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Meta-analytic evidence for a core problem solving network across multiple representational domains

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HIGHLIGHTS:

- Identified meta-analytic brain networks associated with diverse problem solving tasks
- A shared managerial and attentional network supports generalized problem solving
- Problem solving within content areas engages representationally specific sub-networks
- Problem solving relies on cooperation between sub-network and whole-brain systems

ABSTRACT

Problem solving is a complex skill engaging multi-stepped reasoning processes to find unknown solutions. The breadth of real-world contexts requiring problem solving is mirrored by a similarly broad, yet unfocused neuroimaging literature, and the domain-general or context-specific brain networks associated with problem solving are not well understood. To more fully characterize those brain networks, we performed activation likelihood estimation meta-analysis on 280 neuroimaging problem solving experiments reporting 3,166 foci from 1,919 individuals across 131 papers. The general map of problem solving revealed broad fronto-cingulo-parietal convergence, regions similarly identified when

considering separate mathematical, verbal, and visuospatial problem solving domain-specific analyses. Conjunction analysis revealed a common network supporting problem solving across diverse contexts, and difference maps distinguished functionally-selective sub-networks specific to task type. Our results suggest cooperation between representationally specialized sub-network and whole-brain systems provide a neural basis for problem solving, with the core network contributing general purpose resources to perform cognitive operations and manage problem demand. Further characterization of cross-network dynamics could inform neuroeducational studies on problem solving skill development.

KEYWORDS: problem solving; reasoning; cognitive control; functional neuroimaging; meta-analysis; activation likelihood estimation (ALE); domain-general; domain-specificity

1. INTRODUCTION

Problem solving has been investigated across human and animal models for decades; it is a process that is central to numerous everyday tasks involving the execution of a complex, multi-step sequence of goal-oriented objectives. In humans, problem solving has been used to quantify general intelligence (Jung and Haier, 2007; Savage, 1974), assess educational or learning outcomes (Hmelo-Silver, 2004; Jonassen, 1997; Pellegrino and Hilton, 2012; Yerushalmi et al., 2007), understand age-related cognitive declines (Mienaltowski, 2011; Paas et al., 2001), or characterize neurocognitive or developmental disorders (Kodituwakku, 2009; Ozonoff and Jensen, 1999; Sachdev et al., 2014), and has been investigated across multiple research domains including medicine (Elstein, 2002), economics (von Hippel, 1994), education (Jonassen, 2000; NCTM, 2010), physics (Hsu et al., 2004; Maloney, 2011), psychology (Davidson and Sternberg, 2003; Simon A. and Newell, 1971), and cognitive neuroscience (Fink et al., 2009; Unterrainer and Owen, 2006).

Given this universal and multidisciplinary interest in problem solving, numerous definitions of the construct have been articulated by experts from different domains with varying theoretical knowledge bases. In the present study, we adopt the definition of a *problem* as a “situation in which you are trying to reach some goal, and must find a means for getting there” (Chi & Glaser, 1985, pp. 229). The act of *problem solving* then involves identifying and/or performing critical thinking processes related to evaluating the problem, planning or sequencing actions to solve it, and executing operations that conform to some rule set (e.g., semantic, algebraic, logical, mechanical, or other delimiting frameworks) to arrive at a correct, or sometimes most appropriate, previously unknown solution. Within this operational definition, problem solving can be considered as a sequential and/or parallel orchestration

of a series of integrative cognitive maneuvers wherein solutions are systematically, but not necessarily immediately, derived. Such framing acknowledges that problem solving encompasses iterative algorithmic steps, as well as exploratory and innovative processes wherein solution paths draw on creativity and insight. It is of note that an important component of solving a problem may be in the initial characterization of the problem itself, a step in which one must identify the rule set implied or relevant to the problem's context. In this way, the problem solving processes can be highly content-specific while simultaneously grounded in a common framework that is context-independent. Thus, problem solving-related processes are dynamic, frequently involve the confluence of learning, cognitive ability, and previously acquired knowledge, and span developmental stage and social context. Problem solving can range from formative human experiences such as a toddler interacting with environmental affordances as objects and tools are tested to replicate observed functions, to more technical or abstract undertakings such as scientists drawing on experiment, technique, and knowledge to address unresolved questions from their discipline.

In human functional neuroimaging research, numerous and diverse experimental tasks have been used to elicit cognitive processes viewed as central to problem solving. Various neuroimaging studies have considered problem solving from the perspectives of mathematical calculation (e.g., Dehaene et al., 1999), deductive or inductive reasoning (e.g., Goel, 2007), insight solution generation (e.g., Luo and Niki, 2003), verbal or picture-based analogical reasoning (e.g., Bunge et al., 2005), fluid intelligence (e.g., Prabhakaran et al., 1997), or puzzle solving and game-play (e.g., Atherton et al., 2003). However, little is known about the neurobiological processes underlying problem solving as a general endeavor, and a broad comparison of activation results across these multiple diverse problem solving tasks has not been conducted. Thus, it is not known if there exists a constellation of common brain regions supporting general problem solving, irrespective of topic, scope, or discipline, or if problem solving is a relatively specific mental activity that instead relies more strongly on particular neural correlates most relevant to the problem's specific context and features. By addressing this question, we may be better able to characterize the nature of problem solving across its many interdisciplinary conceptions in the service of facilitating improvements to strategies promoting problem solving skill development.

While problem solving remains a relatively equivocally defined construct, particularly within the neuroimaging literature, initial insight into the neural substrates of many of the constituent processes noted above may be gleaned from the *executive function domain*. For example, Minzenberg et al. (2009) and Niendam et al. (2012) characterized executive functions as those mental processes that direct,

regulate, and integrate goal-oriented behavior. *Cognitive control* is a term often used synonymously with, or to emphasize the regulatory aspects of, executive function wherein many cognitive processes together dynamically manage information to guide actions and achieve a common purpose (Miller, 2000). This ‘managerial system’ responsible for directing necessarily coherent, purposeful, and stepwise actions is likely a central element across many, if not all, forms of problem solving. Yet, it remains unclear which of the neural correlates of cognitive control are also essential for problem solving, and whether a common network exists linked with problem solving across contexts.

Brain regions associated with executive function have been relatively well studied, are often collectively referred to as the Central Executive Network (CEN), and typically reveal functionally connected inter- and intra-hemispheric regions across association cortices. Early perspectives on executive function attempted to map specific and theoretically distinct cognitive processes onto individual brain regions (Luria, 1966; Shallice, 1988). However, as experimental techniques in fMRI deepened the scientific understanding of cognitive control, consensus shifted away from simple one-to-one function-structure mappings and towards a more system-based perspective wherein whole-brain distributed networks support multiple cognitive constructs (Carpenter, 2000; Menon and Uddin, 2010). Goal-oriented, complex cognition is maintained by such multiregional interactions (Cocchi et al., 2013), and intra-hemispheric frontoparietal connections may be one neurobiological aspect contributing to species-specific behavioral differences between human and non-human primates (Wey et al., 2013). The dorsolateral prefrontal cortex (dlPFC), medial prefrontal cortex (mPFC), and posterior parietal cortex (PPC) are together frequently implicated across executive function paradigms such as working memory *n-back* tasks (Owen et al., 2005; Curtis, 2003), attentional control tasks including *go/no-go* and *Stroop* paradigms (Cieslik, 2015), and others such as the *oddball* vigilance task, *tower maze* planning task, and *Wisconsin card sorting* flexibility task (Lie et al., 2006; Linden, 1999; Unterrainer and Owen, 2006).

In an extensive meta-analysis across executive function tasks, Niendam and colleagues (2012) considered 193 neuroimaging studies reporting outcomes from flexibility, inhibition, working memory, initiation, planning, and vigilance paradigms. Those authors identified a cross-domain cognitive control system including dlPFC, frontopolar cortex, orbitofrontal cortex, anterior cingulate cortex (ACC), superior and inferior parietal and occipito-temporal cortex, cerebellum, and limbic areas such as the caudate, putamen, and thalamus. This so-called *superordinate cognitive control system* constituted a shared network supporting various disparate paradigm activations, and thus suggested that multiple executive functions are supported across a common set of fronto-cingulo-limbic-parietal brain regions.

Similar observations of common prefrontal, insular, and parietal brain regions responsible for a diversity of goal-oriented tasks have also been demonstrated across attentional processes (Duncan, 2006) and show enhanced involvement when task demands are increased, regardless the type of task performed (Duncan and Owen, 2000; Fedorenko et al., 2013). This system has been termed the *multiple demand* (MD) network because of its high flexibility across contexts and has been argued to be critically involved in task control, attentional focusing, managing cognitive load, and may play a central role in interfacing with different brain systems that accomplish sub-tasks or specific cognitive operations within structured mental operations (Duncan, 2013, 2010). Given the close ties between problem solving and this multitude of diverse cognitive functions, a reasonable working hypothesis is that a similar network is associated with problem solving across diverse representational domains.

While a collection of brain regions commonly activated across problem solving tasks may be indicative of a supervisory control network, there is also evidence for simultaneous domain-specific regional involvement during problem solving. Neural findings from individual problem solving studies support the notion of a supervisory control network that also subtends functionally specific regional interactions. For example, in an investigation of math and word problem solving, Newman and others (2011) identified a common set of CEN regions, including superior parietal lobule (SPL) and horizontal intraparietal sulcus (IPS), that supported both representational modalities of problem solving. In addition to this common problem solving network, they also observed distinct activations across Broca's and Wernicke's areas in word but not number problems, and identified enhanced activation in IPS specific to number but not word problems. These results highlight the importance of not only a common network for problem solving, but also the separate and distinctive interaction of regions specific to problem solving representation.

To date, results from the wide range of neuroimaging problem solving paradigms have not been collectively assessed to identify common and differential brain activation patterns across problem solving representational contexts and distinct domains. To this end, we first identified a set of published neuroimaging experiments that utilized high-level critical thinking and reasoning tasks. If the tasks were consistent with our operational definition of problem solving, we selected related experimental contrasts according to inclusion criteria. These tasks involved healthy adults answering novel questions by way of generating or verifying solutions. We then applied a quantitative, coordinate-based meta-analysis method to comprehensively synthesize this literature corpus with the purpose of identifying the neural networks associated with problem solving. Using this methodology, we sought to: (1) determine

if convergent neurobiological substrates are present across the diversity of problem solving tasks; and conversely, (2) identify those brain regions exhibiting consistent functional specificity within distinct representation domains.

2. METHODS

To identify consistent and dissociable brain activation patterns linked with problem solving, we conducted a series of Activation Likelihood Estimation (ALE) meta-analyses (Turkeltaub et al., 2002; Laird et al., 2005; Eickhoff et al., 2009; 2012; Turkeltaub et al., 2012) delineating convergent results reported within and across distinct representational categories.

