Research report

A hierarchy for relational reasoning in the prefrontal cortex

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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.
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 neuroimaging 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 Bongiolloti, 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 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
analogy task consisted of four-term analogy problems that were presented in a sequential manner (Fig. 2). Initially, subjects viewed a pair of pictures and determined the relation present between them. Next they were shown a third picture with the goal of generating an inference about a possible fourth item that would complete the relational mapping to the first pair. Lastly, subjects were shown a picture of a sample fourth item that did or did not fit the analogy. Subjects responded with a button press whether this last item was a fit or not. We employed two control conditions, a semantic condition and a perceptual condition. These control conditions were identical to the analogy condition except that subjects did not need to process or maintain the relation between the first two items. In these conditions, subjects were instructed to make a button press indicating whether the fourth and final item was a perceptual match or a semantic match compared to the third item.

**Fig. 2** — Examples of the analogy task and control conditions. A. The analogy task required subjects to view a pair of items initially and to determine their relationship at the first relation phase. After a delay, subjects viewed a third item and had to infer an item that could be paired with it to complete the same relation that was discovered in the first relation phase. Finally, the inference phase required subjects to determine whether the item presented was a fit to complete the problem. B. The semantic match condition required no relational encoding at the first relation phase. This was followed by inference of a semantic associate to the third item (without the need to map to the first relation) and finally, verification if the fourth item fit the third. C. The perceptual condition was identical to the semantic condition, except subjects had to infer a fourth item based on visual similarity and then verify whether the provided fourth term fit the problem on that basis.

2. **Method**

2.1. **Participants**

Twenty healthy, right-handed, native English-speaking volunteers participated. They ranged in age from 18 to 45 (mean age: 27.5 years) with normal or corrected vision. This experimental protocol received approval from the Institutional Review Boards of The University of Texas at Dallas and UT Southwestern Medical Center at Dallas. All subjects provided informed consent to participate in accordance with the 1964 Declaration of Helsinki. Behavioral data from one subject was not recorded during performance of the analogy task due to a computer error.

2.2. **Experimental procedure**

2.2.1. Visuo-spatial reasoning task

Subjects received a separate training session on this task prior to scanning. A series of slides were shown with each consisting of three consecutive box frames arranged horizontally (refer to Fig. 1). Each problem was to be solved moving from left to right. Each frame included four shapes occupying specific positions (center, surrounding center, left side, or left upper corner) in the leftmost frame. The shapes continued to change from the middle to the rightmost frames. Thus, a shape always began in one location and either remained the same or began to change in the second frame. Only if it had started to change in the second frame did it finish changing in the third frame. If each changing shape finished its sequence of progressive change in the rightmost frame, the problem was considered to be “true”. Subjects had been trained prior to the task to understand what the shapes in the different positions would do if they altered their position. In half of the problems, one of the shapes that had altered in position from the leftmost to the middle frame returned to its original position in the rightmost frame. Subjects were instructed to respond “false” to such problems making a key press. Subjects were asked to make a judgment on whether or not the progression of boxes from left to right was complete. In other words, they were requested to make a decision about whether or not the shapes completed their designated characteristic across all three boxes.

The experiment consisted of 96 problems varying in number of dimensions of change (1, 2, or 3) and validity (half of the problems required “true” answers and the others required a “false” answer). Subjects verified if all changes in the problem were complete, (e.g., they occurred across all of the frames). Problems were counterbalanced by rotating the shapes through each spatial position across the set. The design was balanced with 32 problems representing each relation number. One of the four shapes always remained stationary to avoid three-relation problems appearing entirely different across the frames, which could allow a pattern match strategy to be used. Subjects responded by pressing either of two buttons corresponding to “true” and “false” problems. Accuracy and
response time (RT) data were recorded. Each trial was displayed for 5 sec with a fixation point between trials. The trial did not terminate when subjects made a response. Subjects were instructed to respond as quickly as possible.

