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Review

The cognition and neuroscience of relational reasoning

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ABSTRACT

There has been a growing interest in understanding the complex cognitive processes that give rise to human reasoning. This review focuses on the cognitive and neural characteristics of relational reasoning and analogy performance. Initially relational reasoning studies that have investigated the neural basis of abstract reasoning with an emphasis on the prefrontal cortex are described. Next studies of analogical reasoning are reviewed with insights from neuropsychological and neuroimaging studies. Additionally, studies of cognitive components in analogical reasoning are described. This review draws together insights from numerous studies and concludes that prefrontal areas exhibit domain independence in relational reasoning, while posterior areas within the temporal, parietal, and occipital lobes show evidence of domain dependence in reasoning. Lastly, future directions in the study of relational reasoning are discussed.

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Abbreviations: DLPFC, dorsolateral prefrontal cortex; ERP, event-related potential; fg, fluid General Intelligence; FTL, frontotemporal lobar degeneration; fMRI, functional Magnetic Resonance Imaging; MRI, Magnetic Resonance Imaging; MFG, middle frontal gyrus; PET, positron emission tomography; PFC, prefrontal cortex; RL, rostral lateral prefrontal cortex; RPM, Raven's Progressive Matrices; TBI, traumatic brain injury

1. Introduction

Reasoning has been of interest to cognitive psychologists for many years and research has been driven primarily by attempts to understand basic problem solving in healthy adult humans. These studies date back to the Gestalt tradition and carried on through the rise of the cognitive approach to psychological inquiry. Relational reasoning has been considered to be an important domain for assessments of fluid intelligence (Spearman, 1904). Prominent examples of this approach such as the Raven's matrices (Raven, 1938), and the Cattell Culture Fair test (1973) are comprised of abstract novel pattern match problems that are not strongly dependent on prior knowledge. Research in cognitive psychology and cognitive science has been highly active over the past several decades with numerous theoretical papers outlining key processes in relational reasoning with a particular emphasis on analogy (Gentner, 1983; Gick and Holyoak, 1983; and Sternberg and Rifkin, 1979). This work led to the development of computational models of relational reasoning (Falkenhainer et al., 1989; Holyoak and Thagard, 1989; Hofstadter, 1995; and Hummel and Holyoak, 1997, 2003). With the establishment of many of the important cognitive operations involved in reasoning, the field has increasingly begun to place the reasoning abilities of healthy adult humans into both cross-species and lifespan developmental contexts. Such integrative approaches have suggested key cognitive capacities that appear to be building blocks for abstract reasoning.

Analogies are important for making sense of novel incoming information based on what has been experienced in the past. Understanding the relations among people, animals, or objects in a situation are critical for drawing successful analogies. This ability to make relational comparisons across domains of knowledge is representative of the elaborated problem solving ability observed in humans. Notably, the cognitive skills needed to detect and map relations improve with age (Goswami, 2001; Holyoak et al., 1984; and Rattermann and Gentner, 1998). As adults, we are able to use analogies to both understand novel situations and to suit our goals in teaching others and highlighting similarities between situations. Blanchette and Dunbar (2001) summarized the types of analogies observed in real world environments such as science lab meetings and in news media. Molecular biologists were observed to use analogies when confronting novel data by referring to known phenomena within their field (Dunbar, 1997). Conversely, politicians have been observed to use analogies between policy situations and remote domains such as magical explanations (Dunbar and Blanchette, 2001). Furthermore, the political analogies tended to involve emotional content to advance political goals. Thus, analogies may be used in both understanding new information and in teaching others about aspects of situations that may be seen as similar. Analogical thinking has also been invoked in the explanations of diverse higher order cognitive abilities including empathy (Barnes and Thagard, 1997), theory of mind (Lillard, 1999), metaphor (Gentner et al., 2001), and mathematics (Novick and Holyoak, 1991; Richland et al., 2007). Thus analogy is a core cognitive ability that serves as a rich tool for human thinking.

From a laboratory-based perspective, an important advance has been to investigate the neural basis of these cognitive building blocks. Major cognitive subcomponents of reasoning include working memory capacity, inhibitory control, and the ability to shift attention toward relevant details and away from inappropriate ones. These aspects are developed through childhood to enable adults to use increasingly abstract representations in their reasoning. Further, these cognitive component processes can be assessed across-species, giving further clues as to what constitutes human reasoning and how it differs from other species.

The cognitive processes involved in relational reasoning have been further identified and specified through investigations of neural processing related to these functions. Notably, the progress in functional brain imaging has enabled the study of higher cognitive reasoning processes. These include studies of deductive reasoning (Goel and Dolan, 2000; Monti et al., 2007), analogical reasoning (Bunge et al., 2005; Green et al., 2006; Krawczyk et al., 2010a; and Luo et al., 2003), as well as neuropsychological studies of problem solving (Goel and Grafman, 1995), and chess cognition (Campitelli et al., 2007). An emerging consensus from many of these studies is that the prefrontal cortex (PFC) contributes extensively to reasoning ability (Robin and Holyoak, 1995). Through improvements in understanding both the functions of the PFC and how they enable abstract reasoning to occur, we are in a position to further refine our understanding of what cognitive factors are involved in reasoning and further constrain models of reasoning.

