J Neural Transm (2008) 115: 545–552
DOI 10.1007/s00702-007-0850-1
Printed in The Netherlands

Journal of Neural Transmission

An fMRI-study of locally oriented perception in autism: altered early visual processing of the block design test

S. Bölte[1], **D. Hubl**[2], **T. Dierks**[2], **M. Holtmann**[1], **F. Poustka**[1]

[1] Department of Child and Adolescent Psychiatry, J. W. Goethe-University, Frankfurt/Main, Germany
[2] Department of Psychiatric Neurophysiology, University Hospital of Clinical Psychiatry, Bern, Switzerland

Received 18 April 2007; Accepted 23 October 2007; Published online 26 February 2008

Summary. Autism has been associated with enhanced local processing on visual tasks. Originally, this was based on findings that individuals with autism exhibited peak performance on the block design test (BDT) from the Wechsler Intelligence Scales. In autism, the neurofunctional correlates of local bias on this test have not yet been established, although there is evidence of alterations in the early visual cortex. Functional MRI was used to analyze hemodynamic responses in the striate and extrastriate visual cortex during BDT performance and a color counting control task in subjects with autism compared to healthy controls. In autism, BDT processing was accompanied by low blood oxygenation level-dependent signal changes in the right ventral quadrant of V2. Findings indicate that, in autism, locally oriented processing of the BDT is associated with altered responses of angle and grating-selective neurons, that contribute to shape representation, figure-ground, and gestalt organization. The findings favor a low-level explanation of BDT performance in autism.

Keywords: Pervasive developmental disorders; brain; neurobiology, fMRI; visual processing; weak central coherence; neuropsychology

Introduction

Alterations in visual perception are cognitive features of autism-spectrum conditions (Dakin and Frith 2005). A multitude of research has identified superior detection of fine detail on spatial or visual search tasks. Various models have been proposed to explain increased piecemeal processing (e.g., Plaisted 2001; Happé and Frith 2006; Mottron et al. 2006), all of them suggesting a default for locally oriented processing in autism. Human information processing in typical development is primarily focused on achieving higher-order holistic global experiences.

Correspondence: Sven Bölte, Klinik für Psychiatrie und Psychotherapie des Kindes- und Jugendalters, Deutschordenstr. 50, 60528 Frankfurt/Main, Germany
e-mail: boelte@em.uni-frankfurt.de

One of the first observations that generated suspicion of local bias in autism was peak performance on the block design test (BDT) from the Wechsler Intelligence Scales. In this task, the subject is presented with four or nine red and white blocks, depending on the item, and is asked to construct replicas of stimuli arranged by the examiner or shown in smaller scale in a two-dimensional picture booklet. Each block has two white sides, two red sides, and two half-red half-white sides with the colors divided diagonally. For successful completion of the BDT, subjects must resist the drive to perceive a global stimulus, in favor of seeing the composition of single blocks. Today, it is well known that individuals with autism show absolute or relative peaks on the BDT (Lockyer and Rutter 1969; Tymchuk et al. 1977; Shah and Frith 1983, 1993; Asarnow et al. 1987; Lincoln et al. 1988; Szatmari et al. 1990; Allen et al. 1991; Happé 1994; Rühl et al. 1995; Siegel et al. 1996). In addition to these results, Caron et al. (2006) examined the performance of people with autism with and without visuospatial peak, as well as control individuals with and without visuospatial peak, on a modified BDT at various levels of perceptual cohesiveness. In subjects with autism, those with and without a BDT peak presented with reduced detrimental effects of growing perceptual coherence compared with the BDT-matched control groups. Thus, superior performance on the BDT is not necessary to infer local bias in autism. To the contrary, locally oriented processing of the BDT seems equally sensitive and specific to autism.

The neurobiological correlates of the BDT in autism are largely unknown. Most published data on brain functioning associated with BDT performance comes from clin-

ical studies in subjects with brain lesions or neurological syndromes. Chase et al. (1984) compared local cerebral glucose metabolism during performance on the Wechsler Adult Intelligence Scale scores in patients with Alzheimer's disease and healthy subjects. They found an association between performance on the BDT and increased glucose metabolism in the right posteroparietal regions. Studies in patients with lateralized lesion confirm the correlation between BDT performance and right hemisphere parietal regions (Warrington et al. 1986; Wilde et al. 2000). In addition, broken configuration errors (missing blocks) are documented for right hemisphere focus epilepsies (Zipf-Williams et al. 2000). However, observations in split-brain patients make it clear that both hemispheres contribute to BDT performance (Geschwind 1979). Mild to moderate traumatic brain injury is not necessarily connected to failure on the BDT (Axelrod et al. 2001). In summary, these studies indicate that a broad range of neurological conditions can be associated with poor results on the BDT. In particular, right hemisphere functions in the parietal lobe are likely to be crucial for BDT processing.