2.2.2. Analogy task
Subjects were trained on the three task conditions prior to entering the MRI scanner. Twenty-four picture analogy problems were presented in the format A:B as C:D. The final picture of the second relation (D from the C:D relation) had three possible conditions: an analogical condition, a perceptual condition, and a semantic condition. Each condition was identified to the subject before the run began and only one condition was used per run to avoid potential confusion about the instructions. Each trial consisted of a three slide series separated by focal point slides. The first relation presentation slide revealed images A and B simultaneously (e.g., sandwich:lunchbox) with a vertical line between them for a duration of 4 sec. A focal point was then presented for 4 sec. The C image (hammer) was presented directly after the previous focal point for a duration of 6 sec followed by another 4 sec focal point. The D image [toolbox (analogy), nail (semantic), hatchet (perceptual)] was then presented for 4 sec. Participants were instructed to judge the analogy to be true or false during the presentation of slide D and to indicate their response via button press. Three button options were available; true, false, and a third button to be used if the subject could not provide a confident answer or was confused regarding the A:B relationship or the C:D relationship, depending on the condition. The true and false buttons were held in each hand with hand placement counterbalanced for the experiment. The third button was consistently positioned centrally.

The design of the experiment enabled subjects to generate an answer at the third phase (C), referred to as the inference phase, while temporally separating the response phase (D). In all three conditions (analogical, perceptual, and semantic) the A, B, and C items remained the same; however, the D item varied depending on the condition. All images were presented in grayscale on a white background.

**Analogical condition:** For the analogy condition, subjects inferred the completion of the relationship C to D by comparing A to B. Using this comparison, subjects generated
<table>
<thead>
<tr>
<th>Region of Interest from Visuo-spatial Task</th>
<th>Analogy Mean fMRI values from Visuo-spatial Region of Interest</th>
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<tbody>
<tr>
<td><strong>RLPFC</strong></td>
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<tr>
<td><strong>y=53</strong></td>
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<tr>
<td><strong>PMC</strong></td>
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<tr>
<td><strong>y=60</strong></td>
<td><img src="image8" alt="Graph for y=60" /></td>
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**Legend**

- Analogy
- Semantic
- Perceptual

**Graphs**

- **First Relation**
- **Inference**
- **Response**

**X-axis** (% Signal Change)

**Y-axis**
a D possibility before the answer choice D was revealed. Once presented, the D image was judged to be a true (e.g., hammer:tool) or a false completion of the analogy. For example a false analogy was toothbrush:teeth as soap:telephone.

**Perceptual condition:** For the perceptual condition, subjects were asked to base their true/false decision on the perceptual similarity of the C to the D item. Subjects were not required to maintain the A to B relationship but were instructed to try to imagine a fit for the D term based on the perceptual properties of the C term. A true or false decision was chosen by comparing the perceptual characteristics of the C and D images. An example of a true perceptual match is football:lemon (on the basis of oblong shapes), while a false perceptual match example is roof:garden (on the basis of no shared visual commonalities).

**Semantic condition:** For the semantic condition, the D answer was based on whether it had high semantic similarity to the C image. Highly correlated words were taken from The University of South Florida Word Association Norms (Nelson et al., 1998) and these were translated into picture form for use in the experiment. As in the perceptual condition, the relationship between the A and B items was not necessary to maintain. A true or false decision was chosen by considering the semantic similarity of the C and D images with a true semantic relationship exemplified by the strong association match baby:crib, while a false example was beehive:hen, in which no clear association was evident.

### 2.2.3. Functional MRI acquisition and analysis

Images were acquired using a 3T Philips MRI scanner with a gradient echoplanar sequence (TR = 2000 ms, TE = 28 ms, flip angle = 20°) sensitive to BOLD contrast. Each volume consisted of tilted axial slices (3 mm thick, .5 mm slice gap) that provided nearly whole brain coverage. Anatomical T1-weighted images were acquired in the following space: TR = 500 ms, TE = 10, slice thickness = 4 mm with no gap at a 90° flip angle. Head motion was limited using foam head padding.

