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

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**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

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3 region that has been associated with analogical reasoning is the left rostrolateral prefrontal  
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5 cortex (rlPFC), as was recently demonstrated by a previous meta-analysis (Vartanian, 2012)  
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7 that analyzed data from 10 functional MRI studies. Similarly, a voxel-based morphometry  
8  
9 approach demonstrated a link between individual analogical reasoning abilities and the  
10  
11 structure of the left rlPFC (Aichelburg et al. 2014). This set of results argues for an important  
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13 role of the rlPFC, particularly the left rlPFC, in analogical process. However, many studies  
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15 have reported bilateral activation (Cho et al. 2010; Geake and Hansen, 2010; Preusse et al.  
16  
17 2011; Wartenburger et al. 2009), or even right activation, of the rlPFC in non-verbal  
18  
19 visuospatial analogy tasks (Kalbfleisch et al. 2007) and in semantic analogy tasks (Luo et al.  
20  
21 2003). Therefore, the left predominance of the rlPFC for analogical reasoning processing is  
22  
23 still unclear and remains to be confirmed.  
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28 If the hypothesis of a left dominance of the rlPFC for analogy proves true, the  
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30 cognitive processes supported by the left rlPFC and underlying a left specialization remain  
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32 unknown. A left dominance could be explained by the domain of the analogy performed  
33  
34 and/or its verbal or semantic nature. Alternatively, some cognitive processes involved in  
35  
36 analogical reasoning **may** require specifically the left rlPFC region. With regard to the first  
37  
38 explanation, literature about cognition has historically supported a left dominance for  
39  
40 language, including semantics, and a right dominance for spatial information processing  
41  
42 (Bates et al. 2003; Catani et al. 2005; Forkel et al. 2014; Heilman et al. 1986; Mesulam, 1981;  
43  
44 Price, 2010; Thiebaut de Schotten et al. 2011). In the analogy field, tasks have used various  
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46 materials requiring the inference of analogies in the semantic domain (i.e., infer semantic  
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48 relationships such as nose-smell :: mouth-taste) or in the visuospatial domain (i.e., analyze  
49  
50 visuospatial relationships to infer a logical, geometrical or mathematical rule such as  
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52 symmetry or linear increase). Semantic analogies depend on knowledge of the semantic  
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54 meaning of the terms and of the relationships between them. In visuospatial analogies, the  
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3 analogy is inferred from the analysis of the visual and spatial relationships between terms that  
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5 can be conceived as transformations from one term to the other (e.g., changes in shape, color,  
6  
7 size, etc.). To our knowledge, only one study has examined directly the question of the  
8  
9 specialization of the analogy network as a function of the analogy domain (Wendelken et al.  
10  
11 2012). This study did not find a left-right specialization of rIPFC according to the analogy  
12  
13 domain: both semantic and visuospatial analogies recruited the left rIPFC. Further studies are  
14  
15 needed in order to better understand the role and organization of the left rIPFC for analogy  
16  
17 domains, and the involvement of the other prefrontal regions.  
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20  
21 This leads us to the second hypothesis relative to the specific or critical processes  
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23 supported by the left rIPFC region. The few patient studies conducted to date have confirmed  
24  
25 the critical role of the prefrontal cortex (PFC) in analogical reasoning (Krawczyk et al. 2008;  
26  
27 Morrison et al. 2004; Schmidt et al. 2012) or in rule inference (Reverberi et al. 2005), but  
28  
29 these studies were unable to determine the role of the rIPFC region specifically. In functional  
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31 imaging, the left rIPFC has been involved in the processing of abstract information (Christoff  
32  
33 et al. 2003) and in the comparison (Wendelken et al. 2008a) or the integration of multiple  
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35 relationships (Bunge et al. 2005; Cho et al. 2010; Christoff et al. 2001).  
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39 These operations are often investigated using other relational reasoning tasks, the  
40  
41 matrix problem tasks such as Raven's Progressives Matrices (Raven, 1941). Matrix problems  
42  
43 typically require the consideration and integration of visuospatial relationships to infer  
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45 logical, geometrical or mathematical rules (Kalbfleisch et al. 2013, 2007; Shokri-Kojori et al.  
46  
47 2012; Yamada et al. 2012). Matrix problem tasks thus share several cognitive processes with  
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49 analogy tasks, such as relational comparison, integration and schema inference. Matrix  
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51 problems and 4-terms analogies are supposed to measure the same type of relational  
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53 reasoning functions (Krawczyk, 2012). In this framework, typical 4-terms analogy tasks and  
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55 matrix problem tasks might thus engage similar brain regions. Functional imaging studies  
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3 have shown that bilateral frontal and parietal regions are involved during matrix problem  
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5 tasks. The most frequently reported regions in these studies were the dorsolateral PFC  
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7 (Christoff et al. 2001; Hampshire et al. 2011; Krawczyk et al. 2008; Kroger et al. 2002;  
8  
9 Perfetti et al. 2009) sometimes extending to the rIPFC (Golde et al. 2010; Hampshire et al.  
10  
11 2011; Krawczyk et al. 2008, see also Wendelken et al. 2008a), the premotor cortex (Golde et  
12  
13 al. 2010; Kalbfleisch et al. 2007; Krawczyk et al. 2008; Perfetti et al. 2009; Yamada et al.  
14  
15 2012), and posterior parietal areas (Hampshire et al. 2011; Krawczyk et al. 2008; Perfetti et  
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17 al. 2009). Some studies have also shown the involvement of the lateral occipitotemporal  
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19 regions (Hampshire et al. 2011; Kalbfleisch et al. 2013; Yamada et al. 2012), the anterior  
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21 cingulate cortex (Kroger et al. 2002; Shokri-Kojori et al. 2012) and the cerebellum  
22  
23 (Kalbfleisch et al. 2007). A recent and comprehensive review indicated that 4-term analogies  
24  
25 and matrix problems might engage differentially the left and right rIPFC (Krawczyk, 2012).  
26  
27 The lesion approach has produced inconsistent results regarding whether the integrity of the  
28  
29 rIPFC is required for matrix problem solving (Baldo et al. 2010; Gläscher et al. 2009; Tranel  
30  
31 et al. 2008; Waltz et al. 1999; Woolgar et al. 2010). Overall, previous studies have suggested  
32  
33 that analogy and matrix reasoning tasks involve largely similar cognitive processes and  
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35 engage both common and specific brain regions, and might not equally rely on the rIPFC. A  
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37 quantitative comparison of functional activation observed during 4-term analogy and matrix  
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39 problem tasks should help to clarify this question.  
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45 In this general context, the aim of the current study was to identify the cerebral  
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47 network involved in analogical reasoning and its specialization or variation based on domains  
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49 of information (semantic or visuospatial) and task specificity (4-terms analogy or matrix  
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51 problem tasks). We conducted a meta-analysis including 27 experiments that used such tasks.  
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53 We contrasted semantic and visuospatial analogy tasks to identify domain-oriented regions in  
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55 the analogy network and to test whether the involvement of the left rIPFC is dependent on the  
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3 analogy domain. We expected a left dominance for the involvement of the rIPFC independent  
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5 of the analogy domain. We additionally compared visuospatial analogy to matrix problem  
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7 tasks to examine the possible differences in their brain correlates. We hypothesized that  
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9 visuospatial analogies and matrix problems would engage, at least in part, distinct cerebral  
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11 networks and involve differently the rIPFC.  
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## 14 15 16 **METHODS**