In a previous study, we examined the functional anatomy of face processing and visual search in autism versus typical development, using a whole brain approach to determine the representation of different classes of objects in higher-order visual areas (Hubl et al. 2003). Herein, an adaptation of the BDT served as the visual search task. During BDT performance, the control group exhibited significantly higher activation in the right fusiform gyrus, inferior parietal lobe, left superior parietal lobe, and bilateral precentral gyrus than did the autism group. This indicates that in autism versus typical development there exist different visual processing strategies for the BDT in later regions of the visual system. However, activation differences in higher-order areas may not be sufficient to explain altered performance of the BDT. We also observed global activation differences in the occipital cortex, i.e., early visual fields. No in-depth analysis of the primary visual area was computed.

Other spatial tasks that have shown local bias in autism also yielded altered activation in occipital regions. During processing of the embedded figures test (EFT) in autism, Ring et al. (1999) found higher activation in the right occipital gyrus and lower activation in the left occipital gyrus. Manjaly et al. (2007) observed specific activations in the right primary visual cortex and bilateral extrastriate areas in a mixed autism/Asperger syndrome sample. During EFT processing in parents of individuals with Asperger syndrome, Baron-Cohen et al. (2006) reported less bilateral activity in the extrastriate cortex. Interestingly, altered activation patterns in early regions of the visual cortex in autism are reported for quite a wide range of paradigms, not exclusively visual search tasks. There is also evidence for attention shifting tasks (Belmonte and Yurgelun-Todd 2003), learning tasks (Hazlett et al. 2006), as well as social and affective tasks (Critchley et al. 2000; Castelli et al. 2002; Hall et al. 2003).

The results of these imaging studies, together with evidence of an apparent absence of a global visual processing deficit in autism (e.g., Plaisted et al. 1999; Iarocci et al. 2006), have led some authors to suggest a model of enhanced perceptual functioning for autism (Mottron et al. 2006), which also applies to BDT processing (Caron et al. 2006). According to this model, enhanced perceptual functioning and local bias in autism are likely to be associated with overfunctioning parvocellular pathways in V1. Bertone et al. (2005) showed that, compared to typical development, individuals with autism were superior in detecting the orientation of simple first order gratings, processed in V1, but inferior in the detection of second order gratings. The latter was interpreted as either a result of diminished top-down modulation from higher order cognitive regions, or mandatory feedback between V1, V2 and V3.

In conclusion, even though there is good evidence that in autism locally oriented visual processing is associated with early perceptual functions, no study has examined in detail the differential responses in the primary and extra-striate cortical areas. Findings from whole brain analyses cannot provide sufficient insight into activation patterns in early visual fields. The objective of this study was therefore to conduct a selective comparison of brain activation during BDT processing in autism and typical development. We expected to see altered processing of the BDT at an early stage in the visual cortex. The current study is a theory-driven in depth analysis of fMRI-data collected during the same scans that led to our previous paper (Hubl et al. 2003).

Material and methods

Participants

The sample comprised seven high-functioning adolescent and adult individuals with idiopathic autism, and seven healthy control subjects. Subjects were male, medication-free, and did not differ with regard to handedness [$\chi^2(1) = 1.1$; $p = 0.41$]. The groups did not differ significantly in age [$t(12) = 0.00$, $p = 1.00$] or nonverbal IQ [$t(12) = 1.9$, $p = 0.09$], as assessed by the Standard Progressive Raven Matrices (SPM, Raven 1996). However, as groups were not matched, all subsequent group comparisons were analyzed for IQ and age using ANCOVAs. Mean age in the autism group was 27.7 ($SD = 7.8$) years and mean nonverbal IQ was 98.4 ($SD = 17.4$). In the control group the average age was 25.3 ($SD = 6.9$) years and average nonverbal IQ was 111.6 ($SD = 9.3$). The SPM was chosen to control for IQ for four reasons. First, it assesses abstract reasoning, a core feature of IQ.

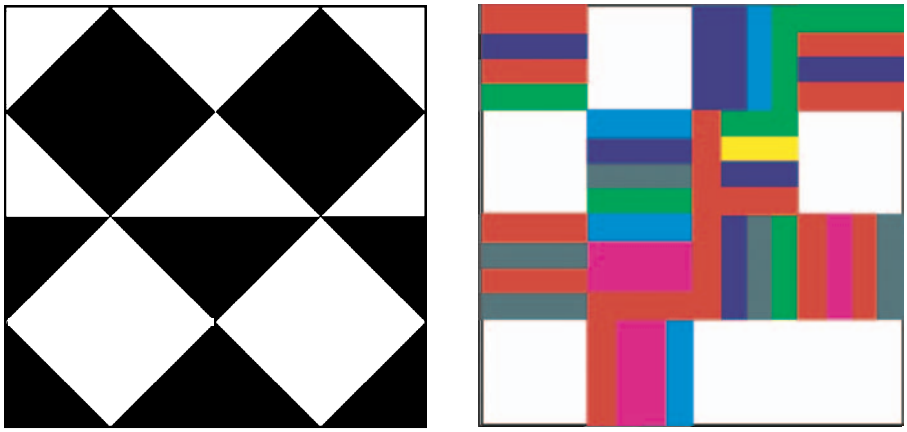


Fig. 1. Examples of 16 block stimuli from the BDT scanner version (**a**) and the color counting control task (**b**)

Second, the SPM is the most complex single test of intelligence (Snow et al. 1984). Third, using a measure of general IQ other than the Wechsler avoids confounds with the BDT. Fourth, and most importantly, the Raven's matrices are fair in autism, unlikely to repress true intellectual capacities (Dawson et al. 2007). Nevertheless, we had complete Wechsler IQ test results available in the autism sample. Mean Wechsler full scale IQ was 98.0 ($SD = 19.2$), with the highest mean scaled scores on object assembly (12.6) and information (12.6), and the lowest scores on comprehension (8.4) and picture arrangement (7.3).

