.
- Andrews-Hanna JR, Reidler JS, Sepulcre J, Poulin R, Buckner RL (2010) Functional-anatomic fractionation of the brain's default network. Neuron 65(4):550–562. https://doi.org/10.1016/ji.neuron.2010.02.005.

- Bauman ML, Kemper TL (1994) Neuroanatomic observations of the brain in autism. Neurobiol Autism 612:119–145.
- Baron-Cohen S, Leslie AM, Frith U (1985) Does the autistic child have a "theory of mind"? Cognition 21:37–46.
- Baron-Cohen S, Ring HA, Wheelwright S, Bullmore ET, Brammer MJ, Simmons A, Williams SC (1999) Social intelligence in the normal and autistic brain: an fMRI study. Eur J Neurosci 11 (6):1891–1898.
- Baron-Cohen S, Wheelwright S, Spong A, Scahill V, Lawson J (2001) Are intuitive physics and intuitive psychology independent? A test with children with Asperger Syndrome. J Dev Learn Disord 5 (1):47–78.
- Barnes JL, Baron-Cohen S (2012) The big picture: storytelling ability in adults with autism spectrum conditions. J Autism Dev Disord 42 (8):1557–1565.
- Bauser DS, Suchan B (2015) Is the whole the sum of its parts? Configural processing of headless bodies in the right fusiform gyrus. Behav Brain Res 281:102–110.
- Blake R, Turner LM, Smoski MJ, Pozdol SL, Stone WL (2003) Visual recognition of biological motion is impaired in children with autism. Psychol Sci 14:151–157.
- Bolte S, Holtmann M, Poustka F, Scheurich A, Schmidt L (2007) Gestalt perception and local-global processing in high-functioning autism. J Autism Dev Disord 37(8):1493–1504.
- Buckner RL, Andrews-Hanna JR, Schacter DL (2008) The brain's default network. Ann N Y Acad Sci 1124:1–38.
- Cai W, Cannistraci CJ, Gore JC, Leung H-C (2014) Sensorimotorindependent prefrontal activity during response inhibition. Hum Brain Mapp 35(5):2119–2136. https://doi.org/10.1002/hbm.22315.
- Cardinale RC, Shih P, Fishman I, Ford LM, Müller R-A (2013) Pervasive rightward asymmetry shifts of functional networks in autism spectrum disorder. JAMA Psychiatry 70(9):975–982. https://doi.org/10.1001/jamapsychiatry.2013.382.
- Carter EJ, Williams DL, Minshew NJ, Lehman JF (2012) Is He being bad? Social and language brain networks during social judgment in children with autism. PLoS ONE 7(10). https://doi.org/10.1371/journal.pone.0047241 e47241.
- Castelli F, Frith C, Happé F, Frith U (2002) Autism, Asperger syndrome and brain mechanisms for the attribution of mental states to animated shapes. Brain 125(8):1839–1849.
- Center for Disease Control and Prevention, Baio J, Wiggins L, Christensen DL, Maenner MJ, Daniels J, Warren Z, et al. (2018) Prevalence of autism spectrum disorder among children aged 8 years—autism and developmental disabilities monitoring network, 11 Sites, United States, 2014. MMWR Surveill Summ 67(6):1.
- Ciaramelli E, Leo F, Del Viva MM, Burr DC, Ladavas E (2007) The contribution of prefrontal cortex to global perception. Exp Brain Res 181(3):427–434.
- Constantino JN, Gruber CP (2012) Social responsiveness scale (SRS). Torrance, CA: Western Psychological Services.
- Corbetta M, Shulman GL, Miezin FM, Petersen SE (1995) Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. Science 270(5237):802–805.
- Critchley HD, Daly EM, Bullmore ET, Williams SCR, Van Amelsvoort T, Robertson DM, Murphy DG (2000) The functional neuroanatomy of social behaviour: changes in cerebral blood flow when people with autistic disorder process facial expressions. Brain 123(11):2203–2212.
- De Gelder B, De Borst AW, Watson R (2015) The perception of emotion in body expressions. Wiley Interdiscip Rev Cognit Sci 6 (2):149–158.
- De Gelder B, Snyder J, Greve D, Gerard G, Hadjikhani N (2004) Fear fosters flight: a mechanism for fear contagion when perceiving emotion expressed by a whole body. PNAS 101 (47):16701–16706.