Another promising avenue in reasoning research is to study the effects of brain damage and disease on reasoning abilities. This neuropsychological approach has established linkages between specific cognitive functions and their associated brain regions. As in the neuroimaging literature, it has become increasingly clear that PFC damage causes profound degradation of reasoning performance. While the PFC has remained an area of strong interest in reasoning, it is also clear that the long term semantic networks constructed from wide-ranging cortical circuits also play a large role in reasoning (Morrison et al., 2004). The effects of cognitive and neurological disorders such as autism, Parkinson's disease, and schizophrenia have also indicated additional brain regions and cognitive components that make up abstract reasoning.

The following sections will review the recent literature describing core cognitive components involved in relational reasoning primarily in healthy and brain-damaged adults. I also focus on the neuroimaging literature and how it has expanded and changed our views of reasoning. Lastly, I will conclude by discussing the future of investigations into reasoning.

2. Relational reasoning

2.1. Abstract relational reasoning

Studies of relational reasoning initially emphasized the contributions of the PFC. Theoretical papers by Robin and Holyoak (1995) and Holyoak and Kroger (1995) postulated that

the operations of the PFC, which include governing selective attention (Posner and Petersen, 1990) and managing working memory (Fuster and Alexander, 1971; Miller and Cohen, 2001; and D'Esposito et al., 1995), may give rise to relational reasoning through integrating multiple relations. Relational integration has been considered to be a core ability that gives rise to higher order relational reasoning. This has been demonstrated in children as a hallmark feature of cognition enabling progress toward more complex reasoning abilities (Andrews and Halford, 2002; Gentner and Rattermann, 1998; Goswami, 2001; and Goswami and Brown, 1989). Anatomically, the PFC is in an advantageous position to contribute to reasoning through integrating relational information, as PFC subregions are densely interconnected and it has reciprocal connections with multiple other brain areas (Petrides and Pandya, 1999). Historically, the importance of the PFC has been emphasized in higher cognitive functions such as avoiding impulsivity (Miller, 1985; Miller and Milner, 1985; and Miller, 1992), supervising and scheduling ongoing activities (Shallice and Burgess, 1991; Sirigu et al., 1995), and making decisions (Damasio, 1994; Krawczyk, 2002).

Initial studies testing the association between relational reasoning and PFC predominantly employed matrix reasoning problems as experimental stimuli. Support for this association came from a patient study by Waltz et al. (1999) that compared patients with selective frontal lobe or temporal lobe damage acquired from frontotemporal lobar degeneration (FTLD) on reasoning tasks. FTLD is a form of dementia that leads to diffuse cortical atrophy of either the frontal lobes, temporal lobes, or both. Results from this study revealed selective deficits in patients with PFC damage on problems that required the integration of relations across matrices relative to simpler matrices that could be solved by perceptual pattern matching. This study also demonstrated similar results with relational transitivity problems. Krawczyk et al. (2008) found similar deficits in PFC damaged FTLD patients using a relational pattern analysis task that manipulated relational complexity. Complementary functional Magnetic Resonance Imaging (fMRI) results were reported by Prabhakaran et al. (1997), who demonstrated that integrating Raven's Progressive Matrices (RPM) (Raven, 1938) problems increasingly activated PFC across progressively more complex relational problems. Similar results were obtained in studies by Kroger et al. (2002) and Christoff et al. (2001), both of whom demonstrated that increasingly anterior areas of PFC became engaged in the task when relational complexity increased. In a related study of math reasoning, Prabhakaran et al. (2000) reported that additive relations in arithmetic problems also led to additional PFC activation as relational complexity increased. Through these studies the PFC emerged as both necessary for relational integration in reasoning performance and increasingly involved as relational integration demands increased.

Having established that the PFC was central in relational reasoning, other studies followed further investigating both the task characteristics that lead to PFC activation as well as the involvement of additional regions that likely interact with the PFC in relational reasoning. Christoff and Gabrielli (2001) proposed that self-generation of information was specifically predictive of anterior PFC activation. Support for this position came from both RPM reasoning (Christoff et al.,

2001) and relational pattern matching that required self-generated inferences (Christoff et al., 2003). Later studies of relational processing have further established that areas including the basal ganglia (Melrose et al., 2007), cerebellum, and visual cortex (Kalbfleisch et al., 2007) are also active in association with PFC regions, but these areas are less selectively involved and complementary patient studies have not been conducted to test for the necessity of these areas in relational matrix reasoning. Supporting the relevance of the PFC in relational reasoning has also come from studies that have linked RPM performance to working memory-related activation (Gray et al., 2002, 2003).

