Relational Integration in the Human Brain: A Review and Synthesis

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Abstract

■ Relational integration is required when multiple explicit representations of relations between entities must be jointly considered to make inferences. We provide an overview of the neural substrate of relational integration in humans and the processes that support it, focusing on work on analogical and deductive reasoning. In addition to neural evidence, we consider behavioral and computational work that has informed neural investigations of the representations of individual relations and of relational integration. In very general terms, evidence from neuroimaging, neuropsychological, and neuromodulatory studies points to a small set of regions (generally left lateralized) that appear to constitute key substrates for component processes of relational integration. These include posterior parietal cortex, implicated in the representation of first-order relations (e.g., *A*:*B*); rostrolateral pFC, apparently central in integrating first-order relations so as to generate and/or evaluate higher-order relations (e.g., *A*:*B*::*C*:*D*); dorsolateral pFC, involved in maintaining relations in working memory; and ventrolateral pFC, implicated in interference control (e.g., inhibiting salient information that competes with relevant relations). Recent work has begun to link computational models of relational representation and reasoning with patterns of neural activity within these brain areas. ■

INTRODUCTION

Relational Integration in Human Reasoning

The human brain supports a tremendous range of cognitive abilities. It has been observed that "human animals—and no other—build fires and wheels, diagnose each other's illnesses, communicate using symbols, navigate with maps, risk their lives for ideals, collaborate with each other, explain the world in terms of hypothetical causes, punish strangers for breaking rules, imagine impossible scenarios, and teach each other how to do all of the above" (Penn, Holyoak, & Povinelli, 2008, p. 109). Cognitive scientists have long debated what mechanism or mechanisms underlie this vast range of intellectual abilities. Over the past quarter century, one general proposal has linked cognitive theories with neuroscientific investigations of human reasoning. The "relational integration hypothesis" has two core assumptions. First, humans are capable of forming explicit representations of relations between entities, thereby assigning entities to functional roles that go beyond perceptual appearances. Second, humans are able to make inferences by integrating multiple relations. That is, a thinker can consider two or more relations together to assess what they jointly imply.

Our aim here is to review what is currently known about the neural substrate of relational integration and the processes that support it. We do not attempt a meta-analysis, and our review does not aim to be exhaustive. Extending other recent reviews and meta-analyses (e.g., Wertheim & Ragni, 2018; Krawczyk, 2012, 2017), we will consider behavioral and computational work that has informed neural investigations. We will focus on the central components of a network underlying relational integration and also consider other varieties of relational processing that are relatively independent of this system for relational integration. In addition to the integration of relations, we will consider the neural basis of representations of individual relations. Finally, we will call attention to open issues that await future investigation.

The general concept of relational integration underlies tasks that exemplify "higher" cognition, including planning and problem solving, deductive and inductive reasoning, and analogical and causal inference. Explicit relations involve internal structure that goes beyond simple associations or statistical covariations among elements. For example, the problem-solving strategy of means–ends analysis requires joint consideration of actions and goals, triggering generation of subgoals that form a goal hierarchy. In propositional deduction, the validity of a conclusion depends on the relation between the truth values of two or more premises. Deduction can involve such relational operations as eliminating negations, substituting constants for variables, and binding quantifiers (e.g., Monti, Osherson, Martinez, & Parsons, 2007). To evaluate an analogy in the form *A*:*B*::*C*:*D*, the reasoner must compare the relation between *A* and *B* to that linking *C* and *D*, assessing the higher-order similarity of the two relations. In a generative analogy problem, stated as *A*:*B*::*C*:?, it is

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necessary to find a *D* such that the *C*:*D* relation is sufficiently similar to the *A*:*B* relation. Here, a candidate *C*:*D* relation is generated under the constraint that it must resemble *A*:*B*, constituting a basic generative operation that allows systematic transfer of ideas by analogy.

The precise nature of the integration process varies from task to task. One relation may be compared to another, two relations may be combined to create a generalization, or one relation may be systematically restructured to form a new one (e.g., constructing the relation *child-of* by creating the converse of *parent-of*; Lu, Wu, & Holyoak, 2019). However, in all cases, the relations to be integrated must be explicit, in the sense of being represented in a manner that permits them to be manipulated in working memory. Both in cognitive development (Karmiloff-Smith, 1992) and in cognitive evolution (Penn et al., 2008), mechanisms for relational re-representation set the stage for higher-order reasoning by transforming perceived relations into mental concepts available as objects of thought. The mature human reasoner goes beyond reacting to perceived relations, achieving the capacity to think about relations that may not be directly observable (Holyoak, 2012; Gentner, 2010; Halford, Wilson, & Phillips, 2010).

Relational Integration in the Brain: Early Work

Because relational integration involves active manipulation of internal representations, it necessarily depends on working memory. For example, imposing an extra load on working memory either directly by adding a secondary task (Waltz, Lau, Grewal, & Holyoak, 2000) or indirectly by increasing state anxiety (Tohill & Holyoak, 2000) impairs relational processing on an analogy task. The neural substrate of working memory is highly complex and distributed across multiple brain regions (D'Esposito & Postle, 2015), but it is generally agreed that subregions of the pFC are critical for the types of cognitive control and flexibility required for relational integration.

Robin and Holyoak (1995) were the first to specifically propose that pFC provides a core substrate for relational integration. The framework they sketched was based on a general survey of deficits in executive functions (notably maintenance of information and inhibitory control) associated with frontal lesions in humans, coupled with studies of contingency learning in nonhuman animals. Two aspects of Robin and Holyoak's proposal proved influential in guiding future work. First, they emphasized that relational reasoning requires multiple subprocesses, which appear to be associated with subregions of pFC. In particular, to manipulate explicit relations, it is necessary to hold active representations in working memory of the entities being related (bridging temporal gaps in their encoding), and to attend to and reason about relations, it is necessary to inhibit interference from salient competing information.

Second, Robin and Holyoak (1995) adopted a taxonomy of relational complexity that had been proposed by Halford and Wilson (1980; Halford, 1993). The Halford and Wilson taxonomy, originally applied to explain transitions in cognitive development, focuses on the number of dimensions of potentially simultaneous variation that jointly determine a response. As the number of such dimensions increases, the cognitive load is hypothesized to increase (with adult human reasoning being limited by the maximum number of dimensions that can be jointly considered, estimated to be four). Robin and Holyoak proposed that variations in relational complexity will impact demands on pFC.

Because relational integration requires at least two relations, it follows that problems requiring joint processing of two relations should be dependent on an intact pFC, whereas problems that depend on a single relation may not be. This hypothesis was tested by Waltz et al. (1999) in a neuropsychological study with patients experiencing frontal or else temporal variants of frontotemporal lobar degeneration (FTLD) and age-matched controls. Waltz et al. systematically varied the complexity of matrix problems (very similar to geometric analogies) and transitive inference problems (given cards stating the relative heights of pairs of individuals, the task was to sort cards that each named one individual in order of height, tallest to shortest). On the basis of Halford and Wilson's complexity taxonomy, subtypes of each problem were created that required consideration of zero, one, or two relations. Frontal-variant patients generally achieved high accuracy on problems involving zero or one relation, but their performance fell to chance on two-relation problems for both the matrix and the transitive inference task. In contrast, temporal-variant patients were almost as accurate as controls regardless of number of relations. At the same time, the frontal-variant patients were more accurate than temporal-variant patients on tasks that assessed semantic memory (e.g., the Boston Naming Test). These findings supported the basic conclusion that joint consideration of at least two relations—that is, relational integration—is dependent on an intact pFC.

The fact that frontal patients were selectively impaired on complex content-free reasoning problems suggests a general connection between relational integration and fluid intelligence. Psychometric studies have found close statistical connections between tasks that require relational integration (particularly analogy problems and the Raven's Progressive Matrices (RPM) test; Raven, 1938) and other tasks used to measure fluid intelligence (Snow, Kyllonen, & Marshalek, 1984). In an early neuroimaging study of human reasoning using PET, Duncan et al. (2000) found that multiple tasks linked to fluid intelligence activated dorsolateral pFC (DLPFC). Another early PET study (Wharton et al., 2000) compared brain responses during a geometric analogy task to those during a matched similarity task, which was based on the same stimuli but did not require integration of relations. A subtraction analysis revealed activation associated with the analogy task in the left dorsomedial pFC and other subareas of pFC as well as in the parietal and superior occipital cortices. Boroojerdi et al. (2001) found that applying low-intensity repetitive TMS over the left pFC selectively decreased RT to solve the same type of analogy problems used by Wharton et al., implying that the left frontal cortex is functionally relevant for performing analogical reasoning.

In summary, the body of research up to the turn of the century suggested intimate connections among relational integration and fluid intelligence, executive functions, and the functions of the human pFC (especially its left lateral surface). We will now explore the more detailed picture of the neural basis for relational integration that has emerged after another two decades of research using multiple methodologies.

NEURAL SYSTEM FOR RELATIONAL INTEGRATION

Overview

The past two decades have brought an explosion of research relevant to the neural basis for relational integration, using a variety of methods including neuropsychology, fMRI, morphometry, and transcranial direct current brain stimulation (tDCS). Here, we aim to sketch the networks that appear to support component processes of relational integration, based on evidence primarily drawn from studies using tasks involving analogical or deductive reasoning. We will first provide an overview of the neural system revealed by this body of research and then briefly review evidence related to each of the major components in the network. We also consider possible neural mechanisms that may support computations related to the representation and integration of relations.

Relational integration has several fundamental prerequisites. To consider the joint implications of multiple relations, it is necessary to represent individual relations, and to represent any individual relation, it is necessary to represent the entities being related. The overall process will be heavily dependent on working memory, as representations of both entities (often objects) and relations among them must be maintained in an active state that allows reasoning processes to operate upon them. Within the population of young adults, measures of individual differences in cognitive capacity predict performance in tasks that require relational reasoning (Gray & Holyoak, 2020; Kmiecik & Krawczyk, this issue).

As a general overview, Figure 1 sketches several major brain regions that appear to play key roles in relational reasoning. These regions participate in the frontoparietal control network, which (often in coordination with additional regions) is critical for tasks that require the ability to coordinate behavior in a rapid, accurate, and flexible goal-driven manner. A wide variety of tasks that require relational reasoning have been linked to the frontoparietal network (e.g., Wendelken, Ferrer, Whitaker, & Bunge, 2016; Watson & Chatterjee, 2012; Acuna, Eliassen, Donoghue, & Sanes, 2002).

