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Enhanced visual processing contributes to matrix reasoning in autism

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Abstract

Recent behavioral investigations have revealed that autistics perform more proficiently on Raven's Standard Progressive Matrices (RSPM) than would be predicted by their Wechsler intelligence scores. A widely-used test of fluid reasoning and intelligence, the RSPM assays abilities to flexibly infer rules, manage goal hierarchies, and perform high-level abstractions. The neural substrates for these abilities are known to encompass a large frontoparietal network, with different processing models placing variable emphasis on the specific roles of the prefrontal or posterior regions. We used functional magnetic resonance imaging to explore the neural bases of autistics' RSPM problem solving. Fifteen autistic and eighteen non-autistic participants, matched on age, sex, manual preference and Wechsler IQ, completed 60 self-paced randomly-ordered RSPM items along with a visually similar 60-item pattern matching comparison task. Accuracy and response times did not differ between groups in the pattern matching task. In the RSPM task, autistics performed with similar accuracy, but with shorter response times, compared to their non-autistic controls. In both the entire sample and a subsample of participants additionally matched on RSPM performance to control for potential response time confounds, neural activity was similar in both groups for the pattern matching task. However, for the RSPM task, autistics displayed relatively increased task-related activity in extrastriate areas (BA18), and decreased activity in the lateral prefrontal cortex (BA9) and the medial posterior parietal cortex (BA7). Visual processing mechanisms may therefore play a more prominent role in reasoning in autistics.

Keywords

fMRI; perception; pattern matching; intelligence

Introduction

Raven's Standard Progressive Matrices (RSPM; Raven 1976) is broadly recognized as an effective means to estimate fluid intelligence, that is, the general ability underlying novel

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problem solving and reasoning (Mackintosh 1998). Consisting of a series of matrix reasoning problems of increasing complexity and difficulty, RSPM assays abilities to infer and integrate rules, to manage goal hierarchies and to form abstractions (Carpenter, et al. 1990). RSPM may be regarded as the most general single test of intelligence, as its measures are highly correlated with a wide range of other intelligence tests (Neisser 1998; Snow, et al. 1984). Recently, we observed that autistics' RSPM performance was better than predicted by their scores on the Wechsler intelligence scales (WISC-III, WAIS-III; Wechsler 1991; Wechsler 1997), the test battery most commonly used to assess autistics' intelligence. For both children and adults, autistics' RSPM scores were on average 30 percentile points higher, and ranged up to 94 percentile points higher, than their Wechsler scores, whereas for non-autistics there was no discrepancy (Dawson, et al. 2007). In related work, Asperger syndrome children were found to have significantly higher RSPM raw scores compared to a group of typically developing children matched on age and Wechsler IQ (Hayashi, et al. 2008). Together, these findings suggest that Wechsler IQ may routinely underestimate intelligence in autism and that autistics' reasoning abilities may be significantly better than reported in much of the existing clinical literature. However, the neural mechanisms responsible for this unexpectedly high level of reasoning skill are not obvious. One way to explore the source of autistics' enhanced RSPM performance is to investigate the brain mechanisms involved in matrix reasoning.

Previous neuroimaging studies exploring fluid reasoning in non-autistics have identified task-related activity in a large, bilateral frontoparietal network, involving multiple regions in lateral prefrontal and posterior parietal cortex (Haier, et al. 1988; Kalbfleisch, et al. 2007; Kroger, et al. 2002; Lee, et al. 2006; Perfetti, et al. 2008; Prabhakaran, et al. 1997). Despite the wide range of cognitive processes involved in complex tasks such as RSPM, the brain regions repeatedly identified across studies are relatively consistent (see Jung and Haier 2007 for a systematic review). Within this network, some authors emphasize the role of dorsolateral and ventrolateral prefrontal cortex in reasoning (Christoff, et al. 2001; Crone, et al. 2009; Duncan, et al. 2000; Kane and Engle 2002). Evidence supporting the importance of prefrontal cortex in reasoning includes impairments in fluid reasoning reported to occur following prefrontal damage (Duncan, et al. 1995; Duncan, et al. 1996; Waltz, et al. 1999), though this finding is not universal (Villa, et al. 1990). In a PET study, Duncan et al. (2000) used two different tasks, one using verbal and the other non-verbal material, that both involve reasoning in the context of novel problem solving, that is, *fluid* reasoning. The overlap in task-related activity, located in lateral frontal cortex, was thought to reflect the reasoning component common to the two tasks. However, using similar reasoning tasks in an fMRI study, Duncan and colleagues recently reported activity in both frontal and parietal cortex, weakening their claims concerning a predominant role of prefrontal cortex in reasoning (Bishop, et al. 2008).

There are numerous alternative accounts of the functional neuroanatomy of reasoning that emphasize the involvement of a larger, more spatially distributed set of cortical regions (Haier, et al. 2003; Jung and Haier 2007; Lee, et al. 2006). Based on their review of 37 structural and functional neuroimaging studies, Jung and Haier (2007) formulated the Parieto-Frontal Integration Theory (P-FIT) of intelligence, a behavioral and physiological account of the regional functional specialization of fluid intelligence. In this model, occipital and temporal cortical activities (Brodman areas 18, 19, 21, 37) are associated with a collection of recognition, elaboration and imagery processes acting on sensory input received from primary visual cortex. Outputs of these processes influence posterior parietal cortical areas (BA 7, 39, 40) responsible for abstraction and elaboration. Parietal regions then interact with dorsolateral and ventrolateral prefrontal cortex (BA 6, 9, 10, 45, 46, 47), to support the need for varying amounts of hypothesis testing. Finally, primary and premotor regions are engaged to generate appropriate responses. This type of spatially and temporally

distributed processing model gives particular emphasis to the contributions of occipital and parietal brain regions to the larger reasoning network.

One experimental strategy for distinguishing among candidate reasoning models involves studying how regional brain activity is differentially modulated according to problem complexity or individual differences in reasoning skill. Activity changes related to problem complexity have been investigated using a figural vs. analytic characterization of RSPM items. While figural items can be largely solved with perceptual strategies such as gestalt completion, analytic items require progressively more complex rule inference and integration (Carpenter, et al. 1990). As problem complexity increases, so does activity across many parts of the reasoning network (Lee, et al. 2006; Prabhakaran, et al. 1997), including changes in prefrontal cortex (Christoff, et al. 2001; Crone, et al. 2009; Kalbfleisch, et al. 2007; Kroger, et al. 2002). As for individual differences, higher intellectual abilities are associated with relatively increased engagement of occipital and parietal cortex and decreased engagement of frontal cortex in abstract reasoning, as is activity associated with a variety of cognitive tasks (Blair 2007).

Because recent findings show a relative advantage for autistics in RSPM performance as compared to their Wechsler IQ, studying the neural mechanisms responsible for autistics' reasoning skills may provide unique insights into the nature of autistic cognition. The complex character of matrix reasoning, and the existing evidence for regional functional specialization of many perceptual and cognitive processes, raises the possibility that, when reasoning, autistics may differentially engage the some components of the frontoparietal reasoning network. This notion is supported by evidence from previous fMRI studies comparing autistic to non-autistic brain activity during reasoning tasks involving semantic categorization, sentence comprehension and working memory. These studies have all found increased activity in extrastriate areas and decreased activity in prefrontal cortex in autistics (Gaffrey, et al. 2007; Kana, et al. 2006; Koshino, et al. 2005). In addition, in developing the enhanced perceptual functioning (EPF) model of autism, we have compiled a wide array of behavioral and physiological evidence regarding the atypical and enhanced role of perception in autism (Mottron, et al. 2006). The EPF model offers a mechanistic account explaining why a significant proportion of autistics display advantages in visual perceptual tasks, including target detection, visual discrimination and visuospatial construction. Extending this model to more complex cognitive phenomena, it is possible that autistics' skill in fluid reasoning reflects stronger engagement of occipital and parietal neural mechanisms responsible for visual attention, object encoding and abstraction.

To explore the neural bases of autistic reasoning, we used fMRI to measure neural activity during RSPM problem solving, making minimal modifications to the test to maximize the ecological validity of the results. This approach has the potential advantage of allowing more accurate inferences about the particular brain processes engaged when RSPM is administered in clinical settings. The EPF model predicts that the neural systems involved in matrix reasoning will include stronger engagement of visual perceptual mechanisms in autistics.

Methods

In this study, autistic and non-autistic control participants completed two related self-paced tasks, the 60 RSPM problems in random order, and a comparison pattern matching task designed to be visually similar to RSPM but requiring minimal reasoning. Task-related changes in brain activity were recorded using fMRI.

Participants

The entire experimental sample comprised 15 autistics and 18 non-autistics, 14 to 36 years old (Table 1). While both groups performed the self-paced RSPM fMRI task with equivalent accuracy, the autistic group responded more quickly. To avoid possible confounds associated with this discrepancy in mean response times, our principal analyses were conducted on participant samples additionally matched on mean RSPM task response times. This matching process was achieved by excluding results from the three fastest autistic participants and the five slowest non-autistic participants, resulting in equivalent mean response times in final groups comprising 12 autistic and 13 non-autistic participants.

All participants gave written informed consent and were compensated for their participation in accordance with protocol # 06-07 018 approved by the Regroupement Neuroimagerie/ Québec IRB. Exclusion criteria were: uncorrectable visual impairment; current use of psychoactive or vasoactive medications; and use of drugs or alcohol exceeding 2 drinks per day. All structural scans were reviewed by a neurologist to rule out the presence of any anatomical abnormalities. Additionally, non-autistics were screened through a questionnaire for any personal or familial neurological or medical conditions known to affect brain function. Groups were matched on age, sex, manual preference and full-scale IQ.

Clinical Characterization—The autistic participants were recruited from the research database of the Pervasive Developmental Disorders Specialized Clinic of Rivière-des-Prairies Hospital (Montreal, Canada). A multidisciplinary evaluation based on DSM-IV criteria is performed at the clinic, including the Autism Diagnostic Interview-Revised (ADI-R; Lord, et al. 1994), the Autism Diagnosis Observation Schedule module 3 or 4 (ADOS-G; Lord, et al. 2000), clinical evaluation and psychometric testing. Twelve autistic participants were characterized with both standardized diagnostic instruments, and three were characterized with the ADI and a clinical interview based on an ADOS-G assessment. Individuals with no history of speech delay, echolalia or pronoun reversal, and who therefore also met criteria for Asperger syndrome, were excluded from the sample.

Psychometric Characterization—Full-scale IQ scores were derived from Wechsler Scales of Intelligence (WISC-III or WAIS-III) scores; autistics in the performance matched sample had a mean IQ of 101.5 and non-autistics 105.31. The corresponding scores for the entire sample were 99.73 and 106.22. Manual preference was estimated using the Edinburgh Handedness Inventory. There was no significant difference between the two groups in IQ or manual preference (Table I).

Task descriptions

Pattern matching task—To allow comparison with a task requiring minimal reasoning, we developed a self-paced 60-item pattern matching task that had similar spatial and temporal properties to the RSPM problems, with a target stimulus displayed above 8 possible answers (Figure 1a). The stimulus was presented until the participant responded. In this self-paced, variable epoch length design, individual problem presentations were separated by periods of fixation whose duration varied from 4 to 7 sec, following an exponential distribution.