Recent developmental studies have begun to address the link between PFC function and the development of relational reasoning ability. Evidence suggests that relational reasoning ability increases with age as people move from early childhood through adolescence (Halford et al., 1994; Richland et al., 2006; and Sternberg and Rifkin, 1979). Crone et al. (2009) investigated the differences in brain activation in children compared to young adults finding that both groups engaged PFC and parietal cortex when solving RPM problems. Further, the adults engaged right RL PFC to a greater degree than children, consistent with an RL PFC-mediated role in integration that is yet present in younger children. In the related area of analogical reasoning, Wright et al. (2007) demonstrated that young adults engaged bilateral RL PFC when solving problems that required integration, while children did not show RL PFC activation during the timeframe critical for solving the problems. Other results have indicated that visuo-spatial reasoning engages superior parietal cortex to a greater degree in adults relative to younger children (Eslinger et al., 2009). This study also indicated that fronto-striatal activity was more involved in younger children's RPM reasoning, while young adults tended to engage fronto-parietal areas. Developmental neuroscience results are converging to indicate that PFC maturity is important for relational reasoning with particular emphasis placed on the RL PFC and the supporting neural regions in parietal cortex in the case of visuo-spatial reasoning.

Other research has investigated the nature of task demands associated with PFC activation. A positron emission tomography (PET) imaging study by Duncan et al. (2000) found that performance of fluid General Intelligence (fG) tasks led to reliable increases in dorsolateral prefrontal cortex (DLPFC) across multiple fG tasks. Forthcoming research by Shokri Kojori et al. (submitted for publication) has revealed that areas of the PFC, along with occipital and parietal cortices are increasingly involved in processing of additional relational information when complexity is increased from one to three relations. Unlike prior studies of matrix reasoning, participants were trained to understand the relations of interest prior to performing the task to control for effect of rule generation processes. This study also demonstrated that directional neural connectivity moves in a posterior-to-anterior direction among neural regions that show increased response to relational complexity variations. The connectivity approach has not yet been fully explored across other relational reasoning tasks, but initial results hold the promise of leading toward a better understanding of how task-related regions coordinate reasoning functions.

2.2. Analogical reasoning

Analogical reasoning is frequently considered to reside at the apex of relational reasoning. Analogies are primarily useful for inferring new knowledge based on prior information. Complex studies have been possible in cognitive psychology investigating multiple aspects of analogical reasoning including analogical retrieval (Wharton et al., 1996), mapping (Krawczyk et al., 2004, 2005; Markman, 1997), and inference (Krawczyk et al., 2005). Neuroscience studies aimed at understanding analogical reasoning have been comparatively limited due to methodology constraints with the majority of studies emphasizing four-term perceptual and semantic analogy tasks. Recent studies are beginning to open up investigation into further subprocesses involved in analogical reasoning at a neural level.

2.2.1. Neuropsychological studies of analogical reasoning

Understanding relational similarity has been considered to be a key skill in the acquisition of analogical reasoning ability (Gentner, 1989; Goswami, 2001). Investigations into the neural basis of analogy have established the importance of PFC, temporal cortex, and axonal connections in making relational similarity comparisons. Tasks that require comparisons of two analogous scenes, such as those developed by Markman and Gentner (1993) and Richland et al. (2006) have been especially useful in this line of investigation. Such tasks allow for comparisons between relational similarity and perceptual or object similarity; the former being a characteristic of analogical reasoning (refer to Fig. 1A). At a cognitive level

scene analogy performance has been linked to working memory ability (Tohill and Holyoak, 2000; Waltz et al., 2000) and RPM task performance (Morsanyi and Holyoak, 2010).

An initial neuroscience study of scene analogy was conducted by Morrison et al. (2004) establishing the importance of both intact PFC and temporal cortex in a scene analogy study conducted with FTLD patients. Their results demonstrated that both frontal and temporal damaged patients choose dramatically fewer relational matches relative to perceptual or object matches among items in analogous cartoon scenes. It was noted that PFC-damaged patients tended to have difficulties particularly when relational match elements were not spatially aligned, suggesting that there were stimulus presentation factors that may have influenced this group.

Additional scene analogy studies have been carried out with individuals with traumatic brain injuries (TBI) which lead to both cortical and white matter connectivity disruptions due to accidents, such as automobile or sports-related collisions. TBI characteristically leads to executive function impairments (Levin and Hanten, 2005; Newsome et al., 2008). Krawczyk et al. (2010a) conducted a scene analogy study with adolescent TBI patients finding that such patients were impaired at forming relational matches overall and showed particular difficulties when perceptual distractor objects were present in the target scene. Their results also linked scene analogy performance with working memory updating abilities through significant correlations with cognitive tasks. Using gray matter thickness measures from Magnetic Resonance Imaging (MRI) scans of the participants, Krawczyk et al. found significant correlations

