General and specialized brain correlates for analogical reasoning: A meta-analysis of functional imaging studies

Lucie Hobeika, Capucine Diard-Detoeuf, Béatrice Garcin, Richard Levy, Emmanuelle Volle

General and specialized brain correlates for analogical reasoning: A meta-analysis of functional imaging studies

Lucie Hobeika*[1,2,3,4,5], Capucine Diard-Detoeuf*[1,2,3,4], Béatrice Garcin[1,2,3,4], Richard Levy[1,2,3,4,5], Emmanuelle Volle[1,2,3,4].

* Contributed equally to this work

[1] Inserm, U 1127, F-75013, Paris, France

[2] CNRS, UMR 7225, F-75013, Paris, France

[3] Sorbonne Universités, UPMC Univ Paris 06, UMR S 1127, F-75013, Paris, France

[4] ICM, Frontlab, F-75013, Paris, France

[5] AP-HP, Hôpital de la Salpêtrière, Behavioural Neuropsychiatry Unit, 75013 Paris, France

Corresponding author:

Dr. Emmanuelle Volle

Frontlab - ICM

Hôpital Pitié-Salpêtrière

47, bld de l'Hôpital, 75013 Paris, France

emmavolle@gmail.com

Running title: Meta-analysis of analogy brain networks

Number of words: 6525

Number of figures: 4 figures

Number of tables: 7 tables

Key words: Analogy, reasoning, rostral prefrontal, abstraction, relational reasoning, functional MRI, neural correlates, meta-analysis

ABSTRACT

Reasoning by analogy allows us to link distinct domains of knowledge and to transfer solutions from one domain to another. Analogical reasoning has been studied using various tasks that have generally required the consideration of the relationships between objects and their integration to infer an analogy schema. However, these tasks varied in terms of the level and the nature of the relationships to consider (e.g., semantic, visuospatial). The aim of the current study was to identify the cerebral networks involved in analogical reasoning and its specialization based on the domains of information and task specificity. We conducted a coordinate-based meta-analysis of 27 experiments that used analogical reasoning tasks. The left rostrolateral prefrontal cortex was one of the regions most consistently activated across the studies. A comparison between semantic and visuospatial analogy tasks showed both domain-oriented regions in the inferior and middle frontal gyri and a domain-general region, the left rostrolateral prefrontal cortex, which was specialized for analogy tasks. A comparison of visuospatial analogy to matrix problem tasks revealed that these two relational reasoning tasks engage, at least in part, distinct right and left cerebral networks, particularly separate areas within the left rostrolateral prefrontal cortex. These findings highlight several cognitive and cerebral differences between relational reasoning tasks that can allow us to make predictions about the respective roles of distinct brain regions or networks. These results also provide new, testable anatomical hypotheses about reasoning disorders that are induced by brain damage.

INTRODUCTION

By identifying similarities between apparently dissimilar objects or situations, humans can solve novel problems, learn and form new concepts, or communicate specific ideas to others. The identification of such similarities allows us to link distinct domains of knowledge and transfer solutions from one domain to another. In analogical reasoning, similarities are typically relational, i.e., they concern the relationships between components of an object or a situation rather than the components themselves (Gentner and Holyoak, 1997; Krawczyk, 2012). In this sense, analogical reasoning is a form of relational reasoning that depends on our ability to consider and compare relationships and to integrate or match those relationships. This relational processing yields the inference of an analogy schema, i.e., a pattern of relational similarities between the analogs. The analogy schema is at a more abstract level of similarities than superficial or perceptual similarities would be, reflecting a mechanism by which relational reasoning supports abstract thinking. Relational reasoning is also considered to be a key process of fluid reasoning (Waltz et al., 1999) and has implications for learning and education (Geake and Hansen, 2005; Gentner et al. 2001), problem solving and creativity (Green et al. 2012). However, the cerebral substrates for this process have not been elucidated.

The cerebral bases of analogical reasoning have been informed primarily through functional imaging. Studies have examined analogical reasoning typically using 4- or sometimes 6-term analogy tasks (e.g., is the A - B relation similar to the C – D relation). Functional magnetic resonance imaging (MRI) studies using these tasks have shown the involvement of a fronto-parietal system (Bunge et al. 2005; Cho et al. 2010; Christoff et al. 2003; Geake and Hansen, 2010, 2005; Green et al. 2010; Volle et al. 2010; Wendelken et al. 2012, 2008a) and an association with the anterior cingulate cortex (Luo et al. 2003; Preusse et al. 2011) and the temporal regions (Luo et al. 2003; Reber et al. 2014). The most consistent region that has been associated with analogical reasoning is the left rostrolateral prefrontal cortex (rlPFC), as was recently demonstrated by a previous meta-analysis (Vartanian, 2012) that analyzed data from 10 functional MRI studies. Similarly, a voxel-based morphometry approach demonstrated a link between individual analogical reasoning abilities and the structure of the left rlPFC (Aichelburg et al. 2014). This set of results argues for an important role of the rlPFC, particularly the left rlPFC, in analogical process. However, many studies have reported bilateral activation (Cho et al. 2010; Geake and Hansen, 2010; Preusse et al. 2011; Wartenburger et al. 2009), or even right activation, of the rlPFC in non-verbal visuospatial analogy tasks (Kalbfleisch et al. 2007) and in semantic analogy tasks (Luo et al. 2003). Therefore, the left predominance of the rlPFC for analogical reasoning processing is still unclear and remains to be confirmed.

If the hypothesis of a left dominance of the rlPFC for analogy proves true, the cognitive processes supported by the left rlPFC and underlying a left specialization remain unknown. A left dominance could be explained by the domain of the analogy performed and/or its verbal or semantic nature. Alternatively, some cognitive processes involved in analogical reasoning may require specifically the left rlPFC region. With regard to the first explanation, literature about cognition has historically supported a left dominance for language, including semantics, and a right dominance for spatial information processing (Bates et al. 2003; Catani et al. 2005; Forkel et al. 2014; Heilman et al. 1986; Mesulam, 1981; Price, 2010; Thiebaut de Schotten et al. 2011). In the analogy field, tasks have used various materials requiring the inference of analogies in the semantic domain (i.e., infer semantic relationships such as nose-smell :: mouth-taste) or in the visuospatial domain (i.e., analyze visuospatial relationships to infer a logical, geometrical or mathematical rule such as symmetry or linear increase). Semantic analogies depend on knowledge of the semantic meaning of the terms and of the relationships between them. In visuospatial analogies, the analogy is inferred from the analysis of the visual and spatial relationships between terms that can be conceived as transformations from one term to the other (e.g., changes in shape, color, size, etc.). To our knowledge, only one study has examined directly the question of the specialization of the analogy network as a function of the analogy domain (Wendelken et al. 2012). This study did not find a left-right specialization of rlPFC according to the analogy domain: both semantic and visuospatial analogies recruited the left rlPFC. Further studies are needed in order to better understand the role and organization of the left rlPFC for analogy domains, and the involvement of the other prefrontal regions.

This leads us to the second hypothesis relative to the specific or critical processes supported by the left rlPFC region. The few patient studies conducted to date have confirmed the critical role of the prefrontal cortex (PFC) in analogical reasoning (Krawczyk et al. 2008; Morrison et al. 2004; Schmidt et al. 2012) or in rule inference (Reverberi et al. 2005), but these studies were unable to determine the role of the rlPFC region specifically. In functional imaging, the left rlPFC has been involved in the processing of abstract information (Christoff et al. 2003) and in the comparison (Wendelken et al. 2008a) or the integration of multiple relationships (Bunge et al. 2005; Cho et al. 2010; Christoff et al. 2001).

These operations are often investigated using other relational reasoning tasks, the matrix problem tasks such as Raven's Progressives Matrices (Raven, 1941). Matrix problems typically require the consideration and integration of visuospatial relationships to infer logical, geometrical or mathematical rules (Kalbfleisch et al. 2013, 2007; Shokri-Kojori et al. 2012; Yamada et al. 2012). Matrix problem tasks thus share several cognitive processes with analogy tasks, such as relational comparison, integration and schema inference. Matrix problems and 4-terms analogies are supposed to measure the same type of relational reasoning functions (Krawczyk, 2012). In this framework, typical 4-terms analogy tasks and matrix problem tasks might thus engage similar brain regions. Functional imaging studies have shown that bilateral frontal and parietal regions are involved during matrix problem tasks. The most frequently reported regions in these studies were the dorsolateral PFC (Christoff et al. 2001; Hampshire et al. 2011; Krawczyk et al. 2008; Kroger et al. 2002; Perfetti et al. 2009) sometimes extending to the rlPFC (Golde et al. 2010; Hampshire et al. 2011; Krawczyk et al. 2008, see also Wendelken et al. 2008a), the premotor cortex (Golde et al. 2010; Kalbfleisch et al. 2007; Krawczyk et al. 2008; Perfetti et al. 2009; Yamada et al. 2012), and posterior parietal areas (Hampshire et al. 2011; Krawczyk et al. 2008; Perfetti et al. 2009). Some studies have also shown the involvement of the lateral occipitotemporal regions (Hampshire et al. 2011; Kalbfleisch et al. 2013; Yamada et al. 2012), the anterior cingulate cortex (Kroger et al. 2002; Shokri-Kojori et al. 2012) and the cerebellum (Kalbfleisch et al. 2007). A recent and comprehensive review indicated that 4-term analogies and matrix problems might engage differentially the left and right rlPFC (Krawczyk, 2012). The lesion approach has produced inconsistent results regarding whether the integrity of the rlPFC is required for matrix problem solving (Baldo et al. 2010; Gläscher et al. 2009; Tranel et al. 2008; Waltz et al. 1999; Woolgar et al. 2010). Overall, previous studies have suggested that analogy and matrix reasoning tasks involve largely similar cognitive processes and engage both common and specific brain regions, and might not equally rely on the rlPFC. A quantitative comparison of functional activation observed during 4-term analogy and matrix problem tasks should help to clarify this question.

In this general context, the aim of the current study was to identify the cerebral network involved in analogical reasoning and its specialization or variation based on domains of information (semantic or visuospatial) and task specificity (4-terms analogy or matrix problem tasks). We conducted a meta-analysis including 27 experiments that used such tasks. We contrasted semantic and visuospatial analogy tasks to identify domain-oriented regions in the analogy network and to test whether the involvement of the left rlPFC is dependent on the analogy domain. We expected a left dominance for the involvement of the rlPFC independent of the analogy domain. We additionally compared visuospatial analogy to matrix problem tasks to examine the possible differences in their brain correlates. We hypothesized that visuospatial analogies and matrix problems would engage, at least in part, distinct cerebral networks and involve differently the rlPFC.

METHODS

Study selection

We searched for all published studies about analogical reasoning using fMRI by conducting a Boolean search in the PubMed database. Specifically, we searched for the following keywords in the text and/or the abstract/title: “analogy”, “analogies”, “analogical reasoning”, “relational reasoning”, “relational integration”, “relational complexity”, “analogizing”, “fluid reasoning”, “analogic reasoning” "progressive matrices", "Ravens’ Standard Progressive Matrices", "Advanced Progressive Matrices", "RSPM", "APM", "Cattell’s Culture Fair Test", together with “brain imaging", "cerebral imaging", "MRI", "fMRI", “functional MRI”, "PET", "neural correlates", "cerebral correlates", "brain activation", "functional magnetic resonance imaging".

