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Cognitive mechanisms, specificity and neural underpinnings of visuospatial peaks in autism

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In order to explain the cognitive and cerebral mechanisms responsible for the visuospatial peak in autism, and to document its specificity to this condition, a group of eight high-functioning individuals with autism and a visuospatial peak (HFA-P) performed a modified block-design task (BDT; subtest from Wechsler scales) at various levels of perceptual cohesiveness, as well as tasks tapping visuomotor speed, global perception, visual memory, visual search and speed of visual encoding. Their performance was compared with that of 8 autistics without a visuospatial peak (HFA-NP), 10 typically developing individuals (TD) and 8 gifted comparison participants with a visuospatial peak (TD-P). Both HFA-P and HFA-NP groups presented with diminished detrimental influence of increasing perceptual coherence compared with their BDT-matched comparison groups. Neither autistic group displayed a deficit in construction of global representations. The HFA-P group showed no differences in performance level or profile in comparison with the gifted BDT-matched [i.e. higher full-scale IQ (FSIQ)] group, apart from locally oriented perception. Diminished detrimental influence of perceptual coherence on BDT performance is both sensitive and specific to autism, and superior low-level processing interacts with locally oriented bias to produce outstanding BDT performance in a subgroup of autistic individuals. Locally oriented processing, enhanced performance in multiple tasks relying on detection of simple visual material and enhanced discrimination of first-order gratings converge towards an enhanced functioning and role of the primary visual cortex (V1) in autism. In contrast, superior or typical performance of autistics in tasks requiring global processing is inconsistent with the global-deficit-driven Weak Central Coherence hypothesis and its neurobiological magnocellular deficit counterpart.

Keywords: autism; visuospatial peak; occipital cortex; parvocellular pathway; magnocellular pathway

Abbreviations: ADI = Autism Diagnosis Interview; BDT = block-design task; CT = construction time; EPF = enhanced perceptual functioning; FSIQ = full-scale IQ; HFA-NP = high-functioning individuals with autism and without a visuospatial peak; HFA-P = high-functioning individuals with autism and a visuospatial peak; ISI = interstimulus interval; PC = perceptual cohesiveness; RT = reaction times; TD-P = typically developing individuals with visuospatial peak; TU = task uncertainty; WCC = Weak Central Coherence; WISC = Wechsler Intelligence Scales

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Introduction

There is accumulating evidence that atypical perception plays a prominent role in the autistic behavioural and cognitive phenotype. Within the visual modality, the performance of persons with autism on tasks necessitating the detection of visual elements embedded in larger fields has been found to be either more locally oriented (Shah and Frith, 1983; Jolliffe *et al.*, 1997; Mottron *et al.*, 2003; Lahaie *et al.*, 2006; see Happé, 1999; and Happé and Frith, 2006, for reviews) or enhanced (Plaisted *et al.*, 1999; O'Riordan *et al.*, 2001; Caron *et al.*, 2004; Pellicano *et al.*, 2005; see Mottron *et al.*, 2006 for a review) when compared with typically developing individuals. This is the case in the embedded figures task (Shah and Frith, 1983; Jolliffe *et al.*, 1997), the impossible figures task (Mottron *et al.*, 1999) and the maze-map task (Caron *et al.*, 2004). Superior performance has also been demonstrated in tasks relying on low-level perceptual processing like pattern (Plaisted *et al.*, 1998*b*) or grating (Bertone *et al.*, 2005) discrimination tasks, in discrimination of elementary stimuli differing at the featural level (Plaisted *et al.*, 2003) and in featural and conjunctive visual search tasks (Plaisted *et al.*, 1998*a*; O'Riordan *et al.*, 2001; O'Riordan, 2004; Jarrold *et al.*, 2005).

Among the large number of visual tasks in which autistic individuals display superior performance, one of the most replicated is the 'block design' (this terminology is unrelated to fMRI terminology, where there can be block or event-related designs) subtest of the Wechsler Intelligence Scales (WISC, WAIS: Wechsler, 1981, 1994). In the block-design task (BDT), the individual is shown a two-dimensional red and white geometric design. The task consists of reproducing this design by assembling a set of blocks composed of six colour surfaces (two red, two white and two diagonally oriented half-red and half-white surfaces). Relative BDT peaks, that is, high level of performance in the BDT as compared with other verbal and non-verbal subtests, is a robust and early finding in autism (Tymchuk *et al.*, 1977; Shah and Frith, 1983, 1993; Asarnow *et al.*, 1987; Happé, 1994; Siegel *et al.*, 1996). However, high level of performance is observed only in a subgroup of individuals satisfying the behavioural criteria for autism. While estimating incidence of the BDT peak as 22–38% in the autistic population of normal intelligence, Siegel *et al.* (1996) concluded that this result could not be used for diagnostic purposes, owing to lack of sensitivity. However, this conclusion has been drawn from performance in the standard Wechsler BDT. This task may not be the most sensitive to autistic particularities, if it does not manipulate the specific dimension that reveals autistic superiority.

Regarding the cognitive mechanisms explaining BDT superiority, a study by Shah and Frith (1993) has shown that the superiority of the autistic group in this task vanishes when the figure to be reproduced is segmented. The authors concluded that BDT superiority in autistic individuals was due to the advantage conferred by spontaneous segmentation, which was evidence for locally oriented processing. This important finding became the cornerstone of Weak Central Coherence (WCC), developed by Frith and Happé (Frith and Happé, 1994; Frith, 2003; Happé and Frith, 2006). In this hypothesis, locally oriented processing is derived from a deficit in the tendency to integrate local elements into a coherent whole. An alternative account attributed BDT superiority to a combination of superior disembodying ability and superior discrimination, within general superior low-level perceptual functioning (Mottron *et al.*, 2006*b*). In the latter explanation, superior performance and locally oriented processing in the BDT would be one among many manifestations of superior performances reflecting overall enhanced perceptual functioning (EPF). However, this model has not been empirically applied to the BDT. In particular, no study has directly tested how EPF may explain the BDT peak, and to date, Shah and Frith's (1993) account for the BDT peak in autism remains without alternative.

Although the WCC model has no explicit neurobiological counterpart, it has been proposed (Milne *et al.*, 2002; Greenaway and Plaisted, 2005) that a putative deficit in perceiving the global aspect of visual information may derive from abnormal functioning of the magnocellular pathway. However, this hypothesis has been criticized on the basis of typical performance in first-order motion perception (Bertone and Faubert, 2005), and overall typical performance in the construction of global visual representations (Mottron *et al.*, 2003, 2006).

This study aims to determine how locally oriented processing and overall superiority in perceptual functioning interact to produce the BDT peak. For this purpose, a BDT allowing manipulation of the variables favouring local (segmentation) and global [perceptual cohesiveness (PC)] processing was constructed. In addition, autistic and non-autistic participants were assessed in a large sample of visual perception tasks (visuomotor speed, global processing, short- and long-term visual memory, visual search and low-level discrimination). In order to disentangle the effects of giftedness, autism and general intelligence in the BDT, this series of tasks was assessed in two groups of autistics—one randomly selected among individuals with a relative BDT peak (HFA-P), and another among individuals without a BDT peak (HFA-NP). Their performance was compared with that of two comparison groups of typically developing individuals—one representative of the general population (TD), and one composed of individuals presenting with an absolute BDT peak (TD-P), that is, exceeding IQ baseline by >1.5 SD. This strategy provides two different matching variables for the autistic group—one on general intelligence (HFA-P and HFA-NP versus TD) and one on visuospatial ability, when it differs from general intelligence owing to autistic or non-autistic giftedness (HFA-P versus TD-P). However, it does not allow for a factorial design (group × BDT peak), which would require identical criteria for both autistic and control groups. Whereas the TD group is representative of the entire population of typically developing individuals, the TD-P group is defined on the basis of the presence of an absolute BD peak only. A relative peak is exceptional in typically developing people, but always accompanies the presence of an absolute peak within the autistic population of normal intelligence. Although BD ability cannot be isolated from autism unequivocally in this design, it detects patterns of performance sensitive to autism when the HFA-P and HFA-NP groups differ from the baseline of the TD sample, and specificity to autism when TD-P and TD behave similarly in this regard.