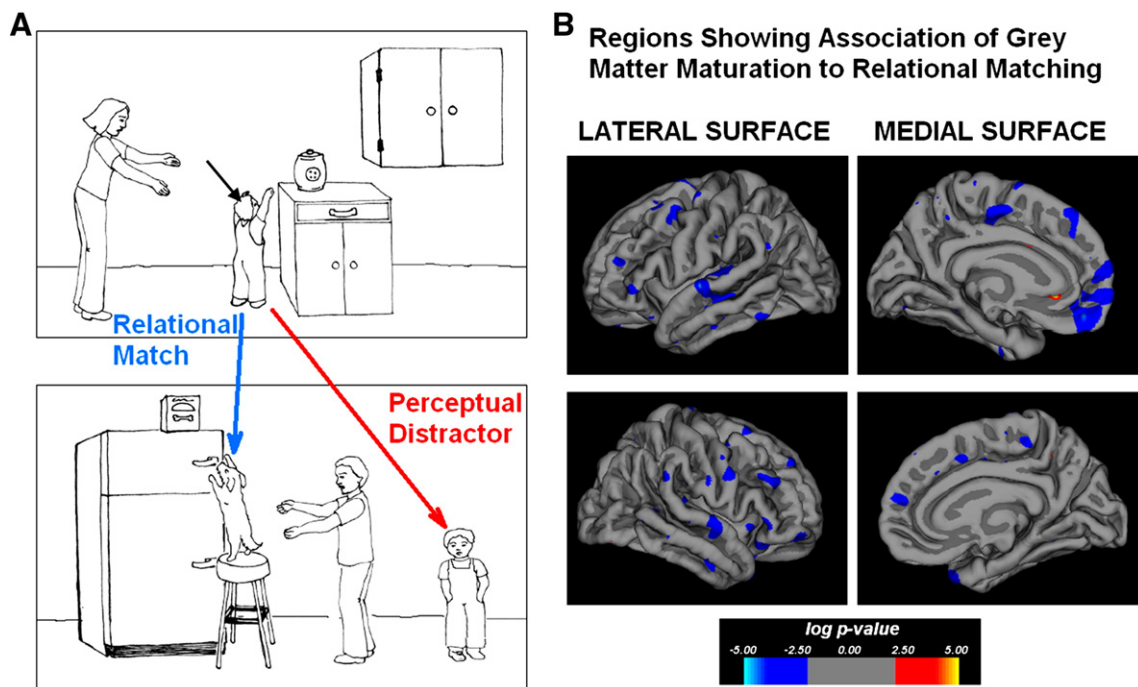


Fig. 1 – A. A scene analogy task is depicted in which participants had to match a highlighted item in the top picture (the boy) with a relational match item in the bottom picture (the dog). A perceptual distractor (the boy) was often present in the bottom picture adapted (from Richland et al., 2006). **B.** Correlational maps between scene analogy performance and gray matter thickness. Areas in blue show significant correlations between cortical maturity (as evidenced by thinning) and analogical reasoning ability (from Krawczyk et al., 2010a).

between gray matter thinning (a marker of cortical maturity) in healthy adolescents predominantly within the anterior frontal pole along with other areas within the temporal, parietal, and occipital lobes (see Fig. 1B). No such relationships between cortical thickness and scene analogy performance were evident in the TBI adolescents indicating that these areas are important for processing relations and avoiding object matches that are compelling, but incorrect. This relational processing deficit has recently been replicated with a TBI and control comparison in adult populations as well (Krawczyk et al., in preparation).

Further progress has been made in understanding relational processing and overcoming non-relational sources of distraction by studying PFC-damaged patients. Morrison et al. (2004) tested FTLD patients with PFC damage and those with temporal damage using a verbal four-term (A:B::C:D) analogy task. Participants had to choose between two alternative D terms, the correct answer and an incorrect distractor, in order to complete the problem with an analogical response. PFC-damaged patients performed worse when distractor D term words were closely associated to the C term, indicating that they had a tendency to make simple semantic association matches between the C and D terms when they were semantically associated. Krawczyk et al. (2008) performed a followup investigation using items that were presented in picture format and participants had to select an appropriate relational item to complete the analogy amid perceptual and semantic distractor items. Their results indicated that patients with PFC-damage had difficulties solving analogies particularly when these distractor items were present compared to patients with temporal damage and control participants. Furthermore, when distractor items were not presented, the scores of PFC-damaged patients rose by over thirty percent. This finding indicates that intact PFC is needed for overcoming the tendency to match the third term to a semantically or perceptually similar item. Note that the analogy can only be solved if this occurs, and when alternative matches were absent PFC damaged patients performance rose to over eighty percent correct. Similar visual distraction results were obtained by Krawczyk et al. (2008) when extraneous distractors were added to a relational pattern matching task with PFC-damaged patients performing approximately thirty percent lower than healthy controls and patients with temporal damage.

Overall, these results from patient studies suggest that the PFC plays a strong role in enabling reasoners to effectively screen out distracting semantic and perceptual similarity while adhering to the goal of making relational responses when alternative matches are available. Meanwhile, intact temporal lobes are important for relational reasoning due to their role in semantic memory storage. The results of Krawczyk et al. (2008) indicated that intact goal maintenance and resistance to distraction are present in individuals with damage to the temporal lobes.