- Delmonte S, Balsters JH, McGrath J, Fitzgerald J, Brennan S, Fagan AJ, Gallagher L (2012) Social and monetary reward processing in autism spectrum disorders. Molecular Autism 3(1):7.
- Dichter GS, Felder JN, Bodfish JW (2009) Autism is characterized by dorsal anterior cingulate hyperactivation during social target

- detection. Soc Cogn Affect Neurosci 4(3):215–226. https://doi.org/10.1093/scan/nsp017.
- Downing PE, Jiang Y, Shuman M, Kanwisher N (2001) A cortical area selective for visual processing of the human body. Science 293 (5539):2470–2473.
- Fink GR, Halligan PW, Marshall JC, Frith CD, Frackowiak RSJ, Dolan RJ (1996) Where in the brain does visual attention select the forest and the trees? Nature 382(6592):626–628.
- Frith U (1989) Autism: explaining the Enigma. Blackwell.
- Frith CD, Frith U (2007) Social cognition in humans. Curr Biol 17(16): R724–R732.
- Frith U, Snowling M (1983) Reading for meaning and reading for sound in autistic and dyslexic children. J Dev Psychol 1:329–342.
- Gilbert SJ, Henson RNA, Simons JS (2010) The scale of functional specialization within human prefrontal cortex. J Neurosci 30 (4):1233–1237. https://doi.org/10.1523/JNEUROSCI.3220-09.2010.
- Goldman A (1998) The mentalizing folk. In: Sperber D, editor. Metarepresentation. London: Oxford. p. 171–196.
- Happé F, Frith U (2006) The weak coherence account: detail-focused cognitive style in autism spectrum disorders. J Autism Dev Disord 36(1):5–25.
- Happé F, Ronald A, Plomin R (2006) Time to give up on a single explanation for autism. Nat Neurosci 9(10):1218–1220.
- Hari R, Forss N, Avikainen S, Kirveskari E, Salenius S, Rizzolatti G (1998) Activation of human primary motor cortex during action observation: a neuromagnetic study. PNAS 95(25): 15061–15065.
- Hauck M, Fein D, Waterhouse L, Feinstein C (1995) Social initiations by autistic children to adults and other children. J Autism Dev Disord 25(6):579–595.
- Holm S (1979) A simple sequentially rejective multiple test procedure. Scand J Stat 6(2):65–70.
- Kaiser MD, Hudac CM, Shultz S, Lee SM, Cheung C, Berken AM, Saulnier CA (2010) Neural signatures of autism. Proc Natl Acad Sci 107(49):21223–21228.
- Kana RK, Keller TA, Cherkassky VL, Minshew NJ, Just MA (2009) Atypical frontal-posterior synchronization of Theory of Mind regions in autism during mental state attribution. Soc Neurosci 4 (2):135–152.
- Kana RK, Liu Y, Williams DL, Keller TA, Schipul SE, Minshew NJ, Just MA (2013) The local, global, and neural aspects of visuospatial processing in autism spectrum disorders. Neuropsychologia 51(14):2995–3003. https://doi.org/10.1016/ji.neuropsychologia.2013.10.013.
- Kana RK, Maximo JO, Williams DL, Keller TA, Schipul SE, Cherkassky VL, Just MA (2015) Aberrant functioning of the theory-of-mind network in children and adolescents with autism. Mol Autism 6:59. https://doi.org/10.1186/s13229-015-0052-x.
- Kana RK, Sartin EB, Stevens C, Deshpande HD, Klein C, Klinger MR, Klinger LG (2017) Neural networks underlying language and social cognition during self-other processing in autism spectrum disorders. Neuropsychologia.
- Kana RK, Travers BG (2012) Neural substrates of interpreting actions and emotions from body postures. Social Cogn Affect Neurosci 7 (4):446–456. http://doi.org.ezproxy3.lhl.uab.edu/10.1093/scan/nsr022.
- Kaping D, Vinck M, Hutchison RM, Everling S, Womelsdorf T (2011) Specific contributions of ventromedial, anterior cingulate, and lateral prefrontal cortex for attentional selection and stimulus valuation. PLoS Biol 9(12). https://doi.org/10.1371/journal.pbio.1001224 e1001224.
- Klin A, Lin DJ, Gorrindo P, Ramsay G, Jones W (2009) Two-year-olds with autism orient to nonsocial contingencies rather than biological motion. Nature 459(7244):257–261. https://doi.org/10.1038/nature07868.