Figure 1 highlights several of the landmarks in the frontoparietal control network that appear to be critical in relational reasoning tasks. In very general terms, evidence from neuroimaging, neuropsychological, and neuromodulatory studies points to a small set of regions (generally left lateralized) that appear to constitute key substrates for component processes of relational integration. These include posterior parietal cortex (PPC), implicated in the representation of first-order relations (e.g., *A*:*B*); DLPFC, which maintains relations in a working memory; ventrolateral pFC (VLPFC), implicated in interference control (e.g., inhibiting salient information that competes with relevant relations); and rostrolateral pFC (RLPFC), apparently central in integrating first-order relations so as to generate and/or evaluate higher-order relations (e.g., *A*:*B*::*C*:*D*). These regions are closely coupled, and some contribute to multiple processes. There are particularly close ties between working memory and interference control (Nee, Wager, & Jonides, 2007), to which both DLPFC and VLPFC contribute. Several other brain areas also support relational integration through more general cognitive processes such as semantic and visuospatial processing as well as attention shifting (Hobeika, Diard-Detoeuf, Garcin, Levy, & Volle, 2016).

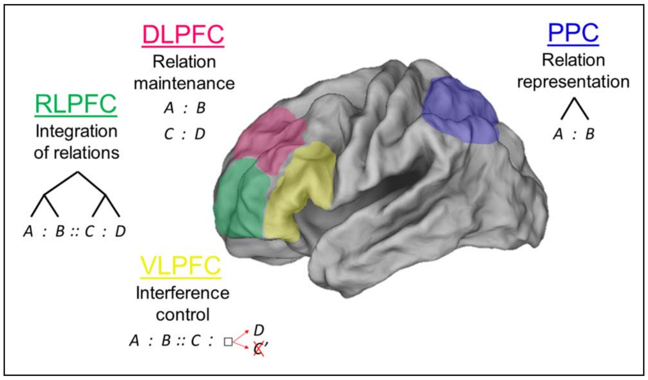

Figure 1. Schematic of major frontal and parietal brain areas that support representation and integration of relations, illustrated for analogical reasoning. Active representations of relations (e.g., *A*:*B*) are formed in the PPC, maintained in working memory based on the DLPFC (*A*:*B*, *C*:*D*), and integrated to identify higher-order relations (e.g., sameness of the relations *A*:*B* and *C*:*D*) in the RLPFC. The VLPFC is involved in inhibiting salient but potentially interfering information (e.g., *C*', a close semantic associate of *C*, might interfere with processing the relation *C*:*D* that is analogous to *A*:*B*).

Substrate of Relational Integration: RLPFC

Nature of the Region

There is now a general agreement that the most anterior region of pFC plays a critical role in the integration of multiple relations (for meta-analyses of fMRI studies of analogical reasoning, see Hobeika et al., 2016; Vartanian, 2012). This region, roughly corresponding to Brodmann's area (BA) 10, is often referred to as the RLPFC (also termed frontopolar). Both comparative and human anatomical evidence suggests this region is wired for integration. BA 10 in the human brain is larger relative to the rest of the brain than it is in the apes, and its supragranular layers have more space available for connections with other higher-order association areas. These anatomical differences suggest that this part of the cortex became enlarged and more specialized during hominid evolution (Semendeferi, Armstrong, Schleicher, Zilles, & Van Hoesen, 2001). An important distinguishing feature of the RLPFC is that the complexity of the dendritic/spine systems (i.e., number and density of dendritic spines per cell) is higher than in primary (e.g., BAs 3, 2, and 1) or unimodal (e.g., BAs 22 and 44) cortices (Jacobs et al., 2001), suggestive of its greater integrative function (Jacobs, Driscoll, & Schall, 1997). Furthermore, the complexity of this region changes over the life span. In the neonatal cortical system, its complexity is lower than that of primary and unimodal cortices, indicating a protracted development of BA 10 (Travis, Ford, & Jacobs, 2005). Its complexity eventually decreases over time in older adults (although remaining relatively more complex than other cortical areas with respect to dendritic/spine systems; Jacobs et al., 1997, 2001). In terms of its connectivity, the RLPFC appears to be heavily and reciprocally interconnected mainly (perhaps exclusively) with other supramodal areas, particularly within pFC, suggesting a specialization in integrating relatively abstract information (Ramnani & Owen, 2004). A recent morphometry study found that individual differences in gray matter volume within the left RLPFC predict performance on an analogy task (Aichelburg et al., 2016).

Relational Complexity

In the area of human reasoning, the earliest line of work supporting the role of the RLPFC in relational integration involved fMRI studies of college students solving variants of RPM problems (Raven, 1938). These are nonverbal, content-free problems based on systematic changes across the horizontal and vertical axes of a matrix (usually 3 × 3) composed of geometric patterns, where the task is to select the best completion for the final missing cell in the matrix from a set of alternatives. RPM-like problems provide sets of well-defined stimuli within which relational complexity can be varied. Prabhakaran, Smith, Desmond, Glover, and Gabrieli (1997) used fMRI to compare neural responses when participants solved “figural” problems, which simply require visuospatial pattern completion, versus “analytic” problems that require systematic relational reasoning (a distinction drawn earlier by Carpenter, Just, & Shell, 1990). In a subtraction of activation between analytic and figural problems, the former yielded greater bilateral activation in pFC (including the RLPFC) as well as left-lateralized activation in parietal, temporal, and occipital lobes.

Two subsequent studies using matrix problems explicitly adopted the Halford and Wilson (1980) taxonomy of relational complexity. Christoff et al. (2001) created RPM-like problems in which the changes across rows and columns of the matrix varied in terms of zero, one, or two relations. pFC activation was specific to the two-relation problems (i.e., those that required relational integration, consistent with the findings observed for frontal patients by Waltz et al., 1999) and was particularly pronounced in the left RLPFC. Kroger et al. (2002) performed a similar parametric study using matrix problems that required attention to zero through four relations, again finding that increasing complexity was associated with greater activation in the anterior pFC. In addition, Kroger et al. included conditions in which behavioral difficulty (assessed by both error rate and solution time) was manipulated by introducing perceptual noise in the stimuli, while holding relational complexity constant. High levels of complexity, but not problems made comparably difficult by perceptual noise, selectively activated anterior left pFC. Studies using content-free analogy problems have also found evidence that the RLPFC is selectively involved in the process of relational comparison (Volle, Gilbert, Benoit, & Burgess, 2010).

Although not focused on the RLPFC per se, several other neuropsychological studies have provided evidence that relational integration depends on pFC more generally. For various types of problems, including both matrices and pictorial analogy tasks, older adults (subject to neural decline in frontal function) are especially impaired in solving problems at higher levels of complexity (Todd, Andrews, & Conlon, 2019; Viskontas, Holyoak, & Knowlton, 2005; Viskontas, Morrison, Holyoak, Hummel, & Knowlton, 2004). Similarly, high relational complexity is problematic for patients experiencing Alzheimer’s disease, especially those with neuropsychological profiles indicative of pFC dysfunction (Waltz et al., 2004), as well as for patients who have had strokes impacting pFC (Andrews, Halford, Chapell, Maujean, & Shum, 2014; Andrews et al., 2013). Most notably, a neuropsychological study using patients with focal damage to the left RLPFC revealed specific deficits in relational integration when solving analogy problems, with the behavioral score in a short analogy task being predictive, with high sensitivity and specificity, of the presence of a lesion within the RLPFC (Urbanski et al., 2016).

The logic of complexity manipulations has also been applied to identify neural areas responsible for domain-general deductive reasoning. Monti et al. (2007) performed two fMRI studies in which college students solved problems that varied in deductive complexity, while holding linguistic complexity constant. To exemplify, simple problems were based on a modus ponens inference, such as “If P or Q then not R; P; therefore not R,” whereas complex problems were based on a more complex modus tollens inference coupled with application of De Morgan’s law, as in “If P or Q then not R; R; therefore not P.” Comparatively, the latter inference relies to a much larger extent on the simultaneous consideration of multiple interacting variables, subgoal processing, and branching (Coetzee & Monti, 2018). Consistent with this view, the left RLPFC was identified as a core region sensitive to deductive complexity. Moreover, this finding held regardless of whether the variables *P*, *Q*, and *R* were in fact single-letter variables (as in the examples above), nonsense single-syllable words, or noun phrases describing visual features of an imaginary geometric object, an imaginary face, or an imaginary house (Monti & Osherson, 2012; Monti, Parsons, & Osherson, 2009). Importantly, recent work has shown that, although the left RLPFC is sensitive to the presence and/or degree of deductive reasoning complexity, it does not responding to increased working memory demands alone (i.e., in the absence of deductive inference-making; Coetzee & Monti, 2018).

Semantic Analogies

The findings summarized so far have focused on content-free problems in which multiple relations can be differentiated quite clearly. Relational complexity is less transparent for problems that depend heavily on semantic knowledge, such as verbal analogy problems in the *A*:*B*::*C*:*D* format (e.g., *bouquet*:*flower*::*chain*:*link*). However, solving such analogies requires assessing the higher-order similarity of the relation between the *A*:*B* concept pair and that between the *C*:*D* pair, a process that would appear to involve the integration of the two relations.[1] Neuroimaging studies have consistently found that solving such analogy problems results in activation of the RLPFC to a greater degree than does categorizing objects in individual pairs, without integrating multiple relations (Krawczyk, McClelland, Donovan, Tillman, & Maguire, 2010; Green, Fugelsang, Kraemer, Shamosh, & Dunbar, 2006; Bunge, Wendelken, Badre, & Wagner, 2005). Other evidence indicates that the integration process is left-lateralized (Bunge, Helskog, & Wendelken, 2009), although the right RLPFC also plays a role in relational processing.

Importantly, for verbal analogies, the response of an area within the left RLPFC increases parametrically with the overall semantic distance between the *A*:*B* and *C*:*D* concepts (Green, Kraemer, Fugelsang, Gray, & Dunbar, 2010). That is, activation is greater when the two pairs are semantically distant (e.g., *blindness*:*sight*::*poverty*:*wealth*) than when they are overall more similar (e.g., *blindness*:*sight*::*deafness*:*hearing*). It thus seems that semantic distance may impact the complexity of the integration process required to compare the two relations (see also Kmeicik, Brisson, & Morrison, 2019). One possible explanation is that the neural code for relations is distributed in nature, such that relations between similar pairs are themselves more similar than are relations between disparate pairs (Chiang, Peng, Lu, Holyoak, & Monti, this issue).