2.1. Literature Search and Experiment Selection Criteria

We began by establishing our definition of problem solving, independent of any literature searches or reviews. Then, a search to compile a comprehensive set of peer-reviewed functional neuroimaging studies investigating problem solving published in English between January 1st 1997 and March 14, 2015 was performed across multiple literature indexing services, including PubMed (www.pubmed.com), Web of Science (www.webofknowledge.com), and Google Scholar (www.scholar.google.com). Searches were constructed to identify functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) studies indexed by keywords such as problem solving, calculation, verbal reasoning, visuospatial reasoning, insight, deductive reasoning, inductive reasoning, or fluid reasoning. References within papers matching these search criteria were examined and appropriate studies not previously identified were added to the pool of potential papers for inclusion. To avoid bias introduced by the selection process, we gathered a large corpus of papers extending across a range of experiments, ensuring cluster convergence was not due to the particular studies selected but rather was representative of a general result across a spectrum of experiments. We determined if tasks in these studies were reasonably described by the two-part problem solving definition we had adopted (i.e., first having a goal, followed by a need to figure out a way to reach it). Once the set of problem solving tasks were identified, associated studies were filtered to identify problem solving experiments/contrasts that isolated one or more of the cognitive processes central to the problem solving task. Of those identified, we selected only those contrasts reporting either blood oxygen level dependent (BOLD) or regional cerebral blood flow (rCBF) signal increases; results associated with BOLD or rCBF decreases were excluded. Group-level effects in healthy adult individuals were targeted, while disease-, age-, and gender-related group comparisons were excluded. Experiments were further filtered to include only

those that reported task-related increases as stereotactic coordinate results in either Talairach or Montreal Neurological Institute (MNI) standardized space. The final set of experiments was constrained to include only whole-brain analyses and exclude region of interest (ROI) results.

Three main paradigm groupings emerged as separate problem solving domains within the neuroimaging literature: tasks in which participants solved computational or *mathematical problems*, language-based or *verbal problems*, or picture-based or *visuospatial problems*. Representational domains were defined by the stimulus modality used: mathematical problems involved number manipulation, verbal problems presented questions with sentence, word, or letter stimuli, and visuospatial problems involved pictorial or spatial tasks. Within these representational sets, five distinct contrast types were included in the meta-analyses: contrasts in which (1) a baseline condition was subtracted from a problem solving task (i.e., problem solving > baseline), (2) problem solving questions were parametrically compared across varying difficulty, abstraction, or complexity (e.g., complex problem solving > simple problem solving), (3) untrained, previously unseen, and novel problems were solved and contrasted with previously memorized or solved problems of the same type (i.e., untrained problem solving > trained problem solving), (4) problem solving was compared across different rule sets or representational modalities (i.e., problem solving type 1 > problem solving type 2; e.g., multiplication problems > addition problems or word problems > number problems), or (5) distinct and sequential problem solving phases were contrasted with each other (e.g., problem solving late phase > problem solving early phase). Several studies used problem solving to investigate differences between healthy controls and either patient populations or populations with intellectually gifted individuals (e.g., mathematical prodigies or high-IQ individuals). Experiments were included from these studies if within-group results for healthy controls were separately reported, without any group interaction effects or comparison with an experimental group.

2.2. Activation Likelihood Estimation

Stereotactic coordinates were extracted from the identified set of problem solving contrasts. To reduce disparity between MNI and Talairach coordinates (Laird et al., 2010), foci originally reported in Talairach space were transformed into MNI space using the tal2icbm algorithm (Lancaster, 2007). A series of activation likelihood estimation meta-analyses was performed in the MATLAB environment to assess concordance across studies and within each problem solving representational domain using the revised non-additive ALE algorithm (Laird et al., 2005; Eickhoff et al., 2009; Turkeltaub et al., 2012). This random-effects approach models activation foci as three-dimensional Gaussian probability distributions

whose widths reflect variances in experimental sample size and uncertainty inherent to spatial normalization. The ALE algorithm first computes a set of modeled activation (MA) maps by selecting the maximum probability associated with any one Gaussian within each experiment (Turkeltaub et al., 2012). This method was employed to alleviate artificial conflation of MA values due to within-experiment coordinate proximity and thus limits the maximum contribution any single experiment can have on the overall ALE results. After the within-experiment activations were modeled, voxel-wise focal overlap across experiments was determined by computing the union of all activation probabilities (known as the voxel's ALE score), a quantity representing convergence of results across studies. This union was anatomically constrained by a grey matter mask based on the ICBM tissue probability maps of Evans et al. (1994). Statistical significance within this so-called ALE map was determined by comparing the distribution of ALE scores to a null-distribution modeled by 10,000 permutations of random data, each containing identical characteristics to those of the actual experiments (e.g., simulated subject and foci numbers). Computationally, foci from the dataset were replaced with coordinates randomly selected from the gray matter template and the union of their values was computed to form the empirically derived null-distribution used to test the null hypothesis of randomly distributed activations. Then, above-chance clustering between experiments was assessed by computing P -values given by the proportion of ALE scores equal to or greater than those obtained under the null-distribution. A correction for multiple comparisons was implemented by using a voxel-level threshold of $P < 0.001$, and then ALE results were family-wise error (FWE) corrected at a cluster extent threshold of $P < 0.05$ (Eickhoff et al., 2017).

First, to identify *common activation patterns* across problem solving, coordinate results from all representational domains (i.e., mathematical, verbal, and visuospatial domains) were pooled and assessed for convergence. The resulting 'global network' was agnostic to variants in problem solving type and therefore useful in evaluating whether a content-general problem solving meta-analytic network could be identified. Here, and in following sections, we refer to the term 'meta-analytic network' (or simply 'network') as a collection of brain regions that together represent the common activation patterns resulting from meta-analytic results. Because clusters revealed by the global network need not be similarly observable across sub-domains, we performed follow-up characterizations of within-domain activation patterns to resolve context-relevant networks. To investigate which brain regions were consistently activated within content-specific tasks, we delineated experiments by representational domain and separately assessed coordinate convergence across mathematical, verbal, and visuospatial problem solving variants. We then inspected these within-domain ALE maps for three-

way conjunctions to identify overlap indicative of common and convergent activation among all types of problem solving (i.e., a core network). Specifically, we conducted a conservative minimum statistic conjunction analysis (Nichols, 2005) to identify significant voxels commonly present across all domain-specific problem solving ALE maps. Next, to decipher the functional role of this core network and identify specific cognitive processes contributing to problem solving in general, we performed functional decoding (which is a statistical approach used to determine psychologically-linked terms given observed brain activation patterns) on the resulting conjunction map (Poldrack, 2011). To do this, we fit a Generalized Correspondence Latent Dirichlet Allocation (GC-LDA; Rubin et al., 2016, 2017) model with 200 topics to the Neurosynth literature corpus (Yarkoni et al., 2011). The GC-LDA model associates each topic with a probability distribution across terms from article abstracts and with a spatial distribution (in this case as a bilateral pair of Gaussian distributions) across voxels in MNI space. These topics reflect words and foci which frequently co-occur across studies in the literature and facilitate distinguishing the conceptual structure associated with terms that can be imprecise or variously defined across studies. Next, we fed the conjunction map into the decoding algorithm, which used the $P(\text{topic}|\text{voxel})$ distribution estimated by the topic model to estimate $P(\text{topic}|\text{map})$. Finally, we expanded the topic weights to word weights by computing the dot product between the $P(\text{topic}|\text{map})$ vector and the $P(\text{word}|\text{topic})$ distribution estimated by the model.

Then, to statistically compare each problem solving domain and isolate *differential activations patterns* selective to each of the three problem solving types, we ran formal contrast ALE meta-analyses using methods described in detail in Laird et al. (2005) and Bzdok et al. (2015). These three-way ALE contrasts were determined by computing difference maps across pairs of domain-specific ALE images and then assessing the conjunction, using the minimum statistic approach, across the difference maps. For example, to isolate the brain activity specifically associated with mathematical problem solving, we first calculated the contrasts of *Mathematical – Verbal* problem solving and *Mathematical – Visuospatial* problem solving. We then computed the conjunction between these two differences (i.e., $[\text{Mathematical} - \text{Verbal}] \cap [\text{Mathematical} - \text{Visuospatial}]$), which isolated brain regions uniquely contributing to mathematical problem solving separated from verbal and visuospatial modalities. Similar conjunction analyses were performed for verbal ($[\text{Verbal} - \text{Mathematical}] \cap [\text{Verbal} - \text{Visuospatial}]$) and visuospatial specific contrasts ($[\text{Visuospatial} - \text{Mathematical}] \cap [\text{Visuospatial} - \text{Verbal}]$). This method for computing the contrasts of multiple ALE images determines which clusters are statistically selective in one ALE map from those regions shared with all other ALE maps. Thus, we assessed domain specificity by examining if one task domain demonstrated greater convergence compared to both of the other task

domains. All contrast analyses were generated with voxel-wise thresholding at $P < 0.01$ (false-discovery rate corrected) using 250 mm³ minimum cluster volumes and 10,000 permutations. The anatomical locations of the observed clusters are labeled and reported in MNI space.

Lastly, we conducted a meta-analysis in which we considered the role of *cognitive demand* within problem solving. Our approach in this analysis was similar to that previously adopted by Duncan and Owen (2000) in their observation of the multiple demand network. We selected contrasts for this final meta-analysis that compared high to low demands across problem tasks (i.e. Complex > Simple Problem Solving) that were otherwise identical. In this way, we assessed convergence across a range of different problem solving experiments, each of which isolated the specific neural underpinning associated with problem difficulty while still controlling for additional factors potentially impacting demand (e.g. task type).

3. RESULTS

3.1. Literature Search Results

The results of the problem solving literature search across mathematical, verbal, and visuospatial domains are described in detail below; the specific contrasts are detailed in Supplementary Table 1, along with the numbers of foci and subjects, task, stimulus, contrast classification, and neuroimaging modality.

3.1.1. Mathematical Problem Solving Paradigms

Numerical calculation was the most widely studied representational domain within the neuroimaging problem solving literature. Overall, the literature search identified 99 mathematical problem solving contrasts, yielding 1,044 activation foci from 41 published papers. A total of 65 of these contrasts compared problem solving with a rest or low-level baseline condition, 21 contrasted two different forms of mathematical problem solving, and 13 compared complex versus simple conditions. Although operand tasks took varying forms, basic paradigm structure involved mental binary operations (i.e., addition, subtraction, multiplication, division) being performed on integer Arabic numerals to arrive at single valued answers. A 2011 meta-analysis on number sense and calculation (Arsalidou and Taylor, 2011) previously identified several mathematical problem solving studies relevant to the investigation at hand. Thus, these experiments were included in this meta-analysis, along with additional neuroimaging studies matching our inclusion criteria. Included paradigms are further described below and in Supplementary Table 1a.

Number Operation Tasks

The majority of included calculation paradigms involved mental quantity manipulations of either one- or two-digit Arabic numerals so as to generate, select, or verify solutions to mathematical expressions (e.g., “6 + 8” or “12 x 55”). Most number operation tasks presented two numeric values on which a single binary operation was performed. However, tasks of this class also included operand manipulations on multi-number lists. Participants responded to numerical and symbolic stimuli by either overtly speaking solutions, internally identifying them, or using a button press to select the correct value from a list of answer choices. Calculation verification paradigms presented participants with numerical equations such as “5 – 13 = -8” and participants decided if the statements were true or false. Most numerical operand paradigms utilized visual stimuli of Arabic digits and/or binary mathematical operands, however some tasks also presented subjects with Roman numerals, auditory Arabic numerals, or English words of Arabic numerals.

Baseline or control conditions for operand tasks took one of several forms including identifying, matching, or comparing target number values. In identification conditions, participants overtly recited values or pressed a button when a target number, letter, word, or symbol appeared on a screen. Baseline matching conditions instructed participants to select an identical number to a previously presented stimulus. In comparison tasks, participants viewed number pairs and identified the digit of larger value. Number comparison, which is sometimes used to measure numeric distance or number sense, did not fit our cognitively demanding definition for problem solving; thus, we considered these tasks as appropriate high-level control conditions for calculation tasks (i.e., Calculation > Comparison).