- Klin A, Shultz S, Jones W (2015) Social visual engagement in infants and toddlers with autism: early developmental transitions and a model of pathogenesis. Neurosci Biobehav Rev:189–203. https://doi.org/10.1016/j.neubiorev.2014.10.006.

- Lerner MD, McPartland JC, Morris JP (2012) Multimodal emotion processing in autism spectrum disorders: an event-related potential study. Dev Cogn Neurosci 3:11–21.
- Libero LE, Stevens CE, Kana RK (2014) Attribution of emotions to body postures: an independent component analysis study of functional connectivity in autism. Hum Brain Mapp 35 (10):5204–5218.
- Libero LE, DeRamus TP, Lahti AC, Deshpande G, Kana RK (2015) Multimodal neuroimaging based classification of autism spectrum disorder using anatomical, neurochemical, and white matter correlates. Cortex 66:46–59.
- Liu Y, Cherkassky VL, Minshew NJ, Just MA (2011) Autonomy of lower-level perception from global processing in autism: evidence from brain activation and functional connectivity. Neuropsychologia 49(7):2105–2111. https://doi.org/10.1016/ji.neuropsychologia.2011.04.005.
- Maldjian JA, Laurienti PJ, Kraft RA, Burdette JH (2003) An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fmri data sets. Neuroimage 19:1233–1239.
- Manjaly ZM, Marshall JC, Stephan KE, Gurd JM, Zilles K, Fink GR (2003) In search of the hidden: an fMRI study with implications for the study of patients with autism and with acquired brain injury. Neuroimage 19(3):674–683.
- Manjaly ZM, Marshall JC, Stephan KE, Gurd JM, Zilles K, Fink GR (2005) Context–dependent interactions of left posterior inferior frontal gyrus in a local visual search task unrelated to language. Cogn Neuropsychol 22(3–4):292–305.
- Mottron L, Dawson M, Soulières I, Hubert B, Burack J (2006) Enhanced perceptual functioning in autism: an update, and eight principles of autistic perception. J Autism Dev Disord 36(1):27–43.
- Murdaugh DL, Nadendla KD, Kana RK (2014) Differential role of temporoparietal junction and medial prefrontal cortex in causal inference in autism: an independent component analysis. Neurosci Lett 568:50–55.
- Murdaugh DL, Shinkareva SV, Deshpande HR, Wang J, Pennick MR, Kana RK (2012) Differential deactivation during mentalizing and classification of autism based on default mode network connectivity. PLoS ONE 7(11). https://doi.org/10.1371/journal.pone.0050064 e50064.
- Navon D (1977) Forest before trees: the precedence of global features in visual perception. Cogn Psychol 9:353–383.
- O'Riordan MA, Plaisted KC, Driver J, Baron-Cohen S (2001) Superior visual search in autism. J Exp Psychol Hum Percept Perform 27:719–730.
- Patriquin MA, DeRamus T, Libero LE, Laird A, Kana RK (2016) Neuroanatomical and neurofunctional markers of social cognition in autism spectrum disorder. Hum Brain Mapp 37(11):3957–3978.
- Peelen MV, Downing PE (2005) Selectivity for the human body in the fusiform gyrus. J Neurophysiol 93(1):603–608.
- Pellicano E, Maybery M, Durkin K, Maley A (2006) Multiple cognitive capabilities/deficits in children with an autism spectrum disorder: "Weak" central coherence and its relationship to theory of mind and executive control. Dev Psychopathol 18(1):77.
- Pelphrey KA, Mitchell TV, McKeown MJ, Goldstein J, Allison T, McCarthy G (2003) Brain activity evoked by the perception of human walking: controlling for meaningful coherent motion. J Neurosci 23(17):6819–6825.
- Pelphrey KA, Morris JP, McCarthy G (2005) Neural basis of eye gaze processing deficits in autism. Brain 128(5):1038–1048.
- Pierce K, Conant D, Hazin R, Stoner R, Desmond J (2011) Preference for geometric patterns early in life as a risk factor for autism. Arch Gen Psychiatry 68(1):101–109.
- Plaisted K, O'Riordan M, Baron-Cohen S (1998) Enhanced discrimination of novel, highly similar stimuli by adults with autism during a perceptual learning task. J Child Psychol Psychiatry 39:765–775.