Then, we included peer-reviewed studies published in English before February 2015 that (1) concerned healthy right-handed adults; (2) involved an analogical or a matrix problem reasoning experimental paradigm; and (3) reported whole brain results with signal change coordinates in the Montreal Neurological Institute (MNI) space or Talairach 3D space. For each study, only independent contrasts were included. If several contrasts in the same study were dependent, only the results from the contrast reporting the most significant maxima were included.

According to these criteria, we ultimately analyzed 27 studies, including 40 fMRI contrasts, 506 subjects and 351 foci of activation (Table 1).

Task categories (Table 1)

We classified each study and experimental contrast according to (1) the type of task used (4-term analogy versus matrix problem tasks) and (2) the domain in which the relational reasoning applied (semantic or visuospatial/logical relationships). The included experiments were distributed into three categories: "Semantic Analogy", "Visuospatial Analogy" and "Matrix Problem" (Matrix Problem tasks always concerned the visuospatial domain).

ALE methods

General principles

We used the Activation Likehood Estimation (GingerALE) software (http://brainmap.org/ale/cli.html; (Eickhoff et al. 2009; Laird et al. 2009; Turkeltaub et al. 2012, 2002) in our meta-analysis. This method determines the brain areas in which the convergence across all included experiments is greater than would be expected by chance (null distribution of randomly generated activation likelihoods) [Eickhoff et al. 2009]. This analysis is based on the compilation of the activation peak coordinates from all the functional imaging studies in a same normalized referential. In other words, ALE evaluates how reliable the involvement of brain regions in given processes across distinct experiments is — in this case in relational reasoning tasks.

Global and task category maps

We performed ALE analyses using the GingerALE software version 2.3.3 (www.brainmap.org; Eickhoff et al. 2012, 2009; Turkeltaub et al. 2012). We converted the activation peak coordinates reported in Talairach space into MNI space using the converter included in the GingerALE toolbox. Activation foci in the same referential from each included contrast were first modeled as Gaussian distributions and then merged into the same volume. We organized the datasets according to subject groups and used the modified ALE algorithm (Turkeltaub et al. 2012) to address the issue of the independence of observation within the same study. The algorithm also modeled spatial uncertainty (Eickhoff et al. 2012, 2009), allowing us to adjust the full-width half maximum (FWHM) using an estimation of between-subject and between-experiment variability. GingerALE then modeled the probability of activation across all studies for each brain voxel, returning localized "activation likelihood estimates" or ALE values. ALE values are the statistical maps created by combined probability distributions centered at each coordinate used in the analysis and reflect the coherency across experiments.

In a second step, ALE values were compared to random distributions of foci to identify significantly activated clusters at each voxel. We used a cluster correction for multiple comparisons: the simulated data was thresholded using a "cluster-forming threshold", identifying the contiguous volumes above the threshold, or clusters. Then ALE tracked the distribution of the volume of the clusters and used a "cluster-level threshold" for thresholding the results. We used an uncorrected cluster-forming threshold at $p < 0.001$ and a cluster-level threshold at $p < 0.05$ (Eickhoff et al. 2012). ALE maps were calculated using 1000 permutations. We also reported the results at a stringent voxel-level family-wise error (FWE) correction when significant.

We computed a global map for all included studies (analogy and matrix problem tasks). To analyze the distinct task categories, an ALE analysis was performed separately for each category (Semantic Analogy, Visuospatial Analogy and Matrix problem tasks). A map for each task category was obtained.

Task comparisons and contrast maps

We next conducted contrast analyses between the task categories to look for specific brain correlates. First, we tested whether analogy in the semantic and spatial domains was associated with specific regions (Table 1, columns 5 and 6) by building subtraction ALE maps that contrasted Semantic versus Visuospatial Analogy tasks. Second, we tested whether Analogy and Matrix Problem tasks had distinct brain correlates by building subtraction ALE maps comparing Visuospatial Analogy versus Visuospatial Matrix Problem tasks.

Contrast analyses were performed by first building ALE maps separately for each condition, and then computing the voxel-wise difference between these two input ALE maps (Laird et al. 2005). ALE contrast maps correspond to the direct subtraction of the two input images, converted into Z-scores. GingerALE creates simulated data of new groupings that are subtracted one from another, and compared to the true data. After 10000 permutations, a voxelwise P value image was obtained, and compared to the true data values. We reported each contrast map with an uncorrected p value < 0.05 and an minimum cluster size of 100 voxels.

ALE results

The anatomical labels of final cluster locations were produced as a GingerALE output. Maps were superimposed on the anatomical Colin27 template (Holmes et al. 1998) using Mricron and MricroGL (http://www.mccauslandcenter.sc.edu/mricro/mricron/) for visualization purposes.

RESULTS

Global analysis (Table 2, Figure 1)

The global ALE map pooling Analogy and Matrix Problem tasks primarily revealed a bilateral fronto-parietal network including a large cluster located in the left rostrolateral PFC that was centered at Brodmann area (BA) 10 and extended to BA 47, 45 and 46, bilateral insula, posterior parietal cortex (BA 7 and 40), several clusters in the posterior region of the inferior frontal gyrus (IFG), middle frontal gyrus (MFG), superior frontal sulcus (SFS), and medial PFC. The clusters in the left rostrolateral PFC, the right dorsolateral region (BA 9, posterior part of the IFG) and the right insular area (BA 13) were significant at a $p < 0.05$ FWE corrected threshold.

Task category maps

1) Semantic Analogy tasks map (Table 3, Figure 2)

The ALE map based on grouping semantic analogy tasks revealed a left-lateral prefrontal network. The primary cluster was located in the rostrolateral part of the left IFG and MFG (BA 10/47 and BA 46). A second cluster was located posteriorly in the posterior part of the left IFG (BA 44). Additional clusters were observed in the superior frontal gyrus, including one in the anterior part (BA 9) and one in the dorsal part (BA 8), and in the bilateral caudate heads.

2) Visuospatial Analogy tasks map (Table 4, Figure 2)

The analysis of Visuospatial Analogy tasks revealed four clusters of activation. The primary cluster was centered in the rostrolateral region of the left inferior frontal sulcus and gyrus (BA 10/47/46). Additional clusters were located in the right MFG (BA 9), the right anterior insula, and the cerebellum.

3) Visuospatial Matrix problems map (Table 5, Figure 2)

The ALE map for Matrix problems revealed a large, bilateral fronto-parietal network distributed into eight clusters of activation. Larger clusters were located bilaterally in the parietal lobe, extending from superior to inferior regions (BA 7 and 40), and in the precuneus (BA 7/31). In the frontal lobe, significant clusters were found bilaterally in the posterior and dorsolateral PFC centered on the posterior inferior frontal sulcus (IFS) (BA 6, 44, 9) with a right predominance, in the posterior region of the superior frontal regions centered on the posterior SFS (BA 6/8), and bilaterally in the medial PFC. Two additional clusters were located in the anterior region of the right insula and in the left cingulate gyrus (BA 32).

4) Visual overlap (Figure 2)

Semantic Analogy and Visuospatial Analogy commonly recruited the rostrolateral part of the left IFG in a similar cluster, while Matrix Problems did not. This corresponded to the cluster that was significant at a voxel-based FWE correction. This region is hereafter referred to as the “left rlPFC ROI”.

Visuospatial Analogy and Matrix problems shared the activation of the right anterior insula.

Contrast maps

1) Comparisons of Semantic and Visuospatial Analogy tasks (Table 6, Figure 3)

The ALE subtraction map of Semantic versus Visuospatial Analogy tasks revealed a cluster located in the rostrolateral part of the left IFG (BA 47) that was located more posterior and ventral to the left rlPFC ROI. The left rostromedial prefrontal cortex (medial BA 10) and the left inferior frontal sulcus (BA 46) were also significantly more strongly activated by Semantic than Visuospatial Analogy tasks.

The ALE subtraction map of Visuospatial versus Semantic Analogy tasks revealed a set of frontoparietal regions including distributed clusters located in the left rostrolateral PFC, the posterior region of the left MFG (BA 6, 8), the posterior right IFG and MFG (BA 9, 45, 46), the left superior parietal lobule (SPL) and inferior parietal lobule (IPL) (angular and supramarginal gyri; BA 7, 39, 40), and the right fusiform gyrus (BA 37). The left rostrolateral PFC cluster was located in the anterior region of the left MFG (BA 10), dorsal to the main analogy region, i.e., the "left rlPFC ROI".

2) Comparison of Visuospatial Analogy versus Matrix problems maps (Table 7, Figure 4)

The ALE subtraction map of Visuospatial Analogy versus Matrix problem tasks revealed a primary cluster in the left rostral region of the PFC (centered on BA 10, extending to BA 9, 45, 46, and encompassing the anterior MFG and IFG) in similar location to the left rlPFC ROI. A second cluster was observed in the left posterior cerebellum.

The ALE subtraction map of Matrix problems versus Visuospatial Analogy tasks revealed a large frontoparietal network containing the bilateral posterior and dorsolateral PFC centered on the posterior IFS (BA 6, 44, 9) with a right predominance, the posterior part of the superior frontal regions centered on the posterior SFS (BA 6/8), the medial PFC (BA 9/32), the left IPL and SPL (BA 7), the right precuneus (BA 7, 19 and 31), and the postcentral gyrus (BA 2 and 3). A left rostral PFC region (BA 10) was also observed, which was in a more medial location than the "left rlPFC ROI".

DISCUSSION

Using the ALE method, our coordinate-based meta-analysis combined data from 27 functional neuroimaging experiments to reveal three lines of findings: (i) the rostral part of the left rlPFC was consistently engaged during analogical reasoning tasks, regardless of the domain of analogy; (ii) additionally activated prefrontal and posterior brain regions were domain-oriented; and (iii) the Visuospatial Analogy and Matrix Problem tasks activated dissociable neural systems across fMRI studies. Matrix Problems network was distributed bilaterally to a greater extent.

The left rlPFC is a reliable domain-general region for analogical reasoning

First, the results from our global analysis of the 27 experiments revealed a reliable activation in the left rlPFC (BA 10/47), which is a region at the rostral end of the IFS that we labeled the "left rlPFC ROI". Previous meta-analyses also reported significant and informative results despite the relatively small number of experiments analyzed (Gonen-Yaacovi et al. 2013; Vartanian, 2012; Prado et al. 2011). Our currently identified association between analogical reasoning and activity in the left rlPFC, and confirmed the findings of Vartanian (2012) when we added 17 new experiments to the meta-analysis. This result is also in agreement with previous findings from different approaches such as morphometry (Aichelburg et al. 2014; Krawczyk et al. 2010), and developmental studies in children. The latter studies suggested that maturation of the PFC and especially of the rlPFC is critical for relational reasoning in Matrix problems (Crone et al., 2009), for semantic analogies (Wright et al., 2008), and visuospatial analogies (Bazargani et al., 2014; Thibaut et al., 2010; Wendelken et al., 2011). These studies showed functional and structural changes in the left rlPFC during development, with decreasing grey matter volume and increasing specificity of left rlPFC activation for relational integration (for a review Dumontheil, 2014). Changes in functional connectivity were also reported between rlPFC and anterior insula, posterior frontal, and posterior parietal cortices (Bazargani et al., 2014), regions that were also reliably observed in the current meta-analysis. Overall developmental studies suggest that the left rlPFC is critical for different types of relational reasoning tasks and domains of relationships used.