RSPM task—We used a slightly modified version of the original, 60-item, untimed, paper version of the RSPM. The RSPM problems are matrices of related geometric designs, from which the final (right-hand bottom) entry is missing and must be chosen from an array of 8 possible answers (Figure 1b and c). In the original version of the test, simple or figural items at the beginning progress to more difficult and complex analytic items. We made modifications to the original RSPM by: (1) horizontally shifting the rows of possible

answers, respectively to the left and right, to simplify the mapping of answers made by pressing buttons with the left or right hand; and (2) reducing non-specific temporal effects by presenting the 60 RSPM items in a counterbalanced order, so that difficulty was not confounded with presentation order. The periods of fixation between problem presentations were the same as those used in the pattern matching task.

Procedure

The first practice session, lasting 5 to 10 min, was done with the participant sitting in front of a computer monitor to gain familiarity with the stimuli and use of the response buttons. Pattern matching items used in this session were similar, but not identical, to those used during the fMRI sessions. Participants were instructed to select the response pattern that best matched the target pattern among the 8 possible choices and then press one of a linear button array for answers “1-4” with their left hand or another button array for answers “5-8” with their right hand.

The second practice session took place in a mock MRI scanner, using the same pattern matching task employed in the previous practice session. After practicing in the mock scanner, the participants were instructed to solve the RSPM problems by “finding the best answer to fill in the missing piece in the large rectangle.” Participants were also told to study each problem until reasonably certain that they had determined the best answer, with no explicit time limit.

The actual fMRI testing session then followed. The imaging session began with a 10 min EPI session with eyes closed to allow participants to acclimate to the gradient noise and confining environment of the MRI system, a procedure employed to minimize between-group differences in sensitivity to the imaging environment. Then the 60-item pattern matching task was presented, which took approximately 9 to 12 min. Participants then completed the 60-item RSPM task, which took 14 to 35 minutes depending on individual speed. A structural MRI scan was done after the RSPM task. Instructions for the two tasks were repeated before going into the fMRI scanner and immediately before each task.

Image acquisition

We used a Siemens Trio 3T scanner with an 8 channel phased-array head coil. Functional data were acquired using an echo planar imaging pulse sequence (48 slices, 3mm cubic voxels, TR = 2850 ms, TE = 30 ms, flip angle = 90°). The first 2 volumes of each session were discarded to allow for longitudinal magnetization equilibration. T1-weighted structural brain images were acquired at the end of the experiment (MP-RAGE, 176 slices, 1 mm cubic voxels, TR = 2530 ms, TE = 3.48 ms, flip angle = 7°).

Stimuli were displayed on a rear projection screen at the back of the scanner bore, with a mirror fixed on the head coil allowing participants to see the screen. Tasks were presented using Presentation (www.neurobs.com).

Image analysis

We used SPM5 (www.fil.ion.ucl.ac.uk/spm/) and MRIcron (www.sph.sc.edu/comd/rorden/mricron/index.html) for image preprocessing, statistical analysis and visualization.

Preprocessing—Image preprocessing steps included: (1) correction for slice timing differences by temporally interpolating voxel time courses in each slice to acquisition time of the middle slice of the EPI volume; and (2) two-pass realignment involving initial registration of all images to the first image of the time series, followed by registration of the

images to the mean of the images computed after first realignment, followed by resampling using 4th degree b-spline interpolation.

Spatial normalization—Images were directly transformed into MNI305 space by directly determining the non-linear mapping between realigned images and the SPM5 EPI template, using 8mm source imaging smoothing, 16 nonlinear iterations and resampling to 2mm cubic voxels using 5th degree b-spline interpolation. To compensate for residual within and between group anatomical differences, spatially normalized images were smoothed with an isotropic Gaussian spatial filter with a full-width at half maximum (FWHM) of 9 mm.

Statistical modeling—For each participant, volumes acquired during the pattern matching and RSPM task sessions were treated as separate time series. For each session, BOLD-contrast signal variance was decomposed with a set of regressors using a general linear model. For both the pattern matching and RSPM tasks, total variance was decomposed into components associated with task performance, with intervening fixation periods serving as an implicit inter-trial baseline for comparison. Regressors for pattern matching, figural RSPM items and analytic RSPM items of various difficulty levels were constructed by first generating boxcar functions of variable width with: (1) amplitudes of 1 during the task periods and 0 for the intervening fixation periods; and (2) durations corresponding to time spent considering each problem. These boxcar functions were then convolved with the SPM5 canonical hemodynamic response function resulting in regressors used to obtain parameter estimates proportional to task-related neural activity per unit time. These regressors, together with other regressors modeling residual movement-related signal modulation, the mean signal for the session, and a discrete cosine transform basis set modeling the low-frequency, presumably artifactual, signal modulations below 0.01 Hz, jointly comprised the full model for each participant. Ordinary least-squares parameter estimates for each regressor were then calculated from the fit of the model to the data using classical restricted maximum likelihood algorithms.

To allow inferences at the population level, a summary statistics second-level analysis was performed using a voxel-wise factorial ANOVA, with Group and Task factors, on images representing the activity associated with the task vs. fixation contrasts derived from each participant. The Group factor (2 levels) was assumed to have unequal variance and independence between levels. The Task factor (6 levels: pattern matching, RSPM with 1 figural and 4 analytical difficulty levels) was assumed to have unequal variance and dependence among levels. For our planned contrasts, the critical threshold for within-group voxel-wise estimates of task-related activity (task vs. fixation) was $p < .05$, FWE-corrected, with an extent threshold of 50 contiguous voxels. Because of the expected weaker strength of between-group comparisons or between-tasks comparisons, the critical threshold used for these contrasts was $p < .001$, uncorrected, with an extent threshold of 50 contiguous voxels, jointly providing sufficient protection from Type I error.

We then computed a series of statistical parametric maps to examine a set of focused hypotheses, including: (1) simple effects contrasts examining the form of pattern matching and RSPM task-related activity within each group, (2) conjunction analysis identifying aspects of the task-related activity common to both groups, (3) between-group contrasts revealing how task-related activity differs between groups, (4) parametric analysis identifying effects of matrix reasoning problem difficulty, (5) prior anatomical specification using small volume correction analysis identifying visual processing areas differentially modulated in the autistic and non-autistic groups, and (6) Group × Task interaction contrasts revealing the regions where matrix reasoning exceeded pattern matching activity in the autistic compared to the non-autistic groups.

The 60 RSPM task items were divided into figural and analytic types, grouping problems of similar type and allowing examination of difficulty effects. Classifications derived from Van der Ven and Ellis (2000) and Lynn (2004) were used to classify 16 of the RSPM items as figural and 44 as analytic. Analytic items were further divided into 4 levels of difficulty, for which the difficulty was estimated from the mean accuracy of a previous sample of 26 non-autistic adults drawn from our research database, who were examined using the original paper version of RSPM. In the image analyses, a parametric analysis was conducted using these 4 levels of difficulty, with the contrast weights for the 4 levels derived from the mean accuracy obtained for that level in the non-autistic 26-adult sample. In addition, contrasting the easiest analytic items with the figural items, matched for accuracy, allowed identification of activity differences related to problem type, while controlling for problem difficulty.

As the EPF model posits that visual processing mechanisms play a central role in autistic cognition, we used it to generate anatomical predictions concerning loci of differential activity between autistic and non-autistic groups engaged in matrix reasoning. Specified regions of interest (ROIs) in occipital and posterior parietal cortex were derived from task vs. fixation contrasts, collected from a separate group of 16 typical adults (21 to 40 years old) performing the same pattern matching task (unpublished results). ROIs centered on the eight most significant local maxima in occipital and parietal cortex, four in each hemisphere, were used to compare task-related activity in autistics and non-autistics in both the pattern matching and RSPM tasks. Critical thresholds were chosen using a small volume correction based on a search radius of 10 mm and a significance level of $p < .05$, FWE-corrected. We hypothesized that activity related to visual matrix reasoning would be higher in autistics relative to non-autistics in the occipital and parietal regions. This procedure represents a relatively strict test of one of the central predictions of the EPF model, because the ROIs to be used for the RSPM task were derived from an independent sample studied at a different site using a different MRI system.

Eye movement—As growing evidence documents atypical oculomotor behavior in autism, we took steps to estimate the net amount of oculomotor activity during each session. Following methods developed to derive estimates of saccadic (Beauchamp 2003) or pursuit (Tregellas, et al. 2002) eye movement density from brain image time series, we used an approach similar to those used in previous autism studies (Haist, et al. 2005; Mizuno, et al. 2006; Villalobos, et al. 2005), in which the variation of BOLD-contrast signal in the orbits serves as an index of the net amount of ocular movement (or saccade density). Two 12.5 mm spherical ROIs were used to extract the time-course of the BOLD-contrast signal for each eye of each participant. For each participant, the standard deviation of the temporal variability of BOLD-contrast signal was averaged for both eyes to obtain an estimate of net saccade density during problem solving. A Group × Task analysis of variance was used to compare the saccade density between the two groups in the two tasks.

Head movement—Between-group differences in head motion can be a concern in studies with clinical populations. To mitigate these effects, the preprocessing realignment process yields estimates of head translation and rotation that are then treated as covariates in the first-level fMRI model. As the incorporation of head motion estimate covariates in the statistical models used to isolate the task-related effects of interest provides incomplete protection from head motion modulation of the MRI signal, we also tested for between-group differences in the estimated head motion. Head motion time series were used to compute estimates of net head translation and rotation in both groups. Then the mean displacement (mm/sec) and rotation (degrees/sec) along each of the x, y and z axes were computed for both tasks. The peak-to-peak translation (mm) for x, y and z axes and the peak-to-peak rotation (degrees) for the pitch, roll and yaw axes were also computed for each

participant in each task. Those parameters were compared in autistics and non-autistics with Group × Task ANOVA.

Results

Behavioral data

Task accuracy and response time—A Group × Task (pattern matching, figural and analytic task types) ANOVA was conducted on accuracy in the RT-matched sample. This analysis revealed a main effect of Task, F (2, 46) = 101.62, $p < .01$, with highest accuracy for the pattern matching task, then the figural items, then the analytic items (pairwise comparisons, all $p < .01$ after Bonferroni correction for multiple tests). However, there was no main effect of Group and no interaction between Group and Task factors, both $F < 1$. A similar ANOVA on RT in the matched samples revealed a main effect of Task, F (2, 46) = 224.95, $p < .01$, with the pattern matching problems being the fastest, then the figural reasoning problems, with the analytic reasoning problems being the slowest (all $p < .01$). There was no effect of Group and no interaction between the Group and Task factors, both $F < 1$. These results confirm that our matching procedure satisfactorily removed between-group differences in RT, while preserving similar accuracy levels in both groups across task levels (see Table II).

In order to verify that both groups had similar performance on an item-per-item basis, mean accuracy of each item was computed for each group. Correlation of item accuracy between groups was very high, $r = .89$, $p < .01$, demonstrating that, regardless of complexity or difficulty, both groups were similar in accuracy across all the RSPM items. We also attempted to assess whether performing RSPM in the scanner, with items presented in a randomized order, influenced item difficulty. We compared the difficulty level of each item in the original RSPM, derived from a 26-adult sample selected from the research database, with the difficulty level of each item for the autistic and non-autistic groups performing the RSPM task in the scanner. The high in vs. out of the scanner item difficulty correlation found in both groups ($r = .60$, $p < .001$, for the autistics and $r = .65$, $p < .01$, for the non-autistics), while not as high as the between-group, in-scanner correlation, suggests that the task modifications made for fMRI compatibility did not significantly modify the relative difficulty associated with solving the RSPM items in the MRI environment.