Detailed descriptions of the procedure used for analyzing activation within trials have been published previously (Buckner et al., 1996; Zarahn et al., 1997) and are summarized below. Activation of each phase of the trials was assessed using multiple regression (Postle et al., 2000). Preprocessing analyses were conducted using Statistical Parametric Mapping Software (SPM 5; Wellcome Trust Centre for Neuroimaging, www.fil.ion.ucl.ac.uk/spm) run in Matlab 6.5 (http://www.mathworks.com). Functional images were realigned to the first volume of acquisition and resliced to 2 mm isotropic voxels, smoothed with a 6 mm 3D Gaussian kernel, and normalized to the Montreal Neurological Institute template.

For the visuo-spatial task, three separate regressors were used to model each phase of the task: 1-Relation, 2-Relation, and 3-Relation regressors were used for modeling each block of eight problems. Each regressor was convolved with a canonical hemodynamic response function (HRF) provided in SPM5 and entered into the modified general linear model of SPM5. Parameter estimates (e.g., β values) were extracted from this GLM analysis for the regressors. Resulting contrast images computed on a subject-by-subject basis were utilized in group map analyses. At the group level, contrasts between conditions were computed by performing one-sample t-tests on the contrasted images. Initially, regions showing a parametric task increase across all three-task complexity levels were isolated. Next, in order to identify PFC regions maximally active toward complexity we used a three-relation (maximal relational complexity load) minus baseline contrast to functionally define regions of interest (ROIs) within PFC search masks. This was carried out by initially defining left and right hemisphere PFC masks comprising Brodmann’s areas 6, 8, 9, 10, 46, and 47 using the WFU Pickatlas toolbox (http://www.fmri.wfubmc.edu/) (Maldjian et al., 2003, 2004). ROIs were defined as any voxel cluster containing 10 or more contiguous voxels and falling within either PFC search mask at an uncorrected p < .005 level.

For the analogy task, four separate regressors, repeated for each of the three conditions, were used to model each phase of the task: encoding, inference, and a response regressor for both true and false analogies. Data was extracted from the independently defined ROIs that had been localized using the three-relation minus baseline condition of the visuo-spatial task. We compared mean signal intensity for one TR (shifted by 4 sec to adjust for hemodynamic lag) for each condition using MarsBar software (sourceforge.net/projects/marsbar). These data were converted to percent-signal change and were then analyzed using pair-wise contrasts [t-tests Bonferroni corrected for multiple comparisons between the analogy condition and the two control conditions within each region of interest (ROI)].

### 3. Results

#### 3.1. Behavior

Behavioral data from the visuo-spatial reasoning task (Fig. 3) demonstrated that there were differences in accuracy based on relation level F(2, 57) = 31.07, p < .001. Bonferroni corrected post-hoc comparisons (p < .05) revealed that all pair-wise differences between categories were significant with higher accuracy for one-relation problems compared to the two- and three-relation problems, as well as higher accuracy for two-relation problems.
over three-relation problems. Additionally, there was a significant effect of RT $F(2, 57) = 7.90, p < .001$ in which one-relation problems were solved significantly faster than the two- and three-relation problems and two-relation problems were solved significantly faster than three-relation problems. These data are consistent with a step-wise increase in complexity that reduces overall accuracy and lengthens RT across the task levels.

Behavioral data from the analogy task showed a significant effect of accuracy $F(2, 54) = 3.55, p < .05$. Post-hoc tests corrected for multiple comparisons ($p < .05$) demonstrated that analogy problems were solved with greater accuracy than the perceptual control task (Fig. 3). An effect of RT was also present $F(2, 54) = 3.66, p < .05$ where analogy problems were solved at a faster rate than both semantic and perceptual control problems.