The present meta-analysis additionally included high-level contrasts such as Multiplication > Addition, Complex > Simple, Number Problems > Word Problems, or Exact Calculation > Approximation. While these control conditions were themselves instances of problem solving, their cognitive subtractions yielded coordinate results specific to characteristics central in mathematical problem solving (i.e., in the respective above examples these were operand type, difficulty level, representation modality, solution method). Because we sought to include results from multiple varieties of questions and across characteristics, we likewise included reverse contrasts such as Addition > Multiplication and so on. Although these reverse contrasts yielded disjoint sets of activation patterns, we considered each contrast as an independent experiment targeting specific qualities inherent to mathematical problem solving. Because both sets of coordinate results highlighted specific characteristics within the general umbrella of mathematical problem solving, they were included. The literature search produced 80 (out

of 99 total mathematical problem solving) number operations contrasts associated with 776 activation foci from 30 papers for inclusion in the meta-analysis.

Paced Auditory/Visual Serial Addition Test

The paced addition serial attention test (PASAT), modified PASAT (mPASAT), or paced visual serial attention test (PVSAT) are neuropsychological tests widely used to study cognitive impairments, attention, information processing speed, and working memory (Tombaugh, 2006). The primary procedure in this paradigm involves mentally and serially adding digits together. Participants are presented with either an auditory (PASAT or mPASAT) or a visual (PVSAT) sequence of numbers, with individual digits ranging between 0 and 9, and are instructed to mentally add the first and second numbers. This sum is then mentally added to the third value, and so on, until the sum of digits equals 10. The participant indicates the sum equals 10 with a button press or hand gesture and begins the serial summation again. While the paradigm has been used to investigate working memory (Lazeron et al., 2003; Mainiero et al., 2004) this calculation task employs sequential addition of an unknown number of random digits until a final value is determined. Thus, the paradigm implicates multi-stepped analytical thinking within the rule set of addition until completion, with the goal of correctly identifying the closing number in the additive sequence. Accordingly, we characterized the PA/VSAT task as a mathematically-based problem solving paradigm and included these tasks in the mathematical meta-analysis. The literature search yielded 7 (out of 99 total mathematical problem solving) PA/VSAT contrasts, which included 138 activation foci from 6 papers.

Additional Mathematical Tasks

Several neuroimaging paradigms targeted mathematical problem solving processes employing less common number or math-based stimuli. Such tasks included percent estimation problems (“what is 44 percent of 70?”; Venkatraman et al., 2006), equation-based algebraic or calculus problem manipulations (Krueger et al., 2008; Newman et al., 2011), or other algorithm-based problems such as pyramid problems (Delazer et al., 2005) or number bisection problems (Wood et al., 2008). In pyramid problems participants viewed non-standard operation expressions such as $54\$3$ and were trained to perform the corresponding “\$” algorithm (in this example, $54+53+52$ where 54 is the ‘base number’ and 3 is the ‘addition span number’). Number bisection problems cued participants with ordered number triplets such as (44,62,87) and participants determined if the middle value was also the mean of the flanking numbers. The literature search yielded 12 additional (out of 99 total) mathematical contrasts reporting 130 activation foci from 5 papers for inclusion in the meta-analysis.

3.1.2. Verbal Problem Solving Paradigms

Neuroimaging problem solving paradigms in the verbal domain asked questions via letter, word, or sentence stimuli, and participants used logic or content knowledge to comprehend, generate, or identify solutions. Overall, the literature search identified 93 verbal problem solving contrasts, which reported 1,028 activation foci from 43 published papers. Of the 93 verbal contrasts identified, 49 compared problem solving with a baseline condition, 13 contrasted complex to simple problem solving in the verbal domain, 22 contrasted differing types of verbal problem solving, 7 identified activation at distinct problem solving phases by contrasting distinct stages in the problem solving process, and two compared untrained to trained verbal problem solving. Paradigms in this category included deductive and inductive reasoning sentences, riddles and insight questions, paragraph-based word problems, and word or letter string analogy sets. These paradigms displayed diversity in stimuli and reasoning methods used, and participants responded via button press to either select from a set of solution options, indicate if a given problem was logical or illogical, or if they had been successfully able to arrive at a solution to the verbal problem before the time expired and an answer was revealed. Included paradigms are described below and in Supplementary Table 1b.

Deductive Reasoning Paradigms

Deduction is a logical process in which specific conclusions are inferred from general rules. Neuroimaging paradigms typically explore mechanisms supporting deductive reasoning across categorical (e.g., All A's are B's, All B's are C's, therefore all A's are C's), relational (e.g., A is to the right of B, B is to the right of C, A is to the right of C), or propositional (e.g., If A then B; A; Therefore B) argument types. In these paradigms, subjects considered sentence- or letter-based arguments and determined if a given conclusion logically followed from the premises. Participants were instructed to respond to questions by pressing a button to indicate if the argument was valid or invalid. Deductive reasoning control conditions typically asked logic questions whose answers were trivially false (e.g., "if A is to the right of B and B is the right of C, is D is to the right of F?") A 2011 neuroimaging meta-analysis (Prado et al., 2011) of deductive reasoning tasks served as an initial model for studies included in our language-based problem solving analysis. We included appropriate studies from this deduction meta-analysis and updated and extended the corpus of deductive linguistic papers for the present study.

While the majority of included verbal deductive reasoning paradigms took one of the conditional forms described above, several paradigms also included in this category presented linguistically challenging word problems that required logical deduction. For example, in Newman et al. (2011) participants

viewed statements such as, “The day before my favorite day is two days after Thursday”, and then determined which day was the favorite. Another study (Kroger et al., 2008) presented word problems such as, “There are five students in a room. Three or more of these students are joggers. Three or more of these students are writers. Three or more of these students are dancers. Does it follow that at least one of the students in the room is all three: a jogger, a writer, and a dancer?”. Some of these studies, as in Zarnhofer et al. (2013), asked participants to solve arithmetic word problems (e.g., “Anna goes for a walk. She walks 4 km/h. What distance does she cover in 3 hours?”). These problems, although mathematical in nature, were included in the verbal meta-analysis because their stimuli were sentence-based. The literature search produced 60 (out of 93 total verbal problem solving) deductive reasoning contrasts associated with 688 activation foci published in 25 papers for inclusion in the meta-analysis.

Verbal Inductive/Probabilistic Reasoning Paradigms

While deductive reasoning is used to make claims on specific information by applying general rules, inductive reasoning is a procedure by which broad rules are inferred from particular instances (e.g., “Mike is a basketball player, Mike is tall. All basketball players are tall.”). While counterexamples can disprove inductive reasoning statements, they can never be fully logically proved. Thus, in inductive neuroimaging paradigms, participants determine if the concluding statements are plausible or not plausible. These inductive tasks are sometimes also referred to as probabilistic reasoning tasks.

Paradigms in this category frequently took a categorical form and the task was to determine if the statement had a greater chance of being true or false (e.g., “House cats have 32 teeth; Lions have 32 teeth; All felines have 32 teeth?”; Goel and Dolan, 2004). Other probabilistic paradigms included in this analysis presented participants with event frequencies from hypothetical experiments with known outcomes and participants probabilistically determined which experiment the results came from. For example, in Blackwood et al. (2004), participants viewed a serial presentation of positive and negative words. They were told these words had been drawn from a survey that received a positive to negative response ratio of either 60:40 or 40:60. Participants were asked to choose which survey the viewed words had likely been drawn from. The literature search yielded 5 (out of 93 total verbal problem solving) inductive reasoning contrasts that included 34 activation foci from 4 papers for inclusion in the meta-analysis.

Verbal Analogy Problems

Analogical reasoning relies on the ability to draw conclusions about relationships from given information and/or by using background knowledge. Typical analogy problems across the neuroimaging literature,

such as those in Luo et al. (2003), present participants with dual word pairs and subjects determine if these formed analogous or general semantically related sets (e.g., analogy: “drummer, band” = “soldier, army”; semantic: “refrigerator, kitchen” = “lounge, room”). Other linguistic analogy tasks were sentence-based and asked participants to complete phrases such as, “black is to white and high is to?” (Wendelken et al., 2008). We also included analogy tasks in this meta-analysis that involved semantic word retrieval (Wagner et al., 2001) in which participants viewed a cue word and then target words that were either unrelated, weakly related, or strongly related to the cue (e.g., strongly related: “cue = rain; targets = pillow, puddle, book, sneaker”; weakly related: “cue = candle; targets = design, halo, exists, bald”); subjects selected the target word most related to the cue.

Analogy tasks sometimes used purely letter-based representations; for example, in Geake and Hansen (2005) participants viewed two successive non-word letters strings that revealed an order- or alphabetic-based transformation rule (e.g., ird implies dri). Subjects were then shown a third letter string and choose or generated the letter string that best followed the transformation rule (e.g., ykw implies ?). Many so-called “fluid analogy” problems, such as in this example, required both semantic and content knowledge to choose the most plausible answer. A similar paradigm, drawn from the Educational Testing Service Kit of Factor Referenced Cognitive Sets (Ekstrom et al., 1976), presented participants with non-word letter strings with some common alphabetic or translational rule, and participants were asked to identify the “odd one out” from a set of choices (Duncan et al., 2000). The literature search produced 9 (out of 93 total verbal problem solving) analogy contrasts that reported a total of 78 activation foci from 5 papers.

Insight Problem Solving

Insight question paradigms are language-based paradigms that targeted the “aha” moment within problem solving and frequently take the form of sentence- or character-based riddle problems. Riddle solving involves careful consideration of phrasings and/or semantic indicators such as syntactic or logographic structure. Neuroimaging riddle paradigms, such as in (Luo and Niki, 2003), used problems like “What can move heavy logs, but cannot move a small nail?” (solution: “a river”). Other riddle-like paradigms relied on word play within Chinese character idioms (or “Chengyu”) whose figurative meanings are often distinct from their literal ones (e.g., an English-language idiom of similar kind is “kick the bucket”, which has the figurative meaning “to die”; Zhang, 2012). The goal of these paradigms is to identify the expression’s metaphoric meaning by decomposing constituent characters into meaningful semantic chunks. For example, in Qiu et al. (2010), participants were given phrases such as 右眼难见,

which translates to “having eyes but being unable to see”, and were asked to derive the idiom’s underlying meaning. In this case, the answer is 盲 (which means “blind”), and is derived by combining the phonetic symbol 亡 with the semantic radical 目 that appears as a constituent chunk in the Chengyu component 眼. Insight paradigms based on chunk decomposition of logograms took multiple but similar forms in the neuroimaging literature and appropriate studies were included in this meta-analysis.

Other neuroimaging paradigms that study insight are anagrams puzzles in which letters from words have been scrambled beyond the point of recognition. Participants, such as those in Aziz-Zadeh et al. (2009), were presented with these scrambled words and are asked to determine the original word. Several additional non-standard insight problem solving paradigms were identified as appropriate for this meta-analysis; one such study (Luo et al., 2013) considered insight in scientific problem solving specifically. In that study, subjects were presented with paragraph-based real world scientific and engineering questions, some of which contained explicit hints towards a solution path. Participants were asked to determine solutions to these scientific/engineering questions and insight moments were facilitated by heuristic use. The literature search yielded 19 (out of 93 total verbal problem solving) insight contrasts reporting 215 activation foci from 12 papers.