In the current meta-analysis, Semantic and Visuospatial Analogy maps overlapped in the “left rlPFC ROI”, suggesting that analogies in distinct domains share a common brain correlate within the rlPFC. For each analogy map, ALE values were significant in the “left rlPFC ROI” but not in the right rlPFC, suggesting a left lateralization of the rlPFC for analogical reasoning regardless of the task domain. As mentioned earlier, left prefrontal dominance for analogical reasoning has been shown in previous functional imaging studies (Vartanian, 2012; Bunge et al. 2009; Krawczyk et al. 2012) and a repetitive transcranial magnetic stimulation study (Boroojerdi et al. 2001). It is unlikely that this left-lateralization could be due solely to verbal or semantic requirements because we observed an activation in the left rlPFC during both Semantic and Visuospatial Analogy tasks, as has been also reported by Wendelken et al. (2012). As shown in a functional imaging study, the activation of the rlPFC across a large range of different tasks using various domains of stimuli (verbal, spatial, visual) reinforces the interpretation of a domain-general function for the rlPFC (Gilbert et al. 2006).

Functional imaging studies have indeed shown the involvement of the rlPFC in various cognitive functions related to analogical reasoning such as working memory (Christoff and Gabrieli, 2000; Narayanan et al. 2005), multitasking and task switching (Braver and Bongiolatti, 2002; Burgess, 2000; Burgess et al. 2000; Koechlin et al. 1999), abstract reasoning and problem-solving (Badre, 2008; Christoff et al. 2003, 2001; Kroger et al. 2002; Smith et al. 2007). However, the precise role of the rlPFC in analogical reasoning, and more widely in cognition, has not been elucidated. Clinical observations have tended to confirm that damage to this region could cause high-level cognitive disorders (Burgess et al. 2009; 2000). Relatively recent theories propose that the rlPFC (or frontal pole) is an integrative and coordinating region, the role of which could be to integrate the outcomes of separate cognitive operations and information of different nature, in the pursuit of long-term or more global behavioral goals (Ramnani and Owen, 2004; Stuss, 2011). Hierarchical models of PFC organization inferred from functional imaging studies place the rlPFC at the top of a cognitive hierarchy in which more anterior portions of the frontal lobes support increasingly abstract representations, greater relational complexity in reasoning, or higher levels of adaptive control (Badre, 2008; Christoff et al. 2009; Koechlin and Summerfield, 2007) in interaction with more posterior regions. Because analogies engage relational integration and the formation of abstract concepts, the involvement of the rlPFC in analogical reasoning is consistent with these theories from both the perspectives of abstraction and relational integration (see also Shokri-Kojori et al., 2012). The rlPFC might also play a role in the coordination or integration of internally (inferred analogy schema) versus externally (stimuli) oriented thoughts (Gilbert et al. 2000; Burgess et al. 2007). The critical role of the rlPFC in these integration, control-related or complexity-dependent functions remains to be tested in patients. These interpretations assume that the role of the rlPFC in the integration of visuospatial, semantic or rule-based relational representations is supported by its interactions with other regions of the analogy network.

Global network of relational reasoning

In addition to the "left rlPFC ROI", the global map showed a distributed set of brain regions bilaterally encompassing the insula, posterior prefrontal regions, posterior parietal cortex, and medial SFG. These regions appeared to belong to distinct brain networks that have been described by resting state functional imaging studies: the fronto-parietal executive/control network, the salience network and the dorsal attentional network (Cole et al. 2012; Power and Petersen, 2013; Power et al. 2011; Vincent et al. 2008)

The fronto-parietal control network includes the dorsolateral prefrontal cortex and the posterior parietal cortex. This network has been largely associated with complex functions related to analogical reasoning, including fluid intelligence (Hampshire et al. 2011; Jung and Haier, 2007; Prado et al. 2011; Reineberg et al. 2015; Wendelken et al. 2015), working memory (Champod and Petrides 2010; Courtney 2004; Curtis 2006; Smith and Jonides 1999), structuration of mental representations into chunks (Bor et al. 2003; Bor and Owen, 2007; see also Wendelken et al., 2008b), and deliberate control of thoughts and actions (Badre and D'esposito 2007; Koechlin et al. 1999; Hampshire and Owen, 2006; Petrides, 2005). The salience network includes the anterior insula and the adjacent ventrolateral prefrontal (posterior IFG) and anterior cingulate cortices (Seeley et al. 2007; Sridharan et al. 2008). An important role of the salience and the fronto-parietal executive networks for fluid reasoning in healthy individuals has been suggested by Yuan and colleagues (2012) using voxel-based morphometry and resting state imaging. Recent studies have postulated that the salience network drives switching between the fronto-parietal control and the default mode networks (Goulden et al. 2014; Jilka et al. 2014; Sridharan et al. 2008), allowing for the engagement of the brain's attentional and higher-order control processes while disengaging other systems that are not task-relevant (Sridharan et al. 2008). This process could be involved in analogical reasoning. Finally, the dorsal attentional system includes regions of the frontal eye fields (posterior SFS), the premotor cortex and the superior parietal lobule. It is associated with externally directed cognition, including covert and overt shifts of spatial attention (Corbetta and Shulman, 2002) and is engaged in tasks involving spatial search and detection. This network could be more involved in visuospatial than semantic analogy tasks, as is discussed below.

Specialization into domain-oriented regions

In contrast to the “left rlPFC ROI”, which was recruited in both Semantic and Visuospatial Analogies, we observed differences in the pattern of brain activity in other areas, depending on the analogy domain.

Compared with Visuospatial Analogy tasks, Semantic Analogy tasks more specifically recruited the left anterior IFG (BA 47), located ventrally and posteriorly to the left rlPFC ROI. The left anterior IFG has been associated with controlling or selecting the retrieved information during semantic retrieval (Badre and Wagner, 2007; Barde and Thompson-Schill, 2002; Thompson-Schill, 2003), with executive aspects of semantic processing (Dronkers et al. 2004; Monti et al. 2007), and with abstract interpretation of metaphors (Rapp et al. 2004). Therefore, it is likely that this region plays a role in the semantic retrieval of relational and abstract information when solving semantic analogies, as has been shown by Bunge et al. (2005).

In addition to the left anterior IFG, Semantic Analogy tasks recruited the posterior region of the left IFG (BA 44) and the anterior and medial region of the left SFG (BA 10) [figure 3]. Rostromedial frontal clusters have been suggested to be part of the semantic memory network (Buckner et al. 2008) and might play a role in relational integration across semantic distance, as has been proposed by Green et al. (2006; 2010) and Brunyé et al. (2015).

These findings are also in agreement with previous functional imaging and lesion studies that have demonstrated a left specialization of the PFC for verbal abstraction using proverb interpretation (Murphy et al. 2013), abstract concepts (Hoffman et al. 2010; Lagarde et al. 2015), or metaphor comprehension (Bohrn et al. 2012; Vartanian 2012).

Conversely, the Visuospatial Analogy tasks more specifically recruited frontal regions located in the bilateral posterolateral PFC, left posterior parietal cortex and intraparietal sulcus, and right fusiform gyrus. Interestingly, this pattern of brain activity is broadly consistent with the brain systems that support visual and spatial processing and spatial attention. The posterior parietal cortex, including both SPL and IPL, is thought to be involved in spatial cognition and has been associated with the formation of spatial representations and the processing of spatial relationships during analogy tasks (Amorapanth et al. 2010; Wendelken, 2015). The fusiform gyrus has previously been shown to participate in visual mental imagery and in the formation of the mental images of the visuospatial schema during analogical thinking (Luo et al. 2003).

In addition, Visuospatial Analogy tasks compared to the Semantic Analogy tasks recruited the anterior MFG (BA 10). This additional rostral PFC region is located dorsal to the shared "left rlPFC ROI" and thus could be associated with the cognitive processes required by spatial and geometrical analogies that are not involved in semantic tasks. Previous authors have emphasized a more dorsal recruitment of the rostral PFC for spatial versus semantic analogies (Wendelken et al. 2012), at the individual level. A greater schema complexity in visuospatial compared to semantic analogies could explain the additional recruitment of a dorsal network, including the anterior MFG and the posterior parietal cortex, as reported by Hampshire et al. (2011) and Krawczyk (2012).

In sum, in addition to the shared domain-general "left rlPFC ROI", semantic and visuospatial analogies recruited unique domain-oriented brain regions. Some of these domain-oriented regions were located in the lateral PFC and were organized along the dorsoventral axis: MFG for Visuospatial Analogies and IFG for Semantic Analogies (Fig. 3). These findings suggest, as has been proposed by Babcock and Vallesi (2015) for inductive reasoning, that analogical reasoning relies on common processes supported by the left rlPFC and recruits content information from domain-oriented regions. This hypothesis is consistent with models of the prefrontal functional architecture that describe a dorsoventral dissociation as a function of the domain of information (Courtney, 2004; Sakai and Passingham, 2003; Smith and Jonides, 1999; Volle et al. 2008).

It is important to mention some limitations in the task comparisons that were performed. A variety of analogy tasks have been used, that employed verbal, figurative or abstract material, and involved semantic, visuospatial, mathematical, or logical relationships (Table 1). Task differences may induce some variability between fMRI studies that decreases the ability of meta-analyses to observe significant results. For instance, stimuli in semantic tasks were relatively homogeneous (written words), but the relationships involved in the analogies varied between studies. The visuospatial tasks were more heterogeneous in terms of materials or stimuli used, such as geometric shapes (Preusse et al. 2011; Wartenburger et al. 2009), symbol strings (Geake and Hansen, 2010, 2005; Volle et al. 2010), pictures (Cho et al. 2010), colors and forms (Christoff et al. 2003; Watson and Chatterjee, 2012), or abstract line drawings (Wendelken et al. 2012), but involved quite similar categories of relationships, for instance increase in size, symmetry, pattern. Thus, we cannot exclude the possibility that these factors impacted the results, and that task-related differences are due to variability in experimental paradigms or materials used rather than to the analogy domain.

Dissociable Visuospatial Analogy and Matrix Problem task networks

The current meta-analysis identified dissociable neural systems activated by the Visuospatial Analogy and the Matrix Problem tasks across fMRI studies, in both the PFC and other brain regions.

In the rostral PFC, a region overlapping the “left rlPFC ROI” was recruited to a significantly greater extent in Visuospatial Analogy than in Matrix Problem tasks (Table 7). This could indicate that the “left rlPFC ROI”, located at the anterior end of the IFS, is a region that is relatively specific to analogical reasoning and is thus less involved in other relational reasoning tasks such as the Matrix Problems. No other regions were significantly different in terms of activation when contrasting Visuospatial Analogy to Matrix Problem tasks.

Conversely when Matrix Problem tasks were compared to Analogy tasks, we observed the recruitment of a set of brain regions including a rostral prefrontal cluster that was located in the anterior part of the SFG and SFS. This cluster was dorsal and medial to the "left rlPFC ROI". This result suggests a functional specialization within the left frontal pole between a ventral region at the end of the IFS that supports analogical reasoning and a more medial region at the end of the SFS supporting relational reasoning in matrix format. However, this interpretation should be taken with caution because this medial rlPFC cluster was not observed in the Matrix Problem tasks map (task related activation) and was significant only when contrasting Matrix Problem to Analogy tasks. In addition, when compared to Analogy tasks, Matrix Problem tasks more consistently recruited a large set of brain regions that can be organized into a superior and an inferior fronto-parieto-occipital brain system with a right predominance. These significant regions appeared to belong to the attentional and fronto-parietal executive networks (Rojkova et al. 2014; Thiebaut de Schotten et al. 2011).