### 3.2. Brain activation

#### 3.2.1. Visuo-spatial reasoning

Results of the parametric increase analysis are shown in Table 1. Areas of the frontal, parietal, and occipital cortex were active in response to the increase from one-, to two-, to three-relation problems. Displayed in Table 1 are MNI coordinates from the peak active voxel from each region (minimum 20 active contiguous voxels, FDR, $p < .05$). We next analyzed brain activation separately for each relational condition in the visuo-spatial task in order to localize regions of the PFC that were responsive to additive relational integration demands across the problems. This was accomplished using contrasts of the one-, two-, and three-relation problems versus baseline after a GLM was performed. Voxel clusters are shown in Fig. 4. We were most interested in active regions of the PFC in response to three-relation problems, as these problems required the greatest degree of relational integration. The three-relation condition showed significant activation ($p < .005$ within the PFC ROI masks) for four regions within the right frontal cortex: RLPFC (MNI space coordinates $x = 42, y = 53, z = 21$), the inferior frontal gyrus (IFG) ($x = 60, y = 26, z = 32$), the dorsolateral PFC (DLPFC) ($x = 48, y = 32, z = 43$), and the premotor cortex (PMC) ($x = 40, y = 0, z = 66$). A subset of these areas (the IFG, the DLPFC, and the PMC) were active for the two-relation problems at these same coordinates, while the one-relation contrast revealed only PMC activation within the frontal lobes. Thus, increases in relational processing load resulted in recruitment of anterior prefrontal regions in an ordered manner moving from posterior to anterior PFC. These results are consistent with a PFC processing hierarchy, as additional areas were engaged additively when processing load increased, while the regions sensitive to lower loads remained active.

#### 3.2.2. Analogue reasoning

We next tested whether these four regions of PFC are also engaged in a hierarchical manner in a four-term analogy task that had been run during the same MRI scanning session. ROI analyses revealed that the series of PFC regions defined in the visuo-spatial task were modulated in a similar manner during the analogy condition (Fig. 4). The RLPFC showed significantly greater activation for the analogy condition over the perceptual condition at the first relation phase ($t_{19} = 2.80, p < .01$), the mapping and inference phase ($t_{19} = 3.13, p < .005$), and the response phase ($t_{19} = 2.92, p < .005$). This region also showed marginal significance for comparisons between the analogy and semantic conditions at each task phase ($p = .07$). Similarly, the IFG ROI showed significant modulation for analogy in comparisons to the perceptual condition at the first relation phase ($t_{19} = 2.13, p < .05$), mapping and inference phase ($t_{19} = 2.34, p < .05$), and marginal significance for the response phase ($t_{19} = 2.00, p = .03$). Differences within the DLPFC ROI were less robust. Here, the analogy condition showed marginally greater activation over the perceptual condition at the mapping and inference ($t_{19} = 2.03, p < .028$) and response phases ($t_{19} = 1.85, p = .06$). Lastly, the PMC region showed no evidence of selectivity among conditions in the analogy task. Notably, the differences were robust between analogy over perceptual processing, but not in comparisons between analogy and the semantic control condition.

### 4. Discussion

The progressive regional involvement of these four PFC areas in visuo-spatial reasoning indicated that increases in relational complexity engage predictable cortical topography within the PFC in an additive manner. The simplest one-relation problems engaged only the PMC significantly. When a second relation was added to the problems, the DLPFC and IFG showed greater activation along with the PMC. Lastly, when a third relation of change was added, the RLPFC was modulated in addition to each of the prior three areas. These results demonstrate that additive complexity of problem representations drives PFC recruitment along a posterior-to-anterior axis. This finding builds upon prior results showing anterior PFC recruitment with complex Raven’s progressive matrices (Kroger et al., 2002), as well as performance deficits in complex matrices and other relational integration tasks in individuals with PFC damage (Krawczyk et al., 2008; Morrison et al., 2004; Waltz et al., 1999). Notably, the right RLPFC was found to be active in the visuo-spatial task and this is consistent with prior studies; however, in addition we identified important other contributing support regions. Unlike prior studies, our two-relation condition did not reliably recruit RLPFC, despite requiring integration of information which is a function commonly associated with the RLPFC (Christoff et al., 2001). Rather the RLPFC was activated when a third level of complexity was added indicating that it holds the highest position of a series of hierarchically organized PFC regions. It is possible that this region is recruited only when sufficient cognitive demands are imposed on the task and that this was the case with the three-relation case only in the visuo-spatial task. It is important to note that several regions showed parametric complexity level modulations in this task including the PFC, parietal, and occipital cortex, thus there is evidence of extended neural involvement.