### 17 18 **Study selection**

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20 We searched for all published studies about analogical reasoning using fMRI by conducting a  
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22 Boolean search in the PubMed database. Specifically, we searched for the following  
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24 keywords in the text and/or the abstract/title: “analogy”, “analogies”, “analogical reasoning”,  
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26 “relational reasoning”, “relational integration”, “relational complexity”, “analogizing”, “fluid  
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28 reasoning”, “analogic reasoning” “progressive matrices”, “Ravens’ Standard Progressive  
29  
30 Matrices”, “Advanced Progressive Matrices”, “RSPM”, “APM”, “Cattell’s Culture Fair Test”,  
31  
32 together with “brain imaging”, “cerebral imaging”, “MRI”, “fMRI”, “functional MRI”, “PET”,  
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34 “neural correlates”, “cerebral correlates”, “brain activation”, “functional magnetic resonance  
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36 imaging”.  
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40 Then, we included peer-reviewed studies published in English before February 2015  
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42 that (1) concerned healthy right-handed adults; (2) involved an analogical or a matrix problem  
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44 reasoning experimental paradigm; and (3) reported whole brain results with signal change  
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46 coordinates in the Montreal Neurological Institute (MNI) space or Talairach 3D space. For  
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48 each study, only independent contrasts were included. If several contrasts in the same study  
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50 were dependent, only the results from the contrast reporting the most significant maxima were  
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52 included.  
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3 According to these criteria, we ultimately analyzed 27 studies, including 40 fMRI  
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5 contrasts, 506 subjects and 351 foci of activation (Table 1).  
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### 8 9 **Task categories (Table 1)**

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

#### 26 *General principles*

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28 We used the Activation Likelihood Estimation (GingerALE) software  
29 (<http://brainmap.org/ale/cli.html>; (Eickhoff et al. 2009; Laird et al. 2009; Turkeltaub et al.  
30 2012, 2002) in our meta-analysis. This method determines the brain areas in which the  
31 convergence across all included experiments is greater than would be expected by chance  
32 (null distribution of randomly generated activation likelihoods) [Eickhoff et al. 2009]. This  
33 analysis is based on the compilation of the activation peak coordinates from all the functional  
34 imaging studies in a same normalized referential. In other words, ALE evaluates how reliable  
35 the involvement of brain regions in given processes across distinct experiments is — in this  
36 case in relational reasoning tasks.  
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#### 51 *Global and task category maps*

52 We performed ALE analyses using the GingerALE software version 2.3.3  
53 ([www.brainmap.org](http://www.brainmap.org); Eickhoff et al. 2012, 2009; Turkeltaub et al. 2012). We converted the  
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3 activation peak coordinates reported in Talairach space into MNI space using the converter  
4 included in the GingerALE toolbox. Activation foci in the same referential from each  
5 included contrast were first modeled as Gaussian distributions and then merged into the same  
6 volume. We organized the datasets according to subject groups and used the modified ALE  
7 algorithm (Turkeltaub et al. 2012) to address the issue of the independence of observation  
8 within the same study. The algorithm also modeled spatial uncertainty (Eickhoff et al. 2012,  
9 2009), allowing us to adjust the full-width half maximum (FWHM) using an estimation of  
10 between-subject and between-experiment variability. GingerALE then modeled the  
11 probability of activation across all studies for each brain voxel, returning localized “activation  
12 likelihood estimates” or ALE values. ALE values are the statistical maps created by combined  
13 probability distributions centered at each coordinate used in the analysis and reflect the  
14 coherency across experiments.

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32 In a second step, ALE values were compared to random distributions of foci to  
33 identify significantly activated clusters at each voxel. We used a cluster correction for  
34 multiple comparisons: the simulated data was thresholded using a “cluster-forming  
35 threshold”, identifying the contiguous volumes above the threshold, or clusters. Then ALE  
36 tracked the distribution of the volume of the clusters and used a “cluster-level threshold” for  
37 thresholding the results. We used an uncorrected cluster-forming threshold at  $p < 0.001$  and a  
38 cluster-level threshold at  $p < 0.05$  (Eickhoff et al. 2012). ALE maps were calculated using  
39 1000 permutations. We also reported the results at a stringent voxel-level family-wise error  
40 (FWE) correction when significant.

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

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3 The global ALE map pooling Analogy and Matrix Problem tasks primarily revealed a  
4  
5 bilateral fronto-parietal network including a large cluster located in the left rostrolateral PFC  
6  
7 that was centered at Brodmann area (BA) 10 and extended to BA 47, 45 and 46, bilateral  
8  
9 insula, posterior parietal cortex (BA 7 and 40), several clusters in the posterior region of the  
10  
11 inferior frontal gyrus (IFG), middle frontal gyrus (MFG), superior frontal sulcus (SFS), and  
12  
13 medial PFC. The clusters in the left rostrolateral PFC, the right dorsolateral region (BA 9,  
14  
15 posterior part of the IFG) and the right insular area (BA 13) were significant at a  $p < 0.05$   
16  
17 FWE corrected threshold.  
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### 20 21 22 23 **Task category maps**

#### 24 25 ***1) Semantic Analogy tasks map (Table 3, Figure 2)***

26  
27 The ALE map based on grouping semantic analogy tasks revealed a left-lateral prefrontal  
28  
29 network. The primary cluster was located in the rostrolateral part of the left IFG and MFG  
30  
31 (BA 10/47 and BA 46). A second cluster was located posteriorly in the posterior part of the  
32  
33 left IFG (BA 44). Additional clusters were observed in the superior frontal gyrus, including  
34  
35 one in the anterior part (BA 9) and one in the dorsal part (BA 8), and in the bilateral caudate  
36  
37 heads.  
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#### 40 41 42 43 ***2) Visuospatial Analogy tasks map (Table 4, Figure 2)***

44  
45 The analysis of Visuospatial Analogy tasks revealed four clusters of activation. The primary  
46  
47 cluster was centered in the rostrolateral region of the left inferior frontal sulcus and gyrus (BA  
48  
49 10/47/46). Additional clusters were located in the right MFG (BA 9), the right anterior insula,  
50  
51 and the cerebellum.  
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#### 54 55 56 57 ***3) Visuospatial Matrix problems map (Table 5, Figure 2)***