The between-task differences in brain activation observed in the current meta-analysis raise the question as to which cognitive processes differ between these two types of visuospatial relational reasoning tasks. Both Analogy and Matrix Problem tasks require inductive and relational reasoning and are considered to be measures of fluid reasoning, i.e., the capacity to think logically and to solve problems in novel situations, independent of acquired knowledge. The two types of tasks may nevertheless differ regarding (1) evaluation versus completion requirements of the task designs; (2) variable visuospatial loads during stimulus display or response choices; and (3) the number of relationships to integrate.

First, analogy and matrix problem tasks could involve distinct cognitive processes because their response requirements are different (Table 1). Two main experimental conditions were used in the included studies: (1) evaluate a proposed analogy ("is A to B as C is to D'') ("Evaluate Yes/No" in Table 1) or (2) complete an analogy ("A is to B as C is to?''), in which participants were asked to select one among several alternatives ("Forced choice completion" in Table 1). All but two studies that used Matrix problems involved a forced choice completion between multiple alternatives, so that all of the lines and columns of the matrix share the same relationships, i.e., are analogs. Among analogy studies, all but four studies involved an evaluation type of response. In only one study the response type was a forced choice completion comparable to the response type in Matrix problem tasks. In two studies participants were to select a target given a source (different from the completion of an incomplete target), and in one study participants freely generated verbally the completion of a target (no forced choice). Therefore, differences in evaluation and completion requirements between analogy and matrix problems could be a confounding factor in our meta-analysis, that can not be controlled for, and might explain some of the differences in their brain correlates. For instance, Wendelken and colleagues' study (2008a) demonstrated that the left rlPFC was involved in evaluating analogies but not in completing a 4-term analogy, which instead was associated with the medial PFC. Here, matrix problem studies rarely included an evaluation condition, which could account for the absence of significant activation in the "left rlPFC ROI", while they recruited a more medial PFC region. Among the two Matrix problem studies that used evaluative responses, one recruited the left rlPFC while the other did not, which did not help to clarify this point. Alternatively, compared to evaluation, completion responses could increase interindividual variability in performance or solving strategy (Shokri-Kojori et al. 2012), and then decrease the power of fMRI to detect significant activation across subjects or increase variability between studies. The issue of response type in relational reasoning should be addressed in further specific experiments controlling for the task type and domain of relationships.

Second, it is likely that the visual and spatial load is greater in matrix problems compared to visuospatial analogy tasks because a greater number of stimuli are usually displayed with regard to both the test items and choice alternatives. Indeed, analogy tasks are usually composed of 4 terms (A:B as C:D) [or sometimes 6 terms for visuospatial analogies; Geake and Hansen, 2010; Volle et al. 2010; Watson and Chatterjee, 2012], whereas matrix tasks usually display a 3-by-3 (or 3-by-2) matrix of terms. Thus, the greater visuospatial processing requirement in matrix problems could explain the additional recruitment of visuospatial regions and the attentional network (Kalbfleisch et al. 2013).

Finally, a greater number of stimuli to analyze also implies more relationships to consider and integrate during matrix problems, which possibly involves additional brain regions (Ackerman and Courtney, 2012). The need to consider and manipulate a greater number of relationships could explain the stronger activation observed in the fronto-parietal control network (Ackerman and Courtney, 2012; Hamsphire et al. 2011; Jia et al. 2015; Volle et al. 2008). This also raises the question of the involvement of "multitasking" or "branching" operations in matrix problem solving, i.e., the need to hold goals in mind while exploring and processing secondary goals (Dreher et al. 2008; Koechlin et al. 1999).

Therefore, visuospatial analogy and matrix problem tasks appear to engage dissociable neural systems across fMRI studies, with more visuospatial, executive, and possibly multitasking requirements in matrix reasoning and possibly greater comparison and matching processing required for analogy tasks.

Conclusion

The current findings showed the distinct brain systems that are involved in relational reasoning and described their task specificities. Several bilateral fronto-parietal systems contributed to different aspects of relational reasoning. The results revealed that the left rlPFC is a domain-general region that is specialized for analogy tasks and is co-activated with different brain regions along the dorsoventral axis as a function of the analogy domain. This suggests that the connectivity of this region with domain-oriented regions has a crucial role in analogical reasoning capacities. Conversely, matrix Problems showed a greater recruitment of the attention network and a fronto-parietal control network compared to analogy tasks, possibly due to greater demands on visuospatial processing and/or the coordination of a greater number of relationships prior to integration. The contrast between matrix problems and analogy tasks also revealed a possible specialization within this region. These findings provide some predictions about the respective roles of distinct brain regions or networks in relational reasoning, which could be tested in neurological patients. Despite the importance of these high-level functions in human cognition, the consequences of brain damage on analogical reasoning are poorly known. The current results provide new anatomical and functional hypotheses to test in patients with focal lesions, and suggest that future neurological studies should use distinct experimental analogy tasks in both semantic and non-semantic domains. For instance, the current results predict that a left rlPFC lesion would alter relational reasoning abilities for all domains of relationships, including real world analogies, whereas lesions in more posterior lesions would impact semantic and non-semantic analogies differently depending on lesion location along the ventral-dorsal axis. Only lesion studies would answer the question of the critical role of the left rlPFC in Matrix problem solving. Such focal lesion studies are needed in order to assess the validity of the results regarding real world analogies, and finally to inform patients and clinicians on the expected deficits after a given lesion.

ACKNOWLEDGMENTS

Funding

This work was supported by the Agence Nationale de la Recherche [grant number ANR-09-RPDOC-004-01, ev], the Société Française de Neurologie (LH) and Journées de Neurologie de Langue Française (CDD). The research leading to these results received funding from the Investissements d'avenir program ANR-10-IAIHU-06.

Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as potential conflicts of interest.

REFERENCES

Ackerman CM, Courtney SM (2012). Spatial relations and spatial locations are dissociated within prefrontal and parietal cortex. J Neurophysiol, 108(9), 2419-2429.

Aichelburg C, Urbanski M, Thiebaut de Schotten M, Humbert F, Levy R, Volle E (2014). Morphometry of Left Frontal and Temporal Poles Predicts Analogical Reasoning Abilities. Cereb Cortex, bhu254.

Amorapanth PX, Widick P, Chatterjee A (2010). The neural basis for spatial relations. J Cogn Neurosci, 22(8), 1739-1753.

Babcock L, Vallesi A (2015). The interaction of process and domain in prefrontal cortex during inductive reasoning. Neuropsychologia, 67, 91-99.

Badre D (2008). Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. Trends Cogn Sci, 12(5), 193-200.

Badre D, Wagner AD (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. Neuropsychologia, 45(13), 2883-2901.

Badre D and D'Esposito M. (2007) Functional Magnetic Resonance Imaging Evidence for a Hierarchical Organization of the Prefrontal Cortex. J Cogn Neurosci, 19, 2082–99.

Baldo JV, Delis DC, Wilkins DP, Shimamura AP (2004). Is it bigger than a breadbox? Performance of patients with prefrontal lesions on a new executive function test. Arch Clin Neuropsychol, 19(3), 407-419.

Barde LHF, Thompson-Schill SL (2002). Models of functional organization of the lateral prefrontal cortex in verbal working memory: evidence in favor of the process model. J Cogn Neurosci, 14(7), 1054-1063.

Bates E, Wilson SM, Saygin AP, Dick F, Sereno MI, Knight RT, Dronkers NF (2003). Voxel-based lesion-symptom mapping. Nat Neurosci, 6(5), 448-450.

Bazargani N, Hillebrandt H, Christoff K & Dumontheil I. (2014). Developmental changes in effective connectivity associated with relational reasoning: DCM of Relational Reasoning Development. Human Brain Mapping, 35, 3262–3276.

Bohrn IC, Altmann U, Jacobs AM (2012). Looking at the brains behind figurative language--a quantitative meta-analysis of neuroimaging studies on metaphor, idiom, and irony processing. Neuropsychologia, 50(11), 2669-2683.

Bor, D and Owen, AM. (2007). A Common Prefrontal–Parietal Network for Mnemonic and Mathematical Recoding Strategies within Working Memory. Cereb. Cortex, **17,** 778–786

Bor, D, Duncan, J, Wiseman, RJ & Owen, AM. (2003) Encoding Strategies Dissociate Prefrontal Activity from Working Memory Demand. Neuron, **37,** 361–367.

Boroojerdi B, Phipps M, Kopylev L, Wharton CM, Cohen LG, Grafman J (2001). Enhancing analogic reasoning with rTMS over the left prefrontal cortex. Neurology, 56(4), 526-8.

Braver TS, Bongiolatti SR (2002). The role of frontopolar cortex in subgoal processing during working memory. Neuroimage, 15(3), 523-536.

Brunyé TT, Moran JM, Cantelon J, Holmes A, Eddy MD, Mahoney CR, Taylor HA (2015). Increasing breadth of semantic associations with left frontopolar direct current brain stimulation: a role for individual differences. Neuroreport, 26(5), 296-301.

Buckner RL, Andrews-Hanna JR, Schacter DL (2008). The brain's default network: anatomy, function, and relevance to disease. Ann N Y Acad Sci, 1124, 1-38.

Bunge SA, Wendelken C, Badre D, Wagner AD (2005). Analogical reasoning and prefrontal cortex: evidence for separable retrieval and integration mechanisms. Cereb Cortex, 15(3), 239-249.

Burgess PW (2000). Strategy application disorder: the role of the frontal lobes in human multitasking. Psychol Res, 63(3-4), 279-288.

Burgess PW, Alderman N, Volle E, Benoit RG, Gilbert SJ (2009). Mesulam's frontal lobe mystery re-examined. Restor Neurol Neurosci, 27(5), 493-506.

Burgess PW, Veitch E, de Lacy Costello A, Shallice T (2000). The cognitive and neuroanatomical correlates of multitasking. Neuropsychologia, 38(6), 848-863.

Catani M, Jones DK, ffytche DH (2005). Perisylvian language networks of the human brain. Ann Neurol, 57(1), 8-16.

Champod AS. and Petrides M. (2010). Dissociation within the frontoparietal network in verbal working memory: a parametric functional magnetic resonance imaging study. J. Neurosci, 30, 3849–3856.

Cho S, Moody TD, Fernandino L, Mumford JA, Poldrack RA, Cannon TD, Knowlton BJ, Holyoak KJ (2010). Common and dissociable prefrontal loci associated with component mechanisms of analogical reasoning. Cereb Cortex, 20(3), 524-533.

Christoff K, Gabrieli JDE (2000). The frontopolar cortex and human cognition: Evidence for a rostrocaudal hierarchical organization within the human prefrontal cortex. Psychobiology, 2(28), 168-186.

Christoff K, Keramatian K, Gordon AM, Smith R, Mädler B (2009). Prefrontal organization of cognitive control according to levels of abstraction. Brain Res, 1286, 94-105.

Christoff K, Prabhakaran V, Dorfman J, Zhao Z, Kroger JK, Holyoak KJ, Gabrieli JD (2001). Rostrolateral prefrontal cortex involvement in relational integration during reasoning. Neuroimage, 14(5), 1136-1149.

Christoff K, Ream JM, Geddes LPT, Gabrieli JDE (2003). Evaluating self-generated information: anterior prefrontal contributions to human cognition. Behav Neurosci, 117(6), 1161-1168.