2.2.2. Neuroimaging studies of analogical reasoning

In recent years the field has witnessed an increasing interest in neuroimaging studies of analogical reasoning. The first modern functional imaging study of analogy was carried out by Wharton et al. (2000) using PET and a relatively simple abstract pattern analogy task in which relations such as

shape and texture were considered among four objects. Their results indicated that the left PFC was predominantly active when a relational strategy was used to solve problems relative to perceptual strategies. Additional activation was observed in the left parietal cortex under relational conditions. Soon additional analogical reasoning studies began to appear in the literature. The next wave of investigations studied individuals performing verbal four-term analogy tasks. Luo et al. (2003) conducted a verbal analogies study using Chinese characters. They observed bilateral PFC activation in association with analogy performance along with activity in other regions including the fusiform gyrus, basal ganglia, left temporal gyrus, and parahippocampal cortex. Bunge et al. (2005) further investigated verbal four-term analogy performance, again revealing left PFC activation foci involved in analogical reasoning. Further, Bunge et al. demonstrated that the left anterior PFC showed a greater sensitivity to processing analogies, while the left inferior PFC was most engaged by semantic memory retrieval. Additional studies by Green et al. (2006, 2009) revealed that a left anterior PFC region sensitive to analogical reasoning over semantic association judgment is also modulated by the remoteness of the semantic association. These studies suggest that the left anterior PFC and DLPFC are important for processing analogical representations with an emphasis on connecting to more remote semantic associations which are characteristic of many analogies. This finding is consistent with recent reports in the metaphor literature indicating that the left inferior frontal gyrus is engaged to a greater degree when metaphorical symbolic associations are considered relative to more straightforward semantic associations (Yang et al., 2009, 2010). Increasingly fMRI studies are beginning to converge in isolating left anterior regions in different cognitive aspects of analogical processing.

Neuroimaging studies have also been targeted at elucidating the common finding from the neuropsychological literature that intact PFC is necessary in order to overcome semantic distraction and thereby enable analogical responses to be made based on relational processing. A recent fMRI study has been performed with the goal of further isolating the PFC responses to inhibitory control in analogical reasoning. Cho et al. (2010) used the people pieces analogy task (Sternberg, 1977; Viskontas et al., 2004; and Cho et al., 2007) which involves a relational complexity manipulation along with an inhibitory component. Cho et al. isolated responses to relational complexity increases and compared these responses with activation related to screening out irrelevant dimensions present within the problems. Both complexity and inhibitory screening had additive effects on response times suggesting that both are key cognitive processes involved in this analogy task. fMRI results revealed that the complexity effects were localized to the middle frontal gyrus, inferior frontal gyrus, and the frontal pole, while interference effects primarily activated the middle frontal gyrus and inferior frontal gyrus regions. Overlapping activation was reported within the bilateral middle frontal gyrus (MFG) and pars opercularis portion of the right inferior frontal gyrus. This study highlights a recent trend in functional imaging studies of analogy that multiple PFC regions contribute to different aspects of analogical

reasoning and that PFC interactivity may be a key aspect of future progress in understanding how multiple subprocesses operate.

2.2.3. Investigating component stages of analogical reasoning
Analogical reasoning is comprised of relational processing along with inhibitory control and interface with semantic memory. All of these aspects have been previously investigated with fMRI using four-term analogies (Bunge et al., 2005; Cho et al.; and Green et al., 2006, 2009). To move toward further understanding of analogy, recent studies have begun to investigate the sequence of processing in analogies. Such studies may clarify the timing of cognitive processes across stages of solving analogies. Wendelken et al. (2008) included two conditions within an fMRI study. In one condition four term verbal analogies were included following the procedure of Bunge et al. (2005). In a second experimental condition, Wendelken et al., presented the first two relational words and separately presented either the second word pair of the analogy, or the third term with a question mark left for the fourth term. This setup required participants to infer a fourth term. This design enabled a comparison between the relational comparison of two associations in an analogy and the process of making semantic comparisons and retrieving a final item. Results showed that the left rostralateral prefrontal cortex (RLPFC) was active in conditions with explicit relational comparisons, but not when either semantic pairs were evaluated alone, or when the final term of the analogy had to be inferred. This suggests that RLPFC is specifically involved in relational integration, consistent with the results of Bunge et al. (2005) and Cho et al. (2010).

In a recent study Krawczyk et al. (2010b) investigated four term analogies across separate processing stages. This was carried out using picture analogies similar to those used in a prior patient study (Krawczyk et al., 2008). The use of pictures also enabled fMRI comparisons of analogy to both semantic and perceptual matching processes, previously shown to degrade analogy performance in PFC-damaged FTLN patients. Fig. 2 shows an example of the timing of presentation employed in this study in which the first relational pair of items in the analogy was initially presented. Next the third item of the analogy was presented independently, thereby enabling the participants to infer a possible analogical match in the fourth term of the analogy. Lastly the final item was presented which either completed an analogical match or did not. Control comparison conditions followed this same sequential presentation of items, but in these conditions participants were instructed to make either semantic association matches or perceptual matches between the third and fourth terms. The analogical reasoning condition resulted in the most accurate performance and the lowest response times over the other conditions. This pattern of results is consistent with the majority of relational processing being accomplished in the first two phases of the task (relational encoding of the first item pair and inference of a second item). The imaging results supported this pattern with the analogy condition resulting in greater activation in a series of left-lateralized PFC regions including the DLPC, inferior frontal gyrus, middle frontal gyrus, and medial PFC areas. These regions all showed graded responses with the analogical condition resulting in