Eye movement

As between-group differences in saccade frequency can confound the interpretation of activity modulations observed during temporally extended visual tasks that involve significant visual search components, saccade frequency was estimated from orbital ROIs used to extract the BOLD-contrast signal fluctuation time series for each session. The temporal variation of each time series was then computed as a measure of saccade frequency averaged over the session. The net saccade density (standard deviation of the fluctuation of the BOLD-contrast signal) was similar in autistics and non-autistics in the pattern matching task (mean 4.21 vs. 4.72) and in the RSPM task (mean 3.96 vs. 4.44). A Group × Task (pattern matching vs. RSPM) ANOVA on net saccade density revealed no between-group differences, F (1, 23) = 0.59, $p = .45$, and no interaction, F (1, 23) = 0.04, $p = .95$. These results suggest that between-group differences in saccade frequency are not a major source of variance in our imaging data.

Head movement

The mean 3D translation and rotation rates, as well as peak-to-peak translation and rotation amplitudes along the x, y and z axes for each participant were examined using a repeated measures ANOVA. In the RSPM task, the mean 3D displacement rate was 0.033 mm/sec in

autistics and 0.040 mm/sec in non-autistics, and the mean 3D rotation rate was 0.026 deg/sec in autistics and 0.037 deg/sec in non-autistics. A Group × Task (pattern matching vs. RSPM) × Displacement rate (translation, rotation) ANOVA revealed no significant between-group difference, F (1, 23) = 0.64, p = .43 and no significant Group × Task interaction, F (1, 23) = 1.54, p = .23, or other interactions involving group. Similarly, a Group × Task (pattern matching vs. RSPM) × Peak-to-peak displacement (x, y, z, pitch, roll, yaw) ANOVA revealed no significant effect of Group, F (1, 23) = 0.94, p = .34, and no Group × Task interaction, F (1, 23) = 1.33, p = .26, or other interactions involving group. These results provide no evidence for between-group head motion effects.

Imaging data

Pattern matching task: simple effects contrasts, conjunctions and between-group contrasts—The pattern matching task contrasted with the fixation inter-trial baseline identified broad areas of activity increases in occipital cortex, posterior parietal cortex, prefrontal cortex, brainstem and cerebellum, with both groups having similar patterns (see Tables III and IV, and Figure 2). Between-group contrasts revealed higher activity in autistics in discrete bilateral frontal areas involving BA 4 and 6 (p < .001 uncorrected).

RSPM task: simple effects contrasts, conjunctions and between-group contrasts—The RSPM task compared to the inter-trial fixation baseline revealed an extended bilateral network of activity in non-autistics (see Table V and Figure 3), encompassing occipital cortex, posterior parietal cortex, lateral premotor cortex, primary motor cortex, insula and cerebellum. This contrast yielded highly similar results in the autistic group, with a similar spatially extended pattern of activity. A between-group conjunction analysis confirmed the impression resulting from visual inspection of the individual group maps that both groups exhibited very similar bilateral activity patterns in occipital cortex, posterior parietal cortex and the inferior and middle frontal gyri (p < .05, FWE corrected; see Table VI).

Between-group contrasts of RSPM task-related activity were conducted to verify if the balance of activity within that network was different in non-autistics and autistics. The autistic > non-autistic contrast revealed lower activity in autistics in the medial posterior parietal cortex and left middle frontal gyrus (p < .001 uncorrected; see Table VI and Figure 4 and 5) and higher activity in autistics in left cuneus and middle occipital gyrus (BA18).

Additional analyses were conducted on the RSPM task data to explore effects of item type and difficulty. First, the figural items were contrasted with the easiest analytic items, matched for difficulty. Increased activity associated with the analytical items was found in left extrastriate area (BA18), superior frontal gyrus (BA6) and medial precuneus (BA7; p < .001 uncorrected). We observed no significant between-group differences associated with processing complexity (analytical vs. figural items). Similarly, a parametric analysis examining 4 difficulty levels within the analytic items revealed increased activity in bilateral extrastriate areas (BA18), the middle frontal gyrus (left BA10 and right BA6) and bilateral superior frontal gyrus (BA6), as well as left supramarginal gyrus (BA40) associated with increasing difficulty (p < .001 uncorrected). There were no significant between-group differences in the effects of difficulty on task-related activity.

Small volume correction analysis using a priori functional ROIs—Eight functional ROIs representing activity associated with the pattern matching task obtained from a previous study were used to test the EPF model prediction that autistic reasoning might more strongly engage higher-order visual processing centers (see Table VII). These

regions were located in occipital and posterior parietal cortex, 4 in the left hemisphere and 4 in the right. In the pattern matching task data, the *a priori* ROI analyses did not reveal any significant differential between-group activity. However, in the analysis of RSPM task data, while none of the ROIs showed greater activity in non-autistics, two clusters of greater activity were observed in the autistics in the middle occipital gyrus and cuneus (BA18; $p <$ .05; FWE-corrected), confirming the findings of the voxel-wise between-group contrasts.

Differential group effects comparing matrix reasoning to pattern matching—A Group × Task interaction was computed to characterize the task specificity of any regional between-group differences. Of particular interest was whether areas in occipital or posterior parietal cortex would exhibit greater differential activity for matrix reasoning compared to the pattern matching conditions, and whether this difference would be larger for the autistics. The voxel-wise *t*-contrast shown in Figure 7 revealed an interaction in both left and right inferior occipital cortex (BA18; $p = .001$ uncorrected). As an additional exploration of these effects, we computed Cohen effect sizes at the coordinates of maximal between-group differences for pattern matching, figural and analytic problems. In the left middle occipital gyrus and the medial precuneus, the between-group effect size increased monotonically across the three task types (see Fig 6), suggesting progressively stronger between-group differences in the engagement of these areas as the reasoning demands of the task increased. In the right middle frontal gyrus, effect size differences were somewhat smaller compared to the corresponding location in the left hemisphere.

Comparative analyses of the complete sample—Assuring the compatibility of groups contrasted in observational imaging studies is not an entirely straightforward matter, as the goal of matching task performance characteristics must be balanced against the need to avoid unduly introducing sample bias. To explore the latter possibility, we repeated the analyses of the behavioral data using the entire participant sample, in which the autistic group responded more rapidly than the non-autistic group (15 autistics and 18 non-autistics). A Group × Task ANOVA on accuracy again revealed a main effect of Task, F (2, 60) = 138.50, $p < .01$. The ANOVA on RT revealed a Group × Task interaction, F (2, 60) = 6.01, $p < .01$. While there was no difference in mean RT between the two groups on the pattern matching task ($p = .37$), autistics were on average 40% faster than non-autistics in the RSPM task (all items; 13.65 s vs. 19 s, $p = .01$), and by item type, 23% faster than non-autistics on the figural (6.55 s vs. 8.07 s, $p = .05$) and 42% faster on the analytic items (16.22 s vs. 22.97 s, $p = .01$). In the RSPM task, the more difficult an item, as indexed by mean accuracy in the 26-adult sample, the greater the speed advantage enjoyed by the autistics, $r = .56$, $p < .01$ (see Table II).

The between-group imaging data analyses were also repeated in the entire sample. In both the pattern matching and RSPM tasks, we observed between-group differences qualitatively similar to those seen in the performance-matched group analyses, confirming that the group performance matching procedure did not appear to materially bias the functional neuroimaging results.

Discussion

While solving the RSPM items, autistic and non-autistic participants activated similar spatially extended networks, encompassing occipital, posterior parietal, prefrontal, insular and cerebellar cortical areas. A difference in the balance of activity between the two groups was evidenced by higher left occipital activity and lower medial posterior parietal and left lateral prefrontal activity in autistics compared to non-autistics. Whereas both groups exhibited similar task accuracy, the autistics generated answers more rapidly than did the non-autistics. The potentially confounding effects of this group performance difference were

dealt with by selecting a subsample of participants additionally matched on response time. Analysis of both the performance-matched and complete samples yielded similar results.

Pattern matching in non-autistics and autistics

The comparison pattern matching task was designed to be similar to the RSPM task with respect to the spatial arrangement of stimuli and requirements for response selection. Task accuracy and response times were not significantly different between groups. Both groups engaged the same regions, including occipital, posterior parietal, frontal and cerebellar cortex. In contrast to the results seen in the RSPM task, we observed no between-group differences in occipital activity. The task-related activity seen in both groups was similar to that observed during visual search tasks involving simple figures, where increases are seen in occipital cortex (BA18 and 19), the intraparietal sulcus (BA7 and 40) and the precuneus (BA7), with increasing recruitment of prefrontal cortex (mainly BA6, 9, 46 and 47) with increasing task difficulty (Anderson, et al. 2007). The mainly occipito-parietal and premotor task-related activity observed in our study is consistent with the results of other studies using pattern matching tasks (Dickins 2005).

We did observe between-group differences bilaterally in the precentral and middle frontal gyri, with relatively greater activity in autistics. These areas are believed to be strongly involved in processes related to response selection and execution. As there were 8 distinct response choices from which participants had to select their answers, a differential between-group efficiency in mapping the selected answer to the corresponding response button is a plausible interpretation.

Non-autistics and the RSPM task

The frontoparietal distribution of activity associated with performance of the RSPM task in non-autistics is in agreement with previous neuroimaging studies of matrix reasoning (Duncan, et al. 2000; Kroger, et al. 2002; Lee, et al. 2006; Prabhakaran, et al. 1997), as well as studies of other types of reasoning (Goel and Dolan 2001; Monti, et al. 2007; Wendelken, et al. 2008b; Wright, et al. 2007) and working memory (Gray, et al. 2003). Our results also correspond well with the core functional and anatomical components of the P-FIT model (Jung and Haier, 2007), which include visual analysis and elaboration (occipital), abstraction (posterior parietal) and hypothesis testing (dorsolateral prefrontal). Additionally, the difficulty analysis and the analytic versus figural item analysis, which revealed increasing activity in bilateral middle frontal and inferior occipital gyri and left posterior parietal cortex, were consistent with previous findings (Kalbfleisch, et al. 2007; Kroger, et al. 2002; Lee, et al. 2006; Perfetti, et al. 2008; Prabhakaran, et al. 1997). Kalbfleisch et al. found prefrontal, posterior parietal and occipital activity to be modulated by difficulty and specifically identified the left middle frontal gyrus as the key region modulated by matrix reasoning difficulty. Overall, the RSPM results obtained in the non-autistic group agree with findings in previous reasoning studies sampling typical populations, confirming that it is possible to study fluid reasoning using an ecologically sound, completely self-paced design employing the same 60 RSPM items comprising the paper version of the test.