Cole MW, Yarkoni T, Repovs G, Anticevic A, Braver TS (2012). Global connectivity of prefrontal cortex predicts cognitive control and intelligence. J Neurosci, 32(26), 8988-8999.

Corbetta M, Shulman GL (2002). Control of goal-directed and stimulus-driven attention in the brain. Nature Rev Neurosci, 3(3), 201-215.

Courtney SM (2004). Attention and cognitive control as emergent properties of information representation in working memory. Cogn Affect Behav Neurosci, 4(4), 501-516.

Crone EA, Wendelken C, van Leijenhorst L, Honomichl RD, Christoff K, Bunge SA. (2009). Neurocognitive development of relational reasoning. Dev Sci, 12, 55–66.

Curtis CE. (2006). Prefrontal and parietal contributions to spatial working memory. Neuroscience 139, 173–80.

Dreher JC, Koechlin E, Tierney M, Grafman J (2008). Damage to the fronto-polar cortex is associated with impaired multitasking. PloS One, 3(9), e3227.

Dronkers NF, Wilkins DP, Van Valin RD, Redfern BB, Jaeger JJ (2004). Lesion analysis of the brain areas involved in language comprehension. Cognition, 92(1-2), 145-177.

Dumontheil I (2014). Development of abstract thinking during childhood and adolescence: The role of rostrolateral prefrontal cortex. Dev Cogn Neurosci, 10, 57-76.

Dumontheil I, Houlton R, Christoff K, Blakemore SJ (2010). Development of relational reasoning during adolescence. Dev Sci, 13(6), F15-24.

Eickhoff SB, Bzdok D, Laird AR, Kurth F, FoxPT (2012). Activation likelihood estimation meta-analysis revisited. Neuroimage, 59(3), 2349-2361.

Eickhoff SB, Laird AR, Grefkes C, Wang LE, Zilles K, Fox PT (2009). Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: a random-effects approach based on empirical estimates of spatial uncertainty. Hum Brain Mapp, 30(9), 2907-2926.

Forkel SJ, Thiebaut de Schotten M, Dell'Acqua F, Kalra L, Murphy DGM, Williams SCR, Catani M (2014). Anatomical predictors of aphasia recovery: a tractography study of bilateral perisylvian language networks. Brain, 137(Pt 7), 2027-2039.

Geake JG, Hansen PC (2010). Functional neural correlates of fluid and crystallized analogizing. Neuroimage, 49(4), 3489-3497.

Geake JG, Hansen PC (2005). Neural correlates of intelligence as revealed by fMRI of fluid analogies. Neuroimage, 26(2), 555-564.

Gentner D, Holyoak KJ, Kokinov BN (2001). The Analogical Mind: Perspectives from Cognitive Science. MIT Press.

Gentner D, Holyoak KJ (1997). Reasoning and learning by analogy. Am Psychol, 52(1), 32-34.

Gilbert SJ, Spengler S, Simons JS, Steele JD, Lawrie SM, Frith CD, Burgess PW (2006). Functional specialization within rostral prefrontal cortex (area 10): a meta-analysis. J Cogn Neurosci, 18(6), 932-948.

Gläscher J, Tranel D, Paul LK, Rudrauf D, Rorden C, Hornaday A, Grabowski T, Damasio H, Adolphs R (2009). Lesion mapping of cognitive abilities linked to intelligence. Neuron, 61(5), 681-691.

Golde M, von Cramon DY, Schubotz RI (2010). Differential role of anterior prefrontal and premotor cortex in the processing of relational information. Neuroimage, 49(3), 2890-2900.

Gonen-Yaacovi G, de Souza LC, Levy R, Urbanski M, Josse G, Volle E (2013). Rostral and caudal prefrontal contribution to creativity: a meta-analysis of functional imaging data. Front Hum Neurosci, 7, 465.

Goulden N, Khusnulina A, Davis NJ, Bracewell RM, Bokde AL, McNulty JP, Mullins PG (2014). The salience network is responsible for switching between the default mode network and the central executive network: replication from DCM. Neuroimage, 99, 180-190.

Green AE, Fugelsang JA, Kraemer DJM, Shamosh NA, Dunbar KN (2006). Frontopolar cortex mediates abstract integration in analogy. Brain Res, 1096(1), 125-137.

Green AE, Kraemer DJM, Fugelsang JA, Gray JR, Dunbar KN (2010). Connecting long distance: semantic distance in analogical reasoning modulates frontopolar cortex activity. Cereb Cortex, 20(1), 70-76.

Green AE, Kraemer DJM, Fugelsang JA, Gray JR, Dunbar KN (2012). Neural correlates of creativity in analogical reasoning. J Exp Psychol Learn Mem Cogn, 38(2), 264-272.

Hampshire A, Owen AM (2006). Fractionating attentional control using event-related fMRI. Cereb Cortex, 16(12), 1679-1689.

Hampshire A, Thompson R, Duncan J, Owen AM (2011). Lateral prefrontal cortex subregions make dissociable contributions during fluid reasoning. Cereb Cortex, 21(1), 1-10.

Heilman KM, Bowers D, Valenstein E, Watson RT (1986). The right hemisphere: neuropsychological functions. J Neurosurg, 64(5), 693-704.

Hoffman P, Jefferies E, Lambon Ralph MA (2010). Ventrolateral prefrontal cortex plays an executive regulation role in comprehension of abstract words: convergent neuropsychological and repetitive TMS evidence. J Neurosci, 30(46), 15450-15456.

Holmes CJ, Hoge R, Collins L, Woods R, Toga AW, Evans AC (1998). Enhancement of MR images using registration for signal averaging. J Comput Assist Tomogr, 22(2), 324-333.

Jia X, Liang P, Shi L, Wang D, Li K (2015). Prefrontal and parietal activity is modulated by the rule complexity of inductive reasoning and can be predicted by a cognitive model. Neuropsychologia 66:67-74.

Jilka SR, Scott G, Ham T, Pickering A, Bonnelle V, Braga RM, Leech R, Sharp DJ (2014). Damage to the Salience Network and interactions with the Default Mode Network. J Neurosci, 34(33), 10798-10807.

Jung RE, Haier RJ (2007). The Parieto-Frontal Integration Theory (P-FIT) of intelligence: converging neuroimaging evidence. Behav Brain Sci, 30(2), 135-154; discussion 154-187.

Kaiser NC, Lee GJ, Lu PH, Mather MJ, Shapira J, Jimenez E, Thompson PM, Mendez MF (2013). What dementia reveals about proverb interpretation and its neuroanatomical correlates. Neuropsychologia, 51(9), 1726-1733.

Kalbfleisch ML, Debettencourt MT, Kopperman R, Banasiak M, Roberts JM, Halavi M (2013). Environmental influences on neural systems of relational complexity. Front Psychol, 4, 631.

Kalbfleisch ML, Van Meter JW, Zeffiro TA (2007). The influences of task difficulty and response correctness on neural systems supporting fluid reasoning. Cognitive Neurodynamics, 1(1), 71-84.

Koechlin E, Basso G, Pietrini P, Panzer S, Grafman J (1999). The role of the anterior prefrontal cortex in human cognition. Nature, 399(6732), 148-151.

Koechlin E, Summerfield C (2007). An information theoretical approach to prefrontal executive function. Trends Cogn Sci, 11(6), 229-235.

Krawczyk DC (2012). The cognition and neuroscience of relational reasoning. Brain Res, 1428, 13-23.

Krawczyk DC, Michelle McClelland M, Donovan CM (2011). A hierarchy for relational reasoning in the prefrontal cortex. Cortex, 47(5):588-597.

Krawczyk DC, Morrison RG, Viskontas I, Holyoak KJ, Chow TW, Mendez MF, Miller BL, Knowlton BJ (2008). Distraction during relational reasoning: the role of prefrontal cortex in interference control. Neuropsychologia, 46(7), 2020-2032.

Kroger JK, Sabb FW, Fales CL, Bookheimer SY, Cohen MS, Holyoak KJ (2002). Recruitment of anterior dorsolateral prefrontal cortex in human reasoning: a parametric study of relational complexity. Cereb Cortex, 12(5), 477-485.

Lagarde J, Valabrègue R, Corvol JC, Garcin B, Volle E, Le Ber I, Vidailhet M, Dubois B, Levy R. (2015). Why do patients with neurodegenerative frontal syndrome fail to answer: 'In what way are an orange and a banana alike?' Brain, 138(2), 456-471.

Laird AR, Eickhoff SB, Kurth F, Fox PM, Uecker AM, Turner JA, Robinson JL, Lancaster JL, Fox PT (2009). ALE Meta-Analysis Workflows Via the Brainmap Database: Progress Towards A Probabilistic Functional Brain Atlas. Front Neuroinform, 3, 23.

Laird AR, Fox PM, Price CJ, Glahn DC, Uecker AM, Lancaster JL, Turkeltaub PE, Kochunov P, Fox PT (2005). ALE meta-analysis: controlling the false discovery rate and performing statistical contrasts. Hum Brain Mapp, 25(1), 155-164.

Luo Q, Perry C, Peng D, Jin Z, Xu D, Ding G, Xu S (2003). The neural substrate of analogical reasoning: an fMRI study. Brain Res Cogn Brain Res, 17(3), 527-534.

Mesulam MM (1981). A cortical network for directed attention and unilateral neglect. Ann Neurol, 10(4), 309-325.

Monti MM, Osherson DN, Martinez MJ, Parsons LM (2007). Functional neuroanatomy of deductive inference: a language-independent distributed network. Neuroimage, 37(3), 1005-1016.

Morrison RG, Krawczyk DC, Holyoak KJ, Hummel JE, Chow TW, Miller BL, Knowlton BJ (2004). A neurocomputational model of analogical reasoning and its breakdown in frontotemporal lobar degeneration. J Cogn Neurosci, 16(2), 260-271.

Murphy P, Shallice T, Robinson G, MacPherson SE, Turner M, Woollett K, Bozzali M, Cipolotti L (2013). Impairments in proverb interpretation following focal frontal lobe lesions. Neuropsychologia, 51(11), 2075-2086.

Narayanan NS, Prabhakaran V, Bunge SA, Christoff K, Fine EM, Gabrieli JDE (2005). The role of the prefrontal cortex in the maintenance of verbal working memory: an event-related FMRI analysis. Neuropsychology, 19(2), 223-232.

Perfetti B, Saggino A, Ferretti A, Caulo M, Romani GL, Onofrj M (2009). Differential patterns of cortical activation as a function of fluid reasoning complexity. Hum Brain Mapp, 30(2), 497-510.

Petrides M (2005). Lateral prefrontal cortex: architectonic and functional organization. Philos Trans R Soc Lond B Biol Sci, 360(1456), 781-795.

Power JD, Cohen AL, Nelson SM, Wig GS, Barnes KA, Church JA, Vogel AC, Laumann TO, Miezin FM, Schlaggar BL, Petersen SE (2011). Functional network organization of the human brain. Neuron, 72(4), 665-678.

Power JD, Petersen SE (2013). Control-related systems in the human brain. Curr Opin Neurobiol, 23(2), 223-228.

Prado J, Chadha A, Booth JR (2011). The brain network for deductive reasoning: a quantitative meta-analysis of 28 neuroimaging studies. J Cogn Neurosci, 23(11), 3483-3497.

Preusse F, van der Meer Elke, Deshpande G, Krueger F, Wartenburger I (2011). Fluid intelligence allows flexible recruitment of the parieto-frontal network in analogical reasoning. Front Hum Neurosci, 5, 22.