Although most studies of verbal analogical reasoning have involved evaluation of complete four-term analogy problems, a few studies have used other formats. The neural response in the RLPFC is very similar when an explicit relation term is substituted for the *A*:*B* pair (e.g., *microphone*:*sound*::*camera*:*light* is replaced with *detects*::*camera*:*light*; Wendelken, Bunge, & Carter, 2008), indicating that relational comparison (rather than mapping of individual concepts; see Footnote 1) is the critical process. Other studies have examined a procedural variant in which participants are asked to generate a completion when the *D* term is missing (e.g., *microphone*:*sound*::*camera*:*?*). When the semantic similarity of the two pairs is relatively high, as in the above example, Wendelken et al. did not observe RLPFC activation in the generation version of the task. It is possible that, for semantically close analogies (particularly when the shared relation is easily named), a satisfactory *D* term can be generated by a process of spreading activation (for the example above, *detect* coupled with *camera* may activate *light*), obviating the need for relational integration.

However, at least for more semantically distant generation problems (e.g., *blindness*:*sight*::*poverty*:*?*), RLPFC activation is reliably observed (Green, Kraemer, Fugelsang, Gray, & Dunbar, 2012). For such distant analogies, the process of generating a *D* term is likely to be guided by relational comparison to ensure that the resulting *C*:*D* relation is sufficiently similar to the *A*:*B* relation. Indeed, generating solutions to distant semantic analogies appears to foster a transient "relational set," encouraging a focus on relations in other tasks administered shortly afterward (Andrews & Vann, 2019; Simms & Richland, 2019; Vendetti, Wu, & Holyoak, 2014). More generally, the generation of solutions to distant analogies appears to be closely linked to creative thinking (Green, 2016).

Green et al. (2017) further explored the role of RLPFC in generating distant semantic solutions to analogy problems with anodal tDCS. This noninvasive neuromodulatory technique has been shown to be capable of increasing (with anodal tDCS) and decreasing (with cathodal tDCS) neuronal excitability through prolonged application of weak currents at the scalp (in the range of 1–2 mA), with effects having been detected up to 1 hr after exposure (see Nitsche et al., 2008, for a review). Consistent with prior work, Green et al. (2017) reported that application of anodal tDCS to the left frontopolar cortex increased the semantic distance of analogical solutions as well as the number of valid solutions produced by participants.

In interpreting these experiments, it should be noted that the frontopolar region identified by Green et al. (2006, 2010) is more medial and caudal (at the intersection of BAs 9 and 10 in the superior frontal gyrus) than the more lateral and ventral region (typically spanning medial and inferior frontal gyri close to the junction of BAs 10 and 47) often associated with relational reasoning (e.g., Cho et al., 2010; Wendelken et al., 2008; Bunge et al., 2005; Kroger et al., 2002; Christoff et al., 2001). Although speculative, an intriguing possibility is that this difference in localization might reflect different aspects of resolving analogies, with the work of Green and collaborators being particularly tuned to the dimension of semantic distance and creativity in relational reasoning. This possibility is consistent with the prior observation that, in typically developing children, the more mediocaudal focus identified by Green and colleagues is also recruited by nonliteral interpretation of an ironic statement (e.g., "Jack just got his test back. Ron sees the F on it and says, 'Way to go.'"; Wang, Lee, Sigman, & Dapretto, 2006).

Alternative Interpretations

A number of alternative (or additional) possible functions of the RLPFC deserve consideration. An obvious possibility is that the RLPFC is simply involved in coping with high problem difficulty, regardless of its basis. However, several studies have shown that tasks requiring relational integration activate the RLPFC more than do control conditions of at least equal behavioral difficulty (Watson & Chatterjee, 2012; Wendelken et al., 2008; Kroger et al., 2002). Conversely, working memory load per se, in the absence of increased relational integration load, does not recruit the RLPFC (Coetzee & Monti, 2018).

There has been considerable debate as to whether relational integration is in fact a core cognitive function of RLPFC or whether it may be a special case of some more general function. There is ample evidence that this brain area plays important roles in performing a variety of demanding cognitive tasks that would not typically be considered reasoning. In particular, the RLPFC is involved in complex episodic memory tasks, especially those that require monitoring over time, postretrieval evaluation, or assessment of the relation between items and their source context (e.g., Westphal, Reggente, Ito, & Rissman, 2016; Ranganath, Johnson, & D'Esposito, 2000). It has been argued that these sorts of mnemonic processes may require forms of relational integration (Wendelken et al., 2008; Christoff & Gabrieli, 2000). That is, explicit consideration of relations (and of relations between relations) may be required for cognitive tasks that are not normally considered "reasoning."

Another proposal is that integrating relations is a special case of coordinating subgoals, where the latter activity is the more general function of the RLPFC (Ramnani & Owen, 2004; Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999). There is a great deal of evidence that performing nonanalogical cognitive tasks involving goal hierarchies can activate the RLPFC (although arguably processing of multiple subgoals is itself a form of relational integration). However, a study by Watson and Chatterjee (2012) found that performing an analogy task yielded greater RLPFC activation than performing a nonanalogical task (matched in overall difficulty) that required coordination of subgoals. This finding suggests that the kind of relational comparison central to analogical reasoning places a particularly high burden on the RLPFC.

The RLPFC has also been suggested to play a key role in cognitive control and, in particular, in control over integration and/or segregation of information in working memory. Prabhakaran, Narayanan, Zhao, and Gabrieli (2000), for example, found increased RLPFC activation when participants had to integrate and maintain verbal and spatial information in working memory as compared to maintaining the same amount of information without any integration. Consistent with this view, De Pisapia, Slomski, and Braver (2007) reported a temporally specific pattern of RLPFC activation before, and during, integration of numerical information held in working memory into a sequentially presented arithmetic problem.

Another credible hypothesis is that the RLPFC represents the top of an abstraction hierarchy (caudal to rostral) across regions of pFC and is activated by internally generated representations of an increasingly abstract nature (Christoff & Gabrieli, 2000). In support of this possibility, Christoff, Keramatian, Gordon, Smith, and Mädler (2009) observed greater RLPFC activation when people were cued to expect an abstract rather than concrete solution to an anagram problem (even on trials where participants failed to find the solution). In general, the higher-order comparison of relations will indeed involve internally generated representations. However, we will see shortly that brain areas other than the RLPFC (notably the parietal cortex) also play important roles in the internal generation of relations. In addition, recall that Wendelken et al. (2008) observed the same degree of RLPFC activity in a semantic analogy task when the *A*:*B* relation was stated directly as a verb cue, thus obviating the need to internally generate the (unstated) *A*:*B* relation (for a similar finding, see Aichelburg et al., 2016). With respect to Christoff et al.'s (2009) findings with the anagram task, it should be noted that abstract concepts are often relational in nature (e.g., *catalyst*, *oppression*; see Goldwater & Schalk, 2016). A cue indicating a task will involve abstract concepts may encourage a state of readiness in the brain region most centrally involved in relational processing. A similar mechanism may be involved in creating a relational set (Vendetti et al., 2014).

It should be emphasized that, in the neuroimaging studies we have reviewed, the RLPFC was almost always active together with multiple other brain areas in pFC and more posterior areas. In general, the RLPFC appears to function as the most anterior area in the broad frontoparietal control network (see Gilbert, Gonen-Yaacovi, Benoit, Volle, & Burgess, 2010). We will now consider other brain regions that play important roles in relational reasoning.

Interference Control: VLPFC

Robin and Holyoak (1995) posited that pFC is likely to be critical for a central process required for systematic relational processing: control of interference. To think about specific relations requires the ability to avoid interference from other salient information—notably, irrelevant perceptual or semantic attributes of specific objects and their strong but nonanalogical semantic associates. Neuropsychological studies have shown that frontal patients are particularly impaired in solving analogy problems that require selecting the relational response from a set of options that includes semantic distractors. For example, Morrison et al. (2004) tested frontal-variant patients with FTLD, along with temporal-variant patients and age-matched controls, on *A*:*B*::*C*:*D* verbal analogy problems that required a forced choice between two options, the correct choice *C*:*D* and a *C*:*D'* foil. On the basis of a measure of semantic similarity between words, for some problems, the two terms in the *C*:*D'* foil were more closely related to each other than were the terms in *C*:*D* (e.g., *play*:*game*::*give*:*party* [*C*:*D*] vs. *give*:*take* [*C*:*D'*]). The frontal group was selectively impaired on such problems, indicating a deficit in their ability to resist responding on the basis of direct similarity between the two words in a response option as opposed to the higher-order similarity of the relations in the two word pairs (see Figure 1).

Krawczyk et al. (2008) performed a similar study using four-term picture analogies, where the task required selecting the analogical completion from a set of four options that included three foils. One foil was semantically related to the *C* picture, one was perceptually similar to it, and one was unrelated. Frontal-variant patients with FTLD were particularly prone to select the semantically similar foil and, to a lesser extent, the perceptually similar foil. Behavioral studies have shown that misleading semantic similarity based on shared attributes leads to increased error rates in analogical reasoning for children (Richland, Morrison, & Holyoak, 2006), older adults (Viskontas et al., 2004), and (using response time as a measure) college students (Wong, Schauer, Gordon, & Holyoak, 2019; Cho, Holyoak, & Cannon, 2007).

A large body of research using many tasks, including some that involve reasoning, has implicated the VLPFC in variants of interference control (for a meta-analysis, see Nee et al., 2007). These variants include inhibition of a motor response (e.g., Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003), executive control (Hampshire, Chamberlain, Monti, Duncan, & Owen, 2010), proactive interference resolution in working memory (e.g., Jonides & Nee, 2006; D'Esposito, Postle, Jonides, & Smith, 1999), selection among competing alternatives (e.g., Novick, Kan, Trueswell, & Thompson-Schill, 2009), selection of task-relevant representations from among retrieved competitors (Nee & Jonides, 2009; Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005), controlled semantic retrieval (e.g., Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997), inhibiting belief bias during deductive reasoning (e.g., Goel & Dolan, 2003), and avoiding heuristic bias during decision-making (e.g., De Neys & Goel, 2011). Furthermore, individuals with a greater ability to control interference in working memory have been shown to exhibit a larger brain volume in the VLPFC (Samrani, Bäckman, & Persson, 2019).