Autistics and the RSPM task: A. Faster performance

The tendency for the autistics to respond much more quickly during the RSPM task, without exhibiting a concomitant accuracy decrement, was an unexpected and striking finding. While no more rapid than the non-autistic group in the pattern matching task, the autistics were 23% faster in solving the figural RSPM items and 42% faster in solving the analytic RSPM items. While the participants were not asked to provide answers as rapidly as possible, instead being told to take the time necessary to be reasonably certain of finding the best answer, the large observed discrepancy in response times could have arisen from a

processing advantage unique to the autistic group. However, we cannot exclude other plausible explanations based on motivational or other transient state differences in the 2 groups that might influence a participant's intent or ability to respond briskly. Of note in this context is the fact that this response time finding is concordant with other studies where autistics have responded more quickly in a range of speeded tasks, including visual search, disembedding figures and block design (Caron, et al. 2006; de Jonge, et al. 2006; Edgin and Pennington 2005; Falter, et al. 2008; Jolliffe and Baron-Cohen 1997; O'Riordan M 2004; O'Riordan and Plaisted 2001; O'Riordan, et al. 2001; Plaisted, et al. 1998; Shah and Frith 1993). Although the response time advantage for difficult RSPM problems we observed may reflect an underlying processing advantage in reasoning mechanisms enjoyed by autistics, additional studies directed at this specific question will be required to fully explore this possibility.

Autistics and the RSPM task: B. Regional differences in activity

The pattern of activity we observed in autistic participants was highly similar in its spatial distribution to that seen in non-autistic participants. However, in autistics the activity within this network was higher in extrastriate areas, and lower in the middle frontal gyrus and medial precuneus.

Occipital findings—Increased activity in autistics during the RSPM task was seen in left cuneus, with a similar trend found in right cuneus. The cuneus is thought to be involved in updating information in working memory (Roth and Courtney 2007) and making comparisons among visual images (Ferber, et al. 2007). Its role in visual attention includes shifts of attention (Makino, et al. 2004) and selective attention, with higher activity in the cuneus when the control of attention is more “bottom-up” and stimulus-driven than “top-down” and guided by expectations (Hahn, et al. 2006; Yeh, et al. 2007). The visual search literature in autism might also be informative regarding the involvement of extrastriate areas in autistic cognition. While searching for a target embedded in a complex figure, autistics performed more rapidly but did not differ from non-autistics in saccade frequency (Keehn, et al. 2008b). Instead, autistics had significantly shorter fixations, suggesting they were faster at encoding and analyzing the visual information contained in the complex figures. In addition, in fMRI studies, autistics show increased activity in right occipital cortex when searching for a target placed among a field of distracters (Keehn, et al. 2008a) or embedded in a complex figure (Manjaly, et al. 2007; Ring, et al. 1999). The possibly stronger engagement of visual encoding, analysis and attention systems in autistics provides a number of plausible physiological mechanisms by which autistics might exhibit faster or more accurate performance in complex cognitive tasks.

There is ample prior evidence for involvement of extrastriate cortical areas during reasoning in typical individuals. For example, a correlation between scores on Wechsler Scales and the volume of gray matter or cortical thickness in BA18 and BA19 has been reported (Colom, et al. 2006; Shaw, et al. 2006). Moreover, half the PET studies and nearly half the fMRI studies in Jung and Haier's (2007) review reported activity in occipital areas BA18 and BA19 in relation to various types of reasoning. The observations that occipital areas are commonly engaged in typical individuals during reasoning make them plausible candidates to support these same roles in autistics. Furthermore, according to Jung and Haier's P-FIT model, if autistics are more facile in the recognition, elaboration or manipulation of visual input, processes presumably carried out in occipital and parietal cortex, the need for subsequent hypothesis testing, manipulation and evaluation, processes relying more heavily on prefrontal mechanisms, might be reduced.

Prefrontal findings—Activity in bilateral middle frontal gyrus and left precentral gyrus was decreased in autistics relative to non-autistics. In the typical population, the dorsolateral prefrontal cortex is thought to be involved in manipulation and integration of information in working memory, decision processes and cognitive control (Cole and Schneider 2007; Koch, et al. 2005; Wendelken, et al. 2008a). The middle frontal gyrus has been more specifically implicated in updating and manipulating the spatial information stored in parietal cortex, managing task difficulty and evaluating response correctness (Kalbfleisch, et al. 2007; Kroger, et al. 2002; Owen 2004; Tanaka, et al. 2005).

There are now many reports of decreased activity in prefrontal cortex in autistics relative to non-autistics. These studies employ a broad range of tasks, including working memory (Koshino, et al. 2005; Luna, et al. 2002), embedded figure search (Lee, et al. 2007; Ring, et al. 1999), spatial attention (Haist, et al. 2005), categorization (Gaffrey, et al. 2007), sentence comprehension (Kana, et al. 2006) and the attribution of mental states to animated shapes (Castelli, et al. 2002). However, there are also reports of relatively increased prefrontal activity in autistics, in tasks involving motor sequence learning (Muller, et al. 2003), visually guided saccades (Takarae, et al. 2007) and visual search (Keehn, et al. 2008a). Therefore, the aggregate findings to date do not support the existence of a *general*, task-independent, and spatially invariant decrease in frontal cortical activity in autistics. In our results, both groups engaged the same prefrontal cortical regions during the RSPM task and the modulation of activity in the cortical regions as a function of difficulty and problem type did not differ. Although speculative, the differential between-group dorsolateral prefrontal activity may represent a reduced need to engage working memory in the autistic group, resulting from their stronger engagement of more posterior visual encoding processes.

Parietal findings—The lower medial precuneus activity seen in autistics might result from more efficient perceptual processing. The precuneus is involved in networks responsible for maintaining and updating visuospatial information in working memory, visual detection and attention, mental rotation and visual imagery (Brown, et al. 2006; Cavanna and Trimble 2006; Hufner, et al. 2008; Owen 2004; Suchan, et al. 2006; Yeh, et al. 2007). Most importantly, better visuospatial skills have been correlated with lower precuneus activity during reasoning (Ruff, et al. 2003), in exactly the same area where we observed lower activity in autistics. Thus, enhanced perceptual functioning in autistics might be causally associated with lower medial precuneus activity. Although increased activity in the right precuneus has been found in autistics in a visual search paradigm (Keehn et al., 2008), the particular part of the precuneus involved in visual search was more lateral and anterior than the area of decreased activity in our study. Interestingly, while we observed a trend towards increased activity in autistics in the right inferior parietal cortex (see Figure 5) in the RSPM task, the test statistic did not exceed our critical threshold for significance.

Task-related decreases in activity—Extensive cortical areas of decreased activity were found during the RSPM task in both groups, with no significant between-group difference in the magnitude of decrease. These regions correspond to the “default network”, whose core components encompass medial prefrontal cortex, posterior cingulate cortex, inferior parietal lobule, lateral temporal cortex and the hippocampal formation (Buckner, et al. 2008; Raichle, et al. 2001). Decreased activity is typically observed within this network when individuals are engaged in demanding cognitive tasks. Accordingly, the areas of decreased activity appeared more extended during the much more demanding RSPM task than during the pattern matching task. The absence of a group difference in the extent of decreased activity is consistent with Cherkassky et al. (2006), who reported a similarly extended default network in both autistics and non-autistics, although there was decreased synchronization within the regions of this network in autistics, compared to non-autistics.

Brain mechanisms for perception and reasoning in autistics

The EPF model predicts stronger engagement of visual perceptual mechanisms in autistic cognition, including in reasoning (Mottron, et al. 2006). Consistent with this prediction, we recently demonstrated that autistics would preferentially rely on perceptual and visuospatial strategies during deductive reasoning, whereas non-autistics would show an advantage for semantic strategies (Sahyoun, et al. 2009). Our current findings add physiological evidence that perception indeed plays an atypically prominent role in autistic reasoning and problem solving.

Existing fMRI studies have already demonstrated increased activity in autistics in brain regions believed primarily to be specialized for perceptual functions, in visuospatial tasks such as the Embedded Figures Test (Manjaly, et al. 2007; Ring, et al. 1999), visual search (Keehn, et al. 2008a) and a modified version of the Wechsler Block Design task (Hubl, et al. 2003). Moreover, accumulating evidence from experiments involving working memory and reasoning tasks also suggests a stronger engagement of brain regions specialized for visual processing. First, autistics performed an n-back task using a sequence of alphabet letters with equivalent speed and accuracy as non-autistics, while displaying increased activity in inferior temporal and extrastriate cortex (Koshino, et al. 2005). Second, a study of sentence comprehension comparing high to low imagery content also showed increased activity in parietal and occipital regions in autistics (Kana, et al. 2006). Finally, in an fMRI study of semantic reasoning (e.g. Does a hammer belong to the tools category?), Gaffrey et al. (2007) found extended bilateral activity in extrastriate areas in autistics, whereas these areas were not active in non-autistics. In agreement with our results, both Kana et al. (2006) and Gaffrey et al. (2007) specifically reported increased activity in the cuneus (BA18 and 19). Finally, the observation of increased activity in posterior cortical areas in autistics was concomitant with decreased activity in left inferior and middle frontal gyri in two of these three studies (Kana, et al. 2006; Koshino, et al. 2005).

In typical individuals, recent studies exploring the functional neuroanatomy of skill acquisition and expertise converge on the notion that, with increasing expertise in a task, increased activity is observed in brain regions fundamental to that task (Bor and Owen 2007; Debaere, et al. 2004; Guillot, et al. 2008; Hanakawa, et al. 2003; Kucian, et al. 2008; Meyler, et al. 2007; Olesen, et al. 2004) and activity in “supportive” brain regions often decreases (Debaere, et al. 2004; Guillot, et al. 2008; Kucian, et al. 2008; Poldrack, et al. 2005). For example, after the acquisition of a complex bimanual skill, decreased activity was seen in attention and action correction systems, and concomitant activity increases were seen in regions supporting memory-driven actions (Debaere, et al. 2004). Similar findings were recently obtained in matrix reasoning studies. When comparing participants with high and average fluid reasoning abilities, those with higher reasoning abilities exhibited stronger activity in posterior parietal cortex during a matrix reasoning task (Lee, et al. 2006). In a similar manner, individuals who have higher activity in occipital BA18 tend to exhibit better performance on Raven's Matrices (Haier, et al. 2003), a finding interpreted by the authors as evidence supporting the role of this region in integrating and resolving competition among visual inputs during reasoning. It is therefore plausible that autistic individuals, who have well-documented advantages in some aspects of visual processing, could use these perceptual strengths to support reasoning.

Alternative accounts

Eye movements—Differences in ocular movements between autistics and non-autistics could confound neuroimaging studies where frequent saccades occur, as is seen during RSPM task performance. Analysis of orbital fluctuations in BOLD-contrast signal revealed no between-group difference in this measure of eye movement, for either the RSPM or

pattern matching task. This finding is consistent with most of the visual saccade studies employing non-social stimuli in autism, in which no between-group differences in latency, peak velocity or amplitude of visually guided saccades have been reported (Kemner, et al. 2004; Luna, et al. 2007; Luna, et al. 2002; Mercadante, et al. 2006; Takarae, et al. 2004; Takarae, et al. 2007; Thakkar, et al. 2008). Moreover, in a recent review of oculomotor activity in childhood disorders it was noted that, "overall, [visually guided saccades] appear normal in autism and there is insufficient evidence to claim difficulties with attentional engagement within the oculomotor domain for children with autism" (Rommelse, et al. 2008 p.401). As for fMRI studies of visual saccades in autism, we found no overlap between the areas showing between-group differences during visual saccades (frontal eye fields, dorsolateral prefrontal cortex, anterior/posterior cingulate cortex, posterior parietal cortex, precuneus, area V5, thalamus and cerebellum) and the occipital and prefrontal activity differences seen in relation to the RSPM task (Takarae, et al. 2007; Thakkar, et al. 2008). Moreover, none of the peaks of saccadic activity reported in the most recent studies employing non-autistic samples (frontal eye fields, supplementary eye fields, supplementary motor area, superior and middle temporal gyrus, intraparietal sulcus, basal ganglia and cerebellum) overlapped with the regions of between-group differences identified in our RSPM task (Anderson, et al. 2008; Hufner, et al. 2008; Schraa-Tam, et al. 2009).