Price CJ (2010). The anatomy of language: a review of 100 fMRI studies published in 2009. Ann N Y Acad Sci, 1191, 62-88.

Ramnani N, Owen AM (2004). Anterior prefrontal cortex: insights into function from anatomy and neuroimaging. Nat Rev Neurosci, 5(3), 184-194.

Rapp AM, Leube DT, Erb M, Grodd W, Kircher TTJ (2004). Neural correlates of metaphor processing. Brain Res Cogn Brain Res, 20(3), 395-402.

Raven JC (1941). Standardization of progressive matrices, 1938. Br J Med Psychol.

Reber TP, Luechinger R, Boesiger P, Henke K (2014). Detecting analogies unconsciously. Front Behav Neurosci, 8, 9.

Reineberg AE, Andrews-Hanna JR, Depue BE, Friedman NP, Banich MT (2015). Resting-state networks predict individual differences in common and specific aspects of executive function. Neuroimage, 104, 69-78.

Reverberi C, Lavaroni A, Gigli GL, Skrap M, Shallice T (2005). Specific impairments of rule induction in different frontal lobe subgroups. Neuropsychologia, 43(3), 460-472.

Sakai K, Passingham RE (2003). Prefrontal interactions reflect future task operations. Nat Neurosci, 6(1), 75-81.

Seeley WW, Menon V, Schatzberg AF, Keller J, Glover GH, Kenna H, Reiss AL, Greicius MD (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. J Neurosci, 27(9), 2349-2356.

Shokri-Kojori E, Motes MA, Rypma B, Krawczyk DC (2012). The network architecture of cortical processing in visuo-spatial reasoning. Sci Rep, 2, 411.

Smith EE, Jonides J (1999). Storage and executive processes in the frontal lobes. Science, 283(5408), 1657-1661.

Smith R, Keramatian K, Christoff K (2007). Localizing the rostrolateral prefrontal cortex at the individual level. Neuroimage, 36(4), 1387-1396.

Smith EE and Jonides J. (1999). Storage and executive processes in the frontal lobes. Science 283, 1657–61.

Sridharan D, Levitin DJ, Menon V (2008). A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. Proc Nat Acad Sci U S A, 105(34), 12569-12574.

Stuss DT. Functions of the Frontal Lobes: Relation to Executive Functions. (2011). Journal of the International Neuropsychological Society, 17, 759–765.

Thibaut J-P, French R & Vezneva M. (2010). The development of analogy making in children: Cognitive load and executive functions. J Exp Child Psychol, 106, 1-19.

Thiebaut de Schotten M, Dell'Acqua F, Forkel SJ, Simmons A, Vergani F, Murphy DGM, Catani M (2011). A lateralized brain network for visuospatial attention. Nat Neurosci, 14(10), 1245-1246.

Thompson-Schill SL (2003). Neuroimaging studies of semantic memory: inferring « how » from « where ». Neuropsychologia, 41(3), 280-292.

Turkeltaub PE, Eden GF, Jones KM, Zeffiro TA (2002). Meta-analysis of the functional neuroanatomy of single-word reading: method and validation. Neuroimage, 16(3 Pt 1), 765-780.

Turkeltaub PE, Eickhoff SB, Laird AR, Fox M, Wiener M, Fox P (2012). Minimizing within-experiment and within-group effects in Activation Likelihood Estimation meta-analyses. Hum Brain Mapp, 33(1), 1-13.

Vartanian O (2012). Dissociable neural systems for analogy and metaphor: implications for the neuroscience of creativity. Br J Psychol, 103(3), 302-316.

Vincent JL, Kahn I, Snyder AZ, Raichle ME, Buckner RL (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. J Neurophysiol, 100(6), 3328-3342.

Volle E, Gilbert SJ, Benoit RG, Burgess PW (2010). Specialization of the rostral prefrontal cortex for distinct analogy processes. Cereb Cortex, 20(11), 2647-2659.

Volle E, Kinkingnéhun S, Pochon JB, Mondon K, Thiebaut de Schotten M, Seassau M, Duffau H, Samson Y, Dubois B, Levy R (2008). The functional architecture of the left posterior and lateral prefrontal cortex in humans. Cereb Cortex, 18(10), 2460-2469.

Waltz JA, Knowlton BJ, Holyoak KJ, Boone KB, Mishkin FS, de Menezes Santos M, Thomas CR, Miller BL (1999). A System for Relational Reasoning in Human Prefrontal Cortex. Psychol Sci, 10(2), 119-125.

Wartenburger I, Heekeren HR, Preusse F, Kramer J, van der Meer E (2009). Cerebral correlates of analogical processing and their modulation by training. NeuroImage, 48(1), 291-302.

Watson CE, Chatterjee A (2012). A bilateral frontoparietal network underlies visuospatial analogical reasoning. Neuroimage, 59(3), 2831-2838.

Wendelken C. (2015). Meta-analysis: how does posterior parietal cortex contribute to reasoning? Front. Hum. Neurosci, 8, 1042.

Wendelken C, Chung D, Bunge SA (2012). Rostrolateral prefrontal cortex: domain-general or domain-sensitive? Hum Brain Mapp, 33(8), 1952-1963.

Wendelken C, Nakhabenko D, Donohue SE, Carter CS, Bunge SA (2008a). « Brain is to thought as stomach is to ?? »: investigating the role of rostrolateral prefrontal cortex in relational reasoning. J Cogn Neurosci, 20(4), 682-693.

Wendelken C, Bunge SA & Carter CS. (2008b). Maintaining structured information: an investigation into functions of parietal and lateral prefrontal cortices. Neuropsychologia, 46, 665–78.

Wendelken C, O'Hare ED, Whitaker KJ, Ferrer E & Bunge SA. (2011). Increased Functional Selectivity over Development in Rostrolateral Prefrontal Cortex. J. Neurosci, 31, 17260–17268.

Wright SB, Matlen BJ, Baym CL, Ferrer E, Bunge SA (2008). Neural correlates of fluid reasoning in children and adults. Front Hum Neurosci, 1, 8.

Yamada T, Ohta H, Watanabe H, Kanai C, Tani M, Ohno T, Takayama Y, Iwanami A, Kato N, Hashimoto R. (2012). Functional alterations in neural substrates of geometric reasoning in adults with high-functioning autism. PloS One, 7(8), e43220.

Yuan Z, Qin W, Wang D, Jiang T, Zhang Y, Yu C (2012). The salience network contributes to an individual's fluid reasoning capacity. Behav Brain Res, 229(2), 384-390.

FIGURE CAPTIONS

Figure 1: Global ALE map showing significant activation associated with all the included tasks. The ALE map is displayed on a surface rendering of the anatomical Colin27 template (Holmes et al. 1996) in the MNI space. A cluster correction for multiple comparisons was used with an uncorrected cluster-forming threshold at $p < 0.001$ and a cluster threshold at $p < 0.05$.

Figure 2: Task category maps. Semantic Analogy map (in green), Visuospatial Analogy map (in red) and Visuospatial Matrix problems map (in blue). ALE maps are displayed on a surface rendering of the anatomical Colin27 template (Holmes et al. 1996) in the MNI space. A cluster correction for multiple comparisons was used with an uncorrected cluster-forming threshold at $p < 0.001$ and a cluster threshold at $p < 0.05$.

Figure 3: Analogy domain subtraction maps. Semantic versus Visuospatial Analogy map (in green) and Visuospatial versus Semantic Analogy map (in red) is compared to the "left rlPFC ROI" from the global ALE map (in cyan). The ALE subtraction maps are displayed on a surface rendering of the anatomical Colin27 template (Holmes et al. 1996) in the MNI space. These contrast maps were thresholded at an uncorrected p value < 0.05 following 10,000 permutations with a minimum cluster size of 100 voxels.

Figure 4: Task subtraction maps. Visuospatial Analogy versus Matrix problems map (in red) is compared to Visuospatial Matrix Problems versus Analogy map (in blue). The ALE subtraction maps are displayed on a surface rendering of the anatomical Colin27 template (Holmes et al. 1996) in the MNI space. These contrast maps were thresholded at an

uncorrected p value < 0.05 following 10,000 permutations with a minimum cluster size of 100 voxels.

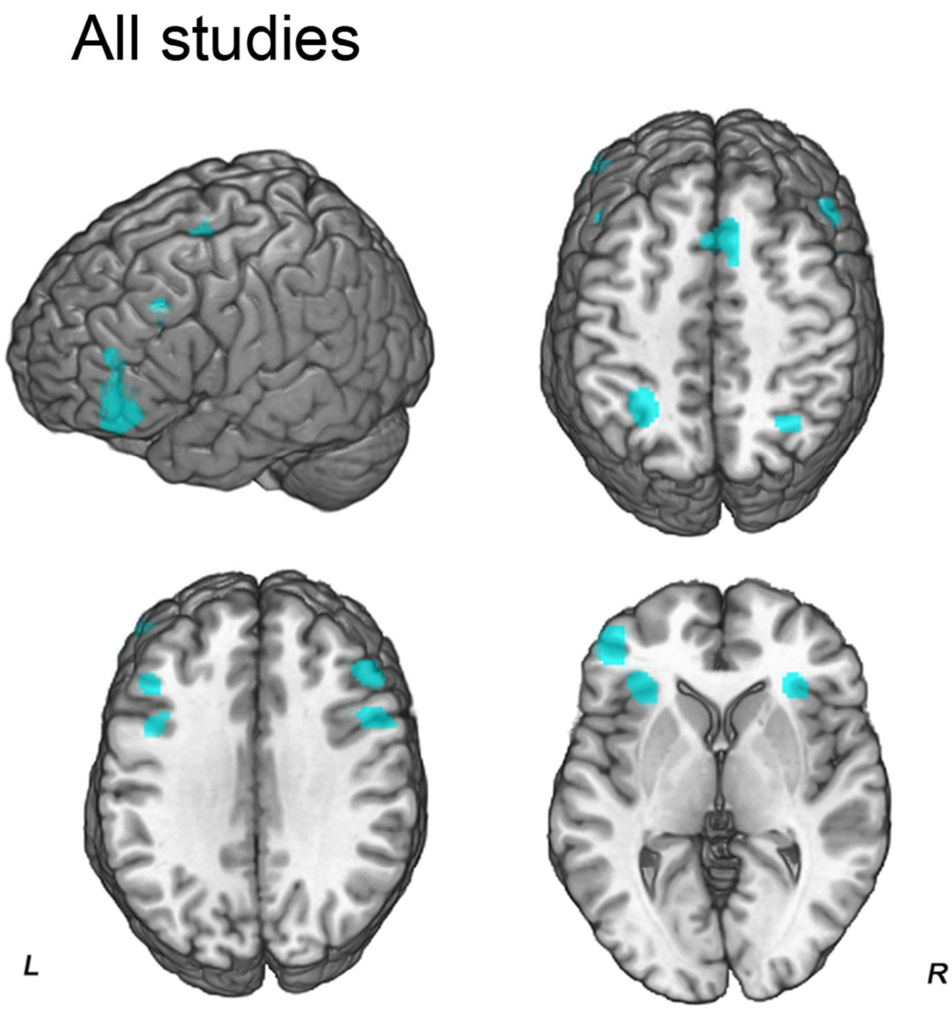

Fig. 1: Global ALE map showing significant activation associated with all the included tasks. The ALE map is displayed on a surface rendering of the anatomical Colin27 template (Holmes et al. 1996) in the MNI space. A cluster correction for multiple comparisons was used with an uncorrected cluster-forming threshold at $p < 0.001$ and a cluster threshold at $p < 0.05$.
88x100mm (300 x 300 DPI)