There is now considerable evidence that similar brain regions are responsible for interference control during analogical reasoning. Cho et al. (2010) performed an fMRI study in which college students solved four-term analogies based on cartoon human figures that varied in a binary fashion on visual dimensions such as gender and clothing color. At the beginning of each trial, it was specified which dimension or dimensions were to be considered relevant to the analogy, thereby manipulating relational complexity (i.e., number of relevant dimensions). An analogy was considered valid if the *A*:*B* and *C*:*D* cartoon figures were both the same or both different on the dimension(s) specified as relevant. The design varied relational complexity and need for interference in a factorial fashion. A dimension was coded as interfering if it was specified as irrelevant but varied in a manner incongruent with the relevant dimensions (e.g., *A* and *B*, and *C* and *D*, might both be "same" on the relevant dimension of clothing color, whereas on the interfering dimension of gender, *A* and *B* might be the same but *C* and *D* might be different). Consistent with the findings reviewed above, Cho et al. found that high relational complexity was associated with greater neural activity in a variety of cortical regions, with unique foci in the RLPFC and right VLPFC, whereas increased interference recruited areas in the bilateral VLPFC and DLPFC, with unique foci in the bilateral DLPFC.

The findings of Cho et al. (2010) provided support for the general hypothesis that multiple regions of pFC contribute to different aspects of analogical reasoning and that the neural basis of interference control is separable from that of relational complexity (see also Kmeicik et al., 2019; Watson & Chatterjee, 2012; Krawczyk et al., 2010). A developmental study by Whitaker, Vendetti, Wendelken, and Bunge (2018) found that developmental improvements in performance on a verbal analogical reasoning were predicted (after controlling for age) by activation in the left inferior frontal cortex, an area associated with controlled semantic retrieval. Brain areas responsible for forms of interference control thus appear to play central roles in analogical reasoning.

Working Memory: DLPFC

Both behavioral experiments (e.g., Waltz et al., 2000) and computational modeling (Hummel & Holyoak, 1997, 2003; Halford, Wilson, & Phillips, 1998) indicate that relational reasoning depends on working memory resources, particularly to maintain active representations of relations that provide the immediate inputs to integration processes. As noted earlier, the neural substrate of working memory is distributed across multiple brain regions, with the DLPFC playing a particularly central role (D'Esposito & Postle, 2015). Neuroimaging studies (e.g., Duncan et al., 2000) have found activation in the DLPFC during complex spatial and verbal reasoning tasks. Indeed, the DLPFC has been involved in maintenance and manipulation of task-relevant information across several domains, including deductive reasoning (Monti & Osherson, 2012; Prado, Chadha, & Booth, 2011), algebraic and arithmetic cognition (Monti, Parsons, & Osherson, 2012; Arsalidou & Taylor, 2011; Menon, Mackenzie, Rivera, & Reiss, 2002; Zago et al., 2001), and analogical reasoning (Hobeika et al., 2016; Cho et al., 2010; Green et al., 2006; Bunge et al., 2005), with the magnitude of the activation being associated with the degree of relational complexity of a task (e.g., Coetzee & Monti, 2018; Feng, Schwemmer, Gershman, & Cohen, 2014; Cho et al., 2010; Kroger et al., 2002; Christoff et al., 2001). In the context of relational integration, this region has most often been characterized as playing a domain-general role (Bunge et al., 2005), most likely tied to working memory (Krawczyk, 2012). The working-memory characterization of DLPFC is also consistent with neuropsychological evidence showing that damage to this region, in the left hemisphere, impairs inference making in proportion to the working memory impairment while sparing meta-deductive judgments about problem difficulty, suggesting some retained appreciation for the deductive relationship tying premises to a conclusion (Reverberi, Shallice, D'Agostini, Skrap, & Bonatti, 2009).

In addition, it is well established that the DLPFC is involved in a large number of processes in addition to working memory, including response conflict, presence of distracting information, novelty, selective attention, and perceptual difficulty (Nee & Jonides, 2009; Nee et al., 2007; Duncan & Owen, 2000). In particular, prior work in the context of analogical reasoning (Valle, Bajo, & Gómez-Ariza, 2020; Cho et al., 2010; Bunge et al., 2005) suggests that the DLPFC could also be involved in interference resolution during response selection (Nee et al., 2007). Bunge et al. (2005) found the right DLPFC to be insensitive to whether participants were evaluating quadruplets of verbal items for analogical validity versus semantic association, or to the degree of association strength tying the items together, and was instead particularly sensitive to the need to avoid accepting invalid responses. The authors interpreted this finding as evidence supporting a role for the DLPFC in response selection.

In a study described earlier, Cho et al. (2010) explored the role of interference in a task in which participants had to verify whether two pairs of simultaneously presented human cartoon characters formed a valid analogy along a subset of four possible visual dimensions. The bilateral DLPFC exhibited the expected positive association with relational complexity but was also recruited (uniquely so in a right-lateralized area) by high-interference problems (i.e., problems in which participants had to evaluate the analogy along a subset of the four dimensions while actively ignoring a different dimension).

Finally, in a tDCS experiment, Valle et al. (2020) leveraged the retrieval-induced forgetting phenomenon (i.e., the finding that, when certain items in a list of words are practiced, nonpracticed related words become inhibited, leading to greater rates of "forgetting" as compared to nonpracticed unrelated words; Anderson, Bjork, & Bjork, 1994) to demonstrate a causal role of the right DLPFC in selection and retrieval of information in the context of analogical reasoning. Specifically, participants first study a list of category/word pairs (e.g., DE-Detective, DE-Debate, FA-Fantasy); then, after an unrelated filler task, they practiced retrieval of a subset of the studied category/word pairs using a cued recall task. Finally, after an additional unrelated distractor task, participants were asked to solve analogies (i.e., generate the fourth term of an A:B::C:? analogy). Consistent with the retrieval-induced forgetting effect, solutions that corresponded to items from the study list that were not practiced but were related to practiced items were generated less frequently than solutions corresponding to items that were not practiced but were not related to practiced items as well as solutions corresponding to novel items. However, participants who received cathodal tDCS (typically considered to be inhibitory) to the right DLPFC during the retrieval practice (as opposed to only sham) did not exhibit this effect. Rather, they generated solutions corresponding to nonpracticed items with similar frequency regardless of whether or not they were related to practiced items. In other words, cathodal neuromodulation of the right DLPFC blocked retrieval-induced forgetting, demonstrating a causal role of this region in the inhibitory mechanisms controlling interference from irrelevant information. Interestingly, however, tDCS did not affect analogical performance directly, confirming the hypothesis that the DLPFC contributes indirectly to analogical reasoning (in part through interference control) but does not contribute to relational mapping itself.

Relation Representation: Parietal Cortex

Relational integration requires representations of individual relations, as well as of the entities between which relations hold, to be generated and maintained in working memory. The representation of individual relations is clearly a prerequisite for relational integration. Indeed, eye-tracking studies of participants solving A:B::C:D analogies have found that a high frequency of saccades between the A and B terms early in processing signals the preferred strategy of mature reasoners and is a strong predictor of success in solving analogies (Vendetti, Starr, Johnson, Modavi, & Bunge, 2017; Thibaut & French, 2016). Establishing a good representation of the A:B relation in working memory is a key initial step in analogical reasoning.

It is generally accepted that the core areas responsible for working memory are located within the lateral frontal cortex (for a review, see D'Esposito & Postle, 2015). A major theory holds that the VLPFC supports basic maintenance of information in any domain, whereas the DLPFC supports manipulation of this information, as by monitoring, updating, or reordering. Notably, other evidence indicates that the PPC, including both the superior parietal lobe (BA 7) and the inferior parietal lobe (BA 40), is also involved in the maintenance and manipulation of spatial as well as phonological representations.

The neural representations of individual semantic relations appear to be broadly distributed across multiple brain regions, including temporal areas associated with semantic memory (Wang, Hsieh, & Bunge, this issue). In the context of an explicit analogical reasoning task, the parietal cortex appears to play a particularly important role. The primary functions of the parietal cortex center on the representation and manipulation of space, as this area serves as the hub of the dorsal "where" system of vision. An intriguing hypothesis is that, by virtue of its rich representational capacity, the parietal cortex provides a core substrate for spatial relations that serve to organize items in working memory (Wendelken et al., 2008). Many basic relations involve orderings and groupings, which lend themselves to quasi-spatial representations. Wendelken et al. found that a working memory task involving a set of items structured by a grouping or ordering selectively activated the PPC. Parietal activation is typically prominent in transitive reasoning tasks, which require integration of comparative relations (e.g., Tom is taller than Bill, Harry is taller than Tom) to infer a further relation (Harry is taller than Tom). Furthermore, the pattern of parietal involvement (in conjunction with anterior frontal activation) is similar for transitive inferences based on physical dimensions such as height, more abstract dimensions such as monetary expensiveness, and even nonsensical dimensions (introduced as orderings) such as "vilchiness" (Alfred, Connolly, Cetron, & Kraemer, 2020; for a review of parietal involvement in reasoning, see Wendelken, 2015).

Such findings support the general view that many abstract relations are derived (perhaps ultimately by analogy) from spatial relations and, furthermore, continue to depend on some of the same neural machinery. Comparative relations provide particularly clear examples. Their acquisition can be modeled by a quantitative comparison of features of the linked terms (e.g., the fact that a dog is larger than a squirrel, or smarter than a slug, can be captured by a model that, in effect, computes the differences between features of the objects being compared; Chen, Lu, & Holyoak, 2014, 2017; Lu, Chen, & Holyoak, 2012; Doumas, Hummel, & Sandhofer, 2008).