The only possible area of concern involves the medial precuneus finding, where there is an overlap with studies of saccades in autism, which also found decreased activity in autistics (Takarae, et al. 2007; Thakkar, et al. 2008). However, the relevance of these findings to our interpretation is tempered by the fact that a third study of visual saccades in autism, which used an ROI approach, did not find any between-group difference in the precuneus or any of the 13 other ROIs examined (Luna, et al. 2002).

In summary, while the difference observed in the precuneus in our study could be related to saccadic activity, the other between-group differences and specifically those involving occipital areas, which are the main findings of our study, are not likely to be explained by differences in ocular movements per se.

Increased sensitivity to visual stimulation—One possibility is that increased activity in occipital cortex simply reflects a general increase in autistic sensitivity to all things visual. Against that account is the fact that our between-group differences were more apparent in the RSPM than in the pattern matching task. Specifically, the higher activity in the left cuneus was only seen in the RSPM task and there was no between-group activity difference in occipital or parietal cortex in a pattern matching task that was specifically designed to be visually similar to the RSPM task, but with minimal reasoning components. Increased recruitment of occipital cortex in autistics was limited to the RSPM task, which could suggest a specific role for visual perceptual mechanisms in autistic reasoning.

Origin of neural differences in matrix reasoning between autistics and non-autistics

Regarding possible developmental mechanisms leading to the atypical autistic activity patterns seen in our study, clues may be found in recent studies of white matter microstructure (Barnea-Goraly, et al. 2004; Courchesne, et al. 2001; Herbert, et al. 2004; Ke, et al. 2008; Keller, et al. 2007) and functional connectivity differences in autism (Just, et al. 2004). In autistics, Just and colleagues have observed reduced functional connectivity between frontal and parietal cortex in a variety of tasks, including sentence comprehension (Just, et al. 2004; Kana, et al. 2006), n-back working memory tasks (Koshino, et al. 2005; Koshino, et al. 2008) and response inhibition tasks (Kana, et al. 2007). Similarly, reduced functional connectivity between early visual areas (BA17) and inferior frontal cortex was found in autistics during a visuomotor coordination task (Villalobos, et al. 2005), but this

decrease was concomitant with increased functional connectivity between the thalamus and its frontal targets (Mizuno, et al. 2006). Given existing reports of atypical connectivity in autism, there are several available explanations for our findings.

One possibility, based on proposals advanced by Just and colleagues (2004), is that increased use of occipital brain regions in autistics reflects compensatory activity arising from an atypical neurodevelopmental trajectory, based on significant communication restrictions between prefrontal and occipital regions. In this scheme, inefficiencies in engaging prefrontal mechanisms could result in the development of compensatory strategies and processing mechanisms more heavily reliant on occipital and posterior parietal cortical regions. These compensatory mechanisms would have to be as effective in supporting reasoning as the more typical mechanisms relying on prefrontal function.

An alternative possibility, based on the EPF model, is that stronger engagement of occipital regions represents a “default” processing mode for autistics, resulting in more locally efficient, and therefore more conveniently engaged, visual processing mechanisms. Decreased prefrontal activity in autistics could be a consequence of an alternate resource allocation strategy based on the availability of more efficient processing in occipital cortex, leading to the sort of reduced functional connectivity observed in other studies.

Another possibility, equally consistent with the EPF model, is that a stronger overall functional independence of perceptual processes from higher-order cognitive control permits autistics a greater engagement of perception in a wide range of tasks which are not typically considered perceptual in nature. In non-autistics, the role of perception would be relatively more restricted through the operation of mandatory or automatic higher-order processes which are optional in autism (Soulières, et al. 2007). Across development, enhanced functional independence could result in the type of atypical activity patterns exemplified in our findings. While non-autistics could easily engage perceptual mechanisms in a pattern matching task, their engagement of visual perceptual mechanisms in the service of abstract reasoning might be, in comparison with autistics, significantly curtailed.

More specific investigations of the differences in structural, functional and effective connectivity will be required to further differentiate these intriguing possible explanations for the differential activity patterns seen in our study.

Summary and conclusion

We have shown that autistics, a group with relatively enhanced performance on the RSPM compared to their performance on Wechsler IQ tests (Dawson, et al. 2007; Hayashi, et al. 2008), rely more extensively on occipital, and less on prefrontal, cortex while solving RSPM problems. While these findings are difficult to interpret in the context of strongly localized prefrontal models of reasoning, they may be more easily interpreted in the context of distributed frontoparietal models of reasoning. These models allow for task-specific spatial redistribution of activity guided by resource allocation mechanisms taking advantage of individual processing strengths. In this regard the distributed frontoparietal model seems more promising as a general model of reasoning, as it provides explanatory mechanisms encompassing differences in reasoning complexity, individual abilities and the unique characteristics of human subgroups.

Higher level visual processes most likely play a more prominent role in reasoning in autistics, with the specific mechanism of this enhanced utilization of occipital regions an obvious object of future study. A next step could be to dissect the components of RSPM in order to better understand *how* atypical perceptual mechanisms, and their more prominent utilization by autistics, support reasoning. This knowledge could potentially inform

educational practice by suggesting ways to optimize the form in which information is made available to autistics during their development.

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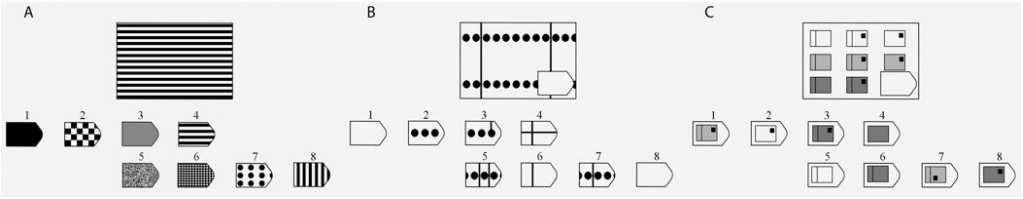

Figure 1.

Sample stimuli for the pattern matching and RSPM tasks. (A) Pattern matching problems required matching the global pattern presented at the top of the screen with one of the patterns presented in the 2 rows below. (B) and (C) RSPM task problems were the 60 items of Raven's Standard Progressive Matrices. The task required selecting the correct answer from the alternatives presented at the bottom of the screen. An example of a figural problem is shown in (B) and of an analytic problem in (C).

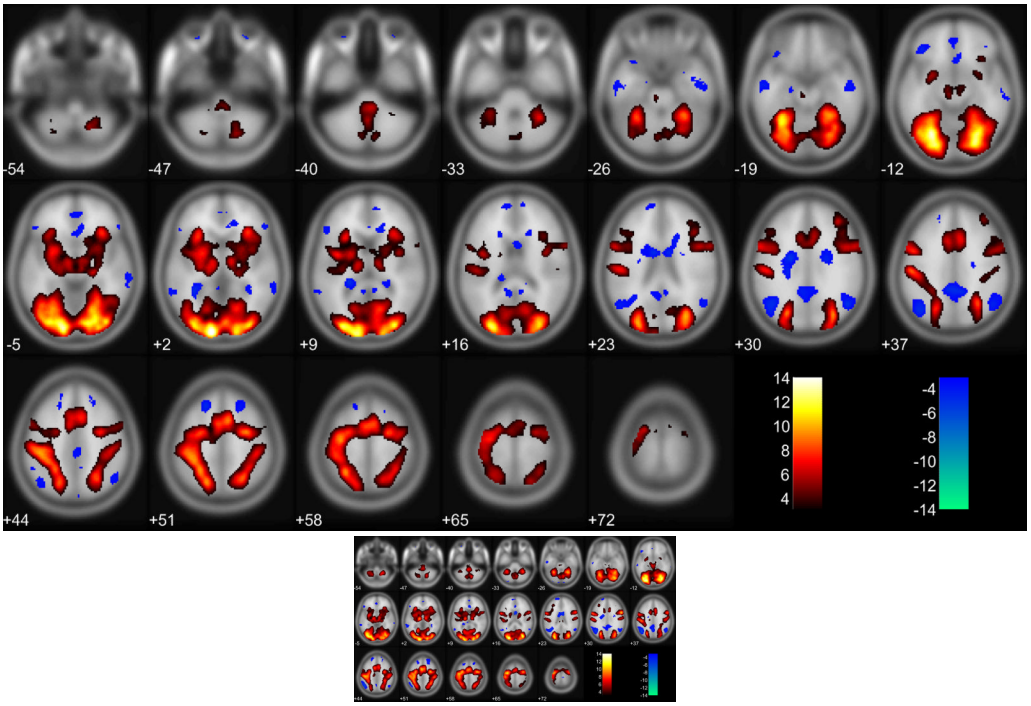

Figure 2.

Relative changes in pattern matching task-related activity contrasted with inter-trial fixation-related activity displayed in axial section. Signal increases are shown in red-yellow and signal decreases are shown in blue-green. Regional variations in task-related activity are displayed using an uncorrected critical threshold of p <.001 for t-statistic maps overlaid on the SPM5 T1 template. Images are displayed using the neurological convention. Results are shown for (A) the non-autistic and (B) the autistic group.