- Puce A, Allison T, Asgari M, Gore JC, McCarthy G (1996) Differential sensitivity of human visual cortex to faces, letterstrings, and textures: a functional magnetic resonance imaging study. J Neurosci 16(16):5205–5215.

- Ring HA, Baron-Cohen S, Wheelwright S, Williams SC, Brammer M, Andrew C, Bullmore ET (1999) Cerebral correlates of preserved cognitive skills in autism. Brain 122(7):1305–1315.
- Rizzolatti G, Craighero L (2004) The mirror-neuron system. Annu Rev Neurosci 27:169–192.
- Rizzolatti G, Fogassi L, Gallese V (2001) Neurophysiological mechanisms underlying the understanding and imitation of action. Nat Rev Neurosci 2(9):661–670.
- Ross PD, de Gelder B, Crabbe F, Grosbras M-H (2014) Body-selective areas in the visual cortex are less active in children than in adults. Front Hum Neurosci 8:941. https://doi.org/10.3389/fnhum.2014.00941.
- Samson F, Mottron L, Soulieres I, Zeffiro TA (2012) Enhanced visual functioning in autism: an ALE meta-analysis. Hum Brain Mapp 33 (7):1553–1581.
- Schultz RT, Gauthier I, Klin A, Fulbright RK, Anderson AW, Volkmar F, Gore JC (2000) Abnormal ventral temporal cortical activity during face discrimination among individuals with autism and Asperger syndrome. Arch Gen Psychiatry 57(4):331–340.
- Senju A (2012) Spontaneous theory of mind and its absence in autism spectrum disorders. The Neuroscientist 18(2):108–113.
- Shah A, Frith U (1983) An islet of ability in autistic children: a research note. J Child Psychol Psychiatry 24(4):613–620.
- Sigala N (2004) Visual categorization and the inferior temporal cortex. Behav Brain Res 149(1):1–7.
- Simmons DR, Robertson AE, McKay LS, Toal E, McAleer P, Pollick FE (2009) Vision in autism spectrum disorders. Vision Res 49:2705–2739.
- Spencer MD, Holt RJ, Chura LR, Suckling J, Calder AJ, Bullmore ET, Baron-Cohen S (2011) A novel functional brain imaging endophenotype of autism: the neural response to facial expression of emotion. Transl Psychiatry 1(7) e19.

- Sucksmith E, Allison C, Baron-Cohen S, Chakrabarti B, Hoekstra RA (2013) Empathy and emotion recognition in people with autism, first-degree relatives, and controls. Neuropsychologia 51 (1):98–105.
- Vatansever D, Menon DK, Manktelow AE, Sahakian BJ, Stamatakis EA (2015) Default mode network connectivity during task execution. Neuroimage 122:96–104.
- von dem Hagen EA, Stoyanova RS, Baron-Cohen S, Calder AJ (2012) Reduced functional connectivity within and between 'social'resting state networks in autism spectrum conditions. Social Cogn Affect Neurosci 8(6):694–701.
- Wandell BA, Brewer AA, Dougherty RF (2005) Visual field map clusters in human cortex. Philos Trans Royal Soc B: Biol Sci 360 (1456):693–707. https://doi.org/10.1098/rstb.2005.1628.
- Wang S, Jiang M, Duchesne XM, Laugeson EA, Kennedy DP, Adolphs R, Zhao Q (2015) Atypical visual saliency in autism spectrum disorder quantified through model-based eye tracking. Neuron 88(3):604–616.
- Wechsler D (1999) Wechsler abbreviated scale of intelligence (WASI). San Antonio, TX: Psychological Corporation.
- Weigelt S, Koldewyn K, Kanwisher N (2011) Face identity recognition in autism spectrum disorders: a review of behavioral studies. Neurosci Biobehav Rev 36(3):1060–1084.
- Weissman DH, Woldorff MG (2005) Hemispheric asymmetries for different components of global/local attention occur in distinct temporo-parietal loci. Cereb Cortex 15(6):870–876.
- Whitfield-Gabrieli S, Nieto-Castanon A (2012) Conn: a functional connectivity toolbox for correlated and anticorrelated brain networks. Brain Connect. https://doi.org/10.1089/brain.2012.0073.

(Received 24 April 2018, Accepted 30 October 2018) (Available online 10 November 2018)