Written informed consent was obtained from all participants and the study was approved by the local ethics committee of the University of Frankfurt/Main. Participants with autism were recruited within the clinic at the Department of Child and Adolescent Psychiatry at the University of Frankfurt/Main or within an ongoing international project on the molecular genetics of autism (www.well.ox.ac.uk/~maestrin/iat.html). Participants fulfilled the ICD-10 research criteria as well as the diagnostic algorithm thresholds for autism in the Autism Diagnostic Interview-Revised (Lord et al. 1994) and the Autism Diagnostic Observation Schedule module 3 or 4 (Lord et al. 2001). None of the members of the control group showed clinically relevant psychopathology on the Youth Self Report (Döpfner et al. 1995) or Young Adult Self-Report (Achenbach 1997), or suffered from any medical disorder.

Material

The BDT from the Wechsler Adult Intelligence Scales-Revised (WAIS-R; Wechsler 1981) is a time-critical three-dimensional visuospatial cognitive task introduced earlier in detail. Twenty-five black and white two-dimensional pictures were presented in fMRI. The pictures included nine originals from the WAIS-R booklet as well as 18 new stimuli. There were 13 four-block, 9 nine-block and 3 sixteen-block pictures (see Fig. 1a). In the scanner version of BDT, the subjects were asked to search for black triangles, indicative of a single block, and name their number as quickly as possible. The crucial aspect for successful performance on the standard BDT is the ability to break down the visual gestalt in single elements. This quality was included in the scanner version of the BDT. As the standard version of the BDT was always administered prior to the scanner version, the probands were familiar with the concept of the BDT and had no difficulty understanding the different formulation of the scanner version.

A color counting control task (CCT) was constructed comprising 25 pictures. The stimuli were composed of colored and white blocks (see Fig. 1b), composed of horizontal or vertical stripes of a maximum of eight different colors. As for the BDT scanner version, there were 13 four-block, 9 nine-block and 3 sixteen-block pictures. Participants had to count and name the number of different colors shown in each stimulus object as quickly as possible.

For all participants, data on the standard BDT was assessed prior to scanning and transformed into scaled scores. Additionally, outside scanner behavioral data on the BDT form and the color counting task were collected. The number of correct answers and the reaction time for both tasks were gathered as dependent behavioral measures.

FMRI procedure

The imaging methodology in this study is identical with the procedure described in Hubl et al. (2003). A 1.5-T whole-body MRI system (Magnetom Vision, Siemens Medical Systems, Erlangen, Germany) was used for the investigation. Fifteen axial slices, covering the whole brain, were acquired for functional imaging. A high-resolution three-dimensional whole brain MPRAGE scan was collected for each subject. The fMRI trial followed a classical block design. It consisted of 16 blocks (total duration: 8 min 32 sec): eight activation blocks (four BDT and four CCT blocks) were alternated with eight resting blocks. Each task was indicated using a one-word cue at the beginning of each block to ensure attention shift. Participants pressed a button with the right index finger when they completed each activation stimuli (counting triangles or colours).

The objective of the fMRI analysis was to determine the contrast between BDT, CCT, and rest in the visual areas V1, V2v, V2d, V3, V3a, V4, V5 and VP. First, GLM statistics (all subjects, all runs) were used to identify regions with $p < 0.05$ and served as the basis for investigating areas of significant activation. Then, regions of interest in the visual cortex were determined manually according to the coordinates provided by Hasnain et al. (1998), with detection accuracy between 73 and 100%, with a median of 100%. Accuracy was 100% for V1, V2d, V2v, VP, V3, V3a and V4 in the right hemisphere, and 100% for V1, V2d, V2v and VP in the left hemisphere.

For data analysis, registration, and visualization, the fMRI software package BrainVoyager 2000® (BrainInnovation, Maastricht, Netherlands) was used. After pre-processing, the two-D statistical maps were superimposed on the original functional scans and incorporated into the three-D anatomical data sets through interpolation of the functional voxels to the same resolution as the anatomical voxels. For each region of the visual pathway, a time activity curve in percent signal change was calculated. Mean BOLD time course (cluster size: $3 \times 3 \times 3$ voxel) for all visual areas were taken independent of the level of significance and formed the dependent imaging variable for the statistical analysis.