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3 The ALE map for Matrix problems revealed a large, bilateral fronto-parietal network  
4 distributed into eight clusters of activation. Larger clusters were located bilaterally in the  
5 parietal lobe, extending from superior to inferior regions (BA 7 and 40), and in the precuneus  
6 (BA 7/31). In the frontal lobe, significant clusters were found bilaterally in the posterior and  
7 dorsolateral PFC centered on the posterior inferior frontal sulcus (IFS) (BA 6, 44, 9) with a  
8 right predominance, in the posterior region of the superior frontal regions centered on the  
9 posterior SFS (BA 6/8), and bilaterally in the medial PFC. Two additional clusters were  
10 located in the anterior region of the right insula and in the left cingulate gyrus (BA 32).  
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#### 23 **4) Visual overlap (Figure 2)**

24 Semantic Analogy and Visuospatial Analogy commonly recruited the rostralateral part of the  
25 left IFG in a similar cluster, while Matrix Problems did not. This corresponded to the cluster  
26 that was significant at a voxel-based FWE correction. This region is hereafter referred to as  
27 the “left rIPFC ROI”.  
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33 Visuospatial Analogy and Matrix problems shared the activation of the right anterior insula.  
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#### 39 **Contrast maps**

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

41 The ALE subtraction map of Semantic versus Visuospatial Analogy tasks revealed a cluster  
42 located in the rostralateral part of the left IFG (BA 47) that was located more posterior and  
43 ventral to the left rIPFC ROI. The left rostromedial prefrontal cortex (medial BA 10) and the  
44 left inferior frontal sulcus (BA 46) were also significantly more strongly activated by  
45 Semantic than Visuospatial Analogy tasks.  
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53 The ALE subtraction map of Visuospatial versus Semantic Analogy tasks revealed a set of  
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3 frontoparietal regions including distributed clusters located in the left rostrolateral PFC, the  
4  
5 posterior region of the left MFG (BA 6, 8), the posterior right IFG and MFG (BA 9, 45, 46),  
6  
7 the left superior parietal lobule (SPL) and inferior parietal lobule (IPL) (angular and  
8  
9 supramarginal gyri; BA 7, 39, 40), and the right fusiform gyrus (BA 37). The left rostrolateral  
10  
11 PFC cluster was located in the anterior region of the left MFG (BA 10), dorsal to the main  
12  
13 analogy region, i.e., the “left rIPFC ROI”.  
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18 **2) Comparison of Visuospatial Analogy versus Matrix problems maps (Table 7, Figure**  
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21 **4)**

22  
23 The ALE subtraction map of Visuospatial Analogy versus Matrix problem tasks revealed a  
24  
25 primary cluster in the left rostral region of the PFC (centered on BA 10, extending to BA 9,  
26  
27 45, 46, and encompassing the anterior MFG and IFG) in similar location to the left rIPFC  
28  
29 ROI. A second cluster was observed in the left posterior cerebellum.  
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31  
32 The ALE subtraction map of Matrix problems versus Visuospatial Analogy tasks revealed a  
33  
34 large frontoparietal network containing the bilateral posterior and dorsolateral PFC centered  
35  
36 on the posterior IFS (BA 6, 44, 9) with a right predominance, the posterior part of the superior  
37  
38 frontal regions centered on the posterior SFS (BA 6/8), the medial PFC (BA 9/32), the left  
39  
40 IPL and SPL (BA 7), the right precuneus (BA 7, 19 and 31), and the postcentral gyrus (BA 2  
41  
42 and 3). A left rostral PFC region (BA 10) was also observed, which was in a more medial  
43  
44 location than the “left rIPFC ROI”.  
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50 **DISCUSSION**

51  
52 Using the ALE method, our coordinate-based meta-analysis combined data from 27  
53  
54 functional neuroimaging experiments to reveal three lines of findings: (i) the rostral part of  
55  
56 the left rIPFC was consistently engaged during analogical reasoning tasks, regardless of the  
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3 domain of analogy; (ii) additionally activated prefrontal and posterior brain regions were  
4  
5 domain-oriented; and (iii) the Visuospatial Analogy and Matrix Problem tasks activated  
6  
7 dissociable neural systems across fMRI studies. Matrix Problems network was distributed  
8  
9 bilaterally to a greater extent.  
10