greater activation than the other two conditions, but notably the semantic condition resulted in numerically greater activation, though this was not significantly different from the perceptual condition. The left inferior frontal gyrus also responded with significantly greater activation in the second phase (presentation of the third term) over the other conditions, consistent with a greater role in analogical retrieval of an appropriate candidate match for the fourth term. Conversely, at the verification period when the fourth term was revealed, greater activation was observed toward the perceptual condition over the analogical condition within the left DLPC, middle frontal gyrus, and medial PFC regions consistent with greater PFC processing occurring in association with the perceptual condition, which was the least constrained by the prior information. Overall, this study indicated that the relational comparison process is maximally demanding at the first phase in which a relational pair is encoded and maintained for use in drawing an analogy. Consistent with prior results RLPFC activation also exhibited differences in which analogical processing was greater than perceptual processing predominantly at the encoding period, as was observed in the other PFC regions. Krawczyk et al. (2010c) compared activation within a geometric relational pattern match task with that observed in this semantic analogy task. The results indicated that right lateralized areas involved in the geometric task were also engaged to a greater degree for analogical processing.

A recent event-related potential (ERP) study conducted by Maguire et al. (submitted for publication) adds additional timing specificity to the stage-wise processing of analogy. In this study Maguire et al. used the same stimuli as Krawczyk et al. (2010b, 2010c) and observed ERP modulation at the left frontal electrode sites at both the initial stage (encoding the first relational pair) and at the second stage in which the third term of the analogy is presented. Analysis of the wave forms associated with the analogical processing indicated early and later left PFC processing associated with analogical reasoning. Further, the increased activation of the left PFC for the initial stage occurred over a longer time period, starting around 400 ms and continuing beyond 1200 ms after the onset of the A:B comparison. In the second stage of the analogy, the differences over the left PFC related to analogical processing were more temporally contained, occurring approximately from 300 to 600 ms after presentation.

Other results investigating the stages of analogy have been performed with non-semantic stimuli. A recent fMRI study by Volle et al. (2010) used letter sequences that varied on dimensions such as color, shape, and size. These investigators used a letter match control condition that did not require analogical mapping. Further, their design incorporated temporal separation between phases of the task which included an exploration and representation phase of the source analog set of items and a separate comparison and mapping phase requiring participants to choose an appropriate analogical match. The results from the first phase of this analogy task indicated that a rostralateral area of BA10 was active in analogical over control conditions along with fronto-parietal network regions. By contrast, a medial rostral PFC region was observed to be engaged at the mapping phase along with a parietal focus of activation. This investigation supports