Statistics

All inference statistics were computed using SPSS/Win.11.5. Separate simultaneous ANCOVAs were calculated to determine between-group effects regarding each of the dependent measures on the imaging and behav-

ioral level: average BOLD responses in V1, V2v, V2d, V3, V3a, V4, V5 and VP bilaterally, number of correct answers, reaction time (BDT scanner version) and scaled scores (standard BDT). A fixed effects analysis was chosen in light of the limited sample size. In all analyses, group (autism versus control) was inserted as predictor, and age and IQ were covariates. An alpha-level of 0.05 was adopted for all statistics. Eta squared (η^2) was computed for group comparisons to provide effect sizes in terms of explained variance. Correlations between dependent measures were computed using Pearson's coefficient.

Results

Behavioral data

In our sample, the performance of the autism group and control group were comparable on the standard BDT [$F(1,10) = 0.38$, $p = 0.55$, $\eta^2 = 0.04$]. The mean scaled score was 10.8 ($SD = 3.6$) in the autism group and 11.9 ($SD = 1.5$) in the control group. Moreover, the number of correct answers [$F(1,10) = 2.8$, $p = 0.12$, $\eta^2 = 0.22$] and the reaction time [$F(1,10) = 1.3$, $p = 0.28$, $\eta^2 = 0.12$] in the BDT scanner version did not differ significantly between the autism and the control group. The mean of correct responses was 18.6 ($SD = 2.7$) in the autism group and 21.5 ($SD = 3.1$) in the control group. The mean reaction time was 9.7 sec ($SD = 3.3$) in the autism sample and 5.9 sec ($SD = 1.8$) in the control group. Satisfactory relations were found between the standard version of the BDT and its adaptation for the scanner. In the total sample, the number of correct answers on the BDT scanner version correlated ($r = 0.42$) with standard BDT performance. Reaction time on the BDT scanner version correlated ($r = -0.44$) with standard BDT.

The behavioral data acquired for the CCT showed no differences between the autism and control group regarding the number of correct answers [$F(1,10) = 0.28$, $p = 0.60$, $\eta^2 = 0.03$] or the reaction time [$F(1,10) = 0.60$, $p = 0.45$, $\eta^2 = 0.06$]. The mean of correct responses was 21.2 ($SD = 3.0$) in the autism group and 22.5 ($SD = 1.6$) in the control group. The mean reaction time was 8.2 sec ($SD = 3.3$) in the autism sample and 4.5 sec ($SD = 1.9$) for controls.

FMRI data

ANCOVA statistics revealed significant between-group effects for V2v and VP during BDT processing, both belonging to the ventral stream located in the right hemisphere (Fig. 2). Furthermore, the autism group and the control group showed significant BOLD response differences in VP on the CCT. No differences in the left hemisphere or in visual regions of the dorsal stream were identified.

In V2v, the average BOLD signal change compared to the rest condition was 0.14% ($SD = 1.25$) for the BDT in the autism group, and 1.18% ($SD = 0.57$) in the control group [$F(1,10) = 6.6$, $p = 0.03$, $\eta^2 = 0.40$]. Regarding VP,

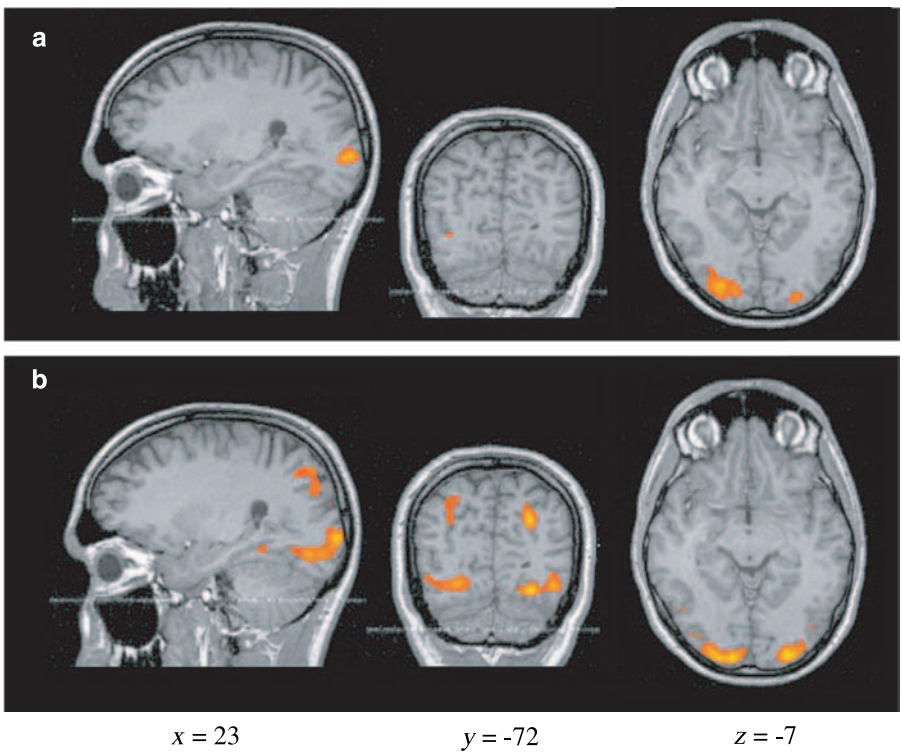
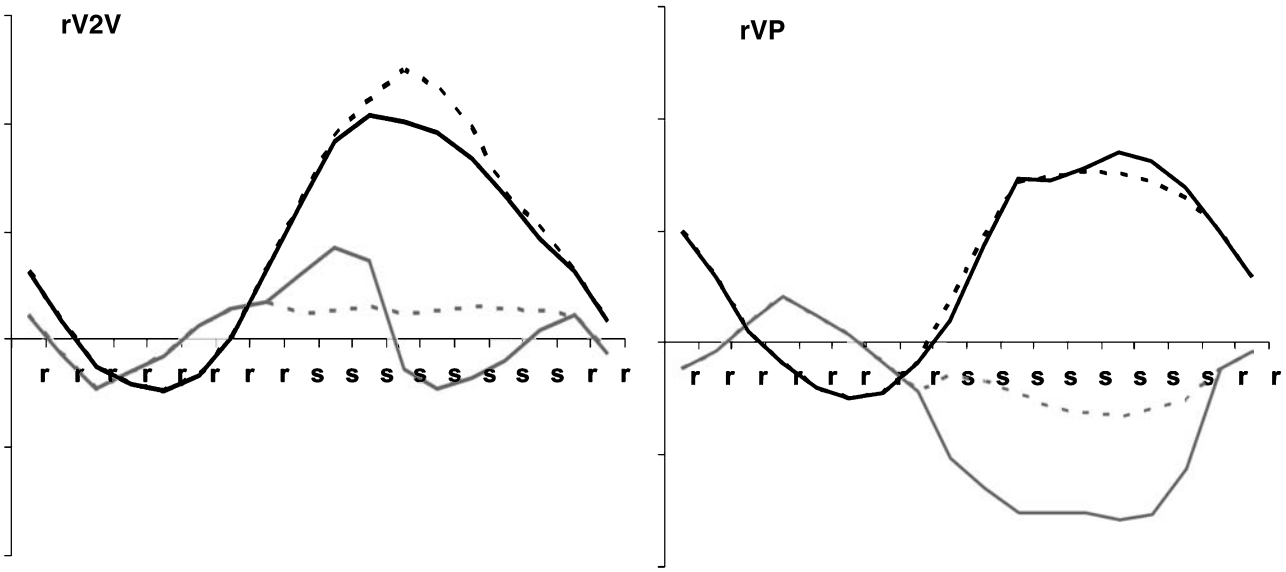