### 14 **The left rIPFC is a reliable domain-general region for analogical reasoning**

16 First, the results from our global analysis of the 27 experiments revealed a reliable  
17  
18 activation in the left rIPFC (BA 10/47), which is a region at the rostral end of the IFS that we  
19  
20 labeled the “left rIPFC ROI”. Previous meta-analyses also reported significant and  
21  
22 informative results despite the relatively small number of experiments analyzed (Gonen-  
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24 Yaacovi et al. 2013; Vartanian, 2012; Prado et al. 2011). Our currently identified association  
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26 between analogical reasoning and activity in the left rIPFC, and confirmed the findings of  
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28 Vartanian (2012) when we added 17 new experiments to the meta-analysis. This result is also  
29  
30 in agreement with previous findings from different approaches such as morphometry  
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32 (Aichelburg et al. 2014; Krawczyk et al. 2010), and developmental studies in children. The  
33  
34 latter studies suggested that maturation of the PFC and especially of the rIPFC is critical for  
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36 relational reasoning in Matrix problems (Crone et al., 2009), for semantic analogies (Wright  
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38 et al., 2008), and visuospatial analogies (Bazargani et al., 2014; Thibaut et al., 2010;  
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40 Wendelken et al., 2011). These studies showed functional and structural changes in the left  
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42 rIPFC during development, with decreasing grey matter volume and increasing specificity of  
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44 left rIPFC activation for relational integration (for a review Dumontheil, 2014). Changes in  
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46 functional connectivity were also reported between rIPFC and anterior insula, posterior  
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48 frontal, and posterior parietal cortices (Bazargani et al., 2014), regions that were also reliably  
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50 observed in the current meta-analysis. Overall developmental studies suggest that the left  
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3 rIPFC is critical for different types of relational reasoning tasks and domains of relationships  
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5 used.  
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7 In the current meta-analysis, Semantic and Visuospatial Analogy maps overlapped in  
8 the “left rIPFC ROI”, suggesting that analogies in distinct domains share a common brain  
9 correlate within the rIPFC. For each analogy map, ALE values were significant in the “left  
10 rIPFC ROI” but not in the right rIPFC, suggesting a left lateralization of the rIPFC for  
11 analogical reasoning regardless of the task domain. As mentioned earlier, left prefrontal  
12 dominance for analogical reasoning has been shown in previous functional imaging studies  
13 (Vartanian, 2012; Bunge et al. 2009; Krawczyk et al. 2012) and a repetitive transcranial  
14 magnetic stimulation study (Boroojerdi et al. 2001). It is unlikely that this left-lateralization  
15 could be due solely to verbal or semantic requirements because we observed an activation in  
16 the left rIPFC during both Semantic and Visuospatial Analogy tasks, as has been also reported  
17 by Wendelken et al. (2012). As shown in a functional imaging study, the activation of the  
18 rIPFC across a large range of different tasks using various domains of stimuli (verbal, spatial,  
19 visual) reinforces the interpretation of a domain-general function for the rIPFC (Gilbert et al.  
20 2006).  
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38 Functional imaging studies have indeed shown the involvement of the rIPFC in  
39 various cognitive functions related to analogical reasoning such as working memory  
40 (Christoff and Gabrieli, 2000; Narayanan et al. 2005), multitasking and task switching  
41 (Braver and Bongiolatti, 2002; Burgess, 2000; Burgess et al. 2000; Koechlin et al. 1999),  
42 abstract reasoning and problem-solving (Badre, 2008; Christoff et al. 2003, 2001; Kroger et  
43 al. 2002; Smith et al. 2007). However, the precise role of the rIPFC in analogical reasoning,  
44 and more widely in cognition, has not been elucidated. Clinical observations have tended to  
45 confirm that damage to this region could cause high-level cognitive disorders (Burgess et al.  
46 2009; 2000). Relatively recent theories propose that the rIPFC (or frontal pole) is an  
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3 integrative and coordinating region, the role of which could be to integrate the outcomes of  
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5 separate cognitive operations and information of different nature, in the pursuit of long-term  
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7 or more global behavioral goals (Ramnani and Owen, 2004; Stuss, 2011). Hierarchical  
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9 models of PFC organization inferred from functional imaging studies place the rIPFC at the  
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11 top of a cognitive hierarchy in which more anterior portions of the frontal lobes support  
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13 increasingly abstract representations, greater relational complexity in reasoning, or higher  
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15 levels of adaptive control (Badre, 2008; Christoff et al. 2009; Koechlin and Summerfield,  
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17 2007) in interaction with more posterior regions. Because analogies engage relational  
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19 integration and the formation of abstract concepts, the involvement of the rIPFC in analogical  
20  
21 reasoning is consistent with these theories from both the perspectives of abstraction and  
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23 relational integration (see also Shokri-Kojori et al., 2012). The rIPFC might also play a role in  
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25 the coordination or integration of internally (inferred analogy schema) versus externally  
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27 (stimuli) oriented thoughts (Gilbert et al. 2000; Burgess et al. 2007). The critical role of the  
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29 rIPFC in these integration, control-related or complexity-dependent functions remains to be  
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31 tested in patients. These interpretations assume that the role of the rIPFC in the integration of  
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33 visuospatial, semantic or rule-based relational representations is supported by its interactions  
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35 with other regions of the analogy network.  
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### 43 **Global network of relational reasoning**

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45 In addition to the “left rIPFC ROI”, the global map showed a distributed set of brain regions  
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47 bilaterally encompassing the insula, posterior prefrontal regions, posterior parietal cortex, and  
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49 medial SFG. These regions appeared to belong to distinct brain networks that have been  
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51 described by resting state functional imaging studies: the fronto-parietal executive/control  
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53 network, the salience network and the dorsal attentional network (Cole et al. 2012; Power and  
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55 Petersen, 2013; Power et al. 2011; Vincent et al. 2008)  
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3 The fronto-parietal control network includes the dorsolateral prefrontal cortex and the  
4 posterior parietal cortex. This network has been largely associated with **complex functions**  
5 **related to analogical reasoning, including** fluid intelligence (Hampshire et al. 2011; Jung and  
6 Haier, 2007; **Prado et al. 2011**; Reineberg et al. 2015; **Wendelken et al. 2015**), working  
7 memory (**Chamod and Petrides 2010**; Courtney 2004; Curtis 2006; **Smith and Jonides 1999**),  
8 **structuration of mental representations into chunks** (Bor et al. 2003; Bor and Owen, 2007; see  
9 **also Wendelken et al., 2008b**), and deliberate control of thoughts and actions (**Badre and**  
10 **D'esposito 2007**; **Koechlin et al. 1999**; Hampshire and Owen, 2006; Petrides, 2005). The  
11 salience network includes the anterior insula and the adjacent ventrolateral prefrontal  
12 (posterior IFG) and anterior cingulate cortices (Seeley et al. 2007; Sridharan et al. 2008). An  
13 important role of the salience and the fronto-parietal executive networks for fluid reasoning in  
14 healthy individuals has been suggested by Yuan and colleagues (2012) using voxel-based  
15 morphometry and resting state imaging. Recent studies have postulated that the salience  
16 network drives switching between the fronto-parietal control and the default mode networks  
17 (Goulden et al. 2014; Jilka et al. 2014; Sridharan et al. 2008), allowing for the engagement of  
18 the brain's attentional and higher-order control processes while disengaging other systems  
19 that are not task-relevant (Sridharan et al. 2008). This process could be involved in analogical  
20 reasoning. Finally, the dorsal attentional system includes regions of the frontal eye fields  
21 (posterior SFS), the premotor cortex and the superior parietal lobule. It is associated with  
22 externally directed cognition, including covert and overt shifts of spatial attention (Corbetta  
23 and Shulman, 2002) and is engaged in tasks involving spatial search and detection. This  
24 network could be more involved in visuospatial than semantic analogy tasks, as is discussed  
25 below.