More recently, computational models of relation learning have been extended to learn distributed representations of abstract semantic relations such as "synonym" (e.g., *big*:*large*), "contrary" (*accept*:*reject*), and "cause–effect" (*accident*:*damage*), by applying supervised learning techniques to feature vectors derived by machine learning algorithms operating on text corpora (Lu et al., 2019). Lu et al.'s Bayesian Analogy with Relational Transformations model has been used to generate model-based predictions of patterns of neural similarity between the responses to different pairs of related words as they are processed in the context of solving *A*:*B*::*C*:*D* analogy problems (Chiang et al., this issue). In their study, each problem was presented sequentially, with the *A*:*B* pair appearing alone for 2 sec before presentation of the *C*:*D* pair. During the *A*:*B* phase, a representational similarity analysis (Kriegeskorte, Mur, & Bandettini, 2008) performed at the level of individual word pairs found that the Bayesian Analogy with Relational Transformations model reliably predicted the similarity pattern of voxels in various brain areas including the superior parietal lobe. During the *C*:*D* phase (when the relational comparison could be performed), the model predicted similarity patterns for voxels distributed over the anterior lateral pFC as well as the parietal cortex.

Such evidence for parietal involvement in the generation and manipulation of active representations of abstract relations supports a general principle: "Spatial thinking is the foundation of abstract thought" (Tversky, 2019, p. 72). In at least a metaphorical sense, to say that two entities are related in a specific way is to "place" each item in some "position" relative to the other such that they can be "compared." Emerging neural evidence suggests that, in the human brain, this description may in fact prove to be stronger than a mere metaphor.

NETWORK DYNAMICS AND RELATIONAL PROCESSING

Role of the Frontoparietal Control Network

As we have emphasized, the frontoparietal control network operates as a general system to support relational reasoning (e.g., Wendelken et al., 2016; Watson & Chatterjee, 2012). In keeping with our earlier review of complexity effects, the RLPFC generally comes into play for reasoning tasks at higher levels of complexity (Monti et al., 2007), whereas other portions of the frontoparietal network (varying across types of reasoning tasks and stimulus modalities) are activated even during performance of less complex reasoning tasks (Wertheim & Ragni, 2018; Prado et al., 2011).

Cocchi et al. (2014) performed an fMRI study that examined patterns of functional connectivity during performance on the Wason selection task (Wason, 1966), which involves assessing whether an option (presented as a card) needs to be examined to test an arbitrary conditional rule. A task analysis was performed to classify the complexity of reasoning required by different options. For example, for the rule "If A then 7" (i.e., if a card shows "A" on the face side, it must show "7" on the reverse side), a card showing "A" (matched to the antecedent) would result in the lowest complexity, whereas a card showing "5" (mismatched to the consequent) would yield the highest complexity. (For both "A" and "5," the correct response is that the reverse side of the card must be examined.) A connectivity analysis revealed a significant increase in connectivity with card complexity in a large-scale functional brain network encompassing the RLPFC, DLPFC, lateral frontal cortex, ACC, parietal and occipital cortices, and anterior insular cortices. These areas correspond to the frontoparietal control network, which has been shown to transiently mediate goal-directed cognition through flexible coupling with other networks (Dixon et al., 2018; Cole et al., 2013; Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013), and a cingulo-opercular network, which is believed to be important for stable "set maintenance" over task-relevant periods (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008). Variations in task demands on relational processing thus appear to result in complexity-dependent modulations of large-scale networks.

Developmental evidence also supports the role of network dynamics in relational reasoning. Wendelken et al. (2016) examined connectivity within the lateral frontoparietal network in relation to performance on a variety of reasoning measures in a large sample of children and adolescents aged 6–18 years. In late childhood and early adolescence, developmental changes in reasoning ability were related to strength of connections within the frontoparietal network. For 9- to 11-year-olds, reasoning ability was most strongly related to connectivity between the left and right RLPFC, whereas for adolescents, the most important connections were between the left RLPFC and the inferior parietal lobe. Overall, these developmental changes in frontoparietal connectivity likely support increasing communication between prefrontal regions and specific parietal targets. The outcome of these changes is an adult system in which different parietal subregions communicate preferentially with different prefrontal subregions (see also Wendelken et al., 2017).

There is also evidence that frontoparietal connectivity patterns can be altered even in adulthood by intensive educational activities related to relational reasoning (for a review, see Bunge & Leib, 2020). For example, Mackey, Miller Singley, and Bunge (2013) examined patterns of connectivity at rest for young adults before and after preparing for the Law School Admissions Test. Compared to age- and IQ-matched controls, those who studied for the reasoning test for about 3 months showed an increase in the strength of frontoparietal connections as well as frontal–striatal connections. Correlations involving the left RLPFC showed particularly large increases over the study interval, particularly with posterior and medial parietal regions.

An important issue concerns how the various hubs of the frontoparietal control network, in conjunction with additional support networks, collaborate to support relational reasoning. The computational requirements include the encoding and maintenance of object representations and relation representations, coupled with systematic comparisons and transformations based on integration of multiple relations. Although the frontoparietal network plays a primary role in supporting these neurocognitive processes, other brain areas also contribute. Hammer et al. (2019) performed a large-scale fMRI study using pictorial analogy problems varying in relational complexity (the same materials used by Cho et al., 2010). They employed machine learning methods to identify multiple networks related to task performance. The study focused on individual differences in analogical reasoning, investigated using multivariate fMRI analyses. Individual analogy capability was positively correlated with activation level in a prefrontal executive network and a visuospatial network and was negatively correlated with activation in the default mode network. The findings from this study imply that individual differences in analogical reasoning depend on multiple executive and visuospatial brain regions and that the contributions of these regions are modulated by individuals' cognitive skills. Moreover, the brain regions associated with individual differences in analogical reasoning only partially overlap with those associated at the group level with relational complexity.

Solving analogies that are more semantic in nature is dependent on brain regions that support the representation of word meanings. The general picture of semantic representation at the level of individual words organized into text is that such representations are highly distributed over the cortex, with major involvement of sensorimotor areas that code features of concrete nouns and action verbs (e.g., Pereira et al., 2018; Huth, de Heer, Griffiths, Theunissen, & Gallant, 2016). More abstract concepts, particularly when systematically organized into meaningful text that conveys relational information, tend to selectively activate a network that includes left-lateralized medial and lateral temporal lobes, as well as subregions of the parietal and frontal cortices, collectively termed the "conceptual hub" (Binder, 2016). This network plays an important role in representing semantic relations between words. Wang et al. (this issue) showed college students pairs of words, with the task of deciding whether or not the words in each pair were related in some way (but without any requirement to make higher-order comparisons of relations across word pairs). When a target pair was immediately preceded by a pair instantiating the same relation (e.g., the target *dog–tail* preceded by the prime *book–page*, where both pairs instantiate the relation *whole–part*), RT to the target pair was facilitated relative to an unprimed pair. In addition, for primed pairs only, a representational similarity analysis (Kriegeskorte et al., 2008) performed at the level of relations (not individual word pairs) yielded reliable patterns of neural similarity in regions involved in the conceptual hub. These findings, considered together with those of Chiang et al. (this issue), suggest that the neural representations of semantic relations are highly sensitive to task requirements. It seems that relatively undirected processing of individual relations depends primarily on the conceptual hub (Wang et al., this issue), whereas an explicit analogical reasoning task also engages the frontoparietal network (Chiang et al., this issue).

Temporal Dynamics Underlying Relational Reasoning

Representations of word meanings are not only distributed in nature but also subject to systematic individual differences (Alfred, Hillis, & Kraemer, this issue). Given that representations of semantic relations also appear to be distributed (Chiang et al., this issue), a difficult computational issue concerns how combinations of semantic representations are organized into structures in which individual objects play specific roles in relations. This issue has been characterized as the problem of how role bindings for relations are dynamically formed and maintained in working memory (Doumas & Hummel, 2012). One computational approach, inspired by neural evidence (for a review, see Ulhaas et al., 2009), is that bindings are coded in the brain by temporal dynamics based on synchronization of neural activity. Computational models based on temporal synchrony (or asynchrony) have been applied to various forms of relational reasoning (Shastri & Ajjanagadde, 1993), including analogy (Hummel & Holyoak, 1997, 2003) and relation learning (Doumas et al., 2008). Wendelken et al. (2008) proposed a general model of relation coding by synchrony in which frontal neurons in the VLPFC and DLPFC serve to maintain activity of posterior neurons that respectively code items (in the inferotemporal cortex) or relations (in the parietal cortex). Knowlton, Morrison, Hummel, and Holyoak (2012) outlined a similar hypothesis as an account of the neural basis for analogical reasoning. Their proposal, which includes the RLPFC as a hub for relational integration, assumes that long-distance communication between pFC and posterior brain regions is enabled by coherent oscillatory activity in multiple frequency bands. Although direct evidence for the function of oscillatory neural activity in reasoning is lacking at present, this general hypothesis isconsistent with evidence that focal lesions in pFC (especially the DLPFC) reduce temporal modulation of alpha-band (10–12 Hz) synchrony within the frontoparietal control network and that these oscillatory changes are accompanied by reduced cognitive flexibility (Sadaghiani et al., 2019).

OPEN ISSUES FOR FUTURE RESEARCH

Although much has been learned over the past quarter century about the neural basis for relational integration, open issues abound. Much remains to be learned about how computational mechanisms capable of human-like reasoning are implemented in the brain. It is likely that further advances in noninvasive neuroimaging techniques capable of high temporal as well as spatial resolution will play a critical role in providing empirical evidence to guide theoretical developments. Techniques such as repetitive TMS (e.g., Boroojerdi et al., 2001) and tDCS (Valle et al., 2020; Green et al., 2017) can be used to test the causal roles of brain regions hypothesized to contribute to relational processing.

Almost all the neural investigations of relational reasoning have used relatively impoverished stimuli, such as analogy problems in the *A*:*B*::*C*:*D* format and content-free deductive reasoning problems. Such problems have methodological advantages for manipulating complexity and in controlling stimulus presentation and the timing of particular cognitive processes. However, a full understanding of human relational reasoning will require investigation of more complex and naturalistic analogies based on stories and other meaningful inputs (e.g., Gick & Holyoak, 1980, 1983). It may be possible to adapt techniques for analyzing semantic processing during text comprehension (e.g., Huth et al., 2016) for this purpose. In addition to further investigating the process of relation comparison, it will be important to explore the neural basis for analogical reminding and relation-based memory retrieval.