Fig. 2. Contrast maps ($p = 0.05$) for BOLD signal responses in the early and intermediate visual cortex during BDT processing in the autism (**a**) and control group (**b**)



Note: *y*-axis = % BOLD signal change, *x*-axis = rest (r) and stimulus (s), autism BDT (—); autism CCT (----), control BDT (—), control CCT (----)

Fig. 3. Hemodynamic response functions in the right V2v and right VP during BDT and CCT in the autism and the normative control sample

the average BOLD signal change compared to the rest condition was −0.43% ($SD = 1.1$) for the BDT in the autism group, and 0.70% ($SD = 0.69$) in the control group [$F(1,10) = 5.0$, $p = 0.048$, $\eta^2 = 0.33$]. In the same region, the BOLD response was −0.91% ($SD = 1.3$) for the CCT in the autism group, and 0.85% ($SD = 0.57$) in the control group [$F(1,10) = 14.1$, $p = 0.004$, $\eta^2 = 0.59$]. A range of other regions, e.g., V3a, with descriptively higher responses in the autism group during the BDT, fell short of statistical significance. Hemodynamic response functions in the right V2v and VP during BDT and CCT in the autism and normative control sample are shown in Fig. 3. For right V2v, the trajectories exhibit expected functions with lower BOLD signal change in the autism sample for the BDT. Nevertheless, despite being lower, BOLD signal change also exhibited an untypical progression in the right VP in autism.

Discussion

In typical development, visual perception is coined by the drive for global processing. That is, grouping single elements into coherent meaningful wholes, in order to limit descriptive complexity. The default perception of people with autism-spectrum conditions might be characterized by the opposite, referred to as local processing. The BDT is a well-known task for demonstrating locally oriented visual processing, independent of performance level (Caron et al. 2006). It has been postulated that local perception bias in autism is an aspect of enhanced perceptual functioning (Motton et al. 2006), which itself is presumed to be associated with altered functioning in the visual cortex, particularly V1. However, this hypothesis has not been examined closely using functional imaging. We investigated the neural correlates of BDT processing in the visual cortex in autism using fMRI. Lower hemodynamic responses to the BDT in the right V2v (V2 ventral) and VP (ventral posterior area) were found. Significant activation differences in the right VP also appeared on a color counting control task, and BOLD signal trajectories were atypical. Thus the finding for V2v must be viewed as the pivotal one in this study. Response differences in VP may not be sufficiently specific to the particular cognitive demands of the BDT and the irregular hemodynamic function may limit valid interpretation. However, VP topographically lies immediately adjacent to V2 with reciprocal connections between these regions (Newsome et al. 1986). The properties of the cells in VP suggest that its role in form and color vision is similar to the V4 color center (Burkhalter and Van Essen 1986).