### 56 **Specialization into domain-oriented regions**

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3 In contrast to the “left rIPFC ROI”, which was recruited in both Semantic and Visuospatial  
4 Analogies, we observed differences in the pattern of brain activity in other areas, depending  
5 on the analogy domain.  
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10 Compared with Visuospatial Analogy tasks, Semantic Analogy tasks more specifically  
11 recruited the left anterior IFG (BA 47), located ventrally and posteriorly to the left rIPFC  
12 ROI. The left anterior IFG has been associated with controlling or selecting the retrieved  
13 information during semantic retrieval (Badre and Wagner, 2007; Barde and Thompson-Schill,  
14 2002; Thompson-Schill, 2003), with executive aspects of semantic processing (Dronkers et al.  
15 2004; Monti et al. 2007), and with abstract interpretation of metaphors (Rapp et al. 2004).  
16 Therefore, it is likely that this region plays a role in the semantic retrieval of relational and  
17 abstract information when solving semantic analogies, as has been shown by Bunge et al.  
18 (2005).  
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30 In addition to the left anterior IFG, Semantic Analogy tasks recruited the posterior  
31 region of the left IFG (BA 44) and the anterior and medial region of the left SFG (BA 10)  
32 [figure 3]. Rostromedial frontal clusters have been suggested to be part of the semantic  
33 memory network (Buckner et al. 2008) and might play a role in relational integration across  
34 semantic distance, as has been proposed by Green et al. (2006; 2010) and Brunyé et al.  
35 (2015).  
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43 These findings are also in agreement with previous functional imaging and lesion  
44 studies that have demonstrated a left specialization of the PFC for verbal abstraction using  
45 proverb interpretation (Murphy et al. 2013), abstract concepts (Hoffman et al. 2010; Lagarde  
46 et al. 2015), or metaphor comprehension (Bohrn et al. 2012; Vartanian 2012).  
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52 Conversely, the Visuospatial Analogy tasks more specifically recruited frontal regions  
53 located in the bilateral posterolateral PFC, left posterior parietal cortex and intraparietal  
54 sulcus, and right fusiform gyrus. Interestingly, this pattern of brain activity is broadly  
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3 consistent with the brain systems that support visual and spatial processing and spatial  
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5 attention. The posterior parietal cortex, including both SPL and IPL, is thought to be involved  
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7 in spatial cognition and has been associated with the formation of spatial representations and  
8  
9 the processing of spatial relationships during analogy tasks (Amorapanth et al. 2010;  
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11 Wendelken, 2015). The fusiform gyrus has previously been shown to participate in visual  
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13 mental imagery and in the formation of the mental images of the visuospatial schema during  
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15 analogical thinking (Luo et al. 2003).  
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18 In addition, Visuospatial Analogy tasks compared to the Semantic Analogy tasks  
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20 recruited the anterior MFG (BA 10). This additional rostral PFC region is located dorsal to  
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22 the shared “left rIPFC ROI” and thus could be associated with the cognitive processes  
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24 required by spatial and geometrical analogies that are not involved in semantic tasks. Previous  
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26 authors have emphasized a more dorsal recruitment of the rostral PFC for spatial versus  
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28 semantic analogies (Wendelken et al. 2012), at the individual level. A greater schema  
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30 complexity in visuospatial compared to semantic analogies could explain the additional  
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32 recruitment of a dorsal network, including the anterior MFG and the posterior parietal cortex,  
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34 as reported by Hampshire et al. (2011) and Krawczyk (2012).  
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39 In sum, in addition to the shared domain-general “left rIPFC ROI”, semantic and  
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41 visuospatial analogies recruited unique domain-oriented brain regions. Some of these domain-  
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43 oriented regions were located in the lateral PFC and were organized along the dorsoventral  
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45 axis: MFG for Visuospatial Analogies and IFG for Semantic Analogies (Fig. 3). These  
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47 findings suggest, as has been proposed by Babcock and Vallesi (2015) for inductive  
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49 reasoning, that analogical reasoning relies on common processes supported by the left rIPFC  
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51 and recruits content information from domain-oriented regions. This hypothesis is consistent  
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53 with models of the prefrontal functional architecture that describe a dorsoventral dissociation  
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3 as a function of the domain of information (Courtney, 2004; Sakai and Passingham, 2003;  
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5 Smith and Jonides, 1999; Volle et al. 2008).  
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7 It is important to mention some limitations in the task comparisons that were  
8 performed. A variety of analogy tasks have been used, that employed verbal, figurative or  
9 abstract material, and involved semantic, visuospatial, mathematical, or logical relationships  
10 (Table 1). Task differences may induce some variability between fMRI studies that decreases  
11 the ability of meta-analyses to observe significant results. For instance, stimuli in semantic  
12 tasks were relatively homogeneous (written words), but the relationships involved in the  
13 analogies varied between studies. The visuospatial tasks were more heterogeneous in terms of  
14 materials or stimuli used, such as geometric shapes (Preusse et al. 2011; Wartenburger et al.  
15 2009), symbol strings (Geake and Hansen, 2010, 2005; Volle et al. 2010), pictures (Cho et al.  
16 2010), colors and forms (Christoff et al. 2003; Watson and Chatterjee, 2012), or abstract line  
17 drawings (Wendelken et al. 2012), but involved quite similar categories of relationships, for  
18 instance increase in size, symmetry, pattern. Thus, we cannot exclude the possibility that  
19 these factors impacted the results, and that task-related differences are due to variability in  
20 experimental paradigms or materials used rather than to the analogy domain.  
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#### 40 **Dissociable Visuospatial Analogy and Matrix Problem task networks**