The analogy task showed a pattern of similar results across separate phases of the task. The analogy condition required relational extraction, maintenance, and inference, unlike the semantic and perceptual control conditions, which required only inference based on single relations between the third and fourth items. The analogy task along with the semantic control condition also required access to stored relationships from semantic memory. In common with the visuo-spatial
task, the analogy condition required processing the relations between items, rather than judgments based on perceptually available features. This may be the essential aspect of cognitive processing that elicits differential activation from this hierarchy of PFC regions, as the other aspects of the visuo-spatial and analogy tasks differed extensively. Alternatively, it is also possible that the additional memory requirement for the encoding phase items in the analogy condition may have contributed to brain activation differences. A memory load interpretation would likely show itself primarily in the encoding and inference phases, as these are the periods most relevant to encoding and maintenance of items in working memory; however, all task phases showed evidence of analogy related differences casting some doubt on this possibility. It was not possible to fully control the influence of memory using the current design, so we are not able to rule out working memory load influences within the present analogy task.

A notable feature of the pattern of activation is that the higher-order PFC regions, the RLPFC and IFG, showed consistent activation across all three task periods of the analogy task when compared to the perceptual control condition. This indicates that these regions may have a temporally extended role in preparation for relational processing, inference, as well as verifying responses. At a lower level of the hierarchy, the DLPFC was only reliably responsive at the verification phase. Meanwhile, the lowest-order region, the PMC, lacked sensitivity to task complexity and demonstrated activation even to the simplest one-relation visuo-spatial problems. This area showed no reliable modulation at any phase of the analogy task relative to the control tasks indicating a more generalized role in relational reasoning at a lower order of operation. Also notable is the pattern of analogy comparisons, which indicated that the analogy versus perceptual processing comparison showed the greatest difference within these ROIs. While, the comparison between the semantic and perceptual control conditions was not reliable, the perceptual control condition may be considered to be the most dissimilar from solving actual analogies, as this condition required no semantic retrieval. Importantly, the RLPFC and IFG regions were maximally recruited when complexity of representation across the two tasks was increased.

When interpreting task-related activation increases in fMRI an important consideration has been how processing time, or accuracy differences may influence the observed activation. In prior reasoning studies RT has been a primary measure of cognitive efficiency (Miller et al., 2009; Viskontas et al., 2004, 2005). Within fMRI studies RT and activation have been of theoretical interest (Rypma et al., 2002, 2006). Prior neuroimaging studies of reasoning have typically controlled for RT variability to avoid the possibility of misinterpretation of activation associated with task manipulations in event-related designs (Christoff et al., 2001; Golde et al., 2009). In our visuo-spatial task it was not possible to control for RT differences in this manner, as the task was run as a block-design; however, the observed ROI responses are more consistent with an abstraction load change affecting activity, rather than an RT influence, as the analogy and visuo-spatial task showed opposing patterns within their behavioral data. This is a rare instance in which RT varies inversely with the complexity conditions and demonstrates that the effect of processing time is unlikely to be responsible for the activation results across these two tasks.

