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Research report

A hierarchy for relational reasoning in the prefrontal cortex

Daniel C. Krawczyk [a,b,c,*], *M. Michelle McClelland* [a,b] *and Colin M. Donovan* [a,b]

[a] *Center for Brain Health, The University of Texas at Dallas, USA*
[b] *School of Behavioral and Brain Sciences, The University of Texas at Dallas, USA*
[c] *Department of Psychiatry, University of Texas Southwestern Medical Center at Dallas, USA*

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ABSTRACT

The human brain possesses a unique capacity to reason about abstract relationships among items in our environment. The neural organization of reasoning abilities has remained elusive. Two approaches toward investigating human reasoning have involved studying visuo-spatial reasoning abilities and studying analogical reasoning. These approaches have both revealed anterior prefrontal cortex (PFC) involvement, but no prior studies have jointly investigated these two forms of reasoning to understand any potential convergence of activation within the PFC. Using fMRI, we tested the extent to which these two forms of reasoning (visuo-spatial and analogical) overlap in PFC activation. We conducted a visuo-spatial reasoning task that required processing multiple changes across three abstract pictures. This task activated a progressively anterior series of PFC regions when multiple relations had to be integrated. We also conducted a four-term analogy task in a stage-wise manner and compared results from this task to semantic and perceptual control conditions that did not require integrating relations across the problems. We found greater activation for analogical reasoning in the series of PFC regions that were sequentially involved in the visuo-spatial reasoning task. These findings indicate that stages of neural processing overlap for different domains within human reasoning. The pattern of differences across the analogy task suggests a hierarchical organization for relational reasoning across domains in which posterior frontal cortex is active across concrete reasoning tasks, while progressively more anterior regions are recruited to process increasingly abstract representations in reasoning.

1. Introduction

Humans have a uniquely developed capacity to reason about relations among items. This includes reasoning by analogy, comprehending metaphors, and solving mathematical problems. One potential source of this ability is our extended capacity to process multiple relations among items (Penn et al., 2008; Robin and Holyoak, 1995). This ability may be nearly unique to humans, as many animal cognition studies indicate that other species are limited to reasoning about perceptual features (Oden et al., 2001). Reasoning about relations may serve as a critical building block in the development of human intelligence, as it enables us to manipulate and maintain information that may be extensively removed from the current context both temporally and spatially.

Numerous psychometric tests of intelligence have centered upon measuring relational capacities including the ability to manipulate and integrate visuo-spatial information.

* *Corresponding author*. Center for Brain Health, The University of Texas at Dallas, 2200 Mockingbird Lane, Dallas, TX 75235, USA.
E-mail address: daniel.krawczyk@utdallas.edu (D.C. Krawczyk).
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The Cattell culture fair test (Institute for Personality and Ability Testing, 1973) requires the ability to sort among increasingly complex figures. Raven's Progressive matrices (Raven et al., 1988) is another standard measure of visuo-spatial intelligence that requires people to integrate spatial and visual aspects of abstract figures across a series of transformations. These tasks are considered to be measures of fluid general intelligence, as they exhibit strong inter-task correlations among several domain-specific measures (Gray and Thompson, 2004). Reasoning by analogy has also been considered to be an important ability that taps into human higher intelligence (Gentner, 1983; Hummel and Holyoak, 1997; Meagher, 2008). A common thread between visuo-spatial and analogical reasoning tasks is that both require people to judge validity of relations among elements, whether they are visual, spatial, or conceptual in nature.

The neural basis of relational processing abilities has been linked to the prefrontal cortex (PFC). This area is disproportionately developed in higher primates and is widely regarded to be important for mental operations such as attention (Posner and Dahaene, 1994), inhibitory control (Lhermitte, 1986), working memory (D'Esposito et al., 1998; Fuster and Alexander, 1971), and higher executive function (Wood and Grafman, 2003). The organization of the PFC continues to be debated. Several recent studies have used functional neruoimaging to investigate the cortical basis for fluid intelligence and have suggested overlap within the dorsolateral PFC for visual, verbal, and abstract reasoning (Duncan et al., 2000; Gray et al., 2003). Other studies have found results that suggest specialization within the anterior PFC for increasingly complex cognition. Notably, recent emphasis has been placed on the rostrolateral PFC (RLPFC) as uniquely relevant to integrating information (Koechlin et al., 1999; Ramnani and Owen, 2004) and processing increasingly abstract complex relations (Christoff et al., 2001; Christoff and Keramatian, 2007; Kroger et al., 2002). Both of these approaches have described integrating rules or cognitive abstraction moving along a posterior-to-anterior direction.