3.1.3. Visuospatial Problem Solving Paradigms

In our third and final representational domain, we identified neuroimaging experiments using visuospatial problem solving to study analogic or relational reasoning by pattern identification, visualization, induction, and visual processing. Overall, the literature search identified 88 visuospatial problem solving contrasts which reported 1094 activation foci published in 50 papers. A total of 47 of these contrasts took the general form of visuospatial problem solving versus a baseline condition, 14 considered complex versus simple visuospatial problem solving, 16 contrasted two types of visuospatial problem solving, 10 contrasted untrained to trained visuospatial problem solving, and one contrasted problem solving across different phases. The visual problems sets identified as part of this literature search varied significantly across studies and many experiments in this representational domain utilized novel task paradigms. In all included visuospatial problem solving paradigms, participants used reasoning to respond to picture stimuli. Included paradigms are described below and in Supplementary Table 1c.

Visuospatial Fluid Reasoning Tasks

Fluid reasoning (sometimes called fluid intelligence, “Spearman's g ”, or simply “ Gf ” or “ g ”; Spearman, 1928) is the ability to reason in novel situations, independent of prior knowledge or culturally embedded context (Ferrer et al., 2009). Two canonical neuropsychological paradigms frequently used to investigate the visuospatial component of fluid reasoning are the Raven’s Progressive Matrices (RPM; Raven, 2000) and the Cattell’s Culture Fair Test (Cattell, 1973). In the former, participants view 3 x 3 picture grids whose images progress horizontally and/or vertically by an analogical rule. Participants must determine the rule(s) of progression and, from a set of options, choose the image that completes the final grid entry. Similarly, the Culture Fair Test presents a set of drawings sharing a relational rule. Participants identify this rule and select either the “odd one out” from the image set, or choose an additional image that follows similarly. Each paradigm contains problems that parametrically increase in complexity level (“low” to “high” g) and simple problems are often used as control conditions to more complex fluid reasoning questions.

Variations of these two visuospatial reasoning tasks have been used across the literature and were also included in this meta-analysis. The Nagliri Nonverbal Intelligence Test (Kalbfleisch et al., 2007), the Fluid Intelligence Test (Ebisch et al., 2012), the Geometric Analogical Reasoning Task (Preusse et al., 2011), and the Nonverbal Reasoning Task (Hampshire et al. 2011) all require subject’s use of relational integration abilities to identify visual pattern-based rules and make rule-based judgments on images. The literature search produced 19 (out of 88 total visuospatial problem solving) fluid reasoning contrasts associated with 200 activation foci from 11 papers that were included in the meta-analysis.

Visual Analogy Problems

Similar to fluid reasoning paradigms, visual analogy problems use picture-based stimuli to depict a deducible visuospatial rule set. In these types of tasks, participants viewed dual shape or image pairs (with A:B and C:D structure) that were related via pattern, color, geometric form, or physical appearance. Participants selected the answer that followed the visual analogical rule or indicated if an item did or did not follow that rule. For example, in Watson and Chatterjee (2012), problems presented colored shape strings illustrating a progression rule and participants choose from answer options putatively illustrating the same rule (e.g., target: red triangle, blue triangle, red circle; answer options: red diamond, blue diamond, red diamond or red diamond, blue diamond, red square). Similarly, Preusse et al. (2010) used a task where the rule set was given by mirror symmetry of geometric ensembles. Participants in this study viewed dual square grids in which blocked shapes depicted transformations

about vertical, horizontal, and/or diagonal axes. The task was to indicate if a second grid pair followed the same reflection rule as the first.

Not all analogical problems of this category portrayed visual rules via abstract shapes. For example, Cho et al. (2010) used the People Pieces Analogy Task (Sternberg, 1977) to elicit analogical reasoning by presenting subjects with two analogical pairs of drawings of human forms. Each pair shared some common quality (e.g., width, height, gender...) and participants were given a list of these dimensions. They were asked if dual sets of people pairs correspond across a given dimension. This task involved problem solving across scales of both relational complexity and levels of attention interference. The literature search across visual analogy problems yielded 5 (out of 88 total visuospatial problem solving) analogical reasoning contrasts reporting 28 activation foci from 4 papers.

Tower of London Task

In the Tower of London (TOL) (Shallice, 1982) or Tower of Hanoi task (Zhang and Norman, 1994), participants are presented with an initial and target configuration of stacked colored balls or disks (e.g., red, green, blue) that lie along three columns. These colored objects can be moved one at a time and from the top of each stack, and placed on the top of any of the three columns. Participants are tasked with identifying the minimum number of moves needed to transform an initial arrangement into a final configuration. This paradigm is frequently used as an assessment of planning within problem solving. Control tasks for TOL sometimes involved simply counting the number of balls present in a configuration or watching balls change positions and counting the number of moves (Wagner et al., 2006). The literature search yielded 12 (out of 88 total visuospatial problem solving) Tower of London and Tower of Hanoi contrasts containing 161 activation foci, as reported in 9 papers included in the meta-analysis.

Spatial Navigation Problem Solving Tasks

Navigation neuroimaging paradigms generally focus on probing the neural mechanisms of spatial memory (e.g., task objective: “remember the location of objects/places encountered in a virtual environment and recall the placements later) or spatial planning and learning (e.g., task objective: “find your way from a starting point to a target location within a map/virtual environment.”) Tasks of the latter variety aligned with our operational definition of problem solving and appropriate experiments of this kind were included in the present meta-analysis. Experiments displayed pictures of mazes or maps from allocentric or egocentric reference frames, and baseline conditions often took the form of route following along visually guided paths. We included relevant experiments identified in a 2014

neuroimaging meta-analysis of spatial navigation (Boccia et al., 2014) and updated and extended the corpus of navigation problem solving papers for the present study.

The majority of included tasks asked participants to make one or several critical decisions at intersection points during navigation, and subjects learned through trial and error which sequence of decisions led to the desired end location. Other contrasts involved navigating mazes that had been learned during a training session but that appeared within scanning as shuffled or with significantly altered visual features, making navigation difficult or in some cases impossible. Tasks of this type sometimes involved navigation along learned routes containing unexpected features inhibiting passage (e.g., a “roadblock” requiring detour planning as in Campbell et al., 2009 or Iaria et al., 2008). Spatial navigation tasks not included in this study were those that lacked the crucial problem solving component of figuring out a means in order to reaching the task goal, for example tasks wherein participants memorized a spatial layout during training and traversed the same environment during scanning, paradigms involving navigation from one familiar landmark to another within a participant's home city, or tasks in which the target location was clearly visible from the starting location. The literature search yielded 39 (out of 88 total visuospatial problem solving) visuospatial navigation problem solving contrasts associated with 531 activation foci from 18 published papers for inclusion in the meta-analysis.

Visuospatial Relational Reasoning

As in verbal deduction paradigms, relational reasoning problems in the visuospatial domain explore transitive inference across relational argument types (e.g., A is to the left of B, B is to the left of C, A is to the left of C). Typically, participants completing these tasks undergo initial out-of-scanner training where they encode multiple ordered shape pairs (e.g., $A < B$, $B < C$, $C < D$, and so on). Taken together these pairs implicitly represented elements drawn from an ordered shape string (e.g., $A < B < C < D < \dots < N$). Then, during MRI scanning, participants viewed non-sequential pairs of encoded relational shapes and selected the right-most shape (e.g., C in $A < C$ or D in $B < D$; Acuna, 2002; Heckers et al., 2004).

Variations on these relational paradigms involved conditional rule completion or falsifications tasks wherein participants viewed colored shape configurations and were asked if they could complete or falsify a relational rule (e.g., “if there is not a red square on the left, then there is a yellow circle on the right”; Eslinger et al., 2009; Houdé et al., 2000). One such falsification task depicted five colored balls of equal or unequal weights appearing across four balance scales (Wendelken and Bunge, 2010). The scales were drawn balanced or tipped to indicate the relative ball weights. The task was to determine if a fifth scale drawing violated or verified the inferred weight rule. The literature search produced 6 (out of 88

total visuospatial problem solving) relational reasoning contrasts associated with 75 activation foci from 5 papers.

Visual Inductive/Probabilistic Reasoning Paradigms

Inductive reasoning paradigms wherein general rules are inferred from specific instances were less ubiquitously used in the visuospatial domain. However, appropriate paradigms that presented visual information and asked participants to decide on generalizable rules or plausible answer choices were included in this analysis. In one such task (Goel and Dolan, 2000) participants considered sets of animal drawings where the animal's physical characteristics (e.g., tail length, abdomen shape) varied along several degrees of similarity. The task was to generate a rule to determine if all animals in a set were likely of the same species. Another task (Blackwood et al., 2004) showed serial images of blue and red balls and participants determined if the balls had been drawn from a bottle containing either a 40:60 or a 60:40 ratio of blue to red balls. In another task (Lu et al., 2010) participants viewed inverted triangles displaying numeric values at each vertex. Each triangle followed a known (e.g., left – right) or unknown (e.g., bottom + right = left, right + left = bottom) calculation rule. Participants performed simple calculation (control condition) or inferred the triangle's rule from a target triangle and then applied that rule to a new triangle (activation condition). We included this paradigm in the visuospatial problem solving meta-analysis, even though numerical calculation was involved, because the target problems used visuospatial stimuli to illustrate spatially encoded induction rules. The literature search yielded 4 (out of 88 total visuospatial problem solving) inductive reasoning contrasts associated with 46 activation foci from 3 published papers for inclusion in the meta-analysis.

Additional Visuospatial Tasks

We also included visual problem solving within game-play contexts. Strategy-based board games such as Chess or Go involve abstract reasoning, planning, and visuospatial processing. Although not prevalent in the literature, some studies (Atherton et al., 2003; Chen et al., 2003) have investigated the neural correlates involved in this level of strategic game-play. Participants in these experiments viewed in-progress game boards and either identified the position of target pieces (control condition) or determined the best next move within a mid-game board configuration (activation condition). The literature search yielded 3 (out of 88 total visuospatial problem solving) additional visuospatial contrasts containing 53 activation foci from 2 papers.

3.2. Global Meta-Analysis

After completing the literature search, an ALE meta-analysis was performed across the total set of 131 papers that examined problem solving within all modalities and paradigms to identify convergent brain regions associated across all problem solving task described above. When multiple contrasts were reported within a single paper they were modeled as separate experiments provided they met our inclusions criteria (with 2.10 contrast included on average per paper, and no single paper contributing more than seven separate contrasts.) **This global problem solving meta-analysis included 280 contrasts, which reported a total of 3,166 foci from 1,919 individuals.** Convergence across experiments was observed in the frontal and parietal cortices, bilaterally including the superior, middle, and inferior frontal gyri (SFG, MFG, and IFG), as well as the dlPFC, dorsomedial prefrontal cortex (dmPFC), and ACC (Figure 1; coordinates listed in Table 1). Bilateral parietal regions were observed across the medial posterior parietal cortex including the SPL, inferior parietal lobule (IPL), and precuneus. In addition to these frontoparietal clusters, consistent activation was observed in the bilateral anterior insular cortex (aIC), extending into the claustrum, lentiform nucleus, caudate, and anterior thalamus. Primary visual regions were also implicated in problem solving with bilateral convergence occurring in the inferior and lateral occipital gyri (IOG and LOG), including the lingual gyrus (LG) and fusiform gyrus (FG).