WCC (and magnocellular) accounts of the BDT peak predict an absence of influence of PC (Experiment 1) on performance, a larger impairment of the HFA-P group in a task tapping holistic processing (Experiment 2) and a superior memory for block patterns deprived of PC (Experiment 3) in the HFA-P group. In contrast, the EPF model applied to the BDT predicts an overall superiority of the HFA-P group in Experiments 1–5, in addition to predictions similar to WCC in Experiment 1, but opposite in Experiment 2.

Methods

Participants

Four groups of adolescents and adults participated in this study: high-functioning autistics with (HFA-P) and without (HFA-NP) a BDT peak, typically developing individuals (TD) and a group of non-autistic gifted individuals with a BDT peak (TD-P). Both groups of HFA participants had full-scale IQ (FSIQ) scores in the average range (IQ > 80). Participants were obtained from the database of the Pervasive Developmental Disorders Specialized Clinic of Rivière-des-Prairies Hospital (Montreal, Canada). The diagnosis of autism was made on the basis of the Autism Diagnosis Interview-Revised (ADI-R; Lord *et al.*, 1994). This diagnosis was confirmed by an explicit assessment of Diagnostic and Statistical Manual of Mental Disorders (DSM) IV criteria through clinical observation, using the Autism Diagnosis Observation Schedule-Generic (ADOS-G, module 3 or 4, Lord *et al.*, 1999). All participants scored above the cut-offs in the algorithms of the two instruments, except for one of the HFA-NP group who scored at 6 (cut-off: 10) in the ADI communication area, but was included as he scored at 5 (cut-off = 3) at the ADOS communication area, had a presentation of classical autism and no other Axis 3 diagnosis. In order to exclude individuals with an attenuated phenotype who may still be positive to these instruments in our experience, the participants were limited to those presenting at least a delay in one- or two-word development. This had the effect of excluding clinical diagnoses of Asperger syndrome in this study, except one who was included owing to a clerical error. Among HFA-P participants, one was taking risperidone, one was taking risperidone and clonidine, and one was taking paroxetine. Among HFA-NP participants, one was taking methylphenidate. Autistic participants were verbal, between 12 and 33 years of age, and all had normal or corrected-to-normal vision, tested by Snoellen Eye Chart before the experiment.

The HFA-P group included eight individuals with autism presenting a BDT scaled score >15, that is, satisfying the 0.05 threshold provided by Wechsler's manual guide to determine an informative difference between the BDT and the average of the other WAIS-III or WISC-III scaled scores (the differences being 3.2 and 2.7, respectively). The HFA-NP group included eight individuals with autism but without a BDT absolute or relative peak as previously defined.

The TD group comprised 10 typically developing participants. One TD participant presented an absolute BDT peak, which corresponds approximately to the incidence of BDT absolute peak in our database of TD individuals. The TD-P group included eight typically developing individuals with a BDT scaled score equivalent to or >15. The typically developing individuals and their first-degree relatives were screened for current or past neurological, developmental or psychiatric disorders. The experiment was formally approved by a local ethics committee. All participants were given financial compensation for their participation. Table 1 shows the characteristics of the four groups.

No statistically significant differences were found between the HFA-P, HFA-NP and TD groups in chronological age, gender, laterality, verbal IQ (VIQ), FSIQ, nor in average scaled scores of the different WAIS or WISC subtests minus BDT. The unique difference was in performance IQ (PIQ) (HFA-P = 108, TD = 96; $P = 0.048$) due to the standard score of the BDT being significantly higher in the HFA-P and in the TD-P group. Relative BDT peaks being practically inexistent in the typical population, TD-P individuals were found only among subjects with overall high IQ. Therefore, the TD-P group had an IQ significantly higher ($\sim$20 points) than the three other groups. The TD-P group was also significantly younger than the HFA-P group.

An overall difference in ADI scores has been reported to falsely produce apparent qualitative differences among subgroups of pervasive developmental disorder (PDD) (e.g. Asperger versus autism: Macintosh and Dissanayake, 2004). Therefore, we assessed differences between individual ADI items and summary scores between the two autistic groups. We did not find differences between groups in any of the summary scores, including the cumulative score for restricted interests and repetitive behaviours. Among the ADI items composing the diagnostic algorithm, only unusual

Table 1 Characteristics of high-functioning participants with autism with (HFA-P) and without (HFA-NP) block-design peak, typically developing participants (TD) and control participants with block-design peak (TD-P)

	Mean (SD)			
	HFA-P	HFA-NP	TD	TD-P
N	8	8	10	8
Age	23.28 (7.4)	18.88 (4.4)	18.6 (3.5)	16.88 (2.0)
VIQ	98.9 (21.5)	98.4 (11.8)	103.8 (8.1)	115,13 (8.2)
PIQ	108.9 (10.0)	99.4 (10.6)	96.5 (9.6)	123.88 (7.9)
FSIQ	103.1 (15.0)	98.5 (10.8)	101.2 (7.2)	121.00 (7.1)
Averaged P s.s.	11.23 (1.3)	9.83 (1.6)	9.4 (1.5)	13.53 (1.2)
BDT s.s.	16.6 (2.0)	10.8 (1.8)	10.1 (2.7)	17.0 (1.4)
Averaged (FS – BDT) s.s.	9.98 (2.0)	9.43 (1.5)	9.77 (0.9)	12.49 (1.1)
Averaged (P – BDT) s.s.	10.01 (1.4)	9.64 (1.6)	9.28 (1.6)	12.66 (1.2)

s.s = scaled score; V = verbal; P = performance; FS = full scale; BDT = block design task.

preoccupations (# 71) and unusual sensory interests (# 77) at the 4–5 years period differed (exact Fisher test, $P = 0.041$), which confirms the hypothesis (see Mottron *et al.*, 2006*a*) that visuospatial peaks and perceptually oriented repetitive behaviour may be related to a low-level perceptual mechanism.

In order to obtain information about the incidence of HFA-P individuals within the autistic population, we examined the proportion of individuals with relative BDT peak in the entire sample of individuals with autism ($n = 92$) and of typically developing ($n = 112$) individuals listed in Rivière-des Prairies' database. A relative BDT peak occurred in 47% of individuals with autism. We therefore consider that the combination of the HFA-P and HFA-NP groups is a representative sample of the autistic population. In contrast, a relative BDT peak was found in only 2% of the non-autistic population (see Fig. 1).

General procedure, tasks and apparatus

The nature of the experiment was explained to all participants at the occasion of signing the research consent. After informed consent was obtained, all participants were individually administered the five tasks in the same order (1—PC in BDT, 2—segmentation versus integration in BDT, 3—long-term visual memory in BDT, 4—visual search in BDT, 5—perceptual discrimination, encoding and retention of visual pattern). The instructions relevant to each particular task were presented and practised before the experiment. The stimuli for computerized tasks were generated by a PC Vectra Pentium II and displayed on a 17-inch colour monitor. Participants were seated 2 ft from the monitor. The entire testing session lasted ~1 h and 30 min.

Experiment 1: Effect of PC on performance in a BDT

Experiment 1 manipulates the PC (minimal, intermediate, maximum) and the presentation form of the design (unsegmented, segmented). PC is a global property of the figure to be reproduced. Figures with high PC require mental segmentation in order to divide them into block-sized units, allowing matching between a part of the design and one of the three possible surfaces of the blocks. PC can be manipulated by varying the number of 'adjacencies' of opposite-coloured edges for the block, or *edge cues*. The higher the number of edge cues, the lower the PC and the easier/faster a successful completion occurs (Royer and Weitzel, 1977; Royer *et al.*, 1984; Schorr *et al.*, 1982). Other variables relevant for task difficulty are *task uncertainty* (TU) and *matrix size*. TU expresses the number of possible decisions required to reproduce a figure. The first level of TU (TU = 1) consists of determining if a required part is red, white or bicolour. If a bicolour part is required, an additional choice (TU = 2) among the four different bicolour face orientations has to be made. The sum of the TUs for each block composing the target figure provides a measure of the total TU involved in constructing this figure. Matrix size expresses the number of blocks (4, 9 or 16) composing the figure. Lastly, the segmentation of the target figure suppresses the detrimental effect of PC on figure construction, leaving only the local–local matching and motor components of the task.