41 The current meta-analysis identified dissociable neural systems activated by the Visuospatial  
42 Analogy and the Matrix Problem tasks across fMRI studies, in both the PFC and other brain  
43 regions.  
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49 In the rostral PFC, a region overlapping the “left rIPFC ROI” was recruited to a  
50 significantly greater extent in Visuospatial Analogy than in Matrix Problem tasks (Table 7).  
51 This could indicate that the “left rIPFC ROI”, located at the anterior end of the IFS, is a  
52 region that is relatively specific to analogical reasoning and is thus less involved in other  
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3 relational reasoning tasks such as the Matrix Problems. No other regions were significantly  
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5 different in terms of activation when contrasting Visuospatial Analogy to Matrix Problem  
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7 tasks.  
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10 Conversely when Matrix Problem tasks were compared to Analogy tasks, we observed  
11  
12 the recruitment of a set of brain regions including a rostral prefrontal cluster that was located  
13  
14 in the anterior part of the SFG and SFS. This cluster was dorsal and medial to the “left rIPFC  
15  
16 ROI”. This result suggests a functional specialization within the left frontal pole between a  
17  
18 ventral region at the end of the IFS that supports analogical reasoning and a more medial  
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20 region at the end of the SFS supporting relational reasoning in matrix format. However, this  
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22 interpretation should be taken with caution because this medial rIPFC cluster was not  
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24 observed in the Matrix Problem tasks map (task related activation) and was significant only  
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26 when contrasting Matrix Problem to Analogy tasks. In addition, when compared to Analogy  
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28 tasks, Matrix Problem tasks more consistently recruited a large set of brain regions that can be  
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30 organized into a superior and an inferior fronto-parieto-occipital brain system with a right  
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32 predominance. These significant regions appeared to belong to the attentional and fronto-  
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34 parietal executive networks (Rojkova et al. 2014; Thiebaut de Schotten et al. 2011).  
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39 The between-task differences in brain activation observed in the current meta-analysis  
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41 raise the question as to which cognitive processes differ between these two types of  
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43 visuospatial relational reasoning tasks. Both Analogy and Matrix Problem tasks require  
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45 inductive and relational reasoning and are considered to be measures of fluid reasoning, i.e.,  
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47 the capacity to think logically and to solve problems in novel situations, independent of  
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49 acquired knowledge. The two types of tasks may nevertheless differ regarding (1) evaluation  
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51 versus completion requirements of the task designs; (2) variable visuospatial loads during  
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53 stimulus display or response choices; and (3) the number of relationships to integrate.  
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3 First, analogy and matrix problem tasks could involve distinct cognitive processes  
4 because their response requirements are different (Table 1). Two main experimental  
5 conditions were used in the included studies: (1) evaluate a proposed analogy (“is A to B as C  
6 is to D”) (“Evaluate Yes/No” in Table 1) or (2) complete an analogy (“A is to B as C is  
7 to?”), in which participants were asked to select one among several alternatives (“Forced  
8 choice completion” in Table 1). All but two studies that used Matrix problems involved a  
9 forced choice completion between multiple alternatives, so that all of the lines and columns of  
10 the matrix share the same relationships, i.e., are analogs. Among analogy studies, all but four  
11 studies involved an evaluation type of response. In only one study the response type was a  
12 forced choice completion comparable to the response type in Matrix problem tasks. In two  
13 studies participants were to select a target given a source (different from the completion of an  
14 incomplete target), and in one study participants freely generated verbally the completion of a  
15 target (no forced choice). Therefore, differences in evaluation and completion requirements  
16 between analogy and matrix problems could be a confounding factor in our meta-analysis,  
17 that can not be controlled for, and might explain some of the differences in their brain  
18 correlates. For instance, Wendelken and colleagues’ study (2008a) demonstrated that the left  
19 rIPFC was involved in evaluating analogies but not in completing a 4-term analogy, which  
20 instead was associated with the medial PFC. Here, matrix problem studies rarely included an  
21 evaluation condition, which could account for the absence of significant activation in the “left  
22 rIPFC ROI”, while they recruited a more medial PFC region. Among the two Matrix problem  
23 studies that used evaluative responses, one recruited the left rIPFC while the other did not,  
24 which did not help to clarify this point. Alternatively, compared to evaluation, completion  
25 responses could increase interindividual variability in performance or solving strategy  
26 (Shokri-Kojori et al. 2012), and then decrease the power of fMRI to detect significant  
27 activation across subjects or increase variability between studies. The issue of response type  
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3 in relational reasoning should be addressed in further specific experiments controlling for the  
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5 task type and domain of relationships.  
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8 Second, it is likely that the visual and spatial load is greater in matrix problems  
9 compared to visuospatial analogy tasks because a greater number of stimuli are usually  
10 displayed with regard to both the test items and choice alternatives. Indeed, analogy tasks are  
11 usually composed of 4 terms (A:B as C:D) [or sometimes 6 terms for visuospatial analogies;  
12 Geake and Hansen, 2010; Volle et al. 2010; Watson and Chatterjee, 2012], whereas matrix  
13 tasks usually display a 3-by-3 (or 3-by-2) matrix of terms. Thus, the greater visuospatial  
14 processing requirement in matrix problems could explain the additional recruitment of  
15 visuospatial regions and the attentional network (Kalbfleisch et al. 2013).  
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25 Finally, a greater number of stimuli to analyze also implies more relationships to  
26 consider and integrate during matrix problems, which possibly involves additional brain  
27 regions (Ackerman and Courtney, 2012). The need to consider and manipulate a greater  
28 number of relationships could explain the stronger activation observed in the fronto-parietal  
29 control network (Ackerman and Courtney, 2012; Hamsphire et al. 2011; Jia et al. 2015; Volle  
30 et al. 2008). This also raises the question of the involvement of “multitasking” or “branching”  
31 operations in matrix problem solving, i.e., the need to hold goals in mind while exploring and  
32 processing secondary goals (Dreher et al. 2008; Koechlin et al. 1999).  
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43 Therefore, visuospatial analogy and matrix problem tasks appear to engage dissociable  
44 neural systems across fMRI studies, with more visuospatial, executive, and possibly  
45 multitasking requirements in matrix reasoning and possibly greater comparison and matching  
46 processing required for analogy tasks.  
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## 51 52 53 54 **Conclusion**

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

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### 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.

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**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 rIPFC 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



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# All studies

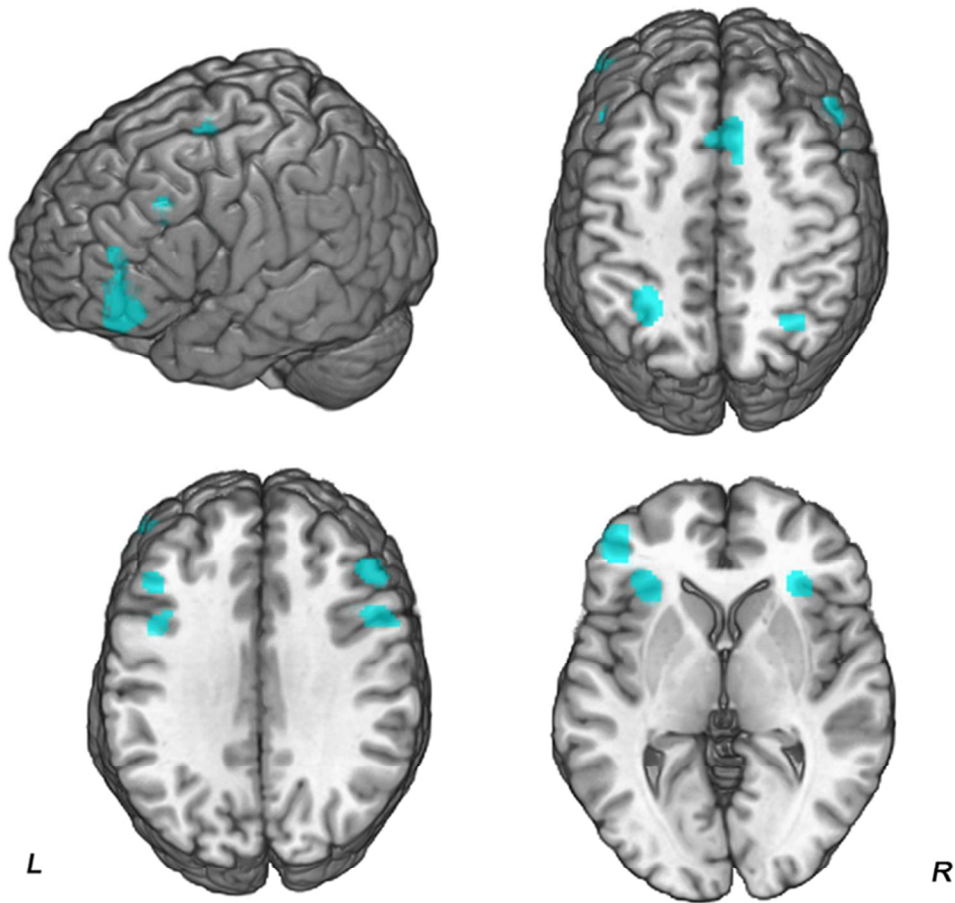
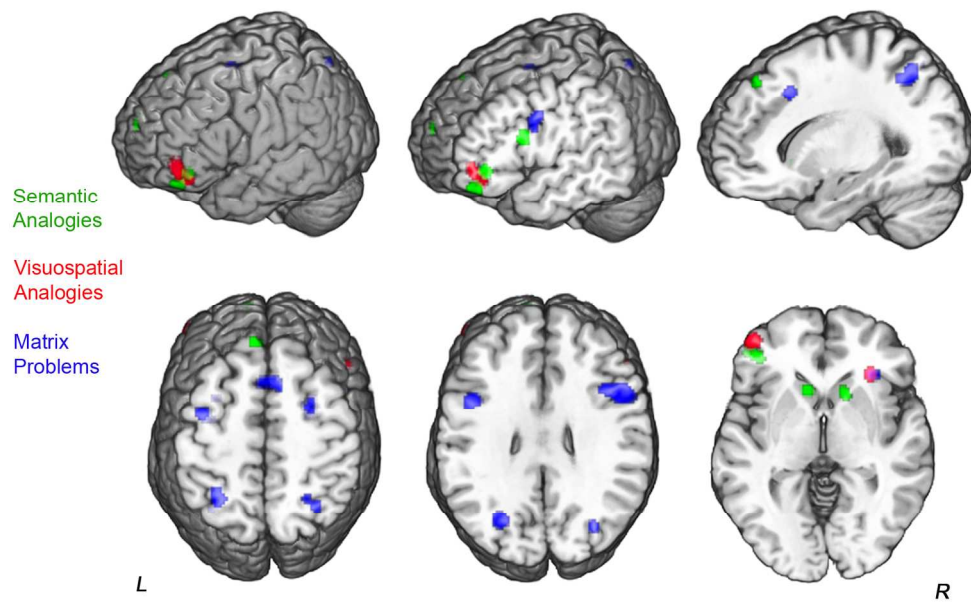