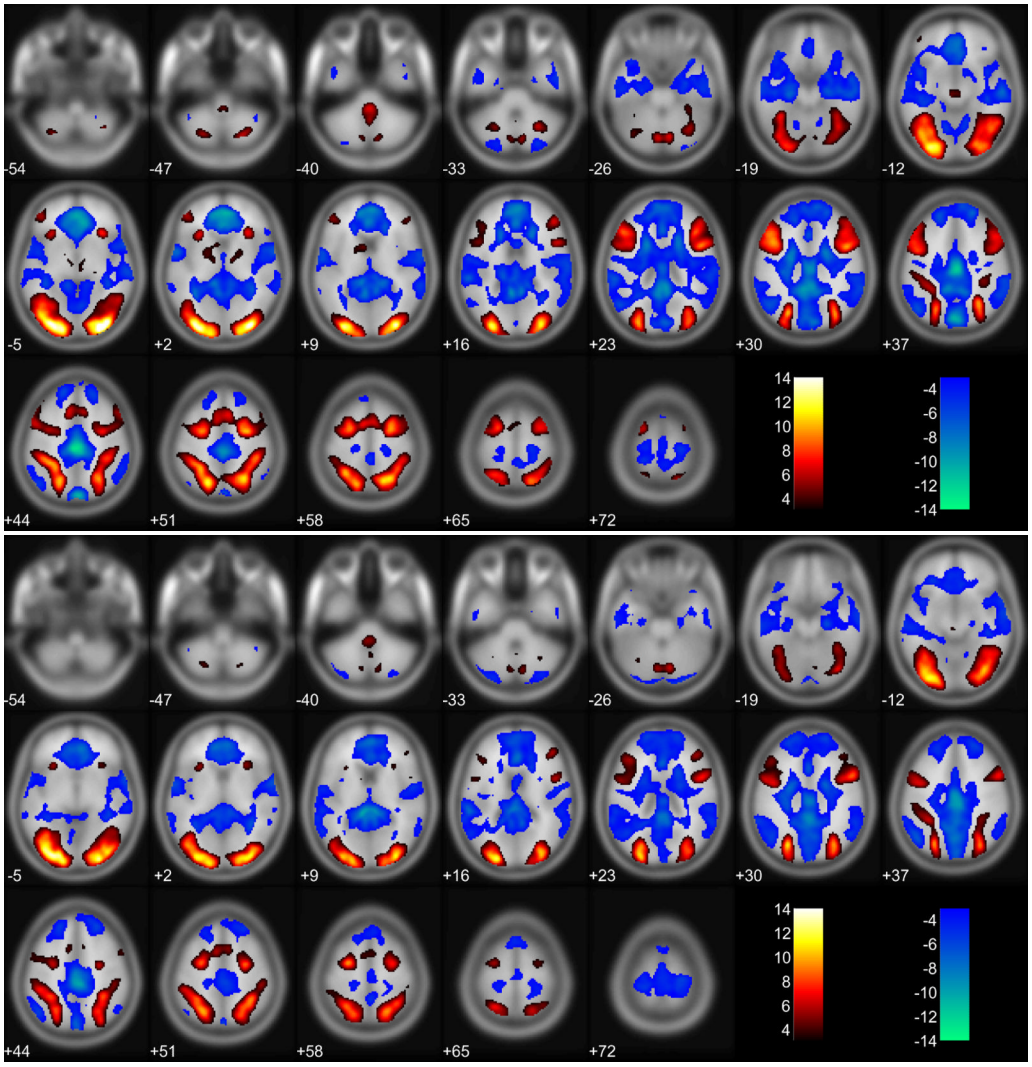

Figure 3.

Relative changes in the RSPM task-related activity contrasted with inter-trial fixation-related activity displayed in axial section. Signal increases are shown in red-yellow and signal decreases are shown in blue-green. The regional variations in task-related activity are displayed using an uncorrected critical threshold of $p < .001$ for t-statistic maps overlaid on the SPM5 T1 template. Images are displayed using the neurological convention. Results are shown for (A) the non-autistic and (B) the autistic group.

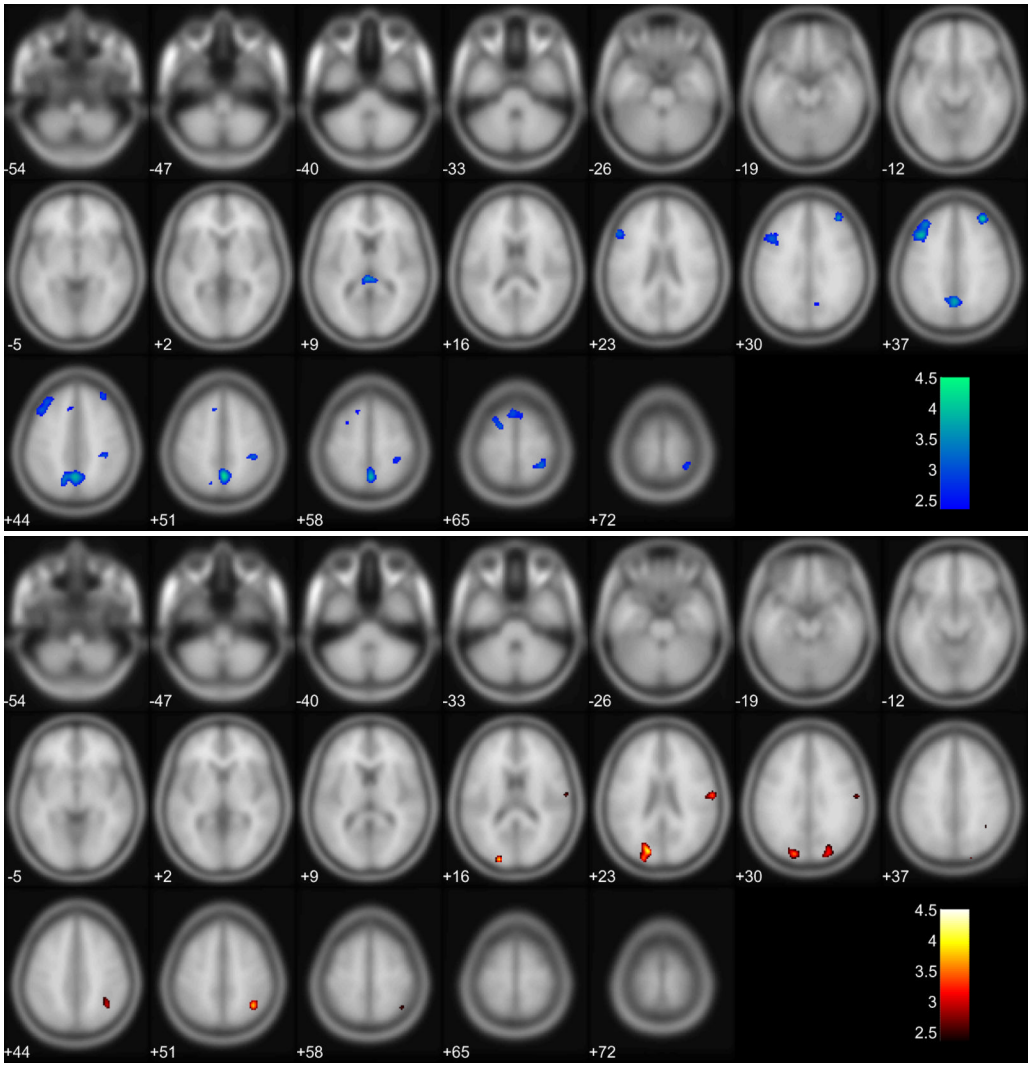

Figure 4.

Group differences in RSPM task-related activity displayed in axial section. Areas in which the signal was greater in (A) the non-autistic compared to the autistic group are displayed in blue-green and areas in which the signal was greater in (B) the autistic compared to the non-autistic group are displayed in red-yellow. To show the spatial distribution of the task-related effects, an uncorrected critical threshold of $p < .01$ and an extent threshold of 140 voxels were used in overlaying the t-statistic maps on the anatomical template. Images are displayed using the neurological convention.

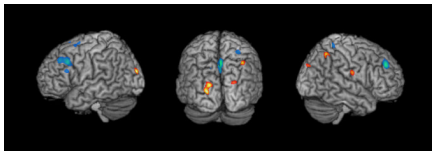

Figure 5.

Volume renderings of group differences in RSPM task activity. Areas in which signal was greater in the autistic compared to the non-autistic group are displayed in red-yellow and areas in which the signal was greater in the non-autistic compared to the AUT group are displayed in blue-green. The spatial distribution of the task-related effects are displayed using an uncorrected critical threshold of $p < .01$ and an extent threshold of 140 voxels. Renderings of the t-statistic maps on LEFT, POSTERIOR and RIGHT views of the anatomical template are shown.

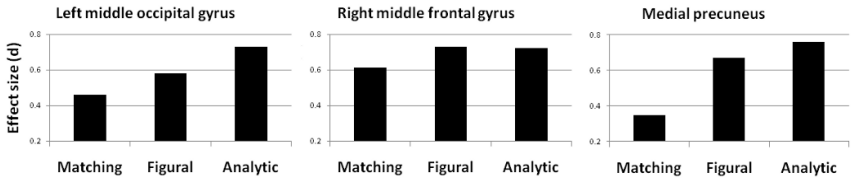

Figure 6.

Effect size (*d*) for the between-group difference in the pattern matching, figural, and analytic problems at the coordinates of maximal between-group difference found in the RSPM tasks. Effect sizes are reported for the left middle occipital gyrus (-22, -92, 18) in the left panel, right middle frontal gyrus (36, 42, 34) in the middle panel, and for the medial precuneus (2, -58, 54) in the right panel.

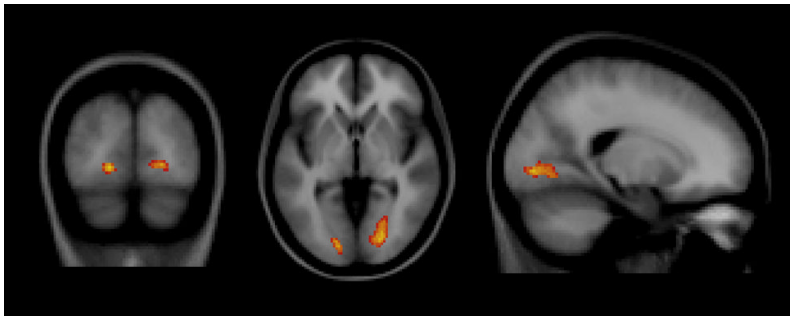

Figure 7.

Group differences in matrix reasoning contrasted with the pattern matching control condition displayed in coronal, axial and sagittal sections. This Group × Task interaction represents additional inferior occipital activity in the autistic group in the matrix reasoning compared to the pattern matching condition. The regional variations in task-related activity are displayed using an uncorrected critical threshold of $p < .01$ for t-statistic maps overlaid on the SPM5 T1 template. Peaks of activity were detected bilaterally in BA 18/19 (MNI coordinates -14,-86,-06 and +24,-78,-04, $p < .001$). Axial and coronal images are displayed in neurological convention.

Table I

Participant Characteristics. Groups were matched on sex, age, full scale IQ and manual preference. These measures are reported for the entire group of participants, as well as for subsamples matched on RT. Age is reported in years. Manual preference is reported as the Edinburgh score (from -100 completely left-handed to +100 completely right-handed). ADI: Autism Diagnostic Interview. Between group differences were examined using ANOVA followed by post-hoc independent sample *t*-tests.

	Entire sample			**Performance matched sample**		
	AUT	**nonAUT**	***p***	**AUT**	**nonAUT**	***p***
Sample size (sex)	15 (2 F, 13 M)	18 (3 F, 15 M)		12 (1 F, 11 M)	13 (2 F, 11 M)	
Age						
M (*SD*)	22.40 (5.95)	21.72 (5.20)	.73	22.08 (4.91)	20.15 (3.02)	.26
Range	14 - 35	14 - 36		16 - 32	16 - 25	
Full scale IQ						
M (*SD*)	100.87 (12.05)	106.22 (12.97)	.23	101.50 (12.56)	105.31 (14.49)	.49
Range	85 - 121	81 - 131		87 - 121	81 - 131	
Verbal IQ						
M (*SD*)	99.20 (14.39)	110.17 (11.50)	.02	100.92 (14.63)	109.62 (12.63)	.13
Range	81-121	85-127		81-121	85-127	
Performance IQ						
M (*SD*)	102.80 (11.98)	100.72 (14.39)	.65	101.92 (12.91)	99.62 (15.47)	.69
Range	95-120	79-133		95-120	79-133	
Manual preference						
M (*SD*)	67.93 (45.68)	57.89 (49.15)	.55	67.67 (49.14)	58.46 (51.29)	.65
Range	-75 - +100	-50 - +100		-75 - +100	-50 - +100	
ADI						
M (cut-off)						
Social	23.27 (10)			22.16 (10)		
Communication	18.47 (8)			17.67 (8)		
Behavior	7.00 (3)			7.08 (3)		

Table II

Behavioral results for the pattern matching and RSPM tasks. Accuracy and RT performance measures are reported for the entire autistic (AUT) and non-autistic (nonAUT) sample, as well as for subsample matched on RT. There were 60 pattern matching and 60 RSPM problems. Of the 60 RSPM items, 16 are considered figural and 44 are considered analytic. Analytic items were further divided into four levels of difficulty from least (analytic 1) to most (analytic 4) difficult. Between group measure differences were assessed using ANOVA followed by independent sample *t* tests. Values are reported as mean and standard deviation - *M* (*SD*). RTs are reported in seconds.