As we have emphasized, the system for relational integration described here can be viewed as a domain-general system heavily dependent on working memory. It is clear, however, that important forms of relational processing involve different, more domain-specific brain systems. In particular, the domain-general system has been dissociated from relational processing based on language (Monti & Osherson, 2012; Monti et al., 2007, 2009), algebra (Monti et al., 2012), and music (Chiang et al., 2018).

In addition to a variety of domain-specific forms of relational processing, additional mechanisms play important roles. In particular, a general basis for acquiring expertise in any domain involves a shift from processes heavily dependent on working memory to processes that rely on knowledge coded into long-term memory (for a review, see Ericsson, 2014). After acquiring rich semantic knowledge, adult humans typically can accomplish important feats involving relational processing, such as comprehension of relatively simple metaphors, using processes that impose lesser demands on working memory (Stamenković, Ichien, & Holyoak, 2019; Holyoak & Stamenković, 2018). An especially important theoretical issue is to clarify how the domain-general relational reasoning system is linked with the manipulation of relations within the language system (Monti, 2017).

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Note

1. The process of comparing the two relations in an *A*:*B*::*C*:*D* analogy problem is often referred to as “mapping.” However, this term is more standardly used to refer to the cognitive processes involved in finding correspondences between the elements in two analogs (or to refer to the resulting set of correspondences; e.g., Gick & Holyoak, 1980). In an *A*:*B*::*C*:*D* analogy, the problem format provides the mapping directly (*A* ➔ *C*, *B* ➔ *D*); hence, the reasoner does not need to perform any further mental operations to discover the correspondences. Moreover, this trivial mapping of elements is unrelated to the validity of the analogy, which simply depends on the similarity of the two relations. Hence, we refer to the solution process for *A*:*B*::*C*:*D* analogies as “relational comparison.”

REFERENCES

Acuna, B. D., Eliassen, J. C., Donoghue, J. P., & Sanes, J. N. (2002). Frontal and parietal lobe activation during transitive inference in humans. *Cerebral Cortex*, *12*, 1312–1321.

Aichelburg, C., Urbanski, M., de Schotten, M. T., Humbert, F., Levy, R., & Volle, E. (2016). Morphometry of left frontal and temporal poles predicts analogical reasoning abilities. *Cerebral Cortex*, *26*, 915–932.

Alfred, K. L., Connolly, A. C., Cetron, J. S., & Kraemer, D. J. M. (2020). Mental models use common neural spatial structure for spatial and abstract content. *Communications Biology*, *3*, 17.

Alfred, K. L., Hillis, M. E., & Kraemer, D. J. M. (this issue). Individual differences in the neural organization of relational networks of semantic concepts.

Anderson, M. C., Bjork, R. A., & Bjork, E. L. (1994). Remembering can cause forgetting: Retrieval dynamics in long-term-memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *20*, 1063–1087.

Andrews, G., Halford, G. S., Chapell, M., Maujean, A., & Shum, D. H. K. (2014). Planning following stroke: A relational complexity approach using the Tower of London. *Frontiers in Human Neuroscience*, *8*, 1032.

Andrews, G., Halford, G. S., Shum, D. H. K., Maujean, A., Chappell, M., & Birney, D. (2013). Relational processing following stroke. *Brain and Cognition*, *81*, 44–51.

Andrews, G., & Vann, D. M. (2019). Solving distant analogies reduces belief-biased responding in transitive inference. *Journal of Cognitive Psychology*, *31*, 760–767.

Aron, A. R., Fletcher, P. C., Bullmore, E. T., Sahakian, B. J., & Robbins, T. W. (2003). Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nature Neuroscience*, *6*, 115–116.

Arsalidou, M., & Taylor, M. J. (2011). Is 2 + 2 = 4? Meta-analyses of brain areas needed for numbers and calculations. *Neuroimage*, *54*, 2382–2393.

Badre, D., Poldrack, R. A., Paré-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron*, *47*, 907–918.

Binder, J. R. (2016). In defense of abstract conceptual representations. *Psychonomic Bulletin & Review*, *23*, 1096–1108.

Boroojerdi, B., Phipps, M., Kopylev, L., Wharton, C. M., Cohen, L. G., & Grafman, J. (2001). Enhancing analogic reasoning with rTMS over the left prefrontal cortex. *Neurology*, *56*, 526–528.

Bunge, S. A., Helskog, E. H., & Wendelken, C. (2009). Left, but not right, rostrolateral prefrontal cortex meets a stringent test of the relational integration hypothesis. *Neuroimage*, *46*, 338–342.

Bunge, S. A., & Leib, E. R. (2020). How does education hone reasoning ability? *Current Directions in Psychological Science*, *29*, 167–173.

Bunge, S. A., Wendelken, C., Badre, D., & Wagner, A. D. (2005). Analogical reasoning and prefrontal cortex: Evidence for separable retrieval and integration mechanisms. *Cerebral Cortex*, *15*, 239–249.

Carpenter, P. A., Just, M. A., & Shell, P. (1990). What one intelligence test measures: A theoretical account of the processing in the Raven Progressive Matrices Test. *Psychological Review*, *97*, 404–431.

Chen, D., Lu, H., & Holyoak, K. J. (2014). The discovery and comparison of symbolic magnitudes. *Cognitive Psychology*, *71*, 27–54.

Chen, D., Lu, H., & Holyoak, K. J. (2017). Generative inferences based on learned relations. *Cognitive Science*, *41*(Suppl. 5), 1062–1092.

Chiang, J. N., Peng, Y., Lu, H., Holyoak, K. J., & Monti, M. M. (this issue). Distributed code for semantic relations predicts neural similarity during analogical reasoning.

Chiang, J. N., Rosenberg, M. H., Bufford, C. A., Stephens, D., Lysy, A., & Monti, M. M. (2018). The language of music: Common neural codes for structured sequences in music and natural language. *Brain & Language*, *185*, 30–37.

Cho, S., Holyoak, K. J., & Cannon, T. D. (2007). Analogical reasoning in working memory: Resources shared among relational integration, interference resolution, and maintenance. *Memory & Cognition*, *35*, 1445–1455.

Cho, S., Moody, T. D., Fernandino, L., Mumford, J. A., Poldrack, R. A., Cannon, T. D., et al. (2010). Common and dissociable prefrontal loci associated with component mechanisms of analogical reasoning. *Cerebral Cortex*, *20*, 524–533.

Christoff, K., & Gabrieli, J. D. E. (2000). The frontopolar cortex and human cognition: Evidence for a rostrocaudal hierarchical organization within the human prefrontal cortex. *Psychobiology*, *28*, 168–186.

Christoff, K., Keramatian, K., Gordon, A. M., Smith, R., & Mädler, B. (2009). Prefrontal organization of cognitive control according to levels of abstraction. *Brain Research*, *1286*, 94–105.

Christoff, K., Prabhakaran, V., Dorfman, J., Zhao, Z., Kroger, J. K., Holyoak, K. J., et al. (2001). Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *Neuroimage*, *14*, 1136–1149.

Cocchi, L., Halford, G. S., Zalesky, A., Harding, I. H., Ramm, B. J., Cutmore, T., et al. (2014). Complexity in relational processing predicts changes in functional brain network dynamics. *Cerebral Cortex*, *24*, 2283–2296.

Coetzee, J. P., & Monti, M. M. (2018). At the core of reasoning: Dissociating deductive and non-deductive load. *Human Brain Mapping*, *39*, 1850–1861.

Cole, M. W., Reynolds, J. R., Power, J. D., Repovs, G., Anticevic, A., & Braver, T. S. (2013). Multi-task connectivity reveals flexible hubs for adaptive task control. *Nature Neuroscience*, *16*, 1348–1355.

De Neys, W., & Goel, V. (2011). Heuristics and biases in the brain: Dual neural pathways for decision making. In O. Vartanian & D. R. Mandel (Eds.), *Neuroscience of decision making* (pp. 125–142). New York: Psychology Press.

De Pisapia, N., Slomski, J. A., & Braver, T. S. (2007). Functional specializations in lateral prefrontal cortex associated with the integration and segregation of information in working memory. *Cerebral Cortex*, *17*, 993–1006.

D'Esposito, M., & Postle, B. R. (2015). The cognitive neuroscience of working memory. *Annual Review of Psychology*, *66*, 115–142.

D'Esposito, M., Postle, B. R., Jonides, J., & Smith, E. E. (1999). The neural substrate and temporal dynamics of interference effects in working memory as revealed by event-related functional MRI. *Proceedings of the National Academy of Sciences, U.S.A.*, *96*, 7514–7519.

Dixon, M. L., De La Vega, A., Mills, C., Andrews-Hanna, J., Spreng, R. N., Cole, M. W., et al. (2018). Heterogeneity within the frontoparietal control network and its relationship to the default and dorsal attention networks. *Proceedings of the National Academy of Sciences, U.S.A.*, *115*, E1598–E1607.

Dosenbach, N. U. F., Fair, D. A., Cohen, A. L., Schlaggar, B. L., & Petersen, S. E. (2008). A dual-networks architecture of top–down control. *Trends in Cognitive Sciences*, *12*, 99–105.

Doumas, L. A. A., & Hummel, J. E. (2012). Computational models of higher cognition. In K. J. Holyoak & R. G. Morrison (Eds.), *The Oxford handbook of thinking and reasoning* (pp. 52–66). New York: Oxford University Press.

Doumas, L. A. A., Hummel, J. E., & Sandhofer, C. M. (2008). A theory of the discovery and predication of relational concepts. *Psychological Review*, *115*, 1–43.

Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neurosciences*, *23*, 475–483.

Duncan, J., Seitz, R. J., Kolodny, J., Bor, D., Herzog, H., Ahmed, A., et al. (2000). A neural basis for general intelligence. *Science*, *289*, 457–460.

Ericsson, K. A. (2014). Expertise. *Current Biology*, *24*, R508–R510.

Feng, S. F., Schwemmer, M., Gershman, S. J., & Cohen, J. D. (2014). Multitasking versus multiplexing: Toward a normative account of limitations in the simultaneous execution of control-demanding behaviors. *Cognitive, Affective & Behavioral Neuroscience*, *14*, 129–146.

Gentner, D. (2010). Bootstrapping the mind: Analogical processes and symbol systems. *Cognitive Science*, *34*, 752–775.

Gick, M. L., & Holyoak, K. J. (1980). Analogical problem solving. *Cognitive Psychology*, *12*, 306–355.