Fig. 1: Global ALE map showing significant activation associated with all the included tasks. The ALE map is displayed on a surface rendering of the anatomical Colin27 template (Holmes et al. 1996) in the MNI space. A cluster correction for multiple comparisons was used with an uncorrected cluster-forming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



28 Fig. 2: Task category maps. Semantic Analogy map (in green), Visuospatial Analogy map (in red) and  
29 Visuospatial Matrix problems map (in blue). ALE maps are displayed on a surface rendering of the  
30 anatomical Colin27 template (Holmes et al. 1996) in the MNI space. A cluster correction for multiple  
31 comparisons was used with an uncorrected cluster-forming threshold at  $p < 0.001$  and a cluster threshold at  
32  $p < 0.05$ .  
33 162x101mm (300 x 300 DPI)

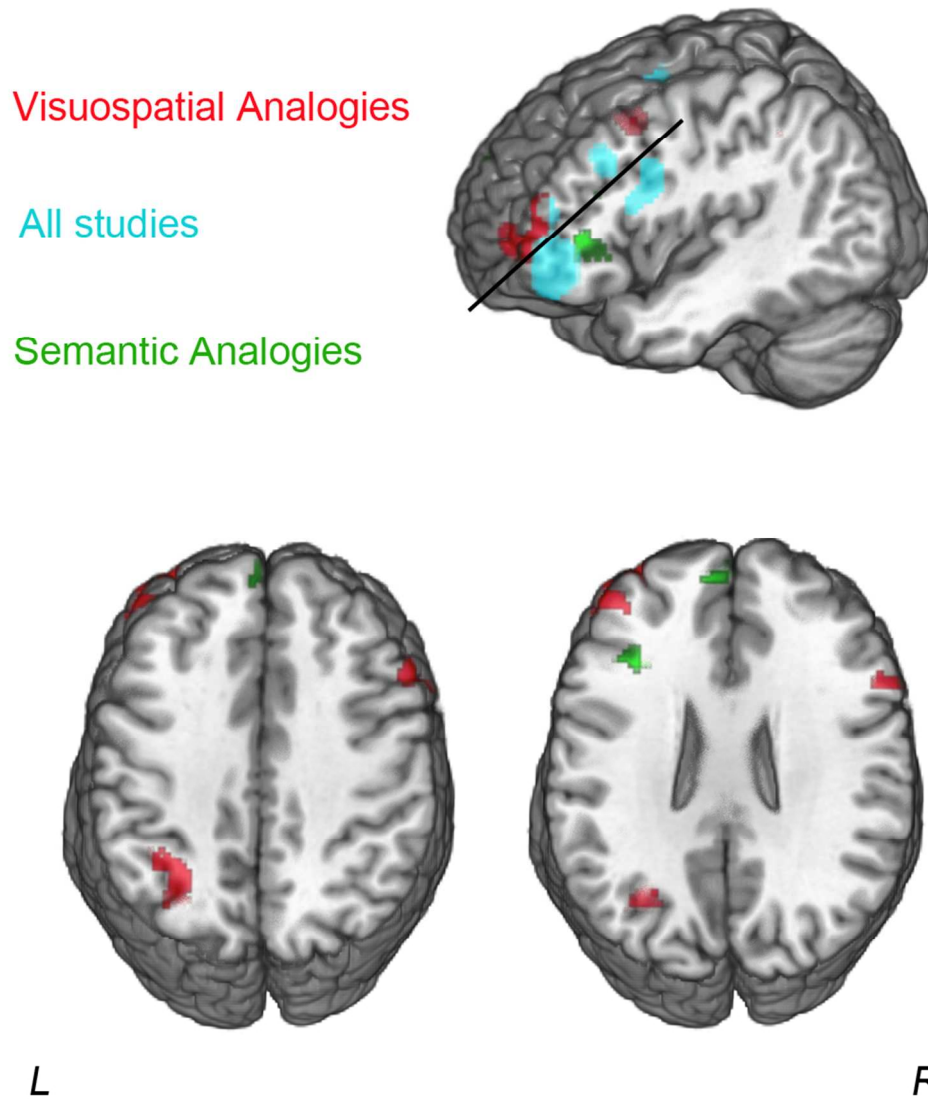


Fig. 3: Analogy domain subtraction maps. Semantic versus Visuospatial Analogy map (in green) and Visuospatial versus Semantic Analogy map (in red) is compared to the "left rIFC ROI" from the global ALE map (in cyan). The ALE subtraction maps are displayed on a surface rendering of the anatomical Colin27 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.  
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## Visuospatial Analogies