V2 is the second retinotopic region in the visual cortex, with a one-to-one mapping of visual space in cortical coordinates. It is the first area of visual association and has strong connections to V3, V4 and V5 as well as connection to V1. V2 neurons fire in response to orientation, color, stereoscopic disparity and motion (Gegenfurtner et al. 1996),

and despite the prominent location of V2 in the visual hierarchy, its function was rather poorly understood until recently (Boynton and Hegdé 2004). However, recent research has consistently shown that V2 neurons are primarily selective for angles, junctions and grating stimuli, which points to a major role of this area in shape representation, figure-ground and gestalt processing (Ito and Komatsu 2004; Qiu and von der Heydt 2005; Hedge and Van Essen 2006). The significance of V2 for other attributes, such as color (Wang et al. 2007), might have been overestimated in the past.

Reduced V2v activation in autism during BDT performance could be explained in several ways, which do not exclude one another. First, as BOLD signal change is associated with task difficulty (Carpenter et al. 1999), our findings may point to decreased efforts in the autism group to recognize and visually segment the stimuli of the BDT, despite comparable overall performance. Second, our findings may indicate a reduced drive for gestalt perception, which has been reported in behavioral studies (Brosnan et al. 2004; Bölte et al. 2007). Third, diminished voluntary top-down attentional modulation reducing global processing in favor of bottom-up salience might result in such V2 activations (Serences and Yantis 2006). Fourth, regional mandatory feedback betweenV2 and neighboring early visual regions (V1 and V3) could also be altered (Bertone et al. 2005). Fifth, in general, the findings for V2v could be a sign of reorganized visual perception in terms of changes in hierarchical processing of stimuli from the retina to higher-order cognitive areas (Lerner et al. 2001). Hence, altered perception could have its origins even earlier in the visual system (e.g., parvocellular pathways), as suggested by the enhanced perception model (Mottron et al. 2006).

The fundamentals of visually coherent perception are generally still poorly understood. Murray et al. (2004) suggest that feedback from higher visual areas reduce lower areas to simplify the description of an image. Bird et al. (2006) found a lack of attentional modulation for social as well as non-social behavior in autism-spectrum disorders. Furthermore, Villalobos et al. (2005) report reduced functional connectivity between V1 and the inferior prefrontal cortex associated with visuomotor performance in autism. Speculatively, these studies could be useful in interpreting our findings. The general evidence for weakened top-down processing in autism owes to attentional modulation, lack of connectivity, lack of activation differences in V1, and, in this study, diminished activation in V2. This may suggest that the BDT is solved on an inferior level in autism. Thus, conservatively, our data favors a low-level explanation for BDT processing in autism.

There are some limitations to our current study. The most prominent is the small sample size. Our findings should not be overly generalized, but regarded as relatively specific to ours, and comparable, samples. Our sample was restricted regarding sex and age; it did not include females and children, only male adolescents and adults. The published coordinates used to define the early visual areas are good approximations, although the gold standard is to map retinotopic areas in each individual as the basis for excluding a bias due to interindividual variations in morphology. Finally, no eye-tracking device was used in the current study, presenting a possible uncontrolled confound (Brenner et al. 2006). Nevertheless, the fact that activation differences between groups in the visual cortex are generally small argue against such a bias. If there had been significant or systematic eye movement differences, one would expect rather broad activation differences throughout many fields of the visual cortex (Kimmig et al. 2001), especially in V1 and along the dorsal stream. No differential influence of eye movements on V2v is known. Overall, one would expect differences within the dorsal, not ventral stream, associated with eye movement differences.

In summary, the present study is the first to explore the neurobiological correlates of the BDT in autism, which is known to be a reliable task of locally oriented processing (Caron et al. 2006). In early and intermediate regions of the visual system, we found diminished response in the right V2v, favoring a low-level explanation of BDT performance in autism.

References

Achenbach TM (1997) Young adult self report (YASR). Arbeitsgruppe Kinder-, Jugend- und Familiendiagnostik (KJFD), Cologne

Allen MH, Lincoln AJ, Kaufman AS (1991) Sequential and simultaneous processing abilities of high-functioning autistic and language-impaired children. J Autism Dev Disord 21: 483–502

Asarnow RF, Tanguay PE, Bott L, Freeman BJ (1987) Patterns of intellectual functioning in non-retarded autistic and schizophrenic children. J Child Psychol Psychiatr 28: 273–280

Axelrod BN, Fichtenberg NL, Liethen PC, Czarnota MA, Stucky K (2001) Performance characteristics of postacute traumatic brain injury patients on the WAIS-III and WMS-III. Clin Neuropsychol 15: 516–520

Baron-Cohen S, Ring H, Chitnis X, Wheelwright S, Gregory L, Williams S, Brammer M, Bullmore E (2006) fMRI of parents of children with Asperger syndrome: a pilot study. Brain Cogn 61: 122–130

Belmonte MK, Yurgelun-Todd DA (2003) Functional anatomy of impaired selective attention and compensatory processing in autism. Brain Res Cogn Brain Res 17: 651–664

Bertone A, Mottron L, Jelenic P, Faubert J (2005) Enhanced and diminished visuospatial information processing in autism depends on stimulus complexity. Brain 128: 2430–2441