Gick, M. L., & Holyoak, K. J. (1983). Schema induction and analogical transfer. *Cognitive Psychology*, *15*, 1–38.

Gilbert, S. J., Gonen-Yaacovi, G., Benoit, R. G., Volle, E., & Burgess, P. W. (2010). Distinct functional connectivity associated with lateral versus medial rostral prefrontal cortex: A meta-analysis. *Neuroimage*, *53*, 1359–1367.

Goel, V., & Dolan, R. J. (2003). Explaining modulation of reasoning by belief. *Cognition*, *87*, B11–B22.

Goldwater, M. B., & Schalk, L. (2016). Relational categories as a bridge between cognitive and educational research. *Psychological Bulletin*, *142*, 729–757.

Gray, M. E., & Holyoak, K. J. (2020). Individual differences in relational reasoning. *Memory & Cognition*, *48*, 96–110.

Green, A. E. (2016). Creativity, within reason: Semantic distance and dynamic state creativity in relational thinking and reasoning. *Current Directions in Psychological Science*, *25*, 28–35.

Green, A. E., Fugelsang, J. A., Kraemer, D. J. M., Shamosh, N. A., & Dunbar, K. N. (2006). Frontopolar cortex mediates abstract integration in analogy. *Brain Research*, *1096*, 125–137.

Green, A. E., Kraemer, D. J. M., Fugelsang, J. A., Gray, J. R., & Dunbar, K. N. (2010). Connecting long distance: Semantic distance in analogical reasoning modulates frontopolar cortex activity. *Cerebral Cortex*, *20*, 70–76.

Green, A. E., Kraemer, D. J. M., Fugelsang, J. A., Gray, J. R., & Dunbar, K. N. (2012). Neural correlates of creativity in analogical reasoning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*, 264–272.

Green, A. E., Spiegel, K. A., Giangrande, E. J., Weinberger, A. B., Gallagher, N. M., & Turkeltaub, P. E. (2017). Thinking cap plus thinking zap: tDCS of frontopolar cortex improves creative analogical reasoning and facilitates conscious augmentation of state creativity in verb generation. *Cerebral Cortex*, *27*, 2628–2639.

Halford, G. S. (1993). *Children's understanding: The development of mental models*. Hillsdale, NJ: Erlbaum.

Halford, G. S., & Wilson, W. H. (1980). A category theory approach to cognitive development. *Cognitive Psychology*, *12*, 356–411.

Halford, G. S., Wilson, W. H., & Phillips, S. (1998). Processing capacity defined by relational complexity: Implications for comparative, developmental and cognitive psychology. *Behavioral and Brain Sciences*, *21*, 803–831.

Halford, G. S., Wilson, W. H., & Phillips, S. (2010). Relational knowledge: The foundation of higher cognition. *Trends in Cognitive Sciences*, *14*, 497–505.

Hammer, R., Paul, E. J., Hillman, C. H., Kramer, A. F., Cohen, N. J., & Barbey, A. K. (2019). Individual differences in analogical reasoning revealed by multivariate task-based functional brain imaging. *Neuroimage*, *184*, 993–1004.

Hampshire, A., Chamberlain, S. R., Monti, M. M., Duncan, J., & Owen, A. M. (2010). The role of the right inferior frontal gyrus: Inhibition and attentional control. *Neuroimage*, *50*, 1313–1319.

Hobeika, L., Diard-Detoeuf, C., Garcin, B., Levy, R., & Volle, E. (2016). General and specialized brain correlates for analogical reasoning: A meta-analysis of functional imaging studies. *Human Brain Mapping*, *37*, 1953–1969.

Holyoak, K. J. (2012). Analogy and relational reasoning. In K. J. Holyoak & R. G. Morrison (Eds.), *The Oxford handbook of thinking and reasoning* (pp. 234–259). New York: Oxford University Press.

Holyoak, K. J., & Stamenković, D. (2018). Metaphor comprehension: A critical review of theories and evidence. *Psychological Bulletin*, *144*, 641–671.

Hummel, J. E., & Holyoak, K. J. (1997). Distributed representations of structure: A theory of analogical access and mapping. *Psychological Review*, *104*, 427–466.

Hummel, J. E., & Holyoak, K. J. (2003). A symbolic-connectionist theory of relational inference and generalization. *Psychological Review*, *110*, 220–264.

Huth, A. G., de Heer, W. A., Griffiths, T. L., Theunissen, F. E., & Gallant, J. L. (2016). Natural speech reveals semantic maps that tile human cerebral cortex. *Nature*, *532*, 453–458.

Jacobs, B., Driscoll, L., & Schall, M. (1997). Life-span dendritic and spine changes in areas 10 and 18 of human cortex: A quantitative Golgi study. *Journal of Comparative Neurology*, *386*, 661–680.

Jacobs, B., Schall, M., Prather, M., Kapler, E., Driscoll, L., Baca, S., et al. (2001). Regional dendritic and spine variation in human cerebral cortex: A quantitative Golgi study. *Cerebral Cortex*, *11*, 558–571.

Jonides, J., & Nee, D. E. (2006). Brain mechanisms of proactive interference in working memory. *Neuroscience*, *139*, 181–193.

Karmiloff-Smith, A. (1992). *Beyond modularity: A developmental perspective on cognitive science*. Cambridge, MA: MIT Press.

Kmeicik, M. J., Brisson, R. J., & Morrison, R. G. (2019). The time course of semantic and relational processing during verbal analogical reasoning. *Brain and Cognition*, *129*, 25–34.

Kmiecik, M. J., & Krawczyk, D. C. (this issue). Reasoning with complex relational structures: The case of the match-to-sample task.

Knowlton, B. J., Morrison, R. G., Hummel, J. E., & Holyoak, K. J. (2012). A neurocomputational system for relational reasoning. *Trends in Cognitive Sciences*, *16*, 373–381.

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

Krawczyk, D. C. (2012). The cognition and neuroscience of relational reasoning. *Brain Research*, *1428*, 13–23.

Krawczyk, D. C. (2017). *Reasoning: The neuroscience of how we think*. San Diego, CA: Elsevier.

Krawczyk, D. C., McClelland, M. M., Donovan, C. M., Tillman, G. D., & Maguire, M. J. (2010). An fMRI investigation of cognitive stages in reasoning by analogy. *Brain Research*, *1342*, 63–73.

Krawczyk, D. C., Morrison, R. G., Viskontas, I., Holyoak, K. J., Chow, T. W., Mendez, M. F., et al. (2008). Distraction during relational reasoning: The role of prefrontal cortex in interference control. *Neuropsychologia*, *46*, 2020–2032.

Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational similarity analysis—Connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience*, *2*, 4.

Kroger, J. K., Sabb, F. W., Fales, C. L., Bookheimer, S. Y., Cohen, M. S., & Holyoak, K. J. (2002). Recruitment of anterior dorsolateral prefrontal cortex in human reasoning: A parametric study of relational complexity. *Cerebral Cortex*, *12*, 477–485.

Lu, H., Chen, D., & Holyoak, K. J. (2012). Bayesian analogy with relational transformations. *Psychological Review*, *119*, 617–648.

Lu, H., Wu, Y. N., & Holyoak, K. J. (2019). Emergence of analogy from relation learning. *Proceedings of the National Academy of Sciences, U.S.A.*, *116*, 4176–4181.

Mackey, A. P., Miller Singley, A. T., & Bunge, S. A. (2013). Intensive reasoning training alters patterns of brain connectivity at rest. *Journal of Neuroscience*, *33*, 4796–4803.

Menon, V., Mackenzie, K., Rivera, S. M., & Reiss, A. L. (2002). Prefrontal cortex involvement in processing incorrect arithmetic equations: Evidence from event-related fMRI. *Human Brain Mapping*, *16*, 119–130.

Monti, M. M. (2017). The role of language in structure-dependent cognition. In M. Moody (Ed.), *Neural mechanisms of language* (pp. 81–101). New York: Springer.

Monti, M. M., & Osherson, D. N. (2012). Logic, language and the brain. *Brain Research*, *1428*, 33–42.

Monti, M. M., Osherson, D. N., Martinez, M. J., & Parsons, L. M. (2007). Functional neuroanatomy of deductive inference: A language-independent distributed network. *Neuroimage*, *37*, 1005–1016.

Monti, M. M., Parsons, L. M., & Osherson, D. N. (2009). The boundaries of language and thought in deductive inference. *Proceedings of the National Academy of Sciences, U.S.A.*, *106*, 12554–12559.

Monti, M. M., Parsons, L. M., & Osherson, D. N. (2012). Thought beyond language: Neural dissociation of algebra and natural language. *Psychological Science*, *23*, 914–922.

Morrison, R. G., Krawczyk, D. C., Holyoak, K. J., Hummel, J. E., Chow, T. W., Miller, B. L., et al. (2004). A neurocomputational model of analogical reasoning and its breakdown in frontotemporal lobar degeneration. *Journal of Cognitive Neuroscience*, *16*, 260–271.

Nee, D. E., & Jonides, J. (2009). Common and distinct neural correlates of perceptual and memorial selection. *Neuroimage*, *45*, 963–975.

Nee, D. E., Wager, T. D., & Jonides, J. (2007). Interference resolution: Insights from a meta-analysis of neuroimaging tasks. *Cognitive, Affective & Behavioral Neuroscience*, *7*, 1–17.

Nitsche, M. A., Cohen, L. G., Wassermann, E. M., Priori, A., Lang, N., Antal, A., et al. (2008). Transcranial direct current stimulation: State of the art 2008. *Brain Stimulation*, *1*, 206–223.

Novick, J. M., Kan, I. P., Trueswell, J. C., & Thompson-Schill, S. L. (2009). A case for conflict across multiple domains: Memory and language impairments following damage to ventrolateral prefrontal cortex. *Cognitive Neuropsychology*, *26*, 527–567.

Penn, D. C., Holyoak, K. J., & Povinelli, D. J. (2008). Darwin's mistake: Explaining the discontinuity between human and nonhuman minds. *Behavioral and Brain Sciences*, *31*, 109–130.

Pereira, F., Lou, B., Pritchett, B., Ritter, S., Gershman, S. J., Kanwisher, N., et al. (2018). Toward a universal decoder of linguistic meaning from brain activation. *Nature Communications*, *9*, 963.