Experimental task and stimuli

The task was constructed following a PC (minimum, intermediate, maximum) × task uncertainty (min, max) × size (4, 9, 16) design, resulting in 18 figures, presented in unsegmented and then in segmented conditions. The segmentation space was 1/3 of the width of one block (0.9 cm). For each matrix size, a control condition measuring the motor velocity component involved in BDT construction was added, in the form of a monochromic square presented in the segmented and the unsegmented condition. Examples of stimuli are presented in Fig. 2.

Procedure

Task procedure followed Wechsler's instruction guide. The participants were first shown the different faces of a block and were informed that all blocks were identical and composed of two red, two white and two bicolour surfaces (see Fig. 2). A 2 × 2 example (not included in the task) was performed by the examiner and then reproduced by the participant. Between each construction, the examiner placed the blocks in front of the participants in order

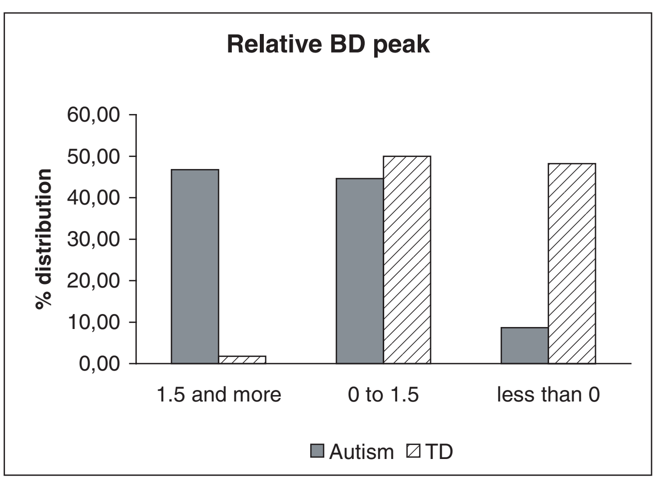


Fig. 1 Relative BDT peak (standard deviation in comparison to FSIQ) distribution in autistic ($n = 92$) and typically developing (TD) individuals ($n = 112$).

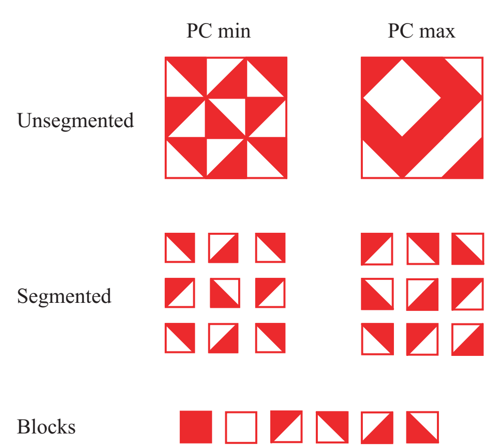


Fig. 2 Examples of the BDT: unsegmented and segmented designs of PC minimum and PC maximum patterns. The design is to be constructed from six surfaces blocks.

that an equivalent variety of block surfaces was facing up. Instructions emphasized speed as well as accuracy. Performance was timed from the moment the design card was placed in front of the participant until the design was completed or the time limit elapsed. Because the designs used in this experiment were more difficult than those in the WISC or WAIS, the maximum allowed time before the construction of a design was considered 'failed' was increased, on the basis of a pilot study. The time limits for the 4-, 9- and 16-block designs were, respectively, 120, 180 and 240 s. One point was credited for each of the correctly reproduced designs. Presentation order of the designs was identical for all participants. Trials were ordered by increasing level of uncertainty within each matrix size, and PC level within each level of uncertainty. The unsegmented condition was presented before the segmented condition to avoid a facilitation effect.

Hypotheses

Following experimental findings demonstrating a generalized local bias in autism and consistent with Shah and Frith's seminal study (1993), the detrimental effect of PC on performance should be inferior in the HFA-P compared with the TD group. In addition, the superiority of the HFA-P group should disappear in the segmented condition, which allows all participants to use a local strategy. Predictions arising from WCC and EPF models would be identical in this regard. No predictions were made for the HFA-NP and the TD-P group.

Results

Average construction time (CT) ranged between 15 and 126 s, that is, within task limits.

Construction time (*CT*). A group (HFA-P, HFA-NP, TD, TD-P) × segmentation (segmented, unsegmented) × PC (minimum, intermediate, maximum) repeated measures ANOVA (analysis of variance), with CT as the dependent variable, revealed an interaction of group × segmentation × PC, $F(6,60) = 3673$; $P = 0.004$, in the unsegmented condition and an interaction of PC × group, $F(6,60) = 5173$; $P = 0.000$. The planned comparison of the group × PC interaction in the unsegmented condition revealed significant interactions when comparing TD to HFA-P [$F(2,32) = 12.908$; $P = 0.000$] and TD-P to HFA-P [$F(2,28) = 6.183$; $P = 0.006$], whereas the interaction is not significant when comparing HFA groups to each other [$F(2,38) = 2.728$; $P = 0.083$]. Therefore, TD and TD-P individuals were slowed by increased PC, whereas HFA-P participants were not. In the segmented condition, the detrimental effect of increasing PC disappeared. However, *post hoc* comparisons (Tuckey HSD) show that whereas the TD-P group was faster than the HFA-NP ($P = 0.000$) and TD ($P = 0.000$) groups in the segmented condition, it was not faster than the HFA-P group ($P = 0.126$) (Fig. 3).

Visuomotor baseline speed. CTs in the segmented and unsegmented condition of the visuomotor control task were pooled, as no hypotheses predicted a difference at this level. Average CTs were, respectively, 11.63, 15.60, 13.25 and 9.92 s for the HFA-P, HFA-NP, TD and TD-P groups, and revealed a significant difference between groups, $F(3,33) = 5631$, $P = 0.003$. The finding of a significant difference between groups in the visuomotor control task led to verification by ANCOVA (analysis of covariance) of whether this variable explained differences in CT found between groups. This analysis pulled out the variance in CT resulting from the visuomotor component. Conclusions pertaining to the group × segmentation × PC and the group × PC interaction in the unsegmented condition were not modified by adding the visuomotor variable.

Accuracy. Overall number of errors was very low, resulting in a non-normal distribution of data, which, combined with the relatively small number of participants per group, precludes statistical analysis. However, qualitative examination of the error curves show the same pattern as CT, with the HFA-P and TD-P groups being the most accurate, the HFA-NP group falling closely behind and the TD group presenting with a larger number of errors. The TD group was the least accurate in the minimum PC condition, where they displayed 15–20% 'local' errors.