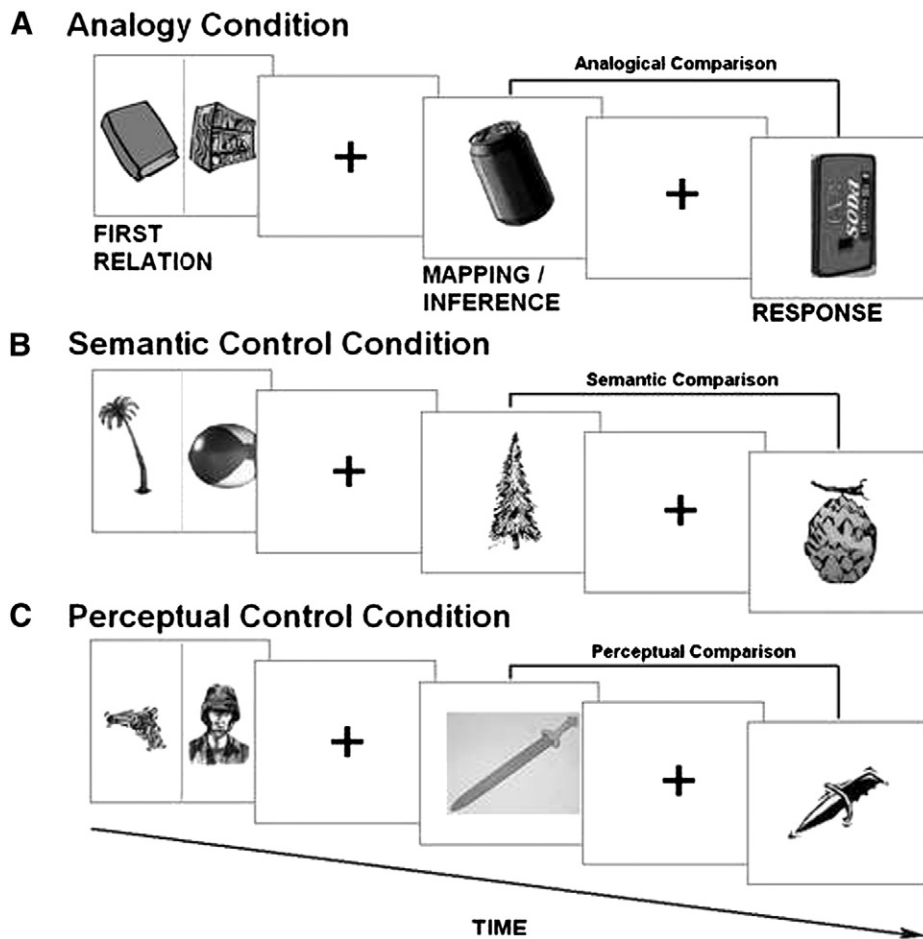


Fig. 2 – Examples of a four-term analogical reasoning task and associated control conditions (from Krawczyk et al., 2010b, 2010c). **A.** The analogy condition required subjects to view a pair of items to determine their relationship at the First Relation phase. After a delay, subjects viewed a third item and were instructed to infer a fourth term that would complete the identical relation at the Mapping/Inference phase. The Inference phase required verification of whether the fourth item fit to complete the problem. **B.** The semantic control condition required inference of a semantic associate to the third item (without the need to map to the first relation) and verification if the fourth item fit. **C.** The perceptual control condition was identical to the semantic control condition, except the inference and verification of a fourth item was based on perceptual similarity.

differential cognitive contributions from areas of left-lateralized BA10 and also verifies that frontal and parietal regions show involvement across non-semantic analogies at the point of processing a source analog. Considered along with the results from semantic analogies (Krawczyk et al., 2010b, 2010c; Maguire et al., submitted for publication) consensus from multiple studies has begun to show differentiation, particularly within PFC areas, between separable phases of analogical reasoning with extensive processing occurring when a source analog is presented relative to periods of mapping, inference, and verification. The RL PFC appears to show left dominance across semantic and non-semantic analogical reasoning, but the contributions of middle and inferior frontal areas have frequently been observed to occur bilaterally.

Another recent ERP investigation of analogical reasoning investigated temporal separability in letter sequence analogies (Qiu et al., 2008) developed for the copycat model (Hofstadter, 1995; Mitchell, 1993). A related fMRI study of similar letter string analogies has revealed bilateral PFC and parietal activation with left DLPFC activation specifically

associated with deeper relational solutions (Geake and Hansen, 2005). Qiu et al. (2008) separated the presentation of the first two terms from the third term letter string analogies. This enabled the investigators to find ERP differences related to analogical encoding, or schema induction, with source localization indicating an anterior medial PFC generator. Left frontal ERPs were implicated in the mapping phase, consistent with prior fMRI findings that left DLPFC is active in analogy tasks and shows modulation by analogical depth (Geake and Hansen, 2005). Unlike the ERP investigation of Maguire et al. (submitted for publication), Qiu et al. (2008) included little semantic information. These studies diverge in that Maguire et al. observed greater left PFC modulation across multiple analogical phases, while Qiu et al. primarily reported mid PFC ERPs associated with analogical encoding. This difference may be attributable to the variation in semantic content between the two studies, which appears to elicit greater left PFC involvement at the encoding phase along with sustained involvement into the mapping and inference processes of analogy.

2.2. Integrating findings from relational reasoning

Relational reasoning involves both content-insensitive neural substrates within the PFC and content-sensitive neural substrates within and outside of the PFC. Fig. 3 provides a brief summary of brain areas relevant to relational reasoning. Studies of the RPM and analogies have demonstrated that visual and spatial processing, mediated by the occipital and parietal cortex, connects to the PFC enabling both bottom-up perception and top-down control over representations relevant to matrix reasoning. Evidence suggests that the involvement of the right RLPFC increases as relational processing demands increase (Crone et al., 2009; Krawczyk et al., 2010a,b, c). The left RLPFC is associated with mediating relational comparisons in analogies (Wendelken et al., 2008) and enabling remote searches for associations (Green et al., 2006, 2009). The bilateral DLPFC, parietal, and occipital cortex support the neural networks associated with executive control in working memory. The left DLPFC and RLPFC are active in making initial relational comparisons. Thus, these areas are important in setting the stage for further analogical and relational comparisons to be made. The DLPFC is also important in inhibitory control in reasoning showing strong association within the MFG and with the LIFG being most relevant to searches for non-dominant meanings, as observed in metaphor (Yang et al., 2009) and semantic retrieval (Bunge et al., 2005). The temporal lobes are important for semantic memory storage processes (Hart and Gordon, 1992; Morrison et al., 2004) relevant to semantic relational reasoning such as analogies. Notably, the RLPFC and DLPFC exhibit activity consistent with domain-independent relational reasoning, while temporal, parietal, and occipital cortex vary depending