3.3. Mathematical Problem Solving Meta-Analysis

We next investigated 99 experiments reporting a total of 1,044 foci across 41 papers wherein 560 participants completed mental mathematical problem solving tasks using number, mathematical symbols, and/or letter- or symbol-based stimuli. Significant ALE-based convergence across these studies was observed in the frontoparietal cortices, including the dlPFC, dmPFC, ACC, SPL, IPL, and precuneus (Figure 2A, Table 2a). Similar to the global analysis, multiple bilateral MFG clusters were observed alongside convergence in SFG extending into the ACC. Peak ALE scores were observed in large bilateral clusters centered about the IFG, aIC, and in portions of anterior prefrontal cortex (PFC). These frontal regions included somewhat larger left-lateralized ALE clusters. In addition to frontal regions, sizeable posterior parietal clusters were observed in the supramarginal gyrus as well as bilateral IPL and SPL. Unlike other representation-specific analyses, the mathematical problem solving analysis displayed bilateral occipital convergence in the IOG, LOG, FG, and LG.

3.4. Verbal Problem Solving Meta-Analysis

Convergence across 93 verbal-based problem solving experiments reporting 1,028 foci in 43 papers and including 650 participants was next tested. Similar patterns of convergence occurred across the bilateral dlPFC, dmPFC, and posterior parietal regions, although somewhat smaller clusters were observed

compared to the calculation analysis (Figure 2B, Table 2b). Verbal problem solving revealed left-emphasized MFG convergence extending from precentral gyrus / presupplementary motor area (Pre-SMA), across dlPFC, left MFG, and left orbitofrontal cortex. Specific to this domain were clusters in the left-lateralized middle temporal gyrus as well as bilateral thalamus. Convergence was also observed in the LG, and clusters were observed in the cerebellar uvula and pyramis/tuber.

3.5. Visuospatial Problem Solving Meta-Analysis

The third and final domain-based ALE meta-analysis included 88 experiments revealing 1094 activation foci appearing in 50 papers in which 745 participants engaged in picture-based problem solving tasks. Within the visuospatial domain, problem solving meta-analysis revealed similar regions of convergence as in the global as well as language- and mathematical-based problem solving analyses, including medial posterior parietal cortex, bilateral horizontal IPS, right SPL, precuneus, bilateral aIC, and bilateral mid and superior frontal gyri (Figure 2C, Table 2c). Multiple precuneus, posterior cingulate, parahippocampus, and retrosplenial cortex clusters were observed for this visuospatial analysis that were not revealed by the other representational domains. Additionally, the cortical clusters were overall more strongly lateralized compared to the mathematical and verbal meta-analyses, and larger regions of dlPFC convergence were observed in the right compared to left hemisphere.

3.6. Conjunction Across Domains

Next, we sought to identify a core set of brain regions commonly linked with problem solving across all representational domains by performing a conjunction analysis (Nichols, 2005) across the mathematical, verbal, and visuospatial ALE results. Nine clusters were identified in this conjunction analysis (Figure 2D, Table 3). These clusters included the dorsal aspect of the cingulate gyrus/SFG, as well as left dlPFC, inferior middle frontal gyri (IMFG), left aIC, and the horizontal segment of the IPS, with greater cluster extent observed in the left hemisphere. Table 4 illustrates the ten top terms most associated with the core problem solving network resulting, as resulting from formal reverse inference analysis.

3.7. Contrast Analyses

Then, to examine functional specialization we performed formal contrast meta-analyses (Bzdok et al., 2015; Laird et al., 2005) and identified regions of domain specificity for mathematical problem solving (Figure 3A, Table 5a), verbal problem solving (Figure 3B, Table 5b), and visuospatial problem solving (Figure 3C, Table 5c). Mathematical problem solving uniquely recruited multiple clusters within a dorsal, frontal, insular, and occipital network of regions. Superior parietal lobules, IPS, and postcentral sulci

were observed bilaterally along with the left posterior precuneus and bilateral pars opercularis/IFG. The left of these IFG clusters showed significant extent along the precentral sulcal boundary towards the precentral gyrus. Mathematical-specific clusters were also observed in the bilateral anterior insula cortices, bilateral occipital poles, and in the left temporo-occipital part of the left inferior temporal gyrus. Verbal problem solving was specifically associated with convergence in a strongly left-emphasized set of frontal, temporal, and occipital areas. Large clusters occurred in Wernicke's area / left posterior temporal gyrus, Broca's area / left pars triangularis, bilateral dorsal striatum (putamen and caudate), and in the left angular gyrus. Clusters with lesser extent were observed in the left dlPFC, left lingual gyrus, and in the dorsomedial PFC. This contrast analysis revealed two additional clusters selectively observed in verbal problem solving studies in the left posterior lobe and the right anterior lobe of the cerebellum. Visuospatial problem solving studies showed domain-specific fronto-parietal convergence bilaterally in the superior frontal sulci, precentral sulci, and in right dlPFC, with cluster extent from rostral to caudal subdivisions. Visuospatial-specific clusters were additionally observed for bilateral precuneus, right inferior parietal lobule, posterior cingulate, retrosplenial cortex, and parahippocampus.

3.8. Problem Demand Analysis

Lastly, we wished to examine the common activation patterns associated with problem solving demand generalized across problem type. We employed a similar selection procedure to that adopted by Duncan and Owen (2000) in their observation of their multiple demand network by locating convergent neural correlates associated with task load while simultaneously controlling for variability across problem type. We selected contrasts that compared problem difficulty across different levels of identical problem tasks (see Supplementary Table 1d). We tested convergence across 41 Complex > Simple problem solving experiments reporting 505 foci in 21 papers and including 355 participants. Patterns of co-activation associated with problem demand were similar to common activity patterns revealed by the global, domain, and conjunction analyses. Bilateral dlPFC, dmPFC/ACC, left precentral sulcus, bilateral aIC, left lateral frontopolar cortex, left precuneus, bilateral SPL, IPL, and horizontal IPS were associated with increased problem demand (Figure 4 purple, Table 6). This problem demand network showed significant overlap with each of the within-domain meta-analytic maps, as well as with the conjunction network.

4. DISCUSSION

We assessed the diverse collection of problem solving neuroimaging studies and performed multiple quantitative coordinate-based meta-analyses to identify common and distinct brain networks

consistently engaged across various tasks. This study is the first to systematically explore convergent brain areas evoked by problem solving across its multiple representationally diverse forms. The meta-analytic corpus of 131 studies included paradigms that, while traditionally considered distinct, met a common operational definition of problem solving wherein participants performed multi-stepped, solution-driven critical thinking operations bounded by mathematical, verbal, or visuospatial rule sets. Global analysis across domains revealed broad involvement of frontal, parietal, insular, and occipital regions. Separate domain-specific analyses revealed consistent but unique convergent activation patterns in the dlPFC, mPFC, IPLs, aIC, and in temporal, occipital, and subcortical structures. To delineate content-general or content-specific convergence of activation, we then performed formal conjunction and contrast analyses across mathematical, verbal, and visuospatial networks. We thus identified a core system of dlPFC, dmPFC, IPS, and SPL areas that subtends all types of problem solving. Domain-specific maps revealed multiple clusters in left temporal gyrus, bilateral insula, occipital pole, bilateral pars opercularis, and areas across the superior parietal lobules that displayed functional selectivity within task sub-types. Lastly, problem demand was associated with activation across a broad set of frontal, parietal, and insular areas similar to those revealed in the domain and conjunction analyses.

4.1. A Core Problem Solving Network

Results from the global problem solving meta-analysis provide evidence that problem solving processes across traditionally distinct paradigms involving diverse content types engage regions within a consistent and broad network of fronto-cingulo-limbic-parietal regions. This network included frontal gyri, especially in dorsal lateral and dorsal medial PFC, anterior cingulate, parietal lobules, precuneus, occipitotemporal gyri, anterior insula, caudate, putamen, and thalamus. Of these regions, robust problem solving-related convergence was observed across principal nodes in the well-characterized central executive (Minzenberg et al., 2009; Niendam et al., 2012), Multiple Demand (Duncan, 2013, 2010, 2006; Duncan and Owen, 2000), and salience networks (Seeley et al., 2007). From a systems-level perspective of brain function, in which distinct distributed networks dynamically interact to flexibly guide complex behaviors (Cohen et al., 2004), our findings suggest generalized problem solving relies on a cooperation between perceptual and regulatory systems. Specifically, the aIC has been described as a node connecting central executive and salience networks which translates pertinent bottom-up information from sensory and limbic inputs to CEN areas, thereby negotiating network switching between internally focused (i.e., autobiographical) and externally directed (i.e., goal-oriented) states (Cocchi et al., 2013; Goulden et al., 2014; Menon and Uddin, 2010; Uddin, 2015). This interaction is

thought to initiate CEN regions to implement top-down control and direct coordinated responses and behavior. Multiple areas across the PFC have been implicated in a range of broad executive functions including working memory (Curtis and D'Esposito, 2003; Owen et al., 2005), planning (Owen, 1997), flexibility (Armbruster et al., 2012; Leber et al., 2008), language comprehension (Ferstl et al., 2008), reasoning (Donoso et al., 2014; Krawczyk et al., 2011), and decision making (Keuken et al., 2014). Observed parietal CEN areas are also associated with a dorsal attention network and regions within the superior and inferior parietal lobules support a range of processes including learning (Sarma et al., 2016), visuospatial working memory (Zago and Tzourio-Mazoyer, 2002), congruency in space, time, and number sense (Riemer et al., 2016), calculation (Arsalidou and Taylor, 2011; Dehaene et al., 2003), metacognitive monitoring of information retrieval (Elman et al., 2012), and visual attention (Behrmann et al., 2004; Blankenburg et al., 2010; Duncan, 2006). The convergent activation within CEN and salience networks identified in the global problem solving analysis suggests the areas and their associated cognitive functions, as influenced by bottom-up signals mediated by aIC, play critical roles in problem solving across content domains.