In summary, the influence of PC on BDT CT is diminished in gifted and non-gifted autistic individuals, when compared with BDT-matched typical participants, and within groups, in gifted participants, when compared with non-gifted participants. This

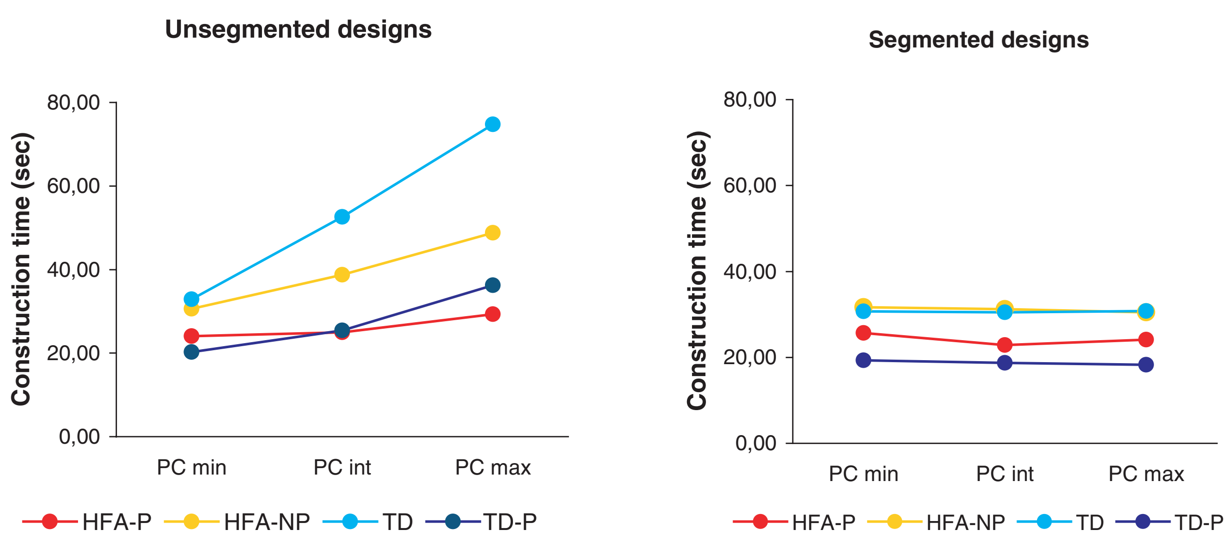


Fig. 3 CT for unsegmented and segmented designs for different levels of PC (minimum, intermediate, maximum).

indicates that diminished influence of PC on BDT in autism is neither dependent on diagnosis nor on general intelligence, nor on visuospatial giftedness only. The autistic superiority in the BDT is revealed only at the maximal level of PC, which conflicts with the local analysis required to perform the task for TD individuals, and confirms Shah and Frith's (1993) interpretation that locally oriented processing contributes to superior BDT performance.

Experiment 2: Testing holistic visual processing through a 'reversed' computerized block-design task

This matching task directly assessed the construction of a global representation in a BDT, to document the role of a deficit at the global level in the local bias evident in Experiment 1.

Experimental task and stimuli

This computerized task consisted of matching an unsegmented figure to a corresponding segmented target figure presented among three segmented distractors. In the condition of minimal PC, the participant can use a local-by-local strategy that is induced both by the large number of edge cues and by the segmented presentation of the figure. In the condition of maximal PC, matching at the global level requires only one operation, whereas matching at the local level requires as many operations as there are blocks in the figure. Eighteen stimuli-target pairs of increasing level of PC, TU and matrix size, corresponding to the same characteristics as those of Experiment 1, were constructed. The distractors used in this task differed from the target by colour inversion, local difference and target rotation. Examples of stimuli are presented in Fig. 4.

Procedure

Subjects were instructed that they would see some designs similar to those used in Experiment 1 at the top of the screen (target stimulus). They were also instructed that they would have to choose, as quickly as possible, from among four segmented designs displayed on the lower part of the screen, the design that corresponds to the target stimuli at the top of the screen. Responses were given by indicating verbally the letter corresponding to the presented items. The experimenter manually recorded the answer by pressing one of four keys of a keyboard recording accuracy and reaction times (RT).

Hypotheses

Whereas WCC explicitly predicts a deficit in processing the configural aspect of the target figure, EPF predicts that a general perceptual hyper-functioning should be manifested by a superiority in processing isolated visuospatial components, even configural ones.

Results

Average RT per individual ranged between 5 and 11 s.

Reaction times (*RT*). A group (HFA-P, HFA-NP, TD, TD-P) × PC (minimum, intermediate, maximum) repeated measures ANOVA, with CT as the dependent variable, revealed a main effect of group, $F(3,30) = 4111$, $P = 0.015$, and PC, $F(2,60) = 118\ 622$, $P = 0.000$, but no group × condition interaction ($P = 0.952$). The facilitation effect on RT of increasing PC was identical across groups, thus demonstrating that global advantage is preserved in autistic participants, whatever their BDT performance. The HFA-P group was faster than the TD group across all levels of PC ($P = 0.029$), and was similar to the TD-P group, demonstrating that perceptual matching is superior in this group, independent of the hierarchical level at which it occurs: local, but also global, processing is faster in HFA-P participants (Fig. 5).

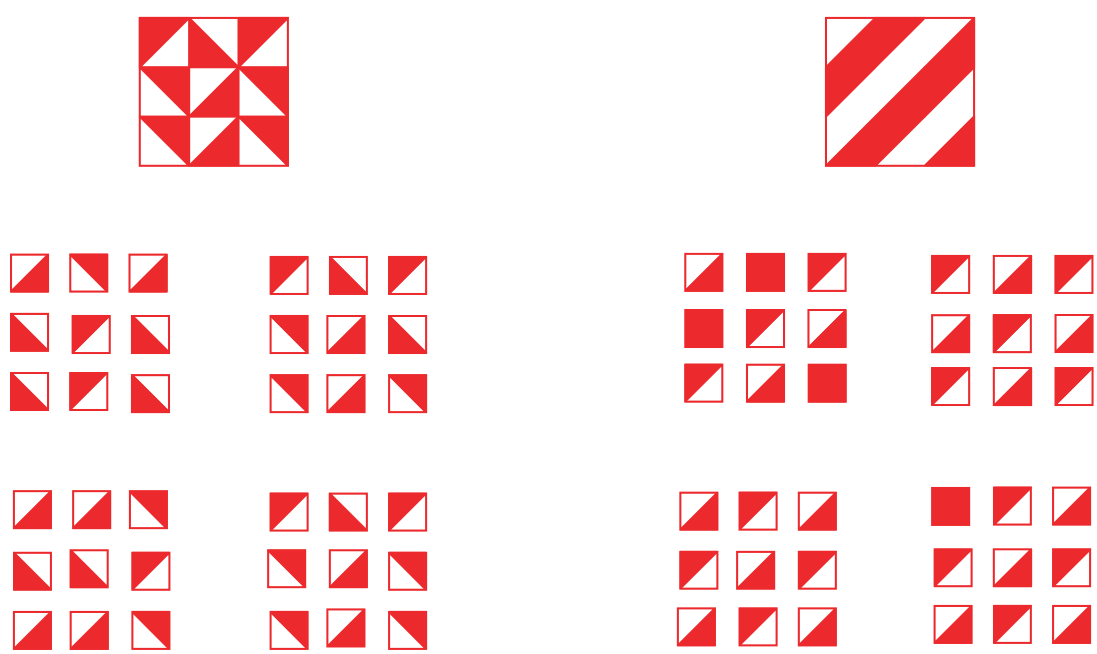


Fig. 4 Example of stimuli (top left: local figure, top right: global figure) and distractors (bottom) used in task 2.

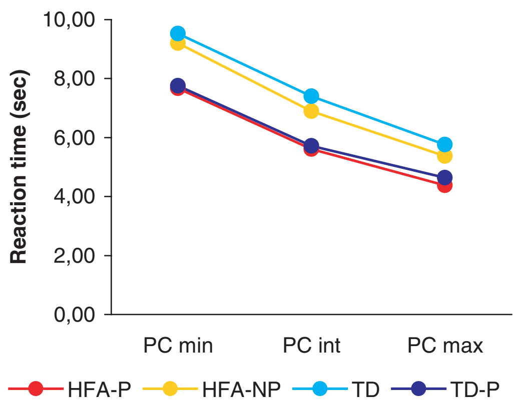


Fig. 5 Local (PC min) versus global (PC max) processing matching speed.

Accuracy. Overall number of errors was very low, which, combined with the small number of participants, precluded statistical analysis. However, qualitative examination of the error curves showed the same pattern as the accuracy measured in Experiment 1, with HFA-P and HFA-NP groups being the most accurate, and TD and TD-P groups being least accurate in the minimal PC condition, where they displayed 15–25% 'local' errors. No speed-accuracy trade-off was found in this task (Spearman Correlation).

The integrity—and, *a fortiori*, the superiority—of performance in a task relying on the construction of a global representation for the HFA groups discards the existence of an integration deficit in autism, and more specifically, its putative role in BDT peak.