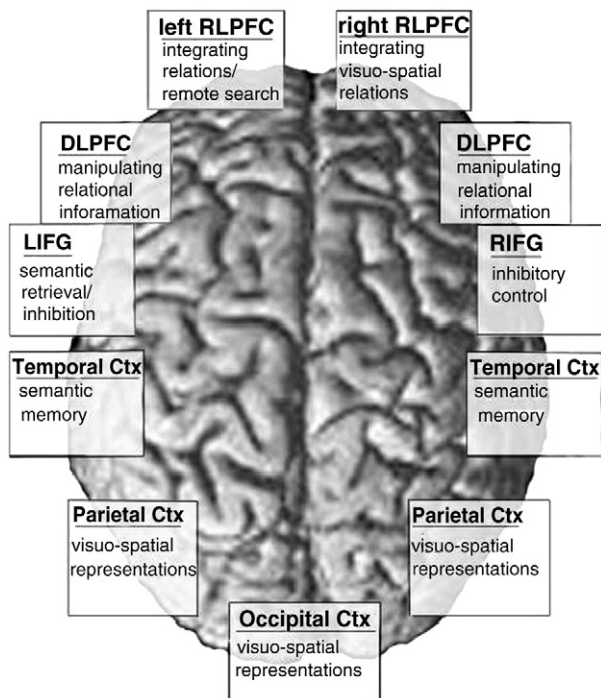


Fig. 3 – Summary of key brain regions and their associated functions in relational reasoning based on results from functional neuroimaging and patient studies.

upon the domain of representations within a given situation or problem type.

3. Future directions

Relational reasoning continues to grow and mature as a research area integrating cognitive and neuroscience studies. There are two paths that future research is likely to take. First, considerable work remains toward further breaking down relational reasoning tasks to investigate cognitive subcomponents through both experimental design and new analysis techniques, such as integrative approaches using multiple methods as well as network and correlational analyses performed on neuroimaging data. A second path for relational reasoning research is to move toward studying more ecologically valid real-world relational reasoning.

Questions remain about the specificity and functional contributions from a variety of brain areas for future neuroscience studies. A clear division has existed between studies of semantic analogies and those that are more abstract, such as RPM, letter string analogies, and visual analogies. Comparing across types of relational tasks appears to be a profitable way forward. Evidence already suggests high overlap between visual relational reasoning and semantic analogical reasoning (Ferrer et al., 2009; Krawczyk et al., 2010c). Future studies may help to isolate regions responsible for operations such as encoding, integration, response selection, and inference that apply to visual relational tasks, transitivity comparison tasks, semantic analogy tasks, and non-semantic analogy tasks. Further, it will be important to tease apart regions that show sensitivity to only the visual or semantic domain. All of these future efforts are likely to benefit from approaching reasoning from a neural network perspective (Fuster, 2006). Reasoning studies have only begun to specify how diverse regions of the brain interact through connectivity to enable the operations of relational reasoning to take place. This is an area that is likely to yield insights into the broader neural basis for reasoning at a basic representational level within the brain.

In time, researchers will likely move toward conducting cognitive neuroscience studies that emphasize greater ecological validity. The existing literature from functional neuroimaging has largely been conducted with either simple visuo-spatial relational reasoning tasks, or with four-term analogies. While these tasks are easier to control experimentally, they have limited our understanding of neural contributions to relational reasoning to cases with either simple arbitrary relations or cases that involve little semantic or relational mapping. Experimental paradigms that better simulate real world reasoning are needed in order to broaden our understanding of other dimensions of human information processing, such as the effect of limited attention, coping with distraction, and variations in goal-directedness. Studies taking this direction will draw more from the basic executive function literature and from the memory literature. Eventually, materials used in neuroimaging tasks will need to investigate the more problematic and complex aspects of real world-information processing such as how non-alignable properties affect neural processing of relations. Further emphasis is also needed on understanding how people detect and make use of different

forms of similarity such as structural versus superficial analogies. A key challenge that will need to be overcome in all of these future efforts will be to avoid simply replicating existing findings from the attention, memory, and similar literatures. Making use of multiple methodologies including fMRI, ERP, patient studies, and eye tracking is likely to be the way forward in avoiding overly general inferences that sometimes come from human neuroscience studies.

To fully appreciate relational reasoning ability in humans it will also remain important to compare cognitive and neuroscience studies of reasoning in humans to those in other species, especially other primates (Flemming et al., 2008; Penn et al., 2008). Humans show a remarkable degree of flexibility in representations and this has largely been attributed to the advanced development within the PFC and anterior frontal pole (Wallis, 2010), but it is also important to note the importance of linguistic representations in relational reasoning, and the extended semantic knowledge capacity of humans which gives rise to some of the most elaborate forms of inference and discovery.

4. Conclusions

Investigations into the neuroscience of relational reasoning remain a vibrant and active area of research with new insights coming from developmental studies, computational models, studies of individuals with neurological and psychiatric impairments, and neuroimaging studies. Each of these methods has its place in future work if we are to gain a greater understanding of brain areas that are associated with common and differing aspects of relational reasoning. The PFC remains the most active cortical area under investigation and intact PFC has been shown to be essential to effective relational reasoning across domains. Furthermore, PFC subregions show selectivity to different aspects of relational reasoning. Further studies are likely to expand our understanding by refining our understanding of brain areas involved in the cognitive subcomponents of reasoning and also emphasizing neural network approaches to reasoning.

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