Semantic analogical reasoning and visuo-spatial relational reasoning are both tasks that tap into fluid general intelligence with their common basis being relational processing. Prior studies of four-term analogical reasoning have found that RLPFC or frontopolar PFC are associated with solving problems that require mapping semantic relations (Green et al., 2006; Bunge et al., 2005; Wendelken et al., 2008). Similar results have been reported with abstract relational tasks in the visuo-spatial domain also reporting anterior PFC activation, typically when subjects solve progressive matrices or math problems (Braver and Bongiolotti, 2002; Prabhakaran et al., 2000). These studies indicate that common integrative mental processes may be shared between these types of tasks and that this is associated with anterior PFC. Additionally, anterior brain activation for visual analogies has recently been associated with fluid general intelligence abilities, as measured using Raven's matrices (Cho et al., 2007). The neural overlap between visuo-spatial and analogical reasoning has not yet been systematically investigated within the same subjects across the PFC.

We investigated the extent to which a series of PFC regions are jointly engaged in relational reasoning across domains. We tested the extent to which a hierarchical series of PFC regions involved in processing abstract visuo-spatial relations was also recruited in processing different relational operations within complex analogies. We initially defined the anterior series of PFC regions by localizing areas involved in integrating visuo-spatial relations. We then investigated whether these regions were also engaged in extracting, maintaining, mapping, and inferring relational information in analogies based on semantic content. Rather than approach relational processing from a single perspective, we sought to characterize a series of relational integration regions that operate systematically across relational operations in different domains that otherwise shared little perceptual or semantic overlap.

Both of the tasks involved a relational reasoning condition and non-relational control conditions. The visuo-spatial reasoning task involved processing one, two, or three variations in dimensions of change across a series of abstract shapes (Fig. 1). Subjects were asked to verify whether the changing item completed a series across all three panels, or whether it reverted back to its original position. Other blocks involved tracking two or three changes across the items. The

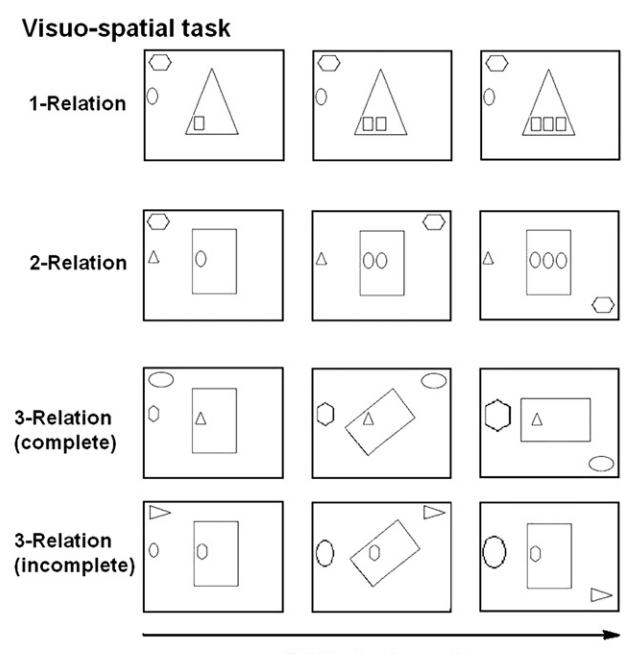

Fig. 1 – Examples of the problems used in the visuo-spatial reasoning task. In each problem one, two, or three relations changed from the leftmost panel to the middle panel. Subjects were to verify whether the problem was complete, meaning that all possible changes continued in the rightmost panel. If all relational changes were complete (for instance the rotation of the central rectangle, the revolution of the satellite oval, and the expansion of the left hexagon in the 3-Relation complete figure) subjects responded with a button press, if any change was not complete in the rightmost panel (see center rectangle in 3-Relation incomplete example), subjects responded with an alternate button press. Items were presented in blocks of eight problems.