Prabhakaran, V., Narayanan, K., Zhao, Z., & Gabrieli, J. D. E. (2000). Integration of diverse information in working memory within the frontal lobe. *Nature Neuroscience*, *3*, 85–90.

Prabhakaran, V., Smith, J. A. L., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1997). Neural substrates of fluid reasoning: An fMRI study of neocortical activation during performance of the Raven's Progressive Matrices test. *Cognitive Psychology*, *33*, 43–63.

Prado, J., Chadha, A., & Booth, J. R. (2011). The brain network for deductive reasoning: A quantitative meta-analysis of 28 neuroimaging studies. *Journal of Cognitive Neuroscience*, *23*, 3483–3497.

Ramnani, N., & Owen, A. M. (2004). Anterior prefrontal cortex: Insights into function from anatomy and neuroimaging. *Nature Reviews Neuroscience*, *5*, 184–194.

Ranganath, C., Johnson, M. K., & D'Esposito, M. (2000). Left anterior prefrontal activation increases with demands to recall specific perceptual information. *Journal of Neuroscience*, *20*, RC108.

Raven, J. C. (1938). *Progressive matrices: A perceptual test of intelligence, 1938, individual form*. London: H. K. Lewis.

Reverberi, C., Shallice, T., D'Agostini, S., Skrap, M., & Bonatti, L. L. (2009). Cortical bases of elementary deductive reasoning: Inference, memory, and metadeduction. *Neuropsychologia*, *47*, 1107–1116.

Richland, L. E., Morrison, R. G., & Holyoak, K. J. (2006). Children's development of analogical reasoning: Insights from scene analogy problems. *Journal of Experimental Child Psychology*, *94*, 249–273.

Robin, N., & Holyoak, K. J. (1995). Relational complexity and the functions of prefrontal cortex. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 987–997). Cambridge, MA: MIT Press.

Sadaghiani, S., Dombert, P. L., Løvstad, M., Funderud, I., Meling, T. R., Endestad, T., et al. (2019). Lesions to the fronto-parietal network impact alpha-band phase synchrony and cognitive control. *Cerebral Cortex*, *29*, 4143–4153.

Samrani, G., Bäckman, L., & Persson, J. (2019). Interference control in working memory is associated with ventrolateral prefrontal cortex volume. *Journal of Cognitive Neuroscience*, *31*, 1491–1505.

Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K., & Van Hoesen, G. W. (2001). Prefrontal cortex in humans and apes: A comparative study of area 10. *American Journal of Physical Anthropology*, *114*, 224–241.

Shastri, L., & Ajjanagadde, V. (1993). From simple associations to systematic reasoning: A connectionist representation of rules, variables and dynamic bindings using temporal synchrony. *Behavioral and Brain Sciences*, *16*, 417–494.

Simms, N. K., & Richland, L. E. (2019). Generating relations elicits a relational mindset in children. *Cognitive Science*, *43*, e12795.

Snow, R. E., Kyllonen, P. C., & Marshalek, B. (1984). The topography of ability and learning correlations. In R. J. Sternberg (Ed.), *Advances in the psychology of human intelligence* (pp. 47–103). Hillsdale, NJ: Erlbaum.

Spreng, R. N., Sepulcre, J., Turner, G. R., Stevens, W. D., & Schacter, D. L. (2013). Intrinsic architecture underlying the relations among the default, dorsal attention, and frontoparietal control networks of the human brain. *Journal of Cognitive Neuroscience*, *25*, 74–86.

Stamenković, D., Ichien, N., & Holyoak, K. J. (2019). Metaphor comprehension: An individual-differences approach. *Journal of Memory and Language*, *105*, 108–118.

Thibaut, J.-P., & French, R. M. (2016). Analogical reasoning, control and executive functions: A developmental investigation with eye-tracking. *Cognitive Development*, *38*, 10–26.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: A reevaluation. *Proceedings of the National Academy of Sciences, U.S.A.*, *94*, 14792–14797.

Todd, J.-A. M., Andrews, G., & Conlon, E. G. (2019). Relational thinking in later adulthood. *Psychology and Aging*, *34*, 486–501.

Tohill, J. M., & Holyoak, K. J. (2000). The impact of anxiety on analogical reasoning. *Thinking & Reasoning*, *6*, 27–40.

Travis, K., Ford, K., & Jacobs, B. (2005). Regional dendritic variation in neonatal human cortex: A quantitative Golgi study. *Developmental Neuroscience*, *27*, 277–287.

Tversky, B. G. (2019). *Mind in motion: How action shapes thought*. New York: Basic Books.

Ulhaas, P. J., Pipa, G., Lima, B., Melloni, L., Neuenschwander, S., Nikolić, D., et al. (2009). Neural synchrony in cortical networks: History, concept and current status. *Frontiers in Integrative Neuroscience*, *3*, 17.

Urbanski, M., Bréchemier, M.-L., Garcin, B., Bendetowicz, D., de Schotten, M. T., Foulon, C., et al. (2016). Reasoning by analogy requires the left frontal pole: Lesion-deficit mapping and clinical implications. *Brain*, *139*, 1783–1799.

Valle, T. M., Bajo, M. T., & Gómez-Ariza, C. J. (2020). Cathodal transcranial direct current stimulation over the right dorsolateral prefrontal cortex cancels out the cost of selective retrieval on subsequent analogical reasoning. *Neuropsychologica*, *141*, 107431.

Vartanian, O. (2012). Dissociable neural systems for analogy and metaphor: Implications for the neuroscience of creativity. *British Journal of Psychology*, *103*, 302–316.

Vendetti, M. S., Starr, A., Johnson, E. L., Modavi, K., & Bunge, S. A. (2017). Eye movements reveal optimal strategies for analogical reasoning. *Frontiers in Psychology*, *8*, 932.

Vendetti, M. S., Wu, A., & Holyoak, K. J. (2014). Far out thinking: Generating solutions to distant analogies promotes relational thinking. *Psychological Science*, *25*, 928–933.

Viskontas, I. V., Holyoak, K. J., & Knowlton, B. J. (2005). Relational integration in older adults. *Thinking & Reasoning*, *11*, 390–410.

Viskontas, I. V., Morrison, R. G., Holyoak, K. J., Hummel, J. E., & Knowlton, B. J. (2004). Relational integration, inhibition and analogical reasoning in older adults. *Psychology and Aging*, *19*, 581–591.

Volle, E., Gilbert, S. J., Benoit, R. G., & Burgess, P. W. (2010). Specialization of the rostral prefrontal cortex for distinct analogy processes. *Cerebral Cortex*, *20*, 2647–2659.

Waltz, J. A., Knowlton, B. J., Holyoak, K. J., Boone, K. B., Back-Madruga, C., McPherson, S., et al. (2004). Relational integration and executive function in Alzheimer's disease. *Neuropsychology*, *18*, 296–305.

Waltz, J. A., Knowlton, B. J., Holyoak, K. J., Boone, K. B., Mishkin, F. S., de Menezes Santos, M., et al. (1999). A system for relational reasoning in human prefrontal cortex. *Psychological Science*, *10*, 119–125.

Waltz, J. A., Lau, A., Grewal, S. K., & Holyoak, K. J. (2000). The role of working memory in analogical mapping. *Memory & Cognition*, *28*, 1205–1212.

Wang, A. T., Lee, S. S., Sigman, M., & Dapretto, M. (2006). Neural basis of irony comprehension in children with autism: The role of prosody and context. *Brain*, *129*, 932–943.

Wang, W.-C., Hsieh, L.-T., & Bunge, S. A. (this issue). Transient incidental activation of abstract concepts in the brain.

Wason, P. C. (1966). Reasoning. In B. M. Foss (Ed.), *New horizons in psychology* (pp. 135–151). Harmondsworth, UK: Penguin.

Watson, C. E., & Chatterjee, A. (2012). A bilateral frontoparietal network underlies visuospatial analogical reasoning. *Neuroimage*, *59*, 2831–2838.

Wendelken, C. (2015). Meta-analysis: How does posterior parietal cortex contribute to reasoning? *Frontiers in Human Neuroscience*, *8*, 1042.

Wendelken, C., Bunge, S. A., & Carter, C. S. (2008). Maintaining structured information: An investigation into functions of parietal and lateral prefrontal cortices. *Neuropsychologia*, *46*, 665–678.

Wendelken, C., Ferrer, E., Ghetti, S., Bailey, S. K., Cutting, L., & Bunge, S. A. (2017). Frontoparietal structural connectivity in childhood predicts development of functional connectivity and reasoning ability: A large-scale longitudinal investigation. *Journal of Neuroscience*, *37*, 8549–8558.

Wendelken, C., Ferrer, E., Whitaker, K. J., & Bunge, S. A. (2016). Fronto-parietal network reconfiguration supports the development of reasoning ability. *Cerebral Cortex*, *26*, 2178–2190.

Wertheim, J., & Ragni, M. (2018). The neural correlates of relational reasoning: A meta-analysis of 47 functional magnetic resonance studies. *Journal of Cognitive Neuroscience*, *30*, 1734–1748.

Westphal, A. J., Reggente, N., Ito, K. L., & Rissman, J. (2016). Shared and distinct contributions of rostrolateral prefrontal cortex to analogical reasoning and episodic memory retrieval. *Human Brain Mapping*, *37*, 896–912.

Wharton, C. M., Grafman, J., Flitman, S. S., Hansen, E. K., Brauner, J., Marks, A., et al. (2000). Toward neuroanatomical models of analogy: A positron emission tomography study of analogical mapping. *Cognitive Psychology*, *40*, 173–197.

Whitaker, K. J., Vendetti, M. S., Wendelken, C., & Bunge, S. A. (2018). Neuroscientific insights into the development of analogical reasoning. *Developmental Science*, *21*, e12531.

Wong, E. F., Schauer, G. F., Gordon, P. C., & Holyoak, K. J. (2019). Semantic and visual interference in solving pictorial analogies. In A. Goel, C. Seifert, & C. Freksa (Eds.), *Proceedings of the 41st Annual Meeting of the Cognitive Science Society* (pp. 3115–3120). Austin, TX: Cognitive Science Society.

Zago, L., Pesenti, M., Mellet, E., Crivello, F., Mazoyer, B., & Tzourio-Mazoyer, N. (2001). Neural correlates of simple and complex mental calculation. *Neuroimage*, *13*, 314–327.