Experiment 3: Long-term visual memory for block-design figures

This task was devised to test the EPF hypothesis that all operations involving simple patterns, from detection up to and including identification and memory, are superior in autism.

Task, stimuli and procedure

The purpose of Experiment 3 was to test if the group of participants showing superior BDT ability in Experiments 1 and 2 were also superior in memorizing the local and global aspects of figures involved in a BDT. An incidental long-term visual recognition task was administrated after Experiment 2 (30 min after Experiment 1) to all participants. The participants had to identify the 18 unsegmented designs of Experiment 1 among a set of 18 distractors corresponding to the same characteristics (PC, TU and Matrix size) as the target designs used in Experiment 1, but different from the stimuli used in Experiments 1 and 2. The series of 18 target figures intermingled with 18 distractors was presented randomly, one at a time. Yes–no responses were recorded on response keys. Accuracy was the dependent variable. Responses on the recognition task were considered correct if the participant accepted an old stimulus or rejected a new stimulus.

Hypotheses

The EPF model predicts a superior memory performance for all figures. EPF and WCC predict that this superiority should be larger for low PC figures, owing to local bias. The WCC model has the same prediction for minimal PC figures (local bias), but this superiority should vanish for high PC figures (global deficit).

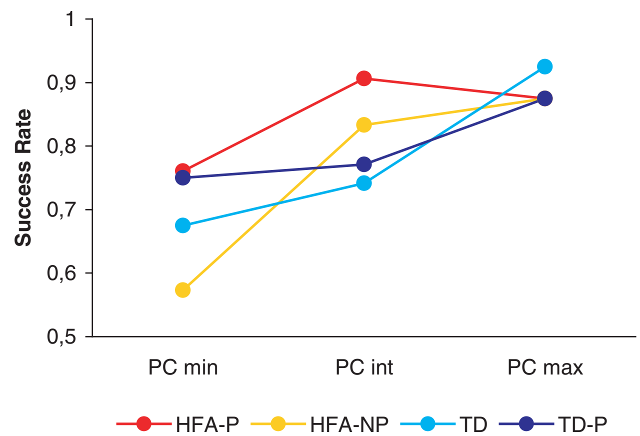


Fig. 6 Long-term visual memory for local (PC minimum) and global (PC maximum) BDT figures.

Results

Accuracy. A group (HFA-P, HFA-NP, TD, TD-P) × PC (minimal, intermediate, maximum) ANOVA, with accuracy as the dependent variable, revealed a group × PC interaction [$F(6,60) = 4917$, $P = 0.000$]. The planned comparison of the group × PC interaction revealed that diminishing PC has a detrimental effect on memory in each group, the classical (Schacter *et al.*, 1990) 'global advantage' in memory. However, this effect was inferior in the HFA-P ($P = 0.023$) and the TD-P ($P = 0.014$) groups than in the HFA-NP and TD groups ($P = 0.000$), owing to a superior performance of the two former groups in recognizing previously encountered, minimum PC (i.e. comprising local details) figures (Fig. 6).

In summary, both autistic groups were better at memorizing high PC (global) figures than low PC (local) figures, showing that global advantage in long-term memory is not impaired in HFA participants. The fact that the HFA-P group equals the TD-P group in this task indicates that visuospatial peaks extend to the memorization of visual material in both groups.

Experiment 4: Visual search using block-design components

Autistic individuals present a characteristic pattern of performance in visual search tasks (Plaisted *et al.*, 1998*a*; O'Riordan and Plaisted, 2001; O'Riordan *et al.*, 2001). In a featural visual search task, the target differs from a unique set of distractors by a single feature. In a conjunctive visual search task, the target shares one feature with one set of distractors and another feature with another set of distractors. Therefore, the target is defined by a combination of features. Autistic individuals are more effective than typically developing individuals in conjunctive visual search tasks. Individuals with autism are also superior to typically developing individuals in featural tasks when featural tasks become more difficult (O'Riordan, 2004). In addition, autistics are less affected by increases in the number of distractors. According to Plaisted (2001), superior ability to discriminate among presented elements (the highly similar blocks required for a construction in BDT, the target and distractors items in a visual search task) may account for superior performance in both types of tasks. In order to facilitate the comparison and the generalization in performance between the two tasks, a visual search task where targets and distractors were identical to block surfaces in the BDT was constructed.

Experimental task and stimuli

Stimuli were constructed by manipulating the structure (bitriangular, birectangular) and the orientation (red angle on right top, left top, right bottom, left bottom; see Fig. 7) of the presented 'blocks'. Birectangular blocks were identical to one of Kohs' blocks (1923), used by Shah and Frith (1993). In the featural condition, the distractors differed from the target by structure and orientation. In the conjunctive condition, distractors were either of identical structure as the target but with different orientation, or different in structure but identical in orientation. Therefore, distractors shared either structure or orientation with the target. In both conditions, each stimulus display occupied an unmarked 16.8 × 16.8 cm square at the middle of the screen. Target or distractors measured 1 cm × 1 cm. The minimum distance between elements was 0.7 cm (rows and columns).

In each condition (featural, conjunctive), level of difficulty was manipulated by varying the number of items displayed (4, 9, 16) and the presence versus absence of the target (50/50), resulting in six possible combinations per condition (see Fig. 8 for example). Two different targets were presented in each condition for a total of 2 sets of 60 trials, separated by a pause. Each set of trials was presented in an individually randomized sequence. Hence, the participant knew in advance the target to search for in each display, but did not know in advance if the target would be present, nor the number of distractors to be searched among for the target.

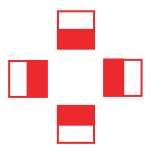
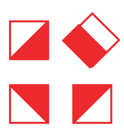
Visual search task	Target	Distractors
Featural		
Conjunctive		

Fig. 7 Targets and distractors used in the 'featural' and 'conjunctive' visual search task.

Procedure

Before each set of test trials, participants were given 12 practice trials. Before starting the test trials, participants were instructed to respond by pressing one of two response keys as quickly and accurately as possible. Each trial was composed of the following sequence: white screen (1 s), central fixation point (1 s), search display (10 s, or until the participant's response). The digital timer was initiated by the presentation of the search display. If the subject did not respond within 10 s, a small clock appeared in the middle of the screen (1 s) followed by a white screen (1 s) and a central fixation point (1 s), announcing the onset of the next trial. If an incorrect response was made, an inverse 'smile' was shown on the screen (1 s). Finally, if a participant pressed on the response key before the search display appeared on the screen, a running 'bunny' was displayed at the middle of the screen (1 s).

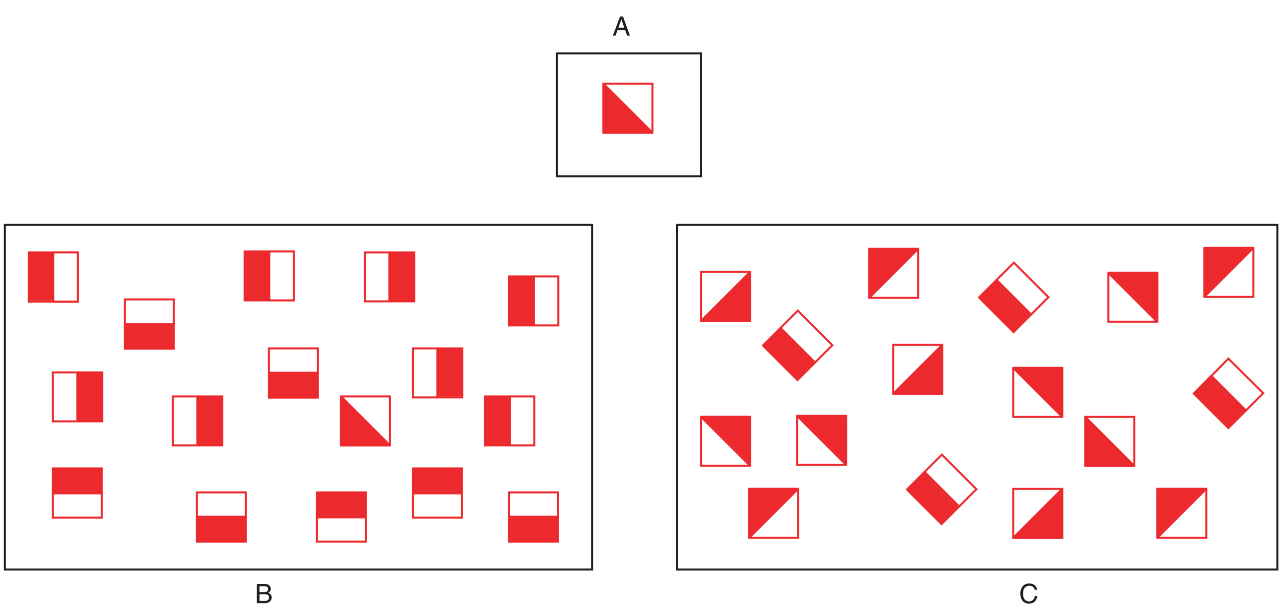


Fig. 8 Visual search task: stimulus (**A**); featural search (**B**); conjunctive search (**C**). The left frame shows an example of a 'featural' search display in which the target is present in a 16-item display. The right frame shows an example of a 'conjunctive' search display in which the target is present in a 16-item display.