Bird G, Catmur C, Silani G, Frith C, Frith U (2006) Attention does not modulate neural responses to social stimuli in autism spectrum disorders. Neuroimage 31: 1614–1624

Bölte S, Scheurich A, Holtmann M, Schmidt L, Poustka F (2007) Gestalt processing and weak central coherence in high-functioning autism. J Autism Dev Disord 37: 1493–1504 [Epub 2006 Oct 7]

Boynton GM, Hegdé J (2004) Visual cortex: the continuing puzzle of area V2. Curr Biol 14: R523–R524

Brenner LA, Turner KC, Müller RA (2006) Eye movement and visual search: are there elementary abnormalities in autism? J Autism Dev Disord, Nov 21 [Epub ahead of print]

Brosnan MJ, Scott FJ, Fox S, Pye J (2004) Gestalt processing in autism: failure to process perceptual relationships and the implications for contextual understanding. J Child Psychol Psychiatr 45: 459–469

Burkhalter A, Van Essen DC (1986) Processing of color, form and disparity information in visual areas VP and V2 of ventral extrastriate cortex in the macaque monkey. J Neurosci 6: 2327–2351

Caron MJ, Mottron L, Berthiaume C, Dawson M (2006) Cognitive mechanisms, specificity and neural underpinnings of visuospatial peaks in autism. Brain 129: 1789–1802

Carpenter PA, Just MA, Keller TA, Eddy W, Thulborn K (1999) Graded functional activation in the visuospatial system with the amount of task demand. J Cogn Neurosci 11: 9–24

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: 1839–1849

Chase TN, Fedio P, Foster NL, Brooks R, Di Chiro G, Mans IL (1984) Wechsler Adult Intelligence Scale performance. Cortical localization by fluorodeoxyglucose F 18-positron emission tomography. Arch Neurol 41: 1244–1247

Critchley HD, Daly EM, Bullmore ET, Williams SC, Van Amelsvoort T, Robertson DM, Rowe A, Phillips M, McAlonan G, Howlin P, Murphy DG (2000) The functional neuroanatomy of social behaviour: changes in cerebral blood flow when people with autistic disorder process facial expressions. Brain 123: 2203–2212

Dakin S, Frith U (2005) Vagaries of visual perception in autism. Neuron 48: 497–507

Dawson M, Soulières I, Gernsbacher MA, Mottron L (2007) The level and nature of autistic intelligence. Psychol Sci 18: 657–662

Döpfner M, Berner W, Lehmkuhl G (1995) Reliabilität und faktorielle validität des youth Self-Report und der child behavior checklist bei einer klinischen stichprobe. Diagnostica 41: 221–244

Gegenfurtner KR, Kiper DC, Fenstemaker SB (1996) Processing of color, form, motion in macaque area V2. Vis Neurosci 13: 161–172

Geschwind N (1979) Specializations of the human brain. Sci Am 241: 180–199

Hall GB, Szechtman H, Nahmias C (2003) Enhanced salience and emotion recognition in Autism: a PET study. Am J Psychiatry 160: 1439–1441

Happé FG (1994) Wechsler IQ profile and theory of mind in autism: a research note. J Child Psychol Psychiatr 35: 1461–1471

Happé FG, Frith U (2006) The weak central coherence account: detail-focused style in autism spectrum disorders. J Autism Dev Disord 36: 5–25

Hasnain MK, Fox PT, Woldorff MG (1998) Intersubject variability of functional areas in the human visual cortex. Hum Brain Mapp 6: 301–315

Hazlett EA, Buchsbaum MS, Hsieh P, Haznedar MM, Platholi J, LiCalzi EM, Cartwright C, Hollander E (2006) Regional glucose metabolism within cortical Brodmann areas in healthy individuals and autistic patients. Cereb Cortex, Jun 19 [Epub ahead of print]

Hegde J, Van Essen DC (2006) A Comparative Study of Shape Representation in Macaque Visual Areas V2 and V4. Cereb Cortex, Jun 19 [Epub ahead of print]

Hubl D, Bölte S, Feineis-Matthews S, Lanfermann H, Federspiel A, Strik W, Poustka F, Dierks T (2003) Functional imbalance of visual pathway indicates alternative face processing strategies in autism. Neurology 61: 1232–1237

Iarocci G, Burack JA, Shore DI, Mottron L, Enns JT (2006) Global-local visual processing in high functioning children with autism: structural vs. implicit task biases. J Autism Dev Disord 36: 117–129

Ito M, Komatsu H (2004) Representation of angles embedded within contour stimuli in area V2 of macaque monkeys. J Neurosci 24: 3313–3324

Kimmig H, Greenlee MW, Gondan M, Schira M, Kassubek J, Mergner T (2001) Relationship between saccadic eye movements and cortical activity as measured by fMRI: quantitative and qualitative aspects. Exp Brain Res 141: 184–194

Lerner Y, Hendler T, Ben-Bashat D, Harel M, Malach R (2001) A hierarchical axis of object processing stages in the human visual cortex. Cereb Cortex 11: 287–297