### Matrix Problems

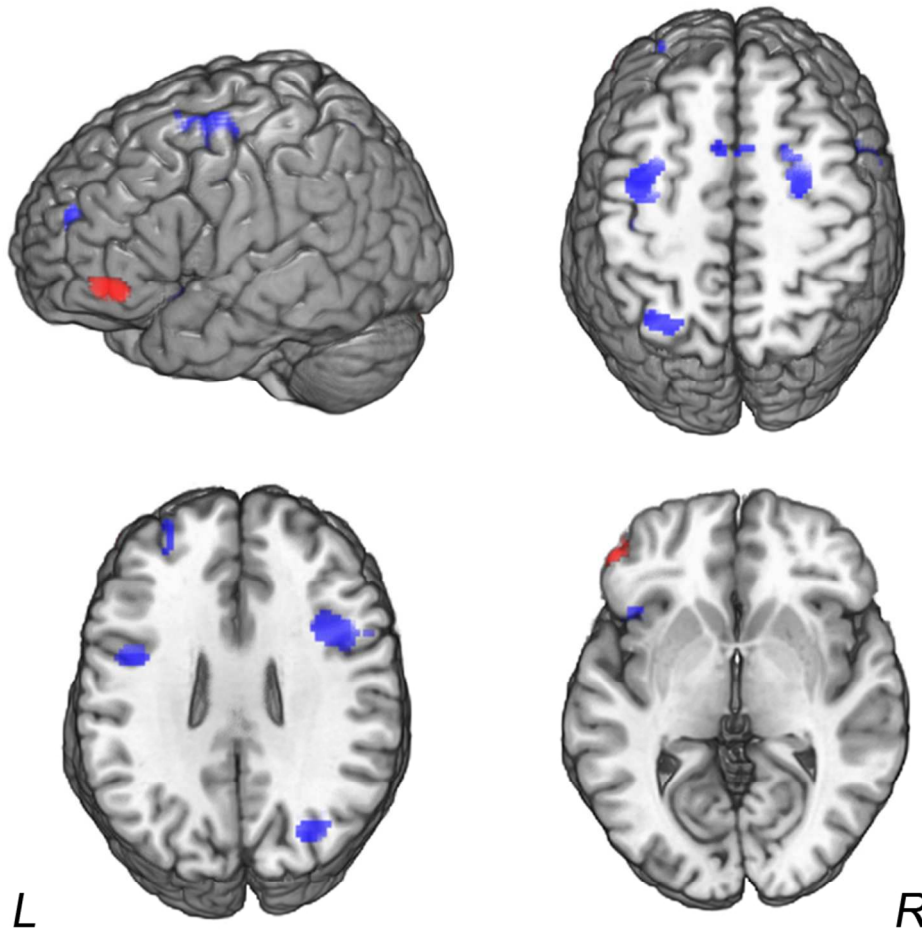


Fig. 4: Task subtraction maps. Visuospatial Analogy versus Matrix problems map (in red) is compared to Visuospatial Matrix Problems versus Analogy map (in blue). The ALE subtraction maps are displayed on a surface rendering of the anatomical Colin27 template (Holmes et al. 1996) in the MNI space. These contrast maps were thresholded at an uncorrected  $p$  value  $< 0.05$  following 10,000 permutations with an arbitrary minimum cluster size of 100 voxels.  
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**Table 1: List and characteristics of all the experiments included in the meta-analysis.**

<b>Authors</b>	<b>Year</b>	<b>N subjects</b>	<b>Task description</b>	<b>Kind of relationship</b>	<b>Task category</b>	<b>Kind of response</b>
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)

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

For Peer Review



**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 (mm <sup>3</sup> )	ALE	x	y	z	Cluster number & size (mm <sup>3</sup> )	ALE	x	y	z
<b>Frontal lobe</b>											
Rostral part of IFS and IFG	10	<b>1 (5192)</b>	<b>0.034</b>	<b>-48</b>	<b>44</b>	<b>-8</b>					
Posterior IFG/ MFG and IFS / Precentral G	9/44/6	2 (1728)	0.023	-48	12	18	<b>5 (1208)</b>	<b>0.028</b>	<b>50</b>	<b>10</b>	<b>26</b>
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
<b>Parietal lobe</b>											
Superior parietal lobe	7	3 (1552)	0.023	-30	-52	48	9 (776)	0.022	34	-60	52

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

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**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.

Location	BA	Left					Right				
		Cluster number & size (mm <sup>3</sup> )	ALE	x	y	z	Cluster number & size (mm <sup>3</sup> )	ALE	x	y	z
<b>Frontal lobe</b>											
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					
<b>Basal ganglia</b>											
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 (mm <sup>3</sup> )	ALE	x	y	z	Cluster number & size (mm <sup>3</sup> )	ALE	x	y	z
<b>Frontal lobe</b>											
Rostral part of IFS and IFG	10	1 (1784)	0.021	-48	44	-10					
MFG	9						4 (304)	0.013	54	28	34
<b>Insula</b>											
Insula	13						2 (368)	0.013	30	28	-4
<b>Cerebellum</b>											
Posterior lobe ( <i>declive</i> )		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 (mm <sup>3</sup> )	ALE	x	y	z	Cluster number & size (mm <sup>3</sup> )	ALE	x	y	z
<b>Frontal lobe</b>											
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
<b>Insula</b>											
Insula							10 (464)	0.014	32	28	-2
<b>Parietal lobe</b>											
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.

<b>Semantic Analogy versus Visuospatial Analogy</b>											
		<b>Left</b>					<b>Right</b>				
<b>Location</b>	<b>BA</b>	<b>Cluster number &amp; size (mm3)</b>	<b>ALE</b>	<b>x</b>	<b>y</b>	<b>z</b>	<b>Cluster number &amp; size (mm3)</b>	<b>ALE</b>	<b>x</b>	<b>y</b>	<b>z</b>
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					

<b>Visuospatial Analogy versus Semantic Analogy</b>											
		<b>Left</b>					<b>Right</b>				
<b>Location</b>	<b>BA</b>	<b>Cluster number &amp; size (mm3)</b>	<b>ALE</b>	<b>x</b>	<b>y</b>	<b>z</b>	<b>Cluster number &amp; size (mm3)</b>	<b>ALE</b>	<b>x</b>	<b>y</b>	<b>z</b>
<b>Frontal lobe</b>											
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
<b>Parietal lobe</b>											
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					
<b>Temporal lobe</b>											
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 (mm <sup>3</sup> )	ALE	x	y	z	Cluster number & size (mm <sup>3</sup> )	ALE	x	y	z
<b>Frontal lobe</b>											
Rostral part of the IFG	10/47	1 (1392)	2.478	-52	50.3	-8					
<b>Cerebellum</b>											
Posterior lobe (Declive, Uvula)		2 (456)	1.812	-18	-86	-16					

Visuospatial Matrix problems versus Visuospatial Analogy											
		Left					Right				
Location	BA	Cluster number & size (mm <sup>3</sup> )	ALE	x	y	z	Cluster number & size (mm <sup>3</sup> )	ALE	x	y	z
<b>Frontal lobe</b>											



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
<b>Insula</b>											
Insula	13	8 (368)	2.273	-41.3	15.3	-14					
<b>Parietal lobe</b>											
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					
<b>Occipital lobe</b>											
Superior occipital G	19						5 (1488)	2.157	36	-72	32
Cuneus	18						5 (1488)	1.935	26	-74	26