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Autistic fluid intelligence: Increased reliance on visual functional connectivity with diminished modulation of coupling by task difficulty

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ABSTRACT

Different test types lead to different intelligence estimates in autism, as illustrated by the fact that autistic individuals obtain higher scores on the Raven's Progressive Matrices (RSPM) test than they do on the Wechsler IQ, in contrast to relatively similar performance on both tests in non-autistic individuals. However, the cerebral processes underlying these differences are not well understood. This study investigated whether activity in the fluid "reasoning" network, which includes frontal, parietal, temporal and occipital regions, is differently modulated by task complexity in autistic and non-autistic individuals during the RSPM. In this purpose, we used fMRI to study autistic and non-autistic participants solving the 60 RSPM problems focussing on regions and networks involved in reasoning complexity. As complexity increased, activity in the left superior occipital gyrus and the left middle occipital gyrus increased for autistic participants, whereas non-autistic participants showed increased activity in the left middle frontal gyrus and bilateral precuneus. Using psychophysiological interaction analyses (PPI), we then verified in which regions did functional connectivity increase as a function of reasoning complexity. PPI analyses revealed greater connectivity in autistic, compared to non-autistic participants, between the left inferior occipital gyrus and areas in the left superior frontal gyrus, right superior parietal lobe, right middle occipital gyrus and right inferior temporal gyrus. We also observed generally less modulation of the reasoning network as complexity increased in autistic participants. These results suggest that autistic individuals, when confronted with increasing task complexity, rely mainly on visuospatial processes when solving more complex matrices. In addition to the now well-established enhanced activity observed in visual areas in a range of tasks, these results suggest that the enhanced reliance on visual perception has a central role in autistic cognition.

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1. Introduction

One of the most stable and intriguing properties of autistic intelligence is that the relative level of difficulty of the different tasks used to estimate intelligence is not the same for autistic and non-autistic people. For instance, autistic individuals obtain a better score when evaluated with the Raven's Progressive Matrices (RSPM) test (Raven, 1976) than with the Wechsler IQ test, whereas non-autistic individuals obtain similar scores on both tests (Dawson et al., 2007; Charman et al., 2011; Nader et al., 2014). In parallel, autistic individuals tend to exhibit a relative advantage on visuospatial tasks in comparison to verbal tasks, as reflected by their ability on visual search, embedded figures, Wechsler's

Block Design, pattern discrimination and mental imagery tasks (Soulières et al., 2011; Stevenson and Gernsbacher, 2013).

The unique pattern of cognitive performance described above is accompanied by an alteration in underlying patterns of cerebral activity and connectivity (Samson et al., 2012; Tyszka et al., 2014). Stronger recruitment of visual perceptual brain regions can be found in a wide array of tasks using faces, objects and words as stimuli (Samson et al., 2012), including higher order tasks such as fluid reasoning (Sahyoun et al., 2010; Soulières et al., 2009; Yamada et al., 2012). In terms of functional connectivity, initial investigations yielded results supporting widespread long-range underconnectivity and local overconnectivity in autism (Courchesne and Pierce, 2005; Just et al., 2007). More recent studies temper this view, demonstrating that local over-connectivity depends on the specific type of analyses conducted (Vissers et al., 2012) and that perceptual long-range functional connectivity is sometimes stronger in autistic relative to non-autistic participants (Keehn et al., 2013; Leveille et al., 2010; McGrath et al., 2012). White matter

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microstructural alterations are also found and correlate with autistic signs and symptoms (Gibbard et al., 2013; Ikuta et al., 2014; McFadden and Minshew, 2013), performance in visuospatial tasks (McGrath et al., 2013), and fluid reasoning abilities (Ellmore et al., 2013).

Fluid reasoning relates to the ability to infer logical solutions when solving novel problems (Cattell, 1987). A spatially extended brain network underlies fluid reasoning, with crucial components in prefrontal and parietal regions (Jung and Haier, 2007; Perfetti et al., 2009). Activity in the fronto-parietal reasoning network is modulated by reasoning complexity and is associated with individual reasoning ability levels (Gray et al., 2003; Lee et al., 2006; Perfetti et al., 2009). Increasing reasoning complexity is associated with widespread increases in activity in the reasoning network, with marked increases in dorsolateral prefrontal cortex (Kalbfleisch et al., 2007; Kroger et al., 2002; Wendelken et al., 2008). Higher reasoning abilities are associated with higher activity in frontal and parietal regions (Perfetti, 2009), and particularly in posterior parietal cortex (Lee et al., 2006).

In autistic individuals, solving fluid reasoning problems is accompanied by higher activity in occipital and temporal regions, but lower activity in some frontal (middle frontal gyrus) and parietal regions (precuneus), compared to non-autistic individuals (Soulières et al., 2009), and lower structural connectivity between frontal language areas and temporal regions (Sahyoun et al., 2010; Yamada et al., 2012). In a previous fMRI study (Soulières et al., 2009), we recorded brain activity while participants performed the RSPM, the emblematic fluid reasoning test (see examples in Fig. 1). Autistic participants performed the self-paced RSPM task with an accuracy similar to that of their comparison group, but unexpectedly exhibited a 40% shorter response time. During the resolution of the matrices, left middle occipital gyrus (BA18) was disproportionally engaged in autistic participants, suggesting that autistic reasoning might rely more heavily on the involvement of occipital regions and their associated perceptual processes during fluid reasoning. However, in light of recent findings identifying increased activity in perceptual areas in autistic individuals in a wide range of tasks (see Samson et al., 2012 for a meta-analysis), one can question whether the increased activity in occipital areas during a reasoning task contributes to reasoning processes per se. We inferred that observing connectivity between this region and other elements of the reasoning network that was modulated by problem complexity would provide further evidence that occipital areas genuinely contribute to autistic reasoning.