	Entire sample			Performance matched sample		
	AUT	**nonAUT**	***p***	**AUT**	**nonAUT**	***p***
Pattern matching task						
Percent correct	99.11 (1.88)	98.15 (3.38)	.38	98.89 (2.05)	97.92 (3.75)	.39
RT	2.43 (0.91)	2.90 (1.33)	.37	2.69 (0.82)	2.60 (0.73)	.76
RSPM task						
Total (60 items)						
Percent correct	75.83 (10.39)	73.70 (9.12)	.54	74.72 (10.87)	72.82 (9.99)	.65
RT	13.65 (4.10)	19 (6.75)	.01	14.59 (3.56)	15.74 (3.94)	.45
Figural (16 items)						
Percent correct	93.30 (8.65)	90.63 (7.80)	.37	93.23 (9.02)	89.90 (8.28)	.35
RT	6.55 (1.89)	8.07 (2.24)	.05	7.01 (1.62)	7.10 (1.80)	.89
Analytic 1 (11 items)						
Percent correct	94.16 (7.65)	94.44 (8.33)	.92	93.18 (7.87)	94.41 (9.49)	.73
RT	9.60 (4.30)	11.05 (4.32)	.35	10.25 (4.31)	9.15 (2.53)	.44
Analytic 2 (12 items)						
Percent correct	78.57 (20.86)	81.48 (15.00)	.65	75.69 (21.16)	78.21 (16.51)	.74
RT	14.04 (5.35)	19.10 (6.70)	.03	15.10 (4.93)	16.03 (4.11)	.61
Analytic 3 (10 items)						
Percent correct	72.14 (20.07)	67.22 (18.73)	.48	70.83 (21.51)	66.15 (19.38)	.57
RT	16.85 (4.84)	23.62 (9.47)	.02	17.82 (4.25)	20.03 (7.55)	.38
Analytic 4 (11 items)						
Percent correct	32.47 (16.62)	25.76 (12.18)	.20	31.82 (17.55)	26.57 (13.10)	.40
RT	24.67 (9.23)	38.53 (17.03)	.01	26.46 (8.72)	30.67 (10.35)	.28

Table III

Activity associated with the pattern matching task. We show t-values for signal increases and decreases for the pattern matching vs. fixation baseline contrast in the non-autistic and autistic groups. Coordinates are in MNI space. Height threshold: $t = 4.88$, $p < .05$, FWE corrected. Extent threshold: k = 50 voxels.

(A) Local maxima of signal change in non-autistics.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Pattern matching > fixation											
Occipital											
Cuneus	17	-12	-98	4	14.53	2.47					
Lingual gyrus	17	-14	-92	-2	14.49	2.47					
	18						26	-80	-10	12.99	2.21
Middle occipital gyrus	18	-20	-86	-8	13.50	2.30					
Fusiform gyrus	19	-28	-70	-12	13.65	2.32	28	-70	-12	12.59	2.14
Parietal											
Inferior parietal lobule	40	-36	-38	48	10.26	1.75					
		-42	-30	46	9.88	1.68					
Superior parietal lobule	7	-28	-50	54	9.67	1.65	26	-62	50	8.86	1.51
Precuneus	7	-18	-66	50	9.62	1.64	28	-62	38	8.39	1.43
Frontal											
Inferior frontal gyrus	9	-58	8	30	6.91	1.18	58	8	30	6.32	1.08
							60	8	22	5.70	0.97
							46	8	26	6.55	1.12
	47						32	26	-2	8.44	1.44
Precentral gyrus	6	-50	2	36	7.81	1.33					
Insula	13	-38	-2	12	7.62	1.30	38	0	14	5.70	0.97
		-28	20	4	8.37	1.43	32	24	8	7.05	1.20
Subcortical											
Thalamus		-12	-14	6	7.25	1.23	12	-10	2	6.53	1.11
							22	-24	-4	6.53	1.11
Brainstem		-8	-14	-4	6.57	1.12	8	-18	-4	5.59	0.95

(A) Local maxima of signal change in non-autistics.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
							2	-36	-42	6.06	1.03
Putamen		-24	0	2	7.65	1.30	22	4	0	5.46	0.93
							26	-4	0	5.02	0.85
Claustrum							30	6	-8	5.28	0.90
Globus Pallidus		-26	-14	0	6.43	1.09					
Pattern matching* < *fixation											
No significant loci											

(B) Local maxima of signal change in autistics.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Pattern matching* > *fixation											
Occipital											
Inferior occip. Gyrus	18	-32	-84	-10	13.56	2.31					
Middle occip. Gyrus	18	-22	-92	16	13.23	2.25	30	-84	16	12.14	2.07
Fusiform gyrus	19	-36	-76	-10	13.24	2.25	34	-76	-12	13.03	2.22
Cuneus	19	-12	-98	2	12.27	2.09					
Parietal											
Postcentral gyrus	40	-46	-28	46	10.27	1.75					
Inferior parietal lobule	40						32	-42	46	8.17	1.39
Superior parietal lobule	7						32	-52	50	8.83	1.50
							24	-60	56	8.31	1.41
Frontal											
Inferior frontal gyrus	9						56	6	30	10.60	1.80
Superior frontal gyrus							2	4	18	6.26	
Precentral gyrus	6	-56	2	32	8.57	1.46					
	44						54	8	12	6.35	1.08
Insula	13	-38	-4	12	7.07	1.20					

(A) Local maxima of signal change in non-autistics.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Subcortical											
Claustrum		-28	20	4	7.39	1.26					
Claustrum		-32	-4	-4	7.20	1.23					
Thalamus		-14	-18	6	9.65	1.64	12	-14	0	7.92	1.35
Medulla		-2	-40	-42	6.97	1.19					
Cerebellum Lobule VIII		-20	-58	-54	5.87	1.00					
Cerebellum Lobule VIII		-26	-50	-54	5.50	0.94					
Cererbellum Lobule VIII		-34	-54	-54	5.50	0.94					
Pattern matching* < *fixation											
Temporal											
Middle temporal gyrus	39	-36	-58	24	5.78	0.98					
Parietal											
Inferior parietal lobule	39	-44	-68	38	6.33	1.08					

Table IV

Group differences and similarities in pattern matching activity.

(A) Conjunction analysis of the pattern matching task in non-autistic and autistic groups. Local maxima of signal increases and decreases are given for the conjunction null of the non-autistic and autistic groups on the pattern matching task vs. fixation baseline contrast. Coordinates are in MNI space. Height threshold: $t = 4.88$, $p < .05$, FWE corrected. Extent threshold: k = 50 voxels.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Pattern matching > fixation											
Occipital											
Middle occipital gyrus	18	-24	-84	-10	12.87	2.19					
		-26	-92	16	12.02	2.05	32	-88	12	11.42	1.94
Fusiform gyrus	19	-30	-76	-10	12.54	2.13	30	-68	-12	12.07	2.05
		-28	-66	-14	11.83	2.01					
Cuneus	17	-12	-98	2	12.27	2.09					
Parietal											
Inferior parietal lobule	40	-44	-30	46	9.78	1.67					
		-36	-34	50	9.63	1.64					
		-32	-44	50	9.09	1.54	34	-48	54	7.04	1.19
Precuneus	7	-28	-58	54	8.46	1.44	28	-56	50	8.05	1.37
Frontal											
Inferior frontal gyrus	9						48	8	28	6.54	1.12
							58	8	30	6.32	1.07
							60	8	22	5.70	0.97
Middle frontal gyrus	6						30	-4	52	9.07	1.55
Precentral gyrus	6	-54	4	34	7.16	1.22					
Insula	13	-38	-4	12	7.07	1.20	32	20	4	6.18	1.05
							28	26	0	6.49	1.11
Subcortical											
Claustrum		-28	20	4	7.39	1.25					
		-34	-2	2	6.22	1.06					
Thalamus		-12	-14	6	7.25	1.24	12	-10	2	6.53	1.11
Putamen		-28	-2	-4	7.14	1.21					

(A) Conjunction analysis of the pattern matching task in non-autistic and autistic groups. Local maxima of signal increases and decreases are given for the conjunction null of the non-autistic and autistic groups on the pattern matching task vs. fixation baseline contrast. Coordinates are in MNI space. Height threshold: $t = 4.88$, $p < .05$, FWE corrected. Extent threshold: k = 50 voxels.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Midbrain		-8	-14	-4	6.57	1.12	8	-18	-4	5.59	0.95
Medulla							2	-36	-42	6.06	1.03
Pattern matching < fixation											
No significant loci											

(B) Between-group differences in the pattern matching task. Local maxima of differential activity for the pattern matching task contrasted with the fixation baseline are shown for the autistic versus non-autistic groups. Coordinates are in MNI space. Height threshold: $t = 3.15$, $p < .001$, uncorrected. Extent threshold: k = 50 voxels.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Non-autistic > Autistic											
No significant foci											
Autistic > Non-autistic											
Frontal											
Middle frontal gyrus	6	-20	-16	58	3.98	0.68	28	-14	46	3.64	0.62
Precentral gyrus	4	-44	-14	42	3.27	0.56	42	-16	40	3.57	0.61
		-32	-14	42	3.95	0.67	46	-18	32	3.98	0.68
	6	-56	0	20	3.71	0.63	22	-18	50	3.88	0.66
		-50	-6	-34	3.84	0.65	22	-16	64	3.82	0.65
							30	-12	70	3.82	0.65

Table V

Activity associated with the RSPM task. We show t-values for signal increases and decreases for the RSPM task vs. fixation baseline contrast in the non-autistic and autistic groups. Coordinates are in MNI space. Height threshold: $t = 4.88$, $p < .05$, FWE corrected. Extent threshold: k = 50 voxels.