Prior analogy studies have shown consistent PFC activation when visual analogies are compared to feature-based matches (Wharton et al., 2000), and when analogy conditions are compared to semantic conditions in verbal domains (Green et al., 2006; Luo et al., 2003). Anterior PFC regions of the RLPFC, or frontopolar PFC, typically on the left side, have been sensitive to complexity in prior abstract reasoning studies (Christoff et al., 2001; Kroger et al., 2002). This has led to the proposal that this area plays an integrative role in cognition. In contrast to a single-region integration area, we demonstrate that a progressive series of frontal areas support relational processing in the visuo-spatial domain. While the RLPFC was activated only in the highest level of relational change, the IFG and DLPFC also showed sensitivity to levels two and three of the visuo-spatial relational processing. Additionally, the regional modulation of these areas across separable phases of the analogy task suggests that the role of PFC areas extends across relational processing requirements, rather than solely focusing upon integration. Other recent evidence from visuo-spatial reasoning also indicates an important role for the middle frontal gyrus and other regions in processing relational information (Kalbfleisch et al., 2007).

This study extends our understanding of the organization of the PFC in higher cognition. Recent theories of PFC organization maintain that there is a progressive topography present within PFC that extends along a posterior-to-anterior axis as greater complexity of information processing occurs. This complexity has been defined in terms of signaling (Koechlin et al., 2003) as well as conflict resolution (Badre, 2008). Our results fit broadly with these ideas, but specifically suggest that multiple relational operations may engage anterior PFC areas, while posterior PFC regions remain active across multi-domain relational processing at lower levels of complexity. It is important to point out that integration of relations is one way to solve the visuo-spatial problems, but it is also possible to sequentially solve each relation individually and hold the result in mind to build a final response. Such a strategy would be more consistent with a working memory load manipulation rather than integration specifically. It is not possible to determine what specific strategy participants engaged in on a trial-to-trial basis in the visuo-spatial task, but if a sequential relational strategy were used, it would suggest that the associated PFC activation may be more related to cognitive control (Badre, 2008; Badre and D’Esposito, 2007; Koechlin et al., 2003; Koechlin and Summerfield, 2007) or cognitive branching (Koechlin et al., 1999).

This study also fits within the literature dealing with the role of the PFC in cognitive abstraction (see Christoff and Keramatian, 2007 for a review). Recent results from neuroimaging studies have lent support to the position that increasingly abstract processing predictably leads to greater recruitment of anterior PFC. This has been demonstrated across studies of abstract meaning in anagram word problems (Christoff et al., 2009), visual problems (Smith et al., 2007) and analogies (Bunge et al., 2005; Green et al., 2006; Wendelken et al., 2008). The current finding support this framework as both high levels of visuo-spatial abstraction and analogies jointly activated the most anterior PFC regions. Recent neurophysiology results also support this view, as anterior
PFC cells appear to have highly flexible response tendencies (Wallis et al., 2001).

It is important to point out that conducting analogical reasoning tasks within neuroimaging environments poses several challenges that constrain the tasks that can be used. The need for large trial numbers and replicable cognitive processing across trials limits our ability to capture the spontaneity and malleability of cognition that frequently accompanies the deepest analogy making. Notably, the mapping stage of analogy contains several steps that are difficult to capture in the fMRI environment. These include the consideration of multiple possible mappings (Krawczyk et al., 2004, 2005; Markman, 1997), aligning different candidate mappings (Gentner, 1983), and using the goals of the analogy to shape the relevance of the relations for mapping. The analogy task employed in the present paper was constrained to a simple one-to-one relation mapping, thus minimizing goal-directed guidance; however, by including an inference of the fourth term we gave participants the opportunity to consider multiple candidate mappings and thus, sort among the best candidate matches. Few other studies have measured the influence of these possible operations using fMRI (Geake and Hansen, 2005; Wendelken et al., 2008). Neuroimaging studies have yet to address one of the core processes in analogy which is mapping when multiple relations are possible.

Reasoning remains a complex area of investigation, but the consideration of neuroscience data enables us to better understand the underlying commonalities across multiple domains. Future studies of human reasoning focused on the hierarchical-organization approach to reasoning may help us to further understand the elusive links between constructs such as fluid intelligence, analogy, and multi-domain problem solving.

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References