The objective of this study was to characterize how regional cerebral activity and connectivity are modulated by task complexity in autistic individuals during fluid reasoning. We were specifically interested in verifying whether the increased activity previously observed in visuospatial areas in autistic individuals during matrix reasoning would be associated with activity and connectivity modulations according to problem complexity. We therefore conducted psychophysiological interaction analyses (PPI) on data from our previous RSPM study (Soulières et al., 2009), with two sets of seed regions. The first set was based on areas of maximal activity common to both groups while solving the RSPM. Often in studies with clinical samples, the selection of seed regions is based on task-related activity patterns observed in the control group, with those seed regions possibly being slightly displaced from activity peaks in the clinical group. This selection approach could result in a bias towards detecting reduced functional connectivity in the clinical sample. Here, we employed a more neutral approach, selecting seed regions based on the conjunction of task-related activity observed in both groups. Then, using a second set of seed regions based on areas of between-group differences in task-related activity, we more specifically addressed our primary goal to examine the contribution of occipital regions to autistic reasoning.

We predicted that autistic participants would exhibit higher functional connectivity involving the occipital seeds with increasing reasoning complexity, relative to non-autistic participants, as suggested by previous observations of stronger reasoning-related activity and anatomical local connectivity in occipital regions (Sahyoun et al., 2010; Soulières et al., 2009). Given numerous previous findings of lower parieto-frontal functional connectivity in autism and the lower frontal activity seen during reasoning in autistic individuals in our previous study, we also predicted lower functional connectivity between prefrontal and posterior parietal regions during the resolution of the more complex reasoning items in autistic relative to non-autistic participants.

2. Methods

2.1. Participants

MRI data were collected from 15 autistic participants (aged 14–35, M = 22.40, SD = 5.95, 2F) and 18 non-autistic participants (aged 14–36, M = 21.72, SD = 5.20, 3F) (dataset from Soulières et al., 2009; see participant characteristics in Table 1). Participants were matched on age, Wechsler Full-Scale IQ and handedness. Autistic participants received a diagnosis according to DSM-IV criteria and were evaluated with two diagnostic instruments, the Autism Diagnosis Observation Schedule (ADOS-G; Lord et al., 2000) and Autism Diagnostic Interview (ADI-R; Le Couteur et al., 1989), by a multidisciplinary team of expert clinicians. A comparison group of participants self-reporting no psychiatric or neurological conditions were recruited from the local population. Primary exclusion criteria for both groups were uncorrected visual impairment, use of psychoactive or vasoactive medication as well as use of illegal drugs or excessive alcohol consumption. A neurologist reviewed all structural scans to rule out any anatomical abnormality. All participants gave written informed consent to participate. The
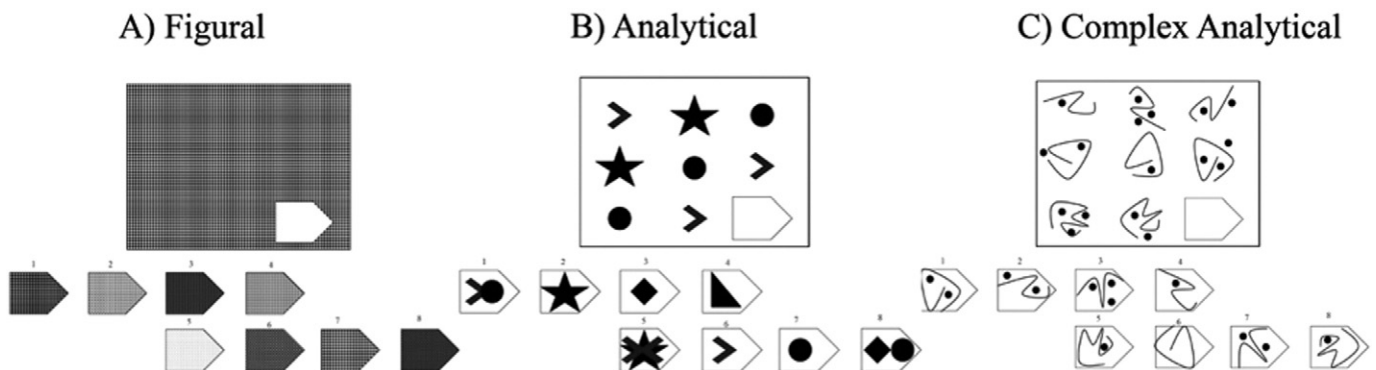

Fig. 1. Examples similar to items from the Raven's Standard Progressive Matrices. This fluid reasoning test is composed of 60 matrix problems of increasing complexity. To solve the matrices, participants have to choose among 8 choices the one that best fill in the missing entry (bottom right of the matrix). The three examples represent the three complexity levels included in our study: figural, analytical and complex analytical.