(A) Local maxima of signal change in non-autistics.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
RSPM > fixation											
Occipital											
Inferior occipital gyrus	18	-30	-88	-8	14.65	2.49	30	-92	-4	17.36	2.96
							38	-86	-4	15.50	2.64
Middle occipital gyrus	18	-30	-92	4	13.79	2.35					
Superior occipital gyrus	19						32	-74	28	9.64	1.64
Cuneus	17	-18	-94	-4	13.58	2.31					
Parietal											
Superior parietal lobule	7	-18	-66	52	11.95	2.03	18	-64	58	11.02	1.88
							28	-62	40	9.65	1.64
							26	-62	52	11.19	1.90
Inferior parietal lobule	40	-34	-42	46	10.49	1.79					
Precuneus	19	-26	-74	32	10.24	1.74					
Frontal											
Middle frontal gyrus	6	-24	-2	54	9.42	1.60	28	-2	54	10.48	1.78
Inferior frontal gyrus	9						46	8	26	10.45	1.78
Middle frontal gyrus	9	-44	14	30	9.66	1.64	50	20	36	7.12	1.21
	46	-48	24	28	9.24	1.57	42	26	24	8.74	1.49
							48	38	16	6.43	1.09
Superior frontal gyrus	6	-6	8	56	7.03	1.20					
	8						6	16	52	6.79	1.16
Medial frontal gyrus	8	-8	18	48	7.02	1.19					
Middle frontal gyrus	10	-42	44	-2	5.72	0.97					
Insula	13	-30	24	-2	6.80	1.16	32	24	-2	8.11	1.38
Subcortical											

(A) Local maxima of signal change in non-autistics.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Cerebellar pyramis		-4	-74	-24	6.45	1.10	8	-74	-24	6.79	1.16
Cerebellar tonsil							0	-52	-40	5.35	0.91
Medulla							2	-38	-42	6.85	1.17
RSPM < fixation											
Temporal											
Superior temp. gyrus	42	-58	-30	20	7.89	1.34					
Superior temp. gyrus	22	-58	2	4	7.66	1.30					
	38	-42	6	-12	5.59	0.95					
Parietal											
Precuneus	19						2	-82	40	11.78	2.00
Postcentral gyrus	43	-50	-12	14	5.41	0.92					
Posterior cingulate gyrus	31	-6	-44	32	9.77	1.66	4	-42	26	9.80	1.67
Frontal											
Anterior cingulate gyrus	32						4	48	0	11.01	1.87
Anterior cingulate gyrus	10						10	38	-4	10.61	1.81
Cingulate gyrus	31						0	-22	42	13.05	2.22
Subcortical											
Cerebellum Lobule VI		-6	-66	-8	5.24	0.89	6	-66	-6	5.58	0.95

(B) Local maxima of signal change in autistics.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
RSPM > fixation											
Occipital											
Inferior occipital gyrus	18	-28	-88	-4	13.62	2.32	28	-92	-4	13.45	2.29
		-38	-82	-6	13.21	2.25	38	-84	-4	11.40	1.94
	19										
Middle occipital gyrus	18	-24	-92	18	12.11	2.06	34	-88	2	11.65	1.98

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(A) Local maxima of signal change in non-autistics.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
	19	-32	-88	12	10.51	1.79	32	-88	10	11.51	1.96
							36	-76	-10	10.55	1.80
Cuneus	19	-26	-74	32	11.08	1.89					
Parietal											
Superior parietal lobule	7	-24	-64	52	10.03	1.71	34	-50	50	9.50	1.62
Frontal											
Inferior frontal gyrus	9						54	10	30	8.58	1.46
Middle frontal gyrus	6	-24	-4	56	9.64	1.64	28	-6	52	8.80	1.50
	9	-42	28	26	5.69	0.97					
	46						44	36	20	5.68	0.97
Precentral gyrus	6	-46	2	34	7.63	1.30					
RSPM < fixation											
Temporal											
Inferior temporal gyrus	20	-54	-22	-16	5.46	0.93	60	-14	-20	5.37	0.91
Middle temporal gyrus	39	-44	-64	28	5.77	0.98					
		-56	-60	12	5.20	0.89					
	21						62	-6	-12	5.85	1.00
Superior temporal gyrus	39	-52	-62	20	4.93	0.84					
	42	-56	-34	16	7.49	1.28					
	22	-64	-44	16	5.13	0.87	62	-46	20	5.38	0.92
		-60	0	0	6.31	1.07	62	4	-2	6.58	1.12
Fusiform gyrus	37						40	-36	-6	6.06	1.03
							36	-46	0	7.24	1.23
Parietal											
Precuneus	7						2	-66	36	8.18	1.39
	19						2	-84	36	7.17	1.22
Inferior parietal lobule	39	-48	-64	38	6.80	1.16					
Supramarginal gyrus	40	-60	-46	30	5.53	0.94	58	-48	32	5.40	0.92

(A) Local maxima of signal change in non-autistics.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Frontal											
Middle frontal gyrus	6	-22	-6	32	7.57	1.29	22	-2	26	7.46	1.27
Medial frontal gyrus	10						4	52	8	7.90	1.34
Superior frontal gyrus	8	-20	42	42	5.71	0.97					
Subcortical											
Cingulate gyrus	31						2	-28	42	10.73	1.83
							2	-42	28	9.10	1.55
Thalamus		-8	-36	10	10.37	1.76					
Anterior cingulate	32	-8	46	2	7.76	1.32	6	44	-4	8.13	1.38
							4	34	14	7.78	1.32
							12	34	-2	7.38	1.26
Parahippocampal gyrus	28						22	-18	-18	6.22	1.06

Table VI

Group differences and similarities in RSPM activity.

(A) Conjunction analysis of the RSPM task in non-autistic and autistic groups. Local maxima of signal increases and decreases are given for the conjunction null of the non-autistic and autistic groups on the RSPM task vs. fixation baseline contrast. Coordinates are in MNI space. Height threshold: $t = 4.88$, $p < .05$, FWE corrected. Extent threshold: k = 50 voxels.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
RSPM > fixation											
Occipital											
Inferior occipital gyrus	18	-28	-88	-4	13.55	2.31	28	-92	-4	13.45	2.29
							38	-84	-4	11.40	1.94
Middle occipital gyrus	18						34	-88	2	11.65	1.98
	19	-32	-88	12	10.51	1.79	32	-88	10	11.51	1.95
		-26	-92	16	11.38	1.94					
Parietal											
Precuneus	19	-26	-74	32	10.24	1.75	32	-74	30	9.50	1.62
	7	-22	-64	52	9.81	1.67					
Superior parietal lobule	7	-30	-50	50	8.72	1.48	22	-64	58	9.44	1.61
Frontal											
Inferior frontal gyrus	9						52	10	28	8.43	1.44
Middle frontal gyrus	6	-24	-2	56	9.26	1.54	28	-6	52	8.80	1.50
	9	-42	28	26	5.69	0.97					
	46						44	36	20	5.68	0.97
Precentral gyrus	6	-46	2	34	7.63	1.30					
RSPM < fixation											
Temporal											
Inferior temporal gyrus	20						60	-14	-20	5.37	0.92
	21						58	-8	-14	5.58	0.95
Middle temporal gyrus	39	-44	-64	28	5.77	0.98					
Sup. temporal gyrus	22	-60	0	0	6.31	1.07	62	2	2	6.38	1.09
	39	-52	-62	20	4.93	0.84					
	42	-58	-32	18	7.30	1.24					

(A) Conjunction analysis of the RSPM task in non-autistic and autistic groups. Local maxima of signal increases and decreases are given for the conjunction null of the non-autistic and autistic groups on the RSPM task vs. fixation baseline contrast. Coordinates are in MNI space. Height threshold: $t = 4.88$, $p < .05$, FWE corrected. Extent threshold: k = 50 voxels.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Fusiform gyrus	37						36	-46	0	7.24	1.23
Fusiform gyrus	37						40	-38	-6	5.92	1.01
Parietal											
Inferior parietal lobule	40	-60	-42	24	5.05	0.86					
	39	-46	-68	38	6.49	1.10					
Frontal											
Middle frontal gyrus	6	-22	-6	32	7.57	1.29	22	-2	26	7.46	1.27
Superior frontal gyrus	8	-20	42	42	5.71	0.97					
Medial frontal gyrus	10						4	52	8	7.90	1.35
Subcortical											
Cingulate gyrus	31						2	-28	42	10.73	1.83
							2	-42	28	9.10	1.55
Posterior cingulate	29	-6	-44	12	7.55	1.28					
Anterior cingulate	32	-8	46	2	7.76	1.32	6	44	-4	8.13	1.38
							2	34	16	7.61	1.30
							12	34	-2	7.38	1.25
Parahippocampal gyrus	28						22	-18	-18	6.22	1.06
	30	-10	-36	6	9.10	1.46					
	36						40	-30	-12	5.37	0.92
Thalamus							14	-38	10	7.61	1.30

(B) Between-group differences in the RSPM task. Local maxima of differential activity for the RSPM task contrasted with the fixation baseline are shown for the autistic versus non-autistic groups. Coordinates are in MNI space. Height threshold: $t = 3.15$, $p < .001$, uncorrected. Extent threshold: k = 50 voxels.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Non-autistic > Autistic											
Precuneus	7	-2	-60	40	3.99	0.68	2	-58	54	4.39	0.75
Precentral gyrus	9	-42	22	36	3.95	0.67					

(A) Conjunction analysis of the RSPM task in non-autistic and autistic groups. Local maxima of signal increases and decreases are given for the conjunction null of the non-autistic and autistic groups on the RSPM task vs. fixation baseline contrast. Coordinates are in MNI space. Height threshold: $t = 4.88$, $p < .05$, FWE corrected. Extent threshold: k = 50 voxels.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Middle frontal gyrus	9	-36	34	38	3.51	0.60	36	42	34	4.30	0.73
Autistic > Non-autistic											
Middle occipital gyrus	18	-22	-92	18	4.17	0.71					
Cuneus	18	-18	-82	24	4.15	0.71					

Table VII

RSPM task: Small volume correction analysis of occipital and posterior parietal brain regions using *a priori* ROIs.

(A) ROIs used for small volume correction analyses. ROIs were defined by taking the four right local maxima and finding their corresponding left local maxima in the pattern matching task vs. fixation baseline contrast in a prior study (unpublished results). Height threshold: $t = 9.17$, $p < 10^{-9}$. The t and d values at those coordinates are reported for non-autistic and autistic groups during performance of the RSPM task.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Non-autistics											
Middle occip. gyrus/cuneus	19	-28	-84	20	9.95	1.69	30	-86	20	9.41	1.60
Middle occipital gyrus	19	-30	-90	10	12.67	2.16	32	-88	12	13.20	2.25
Fusiform gyrus	19	-26	-62	-12	5.73	0.98	30	-72	-12	6.86	1.17
Superior parietal lobule	7	-28	-58	56	9.52	1.62	26	-58	52	10.10	1.72
Autistics											
Middle occip. gyrus/cuneus	19	-28	-84	20	10.50	1.79	30	-86	20	8.43	1.44
Middle occipital gyrus	19	-30	-90	10	10.11	1.72	32	-88	12	11.37	1.94
Fusiform gyrus	19	-26	-62	-12	5.37	0.91	30	-72	-12	6.76	1.15
Superior parietal lobule	7	-28	-58	56	8.98	1.53	26	-58	52	8.82	1.50

(B) Local activity maxima for between-group differences determined using functional ROIs derived from a prior experiment. Local maxima of differential activity for the RSPM task are given for autistic versus non-autistic groups, using small volume corrections based on the ROIs reported in (A). Coordinates are in MNI space. Search radius: 10 mm sphere. Threshold: $p < .01$; FWE-corrected.

		Left					*Right*				
Region label	**BA**	**x**	**y**	**z**	***t***	***d***	**x**	**y**	**z**	***t***	***d***
Non-autistic > Autistic											
No significant loci											
Autistic > Non-autistic											
Middle occipital gyrus	18	-22	-92	20	4.06	0.69					
Cuneus	18	-20	-80	22	3.78	0.64					