Lincoln AJ, Courchesne E, Kilman BA, Elmasian R, Allen M (1988) A study of intellectual abilities in high-functioning people with autism. J Autism Dev Disord 18: 505–524

Lockyer L, Rutter M (1969) A five- to fifteen-year follow-up study of infantile psychosis. Br J Psychiatry 115: 865–882

Lord C, Rutter M, Le Couteur A (1994) Autism diagnostic interview-revised: a revised version of a diagnostic interview for caregivers of individuals with possible pervasive developmental disorders. J Autism Dev Disord 24: 659–685

Lord C, Rutter M, DiLavore P, Risi S (2001) Autism diagnostic observation schedule (ADOS). Los Angeles, CA: Western Psychological Services

Manjaly ZM, Bruning N, Neufang S, Stephan KE, Brieber S, Marshall JC, Kamp-Becker I, Remschmidt H, Herpertz-Dahlmann B, Konrad K, Fink GR (2007) Neurophysiological correlates of relatively enhanced local visual search in autistic adolescents. Neuroimage 35: 283–291

Mottron L, Dawson M, Soulières I, Hubert B, Burack J (2006) Enhanced perceptual functioning in autism: an update, eight principles of autistic perception. J Autism Dev Disord 36: 27–43

Murray SO, Schrater P, Kersten D (2004) Perceptual grouping and the interactions between visual cortical areas. Neural Netw 17: 695–705

Newsome WT, Maunsell JH, Van Essen DC (1986) Ventral posterior visual area of the macaque: visual topography and areal boundaries. J Comp Neurol 252: 139–153

Plaisted K, Swettenham J, Rees L (1999) Children with autism show local precedence in a divided attention task and global precedence in a selective attention task. J Child Psychol Psychiatr 40: 733–742

Plaisted K (2001) Reduced generalization in autism: an alternative to weak central coherence. In: Burack JA, Charman A, Yirmiya N, Zelazo PR (eds) The development of autism: perspectives from theory and research. Mahwah, NJ, Erlbaum, pp 149–169

Qiu FT, von der Heydt R (2005) Figure and ground in the visual cortex: V2 combines stereoscopic cues with gestalt rules. Neuron 47: 155–166

Raven JC (1996) Progressive matrices: a perceptual test of intelligence. individual form. Oxford, UK: Oxford Psychologists Press

Ring HA, Baron-Cohen S, Wheelwright S, Williams SC, Brammer M, Andrew C, Bullmore ET (1999) Cerebral correlates of preserved cognitive skills in autism: a functional MRT study of embedded figures task performance. Brain 122: 1305–1315

Rühl D, Werner K, Poustka F (1995) Untersuchungen zur Intelligenzstruktur autistischer Personen. Z Kinder Jugendpsychiatr 23: 95–103

Serences JT, Yantis S (2006) Selective visual attention and perceptual coherence. Trends Cogn Sci 10: 38–45

Shah A, Frith U (1983) An islet of ability in autistic children: a research note. J Child Psychol Psychiatr 24: 613–620

Shah A, Frith U (1993) Why do autistic individuals show superior performance on the block design task? J Child Psychol Psychiatr 34: 1351–1364

Siegel DJ, Minshew NJ, Goldstein G (1996) Wechsler IQ profiles in diagnosis of high-functioning autism. J Autism Dev Disord 26: 389–406

Snow RE, Kyllonen PC, Marshalek B (1984) The topography of ability and learning correlations. In: Sternberg RJ (ed) Advances in the psychology of human intelligence, vol. 2. Hillsdale, NJ, Erlbaum, pp 47–103

Szatmari P, Tuff L, Finlayson MA, Bartolucci G (1990) Asperger's syndrome and autism: neurocognitive aspects. J Am Acad Child Adolesc Psychiatry 29: 130–136

Tymchuk AJ, Simmons JQ, Neafsey S (1977) Intellectual characteristics of adolescent childhood psychotics with high verbal ability. J Ment Defic Res 21: 133–138

Villalobos ME, Mizuno A, Dahl BC, Kemmotsu N, Müller RA (2005) Reduced functional connectivity between V1 and inferior frontal cortex associated with visuomotor performance in autism. Neuroimage 25: 916–925

Wang Y, Xiao Y, Felleman DJ (2007) V2 thin stripes contain spatially organized representations of achromatic luminance change. Cereb Cortex 17: 116–129

Warrington EK, James M, Maciejewski C (1986) The WAIS as a lateralizing and localizing diagnostic instrument: a study of 656 patients with unilateral cerebral lesions. Neuropsychologia 24: 223–239

Wechsler D (1981) Wechsler Adult Intelligence Scale-Revised (WAIS-R). Psychological Cooperation, San Antonio

Wilde MC, Boake C, Sherer M (2000) Wechsler Adult Intelligence Scale-Revised Block Design broken configuration errors in nonpenetrating traumatic brain injury. Appl Neuropsychol 7: 208–214

Zipf-Williams EM, Shear PK, Strongin D, Winegarden BJ, Morrell MJ (2000) Qualitative block design performance in epilepsy patients. Arch Clin Neuropsychol 15: 149–157