While the global analysis identified common regions of convergence, domain-separated problem solving meta-analyses revealed distinct networks that, importantly, showed agreement across a focused set of frontoparietal areas. These conjunction results suggest problem solving consistently relies on a network-level subdivision of core executive regions that may bring to bear common cognitive and attentional elements fundamental to all problem solving processes. Our functional decoding analysis revealed this core network as being associated with psychologically-linked terms such as “monitoring”, “switching”, “attention”/“attentional”, “working memory”/“memory”, and “demands”, indicating the core network likely provides multiple general purpose resources including supervisory control (e.g., managerial support directing or monitoring cognition), attentional and memory processes, and perceptual and cognitive resources to achieve a broad range of problem solving tasks. One proposed role of such distributed network subdivisions is in actively managing the explicit within-network engagement of brain areas to accomplish specific actions and goals (Cole et al., 2013; Fedorenko and Thompson-Schill, 2014; Mill et al., 2017; Telesford et al., 2016). In this way, particular zones may be differentially engaged based on the demands and resources required to complete a task, and shared zones may be involved with mental operations that are critical to, and potentially transferable across, multiple task types (Cole et al., 2013; Duncan, 2010; Niendam et al., 2012). Common centralized activity across a range of tasks may also be responsible for making available basic cognitive resources, such as working memory maintenance or adaptable processing elements, that are critical in performing demanding tasks (Cabeza

and Nyberg, 2000; Fuster, 2013). Indeed, these core regions are frequently functionally coupled across diverse paradigms (Duncan and Owen, 2000; Niendam et al., 2012) and likely are central in providing flexible attentional focus in many forms of human cognition (Duncan, 2013, 2006). Thus, the within-domain problem solving conjunction map engaging dmPFC, mid-DLPFC, IMFG/inferior frontal junction, left precentral gyrus, precuneus, left horizontal IPS, and bilateral areas in the SPL may represent a shared sub-network that commonly provides subordinate processing resources (e.g., those engaged in order to carry out directed cognitive tasks) as well as broader administrative support across problem solving in general. Focused parietal cortex activity, such as that observed here, has previously been implicated in start-cue processes, and dedicated sections of the dmPFC and dIPFC are believed to form a core system responsible for information maintenance, monitoring, and intentioned sustaining of goal-oriented task-sets (Dosenbach et al., 2006; Miller and Cohen, 2001). Mid-dIPFC and IMFG/IFJ regions are thought to accomplish process-relevant attentional shifting and task coordination (Brass et al., 2005; Bunge et al., 2002; Derrfuss et al., 2004). Additionally, it has been proposed that a similar set of core regions common across demanding cognitive tasks together may also act to flexibly trigger specific context-dependent schemata appropriate for task performance (Cieslik et al., 2015). These observations are consistent with the Multiple Demand system, proposed by Duncan et al. (2010, 2006; Duncan and Owen, 2000), that functions by reducing complex reasoning processes into sub-parts and engaging brain areas to carry out cognitive operations necessary for successive task steps. Thus, it is plausible that the common engagement of these multiple core CEN sub-regions during problem solving may support managerial processes involving initiating, sustaining, and directing attentional demands between multiple sub-goals that are part of inherently complex multi-stepped processes, while simultaneously providing basic cognitive resources to aid in processing within a wider set of functionally- and situationally-relevant sub-networks. Though additional empirical work should be conducted to establish definitive functional roles and mechanisms, we posit that this common network provides shared general purpose cognitive processes that commonly guide cognitive operations during problem solving to access, manage, and allocate relevant executive resources.

4.2. Representational Domain Specificity

The set of regions observed as common across all problem solving contrasts represents a necessary but insufficient neural system for accomplishing the demands of problem solving within particular contexts. Separate verbal, visuospatial, and mathematical meta-analyses revealed robust networks each containing regional dissociations across domains. Therefore, to better characterize domain specificities

in the context of problem solving type, we performed contrast analyses examining brain function selective to each domain. Our aim was to identify any segregated areas that may be responsible for particular roles, and thereby distinguish and describe the multilevel processes occurring within context-specific problem solving.

In the case of mathematical problem solving, the explicit recruitment of fronto-parietal, occipito-temporal, intraparietal sulcal, and aIC sub-regions is consistent with accumulating evidence that a specific constellation of cortical areas is critically involved in calculation and together may act as a circuit for mathematical cognition. Numerical manipulation, number ordering, arithmetic, and magnitude processing all engage a set of such sub-areas (Ansari, 2008; Arsalidou and Taylor, 2011; Buetti and Walsh, 2009; Dehaene et al., 2003; Piazza and Eger, 2016). Moreover, the left temporo-occipital part of the inferior temporal gyrus, which was identified in this analysis, has been characterized as a “number form brain area” responsible for processing visual numerals (Grotheer et al., 2016; Merkley et al., 2016; Shum et al., 2013). The so-called triple-code model of number processing (Dehaene, 1992; Dehaene and Cohen, 1995) conceives of a ventral visual pathway that communicates numeral information from occipital poles to the number form area, where numerals are then represented in a mental scratchpad. Information is then routed along either a temporo-occipital pathway to the IPS/SPL for magnitude representation, or onto language processing areas where numbers are represented syntactically and/or fact-based knowledge is accessed. According to this model, prefrontal circuits then enact the sequential multi-stepped operations necessary for calculation. Our results coincide with this model and we posit that the contrast clusters here revealed constitute a functional sub-system to execute mathematically relevant reasoning processes.

While consensus has not yet been reached on functional pathways subtending linguistic and verbal processes in language-brain research (Poeppel and Hickok, 2004), it is clear that specific cortical areas, in line with those uncovered in the present verbal contrast analysis, play vital roles in language processing (Binder et al., 1997). Significant domain-selective convergence during verbal problem solving occurred in the classical Wernicke’s and Broca’s areas, which support a broad range of language processes (DeWitt and Rauschecker, 2013; Gough et al., 2005; Lesser et al., 1986; Poeppel et al., 2008; Wagner et al., 2001). Left-hemispheric language lateralization (Powell et al., 2006) was observed across several clusters in posterior and superior temporal sulcus/parieto-temporal junction, areas that co-activate with dorsal-stream language regions (Erickson et al., 2017) and may be responsible for verbal working memory subroutines (Poeppel and Hickok, 2004). Additionally, this contrast also identified verbal-selectivity in

the left angular gyrus, a region involved with reading comprehension and semantic processing (Seghier, 2013). Sub-cortical basal ganglia clusters (dorsal striatum/caudate) may support reasoning and decision-making (Robertson et al., 2015), linguistic computation (Monti et al., 2009; Poeppel and Hickok, 2004), and grammatical processing (Ullman, 2001). Thus, within the verbal domain, we posit that these identified regions are responsible for actualizing verbally-relevant operations as they are applied within the context of language-based problem solving.

Visuospatial-selective activity in the superior frontal sulci during problem solving topographically corresponds to the primary cortical oculomotor areas, the so-called human frontal eye fields (FEFs; Cieslik et al., 2016; Grosbras et al., 2005; Lobel et al., 2001; Vernet et al., 2014), associated with eye movements and visual awareness processes, including covert (i.e. non-motor) attention shifts during visual discrimination (Grosbras et al., 2005; Muggleton et al., 2003; Vernet et al., 2014). The observed right hemispheric visuospatially-selective MFG cluster in conjunction with the FEFs has been implicated in visual search and spatial working memory tasks (Grosbras et al., 2005). Further, as part of the brain's gaze control system, the FEFs project to PFC and parietal areas, and increased interaction of regions within this system occurs during visuospatial judgment, visual focus, and when visuospatial cognitive demands are increased (de Graaf et al., 2010; Edin et al., 2007; Vannini et al., 2004). It has been suggested that, when actively managing visuospatial working memory demands (Courtney et al., 1998), FEFs send top-down signals to PPC for visuospatial feature analysis. This analysis is then focused to task-relevant features in the visual stimuli via signals from the MFG (de Graaf et al., 2010), a finding that is consistent with our visuospatially-specific observations. These contrast results suggest that visuospatial problem solving engages a neural subsystem to allocate oculomotor and attentional capabilities for visually salient stimuli.

While these above representational domain results provide convincing evidence that distinct subsystems support problem solving within particular domains, we add a cautious note that these findings should not be interpreted as having an overly selective functional role in modality type. For example, the insula is one of most commonly activated regions of the brain (Behrens et al., 2013; Chang et al., 2013), yet its involvement in the mathematical contrast results certainly should not be interpreted as the region exhibiting functional selectivity for mathematics. The same holds true for the within-domain maps: these results can resemble similar findings from relatively unrelated studies across the literature (e.g., the mathematical domain network shares activity within regions also observed during target detection and response inhibition, tasks which arguably have little mathematical demand;

Hampshire et al., 2010). Rather, we believe our results serve to highlight the full constellation of brain regions that separately and/or cooperatively support problem solving within specific representational types.

4.3. Cognitive Demand in Problem Solving

The above domain-general, representational, and contrast analyses focused on identifying brain activity associated with or independent of problem type, as defined by representational modality. Included experiments spanned a diverse set of contrasts, allowing us to broadly assess convergence in neural activity linked with distinct varieties of problem solving. However, this pooling across varied contrasts simultaneously limited our ability to delineate neural correlates associated with specific cognitive processes central to problem solving. To address this limitation, we adopted the approach of Duncan and Owen (2000) and included only contrasts that clearly isolated the same aspect of problem solving, namely problem difficulty, while also controlling for task type. In this way we were able to cleanly isolate the neural activation patterns associated with cognitive demand across a breadth of problem solving tasks.

The observed clusters in the dlPFC, frontopolar cortex, dmPFC, aIC, and horizontal IPS represent the collection of brain regions that consistently respond to increases in problem demand, independent of problem type. We note that our observations are consistent with previous findings regarding the brain's multiple demand (MD) system (Camilleri et al., 2018; Duncan, 2010, 2006; Duncan and Owen, 2000; Fedorenko et al., 2013). Significant overlap was observed between the problem demand regions and each within-domain problem network. Thus, general problem solving seems to be broadly linked to the wider MD system common across diverse tasks and responsible for flexibly accomplishing multiple attentional and cognitive functions. The MD system is also thought to play a key role in focusing specific cognitive operations and interfacing with multiple brain systems to execute structured and successive goal-oriented subtasks (Duncan, 2010). It is not a particularly surprising result that a challenging problem would draw on enhanced recruitment of this MD system, but what is perhaps more insightful is that our results seem to suggest this is generally the case, regardless of the type or context of the problem task.

4.4. A Model for Multi-Network Cooperation in Problem Solving

Viewed collectively, these global, common, domain-specific, and demand-related results outline a set of related yet dissociable networks engaged during problem solving. The core set of activated regions appears to be centrally involved in problem demand, and formal reverse inference suggests activation

across these areas provide a set of general cognitive resources that, perhaps, interface across broader brain systems and focus attention within directed sequential action (Duncan, 2010). At the same time, contrast results highlight separate representationally-specific sets of coordinated activation patterns that appear to be honed for achieving precise operations. Together, activity across these domain-general and domain-specific areas combine to form different aspects of the overall activation patterns revealed by problem solving within representational domains. Fundamentally, meta-analytic results are unequipped to evaluate such functional network dynamics, although these processes almost certainly play an essential role within problem solving. While the particular analyses we conducted cannot isolate mechanisms in how these dissociable activation patterns come together to achieve the aggregational cognitive maneuvers that make up problem solving, empirical neuroimaging studies have begun to explore these dynamics in regional functional connectivity and network interactions. Additional work is still needed to elucidate how such processes may support the large variety of problem solving processes humans face on a day-to-day basis. Here, we outline one possible interpretation of how our multiple network observations may come together to holistically achieve problem solving across diverse contexts.

We propose a speculative model of general problem solving brain function that arises from a series of sub-network and systems-level interactions that together orchestrate multifaceted cognitive procedures. In our model, the core problem solving network exerts executive control over cognitive steps to flexibly monitor and maintain neural resources. This process may involve top-down signals dispatched from the core regions to trigger and coordinate distinct subroutines adapted to domain or context-specific demands. Sub-processes that occur within broader networks, perhaps similar to those resolved by our within-domain or global analyses, would likely engage multiple whole-brain systems including salience and executive networks (Bressler and Menon, 2010). The role of these system-level interactions in problem solving may be to facilitate integrative cross-network communication, search for and detect solution relevant stimuli, and funnel information into linked sub-routines to adaptively focus attention to achieve smaller, targeted reasoning procedures accomplishing focused cognition (Cohen and D'Esposito, 2016; Duncan, 2013; Uddin, 2017). We propose that honed processes, as directed by the core network, may participate in feedback loops delivering ascending analyzed information back to whole-brain systems to sustain multi-stepped analytics and trigger confirmatory metacognitive processes (e.g., consistency checking or error detection; Mayer, 1998). If this is the case, the core network may aid in sustaining problem solving-related activity by re-dispatching or re-directing reasoning subroutines as needed, ultimately informing decision making processes to produce problem

solutions. Of course, meta-analytic results alone cannot confirm this model, and a considerable amount of additional research is needed to probe the dynamic cross-network connectivity patterns we have here suggested. However, existing work that sheds light on network dynamics within problem solving, outlined below, seem to be consistent with this proposed model.