Hypotheses

WCC predictions about impaired ability to combine two features have already been contradicted by findings of not only preserved but also superior performance of autistics in conjunctive conditions. However, according to the EPF model, lower target detection time and superior accuracy in the autistic group extends also to difficult featural visual search tasks (O'Riordan, 2004).

Results

The four variables (group: HFA-P, HFA-NP, TD, TD-P; condition: featural, conjunctive; display size: 4, 9, 16; presence of the target: yes/no) could not be entered in the same analyses. Therefore, absent and present condition were pooled together in order to document the differential effect of display size among groups and condition. For the same reason, analyses were performed using pooled average RTs and errors across display size (4,9,16).

Group × condition × display size

Reaction times. A group (HFA-P, HFA-NP, TD, TD-P) × condition (featural, conjunctive) × display size (4,9,16) repeated measures ANOVA, with RT as the dependent variable, revealed a main effect of group, $F(3,30) = 3877$, $P = 0.019$, and a condition × display size interaction, $F(2,60) = 92\ 073$ ($P = 0.000$). RT increase between featural and conjunctive conditions and detrimental effect on RT of increasing display size in the conjunctive condition were identical across groups, thus replicating O'Riordan's (2001) and Plaisted's (1998*b*) results for similar display size; however, the HFA-P and TD-P groups were the fastest in all conditions (Fig. 9).

Accuracy. Overall number of errors was small (around 5% in all conditions/display sizes, except 15% in the conjunctive condition for the display size 16), and no differences were observed between groups. No speed-accuracy trade-off was found in this task (Pearson correlation).

Group × condition × target presentation

Results were similar to the previous analyses, with HFA-P behaving like TD-P and HFA-NP like TD participants for present or absent targets.

The observation that the same autistic individuals present with a BDT peak and superior performance in a visual search task confirms Plaisted *et al.* (1998*b*) and O'Riordan and Plaisted's (2001) suggestion that some factor, implicated in a high level of perceptual performance, is shared by these two tasks. It also confirms that the ability to merge two perceptual criteria (conjunctive visual search) is unremarkable in autism.

Experiment 5: Perceptual encoding speed and persistence in iconic memory

This task assesses discrimination threshold and perceptual encoding speed for meaningless visual patterns. Whereas the contribution of local and global perceptual processing to superior BDT performance is assessed in Experiments 1–2, to visual long-term memory in Experiment 3 and to attention/perception interactions in Experiment 4, Experiment 5 tests the possibility that the input of perceptual information is atypically superior in a subgroup of persons with autism. Information in sensory storage typically transfers to short-term visual memory within 100–250 ms after stimulus onset (Phillips, 1974; Purdy *et al.*, 1984).

Stimuli

The stimuli were identical to those used by Phillips (1974) and consisted of 9 × 9 grids, each containing 81 square cells (40 red, 41 white randomly distributed) without borders (see Fig. 10 for example). The difficulty index (proportion of cells differing between a pair of stimuli) qualifies the level of similarity between two stimuli.

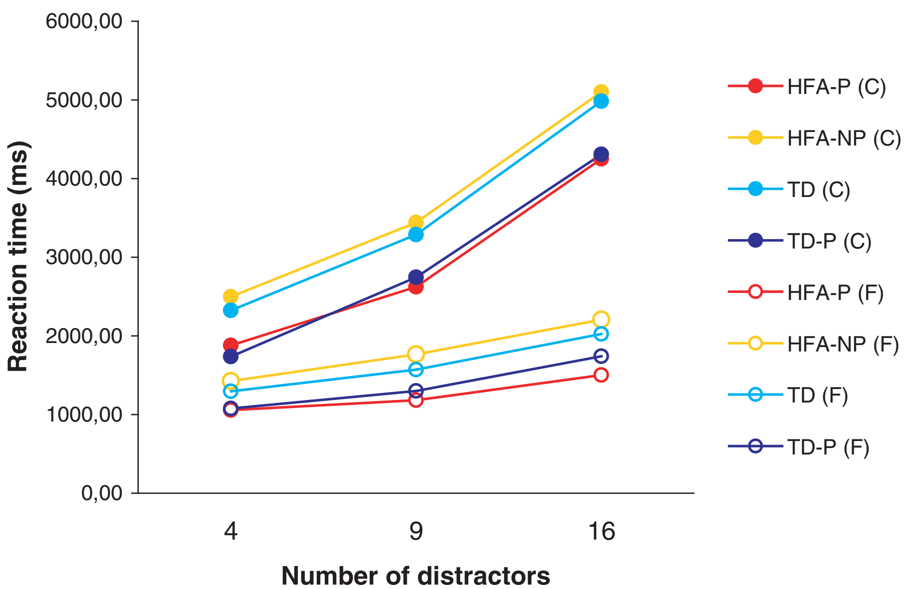


Fig. 9 Average reaction time to detect target among displays of 4, 9 and 16 distractors by group and type of search trial. (C = conjunctive search; F = feature search.)

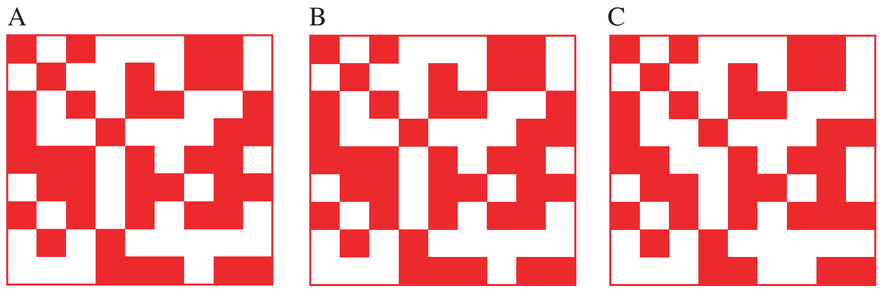


Fig. 10 (**A**) Sample target stimulus (probe), consisting of 9×9 grid of cells, half of which are darkened in a random fashion and exposed for 1000 ms in phase 1 and for 200, 500 or 1000 ms in phase 2. (**B** and **C**) Two test stimuli, which are displayed 1000 ms after presentation of the probe in phase 1 and after a delay of 17 250 or 8000 ms during phase 2. The test stimulus on the left (**B**) matches the probe, whereas the test stimulus on the right (**C**) differs by four cells.

Procedure

Experiment 5 consists of the determination of individual discrimination threshold (phase 1) followed by a delayed matching-to-sample task, at various exposure times and interstimulus intervals (ISIs) (phase 2). Participants were instructed that they would see a geometrical figure on the screen (the probe), followed by a pair of figures (one target, one distractor, differing by having some red cells whitened or vice versa). Responses were recorded by pressing the right or left key, depending on the side on the screen where the target was located.