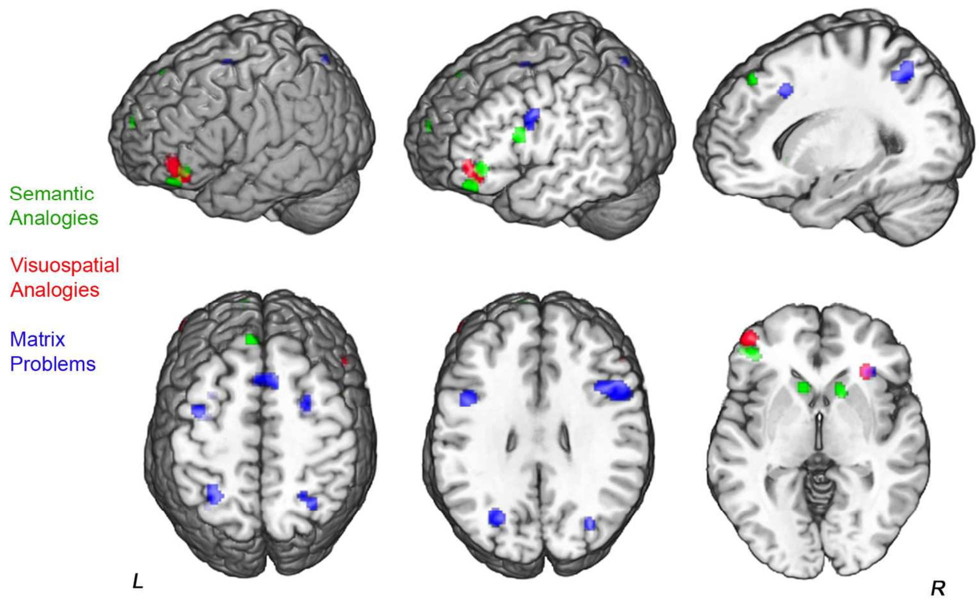

Fig. 2: Task category maps. Semantic Analogy map (in green), Visuospatial Analogy map (in red) and Visuospatial Matrix problems map (in blue). ALE maps are displayed on a surface rendering of the anatomical Colin27 template (Holmes et al. 1996) in the MNI space. A cluster correction for multiple comparisons was used with an uncorrected cluster-forming threshold at $p < 0.001$ and a cluster threshold at $p < 0.05$.
162x101mm (300 x 300 DPI)

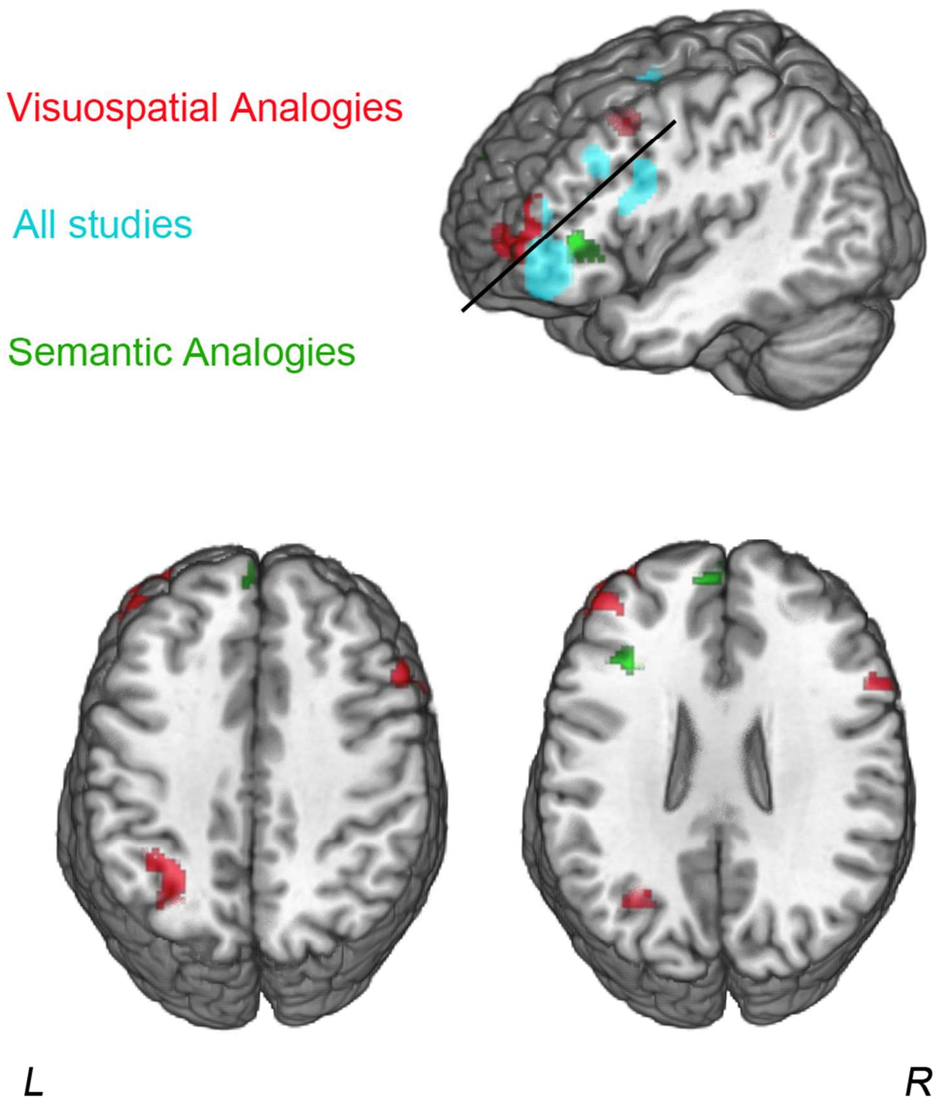

Fig. 3: Analogy domain subtraction maps. Semantic versus Visuospatial Analogy map (in green) and Visuospatial versus Semantic Analogy map (in red) is compared to the "left rlPFC ROI" from the global ALE map (in cyan). The ALE subtraction maps are displayed on a surface rendering of the anatomical Colin27 template (Holmes et al. 1996) in the MNI space. These contrast maps were thresholded at an uncorrected p value < 0.05 following 10,000 permutations with a minimum cluster size of 100 voxels.
88x107mm (300 x 300 DPI)

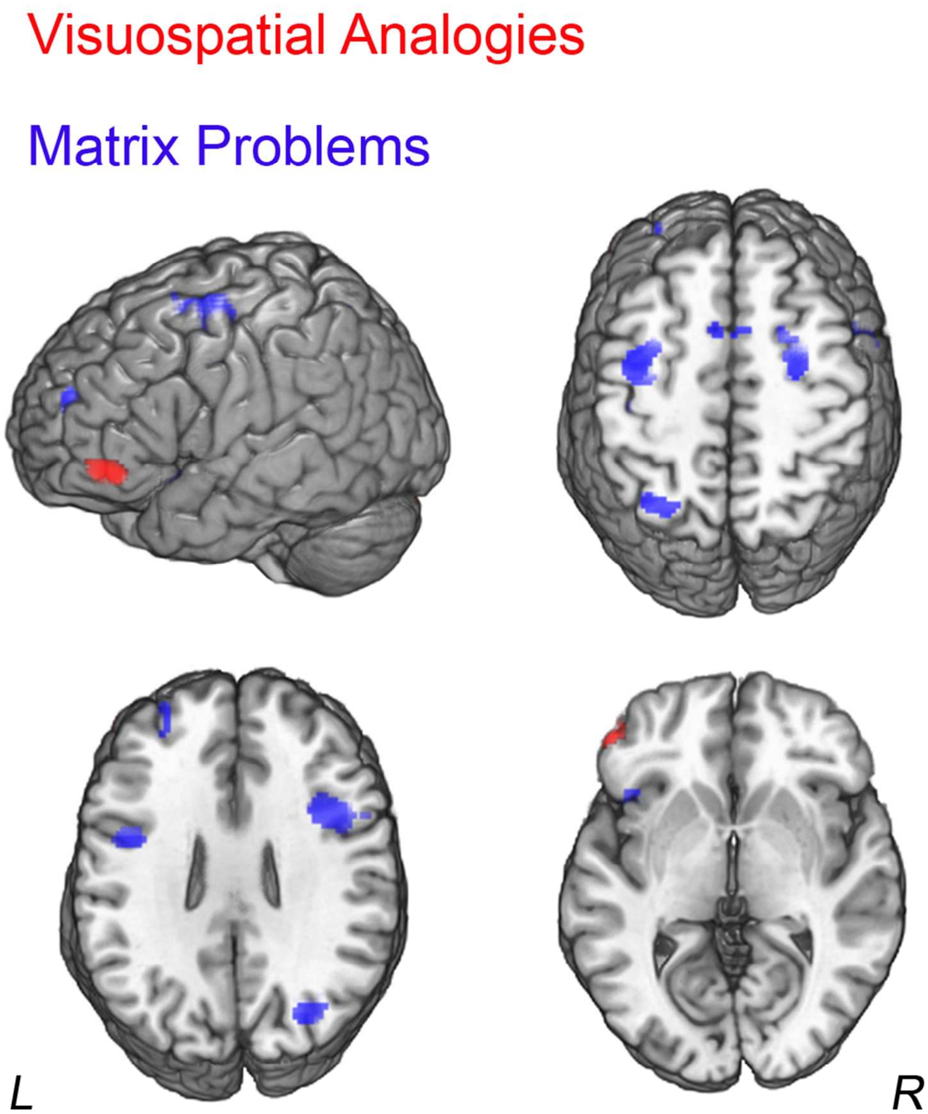

Fig. 4: Task subtraction maps. Visuospatial Analogy versus Matrix problems map (in red) is compared to Visuospatial Matrix Problems versus Analogy map (in blue). The ALE subtraction maps are displayed on a surface rendering of the anatomical Colin27 template (Holmes et al. 1996) in the MNI space. These contrast maps were thresholded at an uncorrected p value < 0.05 following 10,000 permutations with an arbitrary minimum cluster size of 100 voxels.
88x108mm (300 x 300 DPI)

Table 1: List and characteristics of all the experiments included in the meta-analysis.