Complex network interactions such as those we have proposed here would likely take on diverse forms within problem solving, and understanding the ways in which multilevel systems share information may be key in revealing the neural basis of problem solving efficacy. In language tasks, electrocorticography has resolved dynamics across multiple left hemispheric sub-networks, and while these networks appear to coordinate with similar stepwise profiles across subjects, individual differences in response times were also reported alongside subject-by-subject variation in sub-network duration during task engagement (Collard et al., 2016). This suggests common network sequences subtend task completion, but also distinctive contributions from these dynamics may influence behavioral differences. In fact, performance in problem solving has been explicitly linked to variations in how brain systems interact across problem steps. Anderson *et al.* (2012) revealed shifting combinations of whole-brain neural sub-states in children as they solved algebra problems; individuals with high error rates utilized more sub-states at each problem step than their high-performing peers, and reliance on multiple states decreased as error-prone students achieved competency through practice. Such practice-related interactional changes have also been observed in the case of motor learning where connectivity between visual and motor systems decreased as learning occurred over time, suggesting whole-brain systems operate with increased autonomy as procedures become rote and cognitive load diminishes (Bassett et al., 2015). These findings suggest that difficulties in problem solving may be accompanied by increased cross-network complexity, perhaps as characterized by cognitive lingering or looping between unnecessary or convoluted neural states, and that ease in solution derivation may rely on more efficient multileveled network dynamics.

Yet solving truly novel problems is rarely easy, and these network dynamics should be considered in the context of problem solving as an implicitly challenging act that requires forging exploratory paths towards unknown solutions. These processes can demand substantial cognitive load and may require a certain degree of initial lingering within inefficient operations in order to flip positions of uncertainty towards coordinated and meaningful maneuvers. It is likely, then, that successful problem solving relies on a balance of multileveled and complex network crosstalk that eventually transitions towards efficient cooperation between whole-brain systems and targeted sub-processes. The use of creativity within

problem solving is one resource that aids in flipping initial ineffectual processes towards productive solution derivations (Aldous, 2007; Fink et al., 2009; Lubart and Mouchiroud, 2003), and increased dynamic coupling between salience, DMN, and CEN regions has been observed to support such creative idea production (Beaty et al., 2015). At the same time, creative processes in problem solving go hand in hand with shifting attentional focus across problem features (Friedman et al., 2003; Wegbreit et al., 2012; Wiley and Jarosz, 2012), and increased effective connectivity between salience and CEN regions has been observed in individuals with a strong ability to engage in attentional switching, but not for those with reduced capacity to shift attentional stances during tasks (Kondo et al., 2004). It is likely, then, that differences in problem solving success may be characterized by the nature and process of coupling between salience, CEN, and DMN systems. Individuals experiencing difficulty in solving problems may rely on more elongated creativity and attentional shifting mechanisms that drive connectivity loops between fronto-cingulo-parietal regions. In contrast, individuals with more experience in problem solving may be better able to transition that sustained cross-system driving towards more effective honed sub-processes useful in solution derivation. Understanding the processes by which networks interact may prove to be important when understanding individual or group-level differences in problem solving competency. Meta-analytic techniques such as those employed in the present study cannot resolve brain dynamics or measure between-network connectivity, but the broad and processes-specific nature of our results suggest cooperation between large-scale brain systems and functionally specific sub-networks may play a crucial role in problem solving. Observing how these interactions occur may help elucidate remaining questions in how to better support problem solving success across individuals.

4.5. Limitations and Future Work

This study broadly, and for the first time, characterized the common and dissociable neural correlates underlying multiple examples of human problem solving. The investigation synthesized findings from a corpus of neuroimaging experiments reporting coordinate-based results across varied problem solving manifestations in healthy subjects. We included a wide variety of problem tasks and contrasts so that we could determine convergent brain activity associated with domain general problem solving networks. However, this approach had two main limitations. First, while this set of studies was sufficiently diverse, problem solving as a whole is widely investigated across disciplines and contexts. Thus, the mathematical, verbal, and visuospatial paradigms we examined constitute a subset of the larger breadth of human problem solving. However, while the neural substrates uncovered in this study

may best model a particular slice of possible human problem solving processes, it is tenable that similar systems of coordinating perceptual, regulatory, and/or contextually bound channels are also broadly representative of generalizable neural mechanisms across the scope of human problem solving.

The second limitation stems from the diversity of contrasts chosen. We modeled problem solving as a general process by including a wide variety of contrasts. This broad focus identified commonalities across problem tasks and contexts, but simultaneously restricted our ability to resolve the differential contributions specific cognitive processes had on the resulting meta-analytic maps. However, unlike our domain-general or representationally specific results, the problem demand analysis included contrasts of only one type (i.e., complex > simple problems), and was thus able to identify such common activation patterns linked with problem difficulty. Further investigations seeking to isolate other specific constituent processes or characteristics central within problem solving can take a similar approach.

Further, all problem solving instances in this study were conducted in a laboratory environment. Yet, there is a growing cross-disciplinary appreciation of the many ways social, motivational, and affective processes can impact problem solving abilities (Beilock and DeCaro, 2007; DeBellis and Goldin, 2006; Heller et al., 1992; Mayer, 1998). Thus, the mental processes underlying problem solving in a controlled setting may not identically resemble those of problem solving outside the laboratory. Additional studies bridging problem solving neuroimaging investigations with social and affective neuroscience need to be conducted before we are able to explore these topics with meta-analytic tools. Given these limitations, it is likely that the neural representations of problem solving occurring across naturalistic settings and contexts may involve different sets of activation patterns than those reported in this study. However, our finding of a shared core network that may play a role in coordinating, engaging, or negotiating sensory signals likely holds even for more distributed or complex networks. Integrating neuroimaging research in problem solving with multileveled experimental methods that explicitly attend to ecological significance may more appropriately characterize the ways affective and social factors influence the neural makeup of problem solving.

Lastly, meta-analytic results are of course limited by the quality and volume of studies available in the neuroimaging literature. There are several sources of error inherent to fMRI analyses, such as inter-subject anatomical variability and spatial smoothing, that can lead to decreased resolution in group-level fMRI analyses (Nieto-Castañón and Fedorenko, 2012), and in turn cause specious spatial overlap in meta-analytic results. This issue impacts both fMRI group-level analyses and meta-analysis in general. The results we present in this study show centralized and consistent co-activation patterns across

multiple task types and domains, and because of the coherences across our set of problem solving network findings, they are not likely simply the product of sources of noise. However, spatial error may still have contributed to lack of specificity in our observations.

This study leverages the existing wealth of problem solving activation-location findings to reveal patterns of domain-general and context-specific brain networks associated with diverse problem solving tasks. We propose that the coordinated set of these multiple systems may provide supervisory, attentional, and perceptual support to accomplish problem solving across contexts. Promising next steps in problem solving research may be to further measure these stepwise neural profiles, with an explicit consideration on how naturalistic settings and behavioral factors can impact network interactions. Previous work has linked similar brain areas as those revealed here to inter-individual variability in cognitive ability (Goodkind et al., 2015; Muller et al., 2015), but it is currently unclear how variations in network or sub-network connectivity patterns may aid or inhibit individual differences in problem solving success, and by understanding these processes from both a behavioral and neuroscientific perspective we may be better able to characterize how problem solving skills develop across training. Such insight could inform interventions to address the challenges posed by cognitive dysfunction or affective deterrents on problem solving success (Ferrari, 2011). Neuroscience-based interventions have already been used to successfully improve problem solving performance in students via mindset shifting (e.g., from intelligence-as-fixed stances to beliefs in malleable cognitive abilities; Blackwell et al., 2007; Dweck and Leggett, 1988). Such interventions have not yet been widely applied in cases of cognitive deficits, but a detailed mapping of the neural bases of problem solving could be used to develop tools and strategies to mitigate disadvantaging impacts of dyslexia or dyscalculia (Butterworth et al., 2011; Gabrieli, 2009; Kaufmann, 2008). Arguably, one of the fundamental goals of neuroimaging research as a whole is to impact and improve people's everyday experiences and behaviors. In this sense, one of the most promising future directions of neuroimaging problem solving research is to inform evidence-based educational interventions that aid in successful reasoning and skill development. Thus, understanding the neural mechanisms of problem solving, especially with a focus on how cognitive, affective, and environmental factors can influence network dynamics and neural development, has wide reaching applications.

Conclusions

In the present study, we performed multiple problem solving meta-analyses to answer the questions: *"How is content-general problem solving supported in the brain?"*, *"Does a common network direct all*

types of problem solving processes?”, and *“What neural underpinnings selectively represent problem solving within specific content variants?”*. By considering a comprehensive set of problem solving tasks that, heretofore, have only been considered separately, we provide evidence for a common brain-based mechanism for human problem solving in which a shared frontoparietal system provides dual attentional and regulatory support across diverse problem solving tasks, and we identify distinguishable activation patterns that may uniquely contribute to specific representationally-linked functions in problem solving across contexts. Our results suggest multiple convergent neural systems, including salience and cognitive control networks, give rise to generalized problem solving. Unique circuits within these networks support context-specific sub-classes of problem solving, and consistency across diverse stimulus modalities demonstrates a core network that supports problem solving independent of content or focus. This core network appears to play a key role in managing problem demand. The current work provides a novel neurobiological perspective on the wider study of problem solving across knowledge domains and may serve to inform neuroeducational techniques aiming to understand more about the acquisition of problem solving skills.