Phase 1: The purpose of phase 1 was to determine the individual discrimination threshold, expressed in minimum proportion of differing cells allowing discrimination. This was done in order to compare the two groups on this variable, and to separate its role from encoding speed by equating participants on discrimination competency. Probe exposition time and ISIs were both fixed at 1 s. A descending staircase procedure (step = 1 differing cell) was used, beginning by maximum level of difficulty, that is, 1 out of 81 cells differing between targets and distractors. Phase 1 was interrupted when the participant successfully discriminated 16 out of 20 stimuli of a given difficulty level.

Phase 2: The second phase was tested at the difficulty level individually determined during phase 1. Participants were told that exposure time and delay period were modified in phase 2. A sequence of 90 stimuli randomly combining three probe exposure times (200, 500 or 1000 ms) and three ISIs (17, 250 or 8000 ms) was constructed. All ISIs were filled by a neutral grey texture with a fixation cross in the middle of the screen.

Hypotheses

WCC does not entail predictions regarding low-level processing in isolation. The EPF model predicts that discrimination threshold (phase 1) performance as well as encoding speed and persistence of iconic trace (phase 2) should be enhanced in the HFA-P group.

Results

Discrimination. Groups were virtually identical in terms of average difficulty index: HFA-P: 89% (SD = 4%), HFA-NP: 91% (SD = 4%), TD: 89% (SD = 4%), TD-P: 90 (SD = 5%). Between 1 and 16 differing cells were required to discriminate two displays.

Group $\times$ exposure time ANOVA. A group (HFA-P, HFA-NP, TD, TD-P) $\times$ exposure time (200, 500, 1000 ms) repeated measures ANOVA, with accuracy as dependent variable, revealed a group $\times$ exposure time interaction, $F(6,60) = 4000$ ($P = 0.002$). *Post hoc* analyses revealed a clear superiority in accuracy for the HFA-P and TD-P groups at 200 ms of exposure, $F(3,30) = 5485$ ($P = 0.004$), as compared with HFA-NP and TD participants (Fig. 11). The HFA-P and TD-P groups required less exposure time to obtain a comparable performance in discrimination

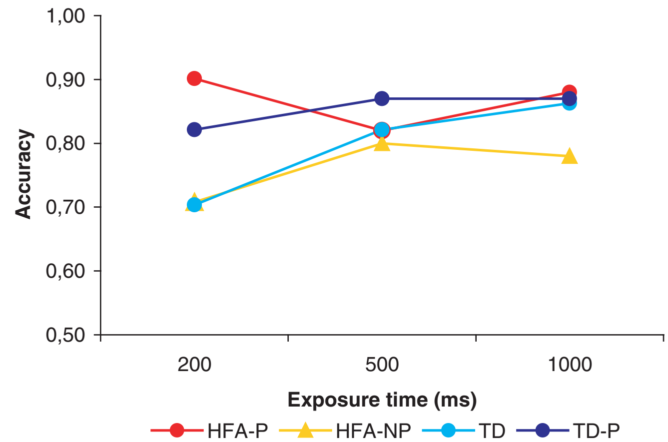


Fig. 11 Accuracy at different exposure times in Experiment 5.

Group $\times$ ISI ANOVA. A group (HFA-P, HFA-NP, TD, TD-P) $\times$ ISI (17, 250, 8000 ms) repeated measures ANOVA, with accuracy as dependent variable, did not reveal a difference between groups.

The fact that HFA-P participants perform like TD participants with a FSIQ ~20 points higher indicates that availability of visual information is superior to what FSIQ could predict in autism (see also Scheuffgen *et al.*, 2000), but indicates that this is true only for the endophenotype characterized by an overall superiority in perceptual tasks. These results also suggest that not all dimensions of early stage visual processing are superior in the HFA-P group (see also Bertone *et al.*, 2005).

General discussion

With the purpose of explaining the mechanisms responsible for the BDT peak in autism, and to document its sensitivity and specificity to autism, a group of HFA individuals with a BDT peak of ability performed a BDT in conditions orienting towards local (segmentation) or global (increasing PC) processing, and four tasks tapping different levels of visual perception. The performance of the HFA-P group was compared with that of autistics without a BDT peak, typical individuals of similar general intelligence and typical individuals matched in BDT peak but with a superior general intelligence measured with Wechsler scales. The two HFA groups displayed a diminished influence of increasing PC, and three results indicate that their ability to integrate features into a coherent whole was preserved: a typical advantage in matching block patterns at the global level, in memorizing figures with high PC and in detecting conjunctive pattern in a visual search task. The HFA-P group displayed a consistent superiority to FSIQ-matched participants but an equivalent performance to that of BDT-matched participants, in one or several aspects of the entire range of tasks. We shall now examine how these findings allow for the disentangling of factors that have been proposed to account for the BDT peak in autism, to which extent BDT peak and overall superiority in perceptual tasks are sensitive to autism and how this may be explained at the neural level.

Understanding BDT peak in autism

Disembedding ability

The limitation of BDT superiority of the autistic group to the unsegmented condition, as reported by Shah and Frith (1993), is replicated. Segmentation of the figure to be reproduced considerably reduces the difficulty of the task but is at risk of producing a ceiling effect, which obscures effects more specific to each of the groups under study. This is not the case for the manipulation of perceptual coherence, which reveals an increase of difficulty that interacts with group and level of performance. For TD individuals, both gifted and non-gifted groups display an increase of CT following increase in PC. However, this increase is more important for non-gifted people than for gifted people, autistic or not, and more important for non-autistics than for autistics, gifted or not. In the autistic group, only the non-gifted group displays a cost of increasing PC. However, when autistic and non-autistic groups of similar level of performance in a standard BDT are compared, autistics are consistently less slowed by maximal level of PC. Therefore, diminished influence of PC plays a role in BDT peak in autism, although it interacts with task difficulty and abilities in perceptual tasks.

Global deficit

Could a deficit in the ability to combine elements in a higher-order representation be responsible for superior BDT performance, as initially proposed by the WCC model (Frith, 2003; Happé and Frith, 2006)? Combined findings of Experiments 2, 3 and 4, based on intact or superior construction of a visual perceptual representation, indicate that this is not the case. The autistic participants without BDT peak are comparable with IQ-matched participants in these tasks, and those with BDT peak are also superior to IQ-matched typical participants in these tasks. Taken together, these findings indicate that the 'default setting' of autistic perceptual analysis towards local elements, demonstrated in Experiment 1, may be bypassed either when the construction of a global perceptual representation optimizes performance (Experiment 2) or when it is mandatory for a successful performance (Experiment 4, conjunctive condition). The autistic group appears to be more cognitively versatile than the TD group: they may use a locally oriented (Experiment 1, maximum PC) or a globally oriented (Experiment 2, maximum PC) strategy. Normalcy of global level analysis has also been reported following explicit instruction in a Navon-type task (focused attention condition; Plaisted, 1999; Experiment 1). Likewise, an ability of autistic participants to re-configure their default setting according to task demands has recently been demonstrated by Iarocci *et al.* (2006), who showed that autistic participants (regardless of their BDT performance) adapt more easily to modification of frequency of target occurrence at the local and global level than comparison individuals, although they are superior for local targets.

Enhanced perceptual functioning

In an updated version of the EPF model (Mottron *et al.*, 2006*b*), we proposed that superior perceptual functioning could be involved in BDT peak. A contribution of EPF to an absolute BDT peak is plausible, as the HFA-P group also displays superiority in five other perceptually related tasks. Conversely, superior disembedding ability has to be combined with overall superior perceptual performance to produce a high BDT performance in autistics. Accordingly, the HFA-NP group, by definition, does not reach the level of absolute and relative BDT peak, and performs at an unremarkable level in Experiments 2–5, everything else (ADI scores, FSIQ, VIQ, PIQ) being equal. With locally oriented processing being found in the entire autistic population and superior perceptual performance being found only in half of them, locally oriented processing may be a necessary, but not sufficient, condition for the development of BDT peak. An indication that visuospatial peaks are a developmental ongoing process has been proposed by Joseph *et al.* (2002), who found greater visuospatial peak versus base line discrepancy in autistic children aged 8 years 11 months than in children aged 5 years 5 months. The fact that the HFA-P group presents with a greater level of unusual preoccupations and sensory interests than the HFA-NP group suggests that locally oriented visual processing might be causally related to these behaviours in a fraction of autistic individuals, thereby overtraining low-level perception in this subgroup. However, a reverse causality (e.g. absence of development of peaks of ability in a subgroup of autistics due to environmental suppression of repetitive behaviours) is also possible.