Authors	Year	N subjects	Task description	Kind of relationship	Task category	Kind of response
Bunge et al.	2005	20	4 terms analogy	Semantic	Semantic Analogy	Evaluate (Yes/No)
Cho et al.	2010	17	4 terms analogy	Visuospatial	Visuospatial Analogy	Evaluate (Yes/No)
Christoff et al.	2001	10	Raven-like	Visuospatial	Matrix Problem	Forced choice completion
Christoff et al.	2003	12	4 terms analogy	Visuospatial	Visuospatial Analogy	Evaluate (Yes/No)
Geake and Hansen	2005	12	4 terms analogy	Visuospatial	Visuospatial Analogy	Forced choice completion
Geake and Hansen	2010	16	6 terms analogy	Visuospatial	Visuospatial Analogy	Evaluate (Yes/No)
Golde et al.	2010	16	Raven-like	Visuospatial	Matrix Problem	Forced choice completion
Green et al.	2010	23	4 terms analogy	Semantic	Semantic Analogy	Evaluate (Yes/No)
Green et al.	2012	23	4 terms analogy	Semantic	Semantic Analogy	Free completion
Hampshire et al. (expe 1)	2011	16	Raven matrices	Visuospatial	Matrix Problem	Forced choice completion
Hampshire et al.	2011	21	Raven matrices	Visuospatial	Matrix Problem	Forced choice completion

(expe 2)						
Kalbfleisch et al.	2007	14	Raven-like	Visuospatial	Matrix Problem	Forced choice completion
Kalbfleisch et al.	2013	34	Raven-like	Visuospatial	Matrix Problem	Forced choice completion
Krawczyk et al.	2011	20	Raven-like	Visuospatial	Matrix Problem	Evaluate (Yes/No)
Kroger et al.	2002	8	Raven-like	Visuospatial	Matrix Problem	Forced choice completion
Luo et al.	2003	10	4 terms analogy	Semantic	Semantic Analogy	Evaluate (Yes/No)
Perfetti et al.	2009	18	Raven-like	Visuospatial	Matrix Problem	Forced choice completion
Preusse et al.	2011	40	4 terms analogy	Visuospatial	Visuospatial Analogy	Evaluate (Yes/No)
Reber et al. (2 expe)	2014	12	4 terms analogy	Semantic	Semantic Analogy	Evaluate (Yes/No)
Shokri-Kojori et al.	2012	20	Raven-like	Visuospatial	Matrix Problem	Evaluate (Yes/No)
Volle et al.	2010	16	6 terms analogy	Visuospatial	Visuospatial Analogy	Target selection among 2 options
Wartenburger et al.	2009	15	4 terms analogy	Visuospatial	Visuospatial Analogy	Evaluate (Yes/No)
Watson and Chatterjee	2012	23	6 terms analogy	Visuospatial	Visuospatial Analogy	Target selection among 2 options
Wendelken et al.	2008	20	4 terms analogy	Semantic	Semantic Analogy	Evaluate (Yes/No) + Free completion
Wendelken et al.	2012	22	4 terms analogy	Semantic	Semantic Analogy	Evaluate (Yes/No)

(expe 1)						
Wendelken et al. (expe 2)	2012	22	4 terms analogy	Visuospatial	Visuospatial Analogy	Evaluate (Yes/No)
Yamada et al.	2012	26	Raven matrices	Visuospatial	Matrix Problem	Forced choice completion

Table 2: Locations of clusters with significant ALE values for the global analysis. Columns number 3-7 represent data associated with the left hemisphere and 8-12 represent data associated with the right hemisphere. The clusters displayed in bold were significant at a p < 0.05 FWE corrected threshold. Abbreviations: BA: approximate Brodmann area; ALE: activation likelihood estimation; S: sulcus; G: gyrus; IFG: inferior frontal gyrus; IFS: inferior frontal sulcus; MFG: middle frontal gyrus; SFG: superior frontal gyrus; SFS: superior frontal sulcus; x, y, z coordinates: peak voxel in the Montreal Neurologic Institute (MNI) space.

		Left					**Right**				
Location	**BA**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**
Frontal lobe											
Rostral part of IFS and IFG	10	**1 (5192)**	**0.034**	**-48**	**44**	**-8**					
Posterior IFG/ MFG and IFS / Precentral G	9/44/6	2 (1728)	0.023	-48	12	18	**5 (1208)**	**0.028**	**50**	**10**	**26**
Superior and lateral part of the MFG	9	11 (528)	0.018	-46	26	34	6 (936)	0.019	46	30	30
Medial SFG / Cingulate	6/32						4 (1296)	0.021	6	20	48
Posterior MFG / SFS / Precentral S	6	10 (776)	0.015	-28	0	62	8 (800)	0.023	30	0	56
Parietal lobe											
Superior parietal lobe	7	3 (1552)	0.023	-30	-52	48	9 (776)	0.022	34	-60	52

Inferior parietal lobe	40	3 (1552)	0.018	-34	-46	38					
Insula											
Insula	13	1 (5192)	0.021	-32	26	2	**7 (832)**	**0.027**	**32**	**28**	**-4**

Table 3: Location of the clusters with significant ALE values for Semantic Analogy tasks. Columns number 3-7 represent data associated with the left hemisphere and 8-12 represent data associated with the right hemisphere. Abbreviations: BA: approximate Brodmann area; ALE: activation likelihood estimation; IFG: inferior frontal gyrus, MFG: middle frontal gyrus; SFG: superior frontal gyrus; x, y, z coordinates: peak voxel in the Montreal Neurologic Institute (MNI) space.

		Left					**Right**				
Location	**BA**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**
Frontal lobe											
Rostral part of the MFG	47	1 (1800)	0.018	-44	48	-16					
Rostral part of the IFG	46	1 (1800)	0.016	-50	42	-6					
Posterior part of the IFG	44	2 (432)	0.014	-48	14	18					
Anterior part of the SFG	10	5 (272)	0.010	-10	64	22					
Dorsal part of the SFG	8	6 (272)	0.010	-6	42	50					
Basal ganglia											
Caudate Head		3 (424)	0.015	-10	18	-4	4 (296)	0.012	14	16	-4

Table 4: Location of the clusters with significant ALE values for Visuospatial Analogy tasks. Columns number 3-7 represent data associated with the left hemisphere and 8-12 represent data associated with the right hemisphere. Abbreviations: BA: approximate Brodmann area; ALE: activation likelihood estimation; IFS: inferior frontal sulcus; IFG: inferior frontal gyrus; MFG: middle frontal gyrus; x, y, z coordinates: peak voxel in the Montreal Neurologic Institute (MNI) space.

		Left					**Right**				
Location	**BA**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**
Frontal lobe											
Rostral part of IFS and IFG	10	1 (1784)	0.021	-48	44	-10					
MFG	9						4 (304)	0.013	54	28	34
Insula											
Insula	13						2 (368)	0.013	30	28	-4
Cerebellum											
Posterior lobe (*declive*)		3 (320)	0.013	-18	-92	-20					

Table 5: Location of the clusters with significant ALE values for Visuospatial Matrix problem tasks. Columns number 3-7 represent data associated with the left hemisphere and 8-12 represent data associated with the right hemisphere. Abbreviations: BA: approximate Brodmann area; ALE: activation likelihood estimation; G: gyrus; IFG: inferior frontal gyrus; IFS: inferior frontal sulcus; MFG: middle frontal gyrus; SFG: superior frontal gyrus; SFS: superior frontal sulcus; x, y, z coordinates: peak voxel in the Montreal Neurologic Institute (MNI) space.

		Left					**Right**				
Location	**BA**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**
Frontal lobe											
Posterior IFG/ MFG and IFS / Precentral G	9/44/6	6 (1040)	0.020	-42	6	26	2 (1696)	0.027	50	10	26
Posterior MFG / SFS	6/8	3 (1416)	0.015	-38	-4	56	4 (1160)	0.022	30	0	54
Medial SFG / Cingulate	6/32	12 (384)	0.016	-10	20	40	5 (1144)	0.016	6	18	48
Insula											
Insula							10 (464)	0.014	32	28	-2
Parietal lobe											
Superior parietal lobe	7	1 (1864)	0.018	-30	-52	48	9 (536)	0.015	32	-62	54
Inferior parietal lobe	40	1 (1864)	0.017	-34	-46	38	11 (456)	0.017	34	-44	40
Precuneus	19/31	8 (648)	0.019	-26	-70	28	7 (656)	0.017	32	-74	24
Precuneus	7						9 (536)	0.010	26	-56	50

Table 6: Locations of the clusters with significant ALE values for the contrast of Semantic Analogy versus Visuospatial Analogy and the reverse contrast. Columns number 3-7 represent data associated with the left hemisphere and 7-12 represent data associated with the right hemisphere. Abbreviations: BA: approximate Brodmann area; G: gyrus; IFG: inferior frontal gyrus; IFS: inferior frontal sulcus; MFG: middle frontal gyrus; SFG: superior frontal gyrus; ALE: activation likelihood estimation; x, y, z coordinates: peak voxel in the Montreal Neurologic Institute (MNI) space.

Semantic Analogy versus Visuospatial Analogy											
		Left					**Right**				
Location	**BA**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**
IFG	47	1 (896)	2.404	-47.5	31.8	0					
Medial part of the SFG	10	2 (368)	1.913	-5	59.6	7.5					
SFG	9	3 (280)	1.672	-2.3	62.3	25.6					
IFS	9 / 46	4 (232)	2.028	-32	26	20					

Visuospatial Analogy versus Semantic Analogy											
		Left					**Right**				
Location	**BA**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**
Frontal lobe											
Anterior part of the MFG	10	1 (2696)	2.181	-46	54	4					

Posterior part of the MFG	8/6	3 (1136)	2.506	-48	11	49					
Lateral part of the MFG	9/45						4 (816)	1.792	56.2	30.7	25.7
Lateral part of the IFG	9/46						4 (816)	1.972	57.7	22.3	20
Parietal lobe											
Angular G	39	2 (2512)	2.473	-30.7	-59.3	38.8					
Superior parietal lobe	7	2 (2512)	2.260	-30	-58	48					
Supra-marginalis G / Inferior parietal lobe	40	2 (2512)	2.122	-34	-48	48					
Temporal lobe											
Fusiform G	37						5 (480)	2.044	49.2	-57.2	-13.2

Table 7: Locations of the clusters with significant ALE values for the contrast of Visuospatial Analogy versus Visuospatial Matrix problem tasks and the reverse contrast. Columns number 3-7 represent data associated with the left hemisphere and 7-12 represent data associated with the right hemisphere. Abbreviations: BA: approximate Brodmann area; G: gyrus; IFG: inferior frontal gyrus; IFS: inferior frontal sulcus; MFG: middle frontal gyrus; SFG: superior frontal gyrus; SFS: superior frontal sulcus; ALE: activation likelihood estimation; x, y, z coordinates: peak voxel in the Montreal Neurologic Institute (MNI) space.

Visuospatial Analogy versus Visuospatial Matrix problems											
		Left					**Right**				
Location	**BA**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**
Frontal lobe											
Rostral part of the IFG	10/47	1 (1392)	2.478	-52	50.3	-8					
Cerebellum											
Posterior lobe *(Declive, Uvula)*		2 (456)	1.812	-18	-86	-16					

Visuospatial Matrix problems versus Visuospatial Analogy											
		Left					**Right**				
Location	**BA**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**	**Cluster number & size (mm3)**	**ALE**	**x**	**y**	**z**
Frontal lobe											

Posterior IFG/ MFG and IFS / Precentral G	6/44/9	6 (1096)	1.881	-41.9	0.4	26.8	1 (5016)	3.540	44.4	11	33.2
Posterior MFG	9						1 (5016)	3.291	41	17	27
Posterior MFG and SFS	6/8	2 (3736)	3.036	-36.2	1	49.9	3 (1976)	2.518	26	6	48
Anterior SFG and SFS	10	4 (1656)	2.518	-26	46	12					
Medial SFG	32/6	11 (128)	1.852	-4	12	46	10 (152)	1.868	4	14	48
Insula											
Insula	13	8 (368)	2.273	-41.3	15.3	-14					
Parietal lobe											
Precuneus	19/ 31						5 (1488)	2.139	26	-72	36
Superior parietal lobe	7	7 (504)	2.155	-34	-58	54					
Postcentral G	2/3	9 (168)	2.248	-42	-18	42					
Occipital lobe											
Superior occipital G	19						5 (1488)	2.157	36	-72	32
Cuneus	18						5 (1488)	1.935	26	-74	26