Specificity and sensitivity to autism of locally oriented processing and of EPF

Diminished sensitivity to perceptual coherence is found in both HFA-P and HFA-NP groups. In contrast, absolute

BDT peak is not specific: its estimated incidence in TD participants from our database is 19% (FSIQ: mean = 107, SD = 16, range = 65–137), whereas it is found in 21% of the autistic population (FSIQ: mean = 84, SD = 21, range = 40–120). However, relative BDT peak is clearly more frequent in autistic (47%) than in typical individuals (2%). Although frequently 1 to 3 SD above IQ baseline, BDT performance in autism is highly correlated with FSIQ (0.613, $P < 0.000$; Mottron *et al*., 2004). Less than 10% of autistic individuals perform at an inferior level in BDT compared with their IQ baseline, whereas this happens in 50% of typically developing individuals. However, although BDT performance of HFA-P and NP groups is unremarkable for minimal level of PC, they become superior to the TD group for intermediate and maximal levels of PC. This suggests that the standard BDT of the Wechsler scales, on which our initial division of HFA-P versus HFA-NP was grounded, was not difficult/sensitive enough to reveal the superiority of the HFA-NP participants. In consequence, the poor sensitivity of BDT peak (38%) reported by Siegel *et al.* (1996), also based on a standard BDT, represents a clear underestimation of the incidence of relative BDT superiority to other Wechsler subtests. In summary, a relative BDT peak appears as relatively sensitive to autism, inasmuch as high levels of perceptual coherence in the figure to be reproduced reveals an autistic superiority in this task, and that performance of autistic participants is compared with that of non-autistic participants of similar FSIQ measured by Wechsler scales.

Regarding perceptual superiority of the HFA–P group in other visual tasks, it could also be seen as poorly specific, as this superiority vanishes when performances of the HFA-P group are compared with those of typically developing participants with similar BDT performance, the TD-P group. However, the specificity of EPF increases considerably if one considers the relation between perceptual performance and average FSIQ. Accordingly, the TD-P group was, on average, 20 points higher in FSIQ than both the TD and the HFA-P group. Therefore, the relative performance of the HFA-P group, that is, having higher perceptual strength than their FSIQ predicts, appears as unique to the HFA-P group.

Neural models for BDT peak and visual EPF

Typical or superior performances in a series of tasks relying on binding of local features do not support a magnocellular involvement in autism. The association of locally oriented processing with enhanced performance in a wide range of visual tasks relying on the detection and discrimination of simple visual material instead suggests an enhanced functioning and role of V1. In typical individuals, feed-forward visual processing follows a double hierarchical pattern. More posterior regions of the occipital lobe are devoted to extraction of unique dimensions and to small areas of the visual field, and more anterior regions both to large areas of the visual field and increasingly abstract, higher-order operations like global processing and categorization (Grill-Spector and Malach, 2004). According to this view, both superior performances in extracting one-dimensional aspects of visual information and locally oriented processing would therefore result from superior functioning of the same region of the posterior-central visual cortex, V1. The fact that these two aspects are found atypically enhanced in a substantial portion of the autistic population, and that one aspect (locally oriented processing) is observed in a large majority of the autistic population makes the implication of this region a strong candidate for visual perceptual atypicalities in autism.

Within V1, the enhanced functioning of the early parvocellular pathway may be a candidate to account for both locally oriented and superior low-level performances in autism. The parvocellular pathway conducts high-resolution visual information and is involved in processing fine-grained stimulus configurations, initial detection and segregation of objects from the background, and object identification (Merigan *et al*., 1993; Steinman *et al*., 1997). It is optimized for encoding information about colour/wavelength and stationary stimuli, and is also more sensitive to details of objects (high spatial frequency; Kaplan, 1991; Merigan *et al*., 1991; Merigan *et al*., 1993). The detection of form contours from individually oriented line elements may be achieved though lateral interaction of orientation selective cells operating in V1, in addition to integrating feedback from higher levels (see Hess *et al*., 2003, for a review). Therefore, local structure can be encompassed by single neurons in V1 (Dakin and Frith, 2005). The 'blocks' used in Experiments 1–4 and in the visuomotor control task share the property of being static, contour and plain colour-defined, and simple (squares and triangles). Most of their detection should plausibly be accomplished at the earliest part of the parvocellular pathway. Although Experiment 5 involves apparently more complex stimuli, these are also composed of coloured squares at the local level, and their processing relies mostly on lateral and anterior occipital sulci and the occipitotemporal sulcus (Ciesielski *et al*., 2005).

Other converging arguments for the implication of a V1 'overfunctioning' in enhanced visual functioning evident in autism come from a recent study by Bertone *et al.* (2005), which investigated a group of 13 HFA individuals, 5 of whom were also in the current HFA-P group. Bertone *et al.* (2005) measured first- and second-order information processing along the parvocellular pathway in autism. Their HFA group was superior for identifying the orientation of simple, first-order gratings, processed in V1, but inferior for identifying the orientation of second-order gratings when compared with typically developing participants. Eighty-three per cent of the autistic participants in Bertone *et al.*'s study presenting superior discrimination of first-order gratings also had a relative BDT peak.

Such a specific dissociation between first- and second-order stimuli could result from diminished (or different, e.g. non-mandatory) long-range feedback from higher-order cognitive processes (Frith, 2003). It could also result from non-mandatory regional feedback, here between V2V3 and V1. In the same direction, a superior activation of right lateral occipital cortex (Brodmann Area—BA-17, 18 and 19) during an EFT was reported by the unique fMRI design exploring pattern detection in autism (Ring *et al*., 1999). However, the absence of a control perceptual task in this study prevents the attribution of this finding to disembedding or enhanced performance *per se*. Considering that V1 typically reduces activity when elements form coherent shapes, and that greater activity in V1 indicates that a collection of lines cannot be resolved into shapes (Murray *et al*., 2002), this superior activity may be explained by atypical spatiotemporal dynamics of V1 during object features binding or to an atypical functional dedication of V1 in autism. Currently, the unique argument for a reduced synchrony between V1 and another level of processing is derived from the finding of diminished functional synchrony between V1 (BA 17) and frontal area 44 in a task involving the observation of visual material (Villalobos *et al*., 2005).

We therefore propose that in a significant proportion of autistic individuals a superior visual input issuing from early stages of visual processing increases the level of performance of subsequent feed-forward flow of visual information as local–global hierarchical processes (Experiments 1 and 2), long-term visual memory (Experiment 3), visual selective attention (Experiment 4) and texture discrimination (Experiment 5). If confirmed, V1 overfunctioning itself calls for explanation, and various candidates are currently available: overall diminished cross-talk between brain regions (Just *et al*., 2004; McAlonan *et al*., 2004); atypical neural connectivity, in the form of enhanced lateral inhibition, more beneficial to 'simple' visual tasks (Bertone *et al*., 2005); diminished feedback of higher-order mechanisms (C. Frith, 2003) or within low-level visual areas (from V3-V2 to V1; Bertone *et al*., 2005); local overconnectivity combined with long-range underconnectivity (Belmonte *et al*., 2004); less specified mechanisms dedicated to high and low spatial frequencies (Boeschoten *et al*., submitted for publication); and long-term effects of the 'optional' use of higher-order processes (Mottron *et al*., 2006*b*). Whatever existing or emerging explanation prevails, we contend that overall skewing of visual processing toward posterocentral occipital brain regions represents an adequate description of the autistic endophenotype, regarding low-level visual perception. Moreover, the finding of similar superior performances in functions accomplished by the primary auditory cortex (Bonnel *et al*., 2003; see Samson *et al*., 2005, for a review) indicates that perception *per se* may be reorganized in autism.

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