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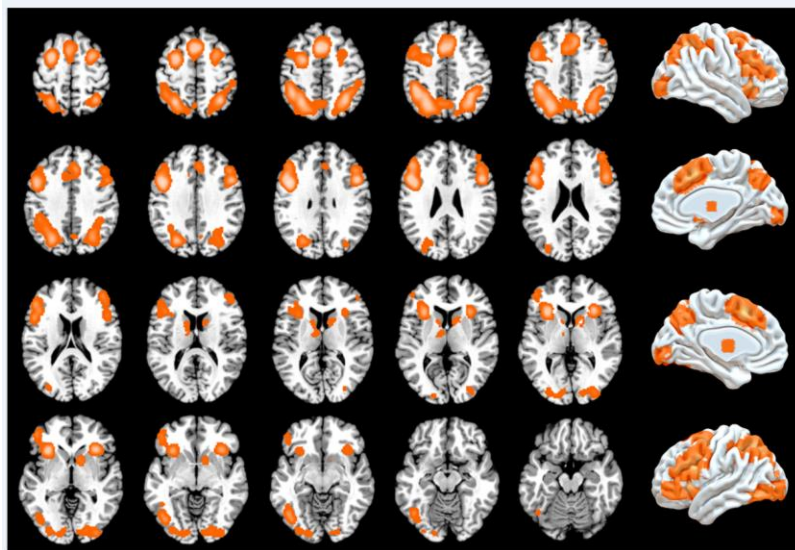
FIGURE CAPTIONS

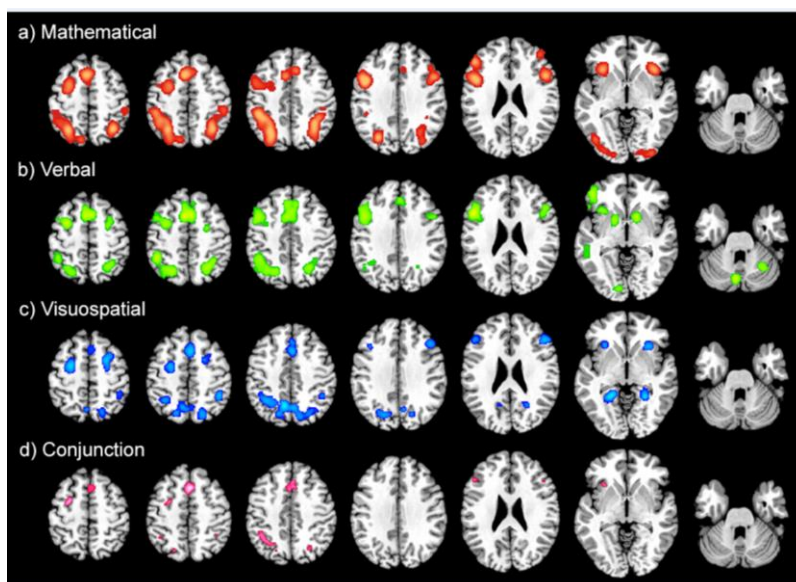
Figure 1. Global Problem Solving Meta-Analysis. The global problem solving meta-analysis identified convergence across 131 papers reporting coordinate results from a diverse range of problem solving experiments. Multiple problem solving modalities were represented in this set, with 280 experimental contrasts across 1,919 subjects. The broad engagement across whole-brain systems depicted by this map represents the overall neural underpinnings of problem solving.

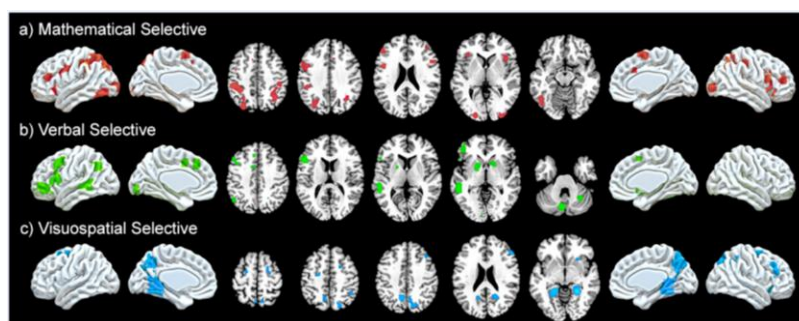
Figure 2. Representational Domain-specific and Conjunction Problem Solving Meta-Analyses. Problem solving experiments were categorized into three representational variants. Within-domain meta-analytic maps are shown for (a) mathematical problem solving (red) = 99 experiments, (b) verbal problem solving (green) = 93 experiments, and (c) visuospatial problem solving (blue) = 88 experiments. A common set of brain regions, present across this heterogeneous set of 280 problem solving contrasts, is depicted in (d), which shows the minimum statistic conjunction between all three within-domain maps (pink).

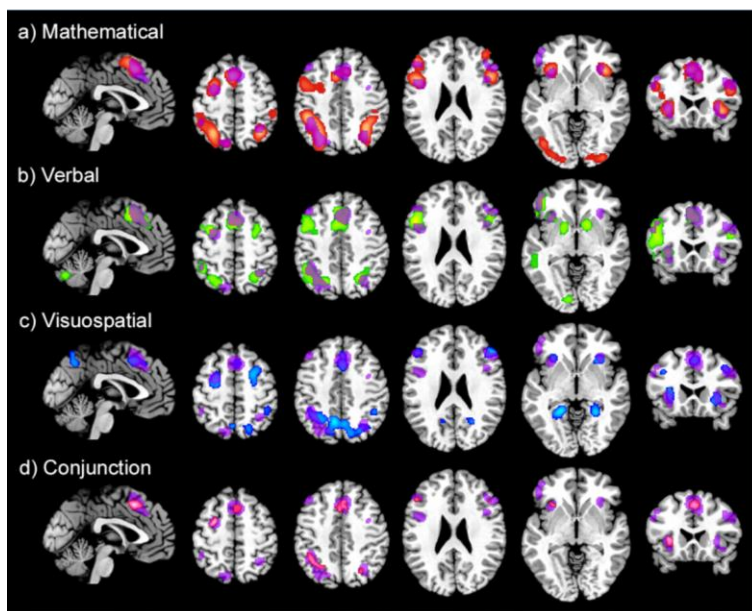
Figure 3. Contrast Problem Solving Meta-Analyses. Contrast analysis for (a) mathematical problem solving ($[Mathematical - Verbal] \cap [Mathematical - Visuospatial]$; rose), (b) verbal problem solving ($[Verbal - Mathematical] \cap [Verbal - Visuospatial]$; green), and (c) visuospatial problem solving ($[Visuospatial - Verbal] \cap [Visuospatial - Mathematical]$; light blue) shows representational specificity across distinct cortical areas. The difference maps show context-bound variations across problem solving types, confirming problem solving within specific domains relies on differential sets of functionally precise neural circuitry.

Figure 4. Problem Demand Meta-Analyses and Domain-Specific Overlays. High vs. low demand problem solving meta-analysis (= 41 experiments), as compared across problem solving by representational domains. Meta-analysis of problem solving tasks contrasting high vs. low demand (transparent purple) are overlaid with the three representational domain meta-analysis and the conjunction meta-analysis: (a) mathematical domain (red), (b) verbal domain (green), (c) visuospatial domain (blue), and (d) conjunction across domains (pink).









TABLES

Table 1. Coordinates of convergent activation from the global problem solving meta-analysis.

Table 2. Coordinates of convergent activation from the (a) mathematical, (b) verbal, and (c) visuospatial problem solving meta-analyses.

Table 3. Coordinates of convergent activation from the minimum statistic conjunction across mathematical, verbal, and visuospatial problem solving meta-analyses.

Table 4. Top ten associated terms resulting from the functional decoding of the conjunction network.

Table 5. Coordinates of convergent activation from the contrast analyses across (a) mathematical, (b) verbal, and c) visuospatial problem solving meta-analyses.

Table 6. Coordinates of convergent activation from the problem demand analysis.

Table 1.**Global Problem Solving Meta-Analysis: Cluster Results**

Cluster	Center of Mass (MNI space)			Cluster Extent (mm ³)	Mean ALE Score
	X	Y	Z		
1	-8	-60	44	43272	4.963767915
2	-40	14	28	34880	5.141902878
3	0	16	48	14136	5.19457248
4	48	22	26	10424	4.716323501
5	34	24	-2	4376	4.996635954
6	28	4	56	4152	4.715339105
7	26	-90	-2	3944	3.877476901
8	-44	-68	-10	3392	4.341783053
9	-22	-90	-6	3256	3.65327546
10	12	8	0	1824	4.033060065
11	-10	-2	8	1184	3.545771589

Table 2.**a) Mathematical Problem Solving Meta-Analysis: Cluster Results**

Cluster	Center of Mass (MNI space)			Cluster Extent (mm ³)	Mean ALE Score
	X	Y	Z		
1	-40	12	28	23472	4.757348649
2	-32	-58	46	20760	4.952114314
3	34	-56	46	12232	4.66749558
4	-2	14	50	8520	4.587236176
5	-38	-78	-8	6000	4.090342946
6	48	14	26	5776	4.553845298
7	36	22	-2	4048	4.601554238
8	30	-92	-2	2136	3.88118772
9	44	44	18	1744	4.158273835

b) Verbal Problem Solving Meta-Analysis: Cluster Results

Cluster	Center of Mass (MNI space)			Cluster Extent (mm ³)	Mean ALE Score
	X	Y	Z		
1	-44	12	32	15312	4.33758957
2	0	18	46	9480	4.318861886
3	-36	-58	46	9040	3.971342055
4	28	-58	48	3912	4.051548754
5	-46	42	-4	3096	4.057574112
6	-56	-38	2	2296	3.895057602
7	46	16	26	2056	3.709159944
8	14	10	-6	1536	4.127226892
9	28	0	56	1528	3.712928623
10	-32	18	-2	1472	3.861140029
11	-6	-76	-32	1296	4.355912738
12	-16	6	-2	1248	4.056552219
13	32	-60	-32	1088	3.83674567
14	-14	-90	-6	1072	3.594205998

c) Visuospatial Problem Solving Meta-Analysis: Cluster Results

Cluster	Center of Mass (MNI space)			Cluster Extent (mm ³)	Mean ALE Score
	X	Y	Z		
1	-6	-64	44	12112	3.716603808
2	-26	-2	56	3848	4.211441027
3	26	2	56	3104	3.989812445
4	46	28	28	2912	3.76056968
5	-22	-48	-8	2832	4.16922139
6	2	18	46	2424	3.894823741
7	26	-44	-8	2136	4.227535089
8	16	-50	10	1920	3.638302641
9	-30	22	2	1672	3.901817582
10	-14	-56	10	1504	3.596709638
11	30	22	-4	1416	3.786637829
12	-46	30	26	1000	3.550904407
13	42	-46	48	984	3.81960495

Table 3.**Conjunction Across Domains: Cluster Results**

Cluster	Center of Mass (MNI space)			Cluster Extent (mm ³)	Mean ALE Score
	X	Y	Z		
1	2	18	48	1536	3.795474291
2	-36	-54	42	864	3.402106762
3	-28	0	56	800	3.845850468
4	-32	20	0	560	3.640799761
5	-48	28	24	120	3.228693962
6	-20	-70	48	96	3.411124468
7	26	-66	42	88	3.235001564
8	48	26	26	40	3.147454739
9	38	-48	48	32	3.250995159

Table 4.**Functional Decoding Analysis: Conjunction Network**

	Term	Weight
1	Monitoring	17.511787
2	Attention	16.065172
3	Working_memory	15.301581
4	Switching	14.103548
5	Motor	13.420883
6	Number	12.446875
7	Aging	10.583265
8	Memory	10.412371
9	Demands	9.7924593
10	Attentional	9.4440851

Table 5.**a) Mathematical Contrast Analysis: Cluster Results**

Cluster	Center of Mass (MNI space)			Cluster Extent (mm ³)	Mean ALE Score
	X	Y	Z		
1	-36	-54	46	7128	2.340867996
2	36	-58	48	3560	2.346692562
3	-48	6	30	2120	2.027558804
4	-48	-66	-14	1176	2.018541098
5	40	20	-4	1096	2.078261852
6	52	14	22	1096	2.07727766
7	-22	-96	0	664	2.101318121
8	34	-94	0	528	2.133773804
9	-36	28	-2	504	1.951239109
10	-48	36	20	464	1.945821404
11	2	4	62	464	1.890849352
12	46	-32	48	424	2.093444824
13	40	44	16	392	1.966767192
14	-10	-76	54	264	1.927932382
15	-10	18	48	24	1.77411747
16	10	20	34	24	1.752256036
17	42	46	28	16	1.736196518

b) Verbal Problem Solving Meta-Analysis: Cluster Results

Cluster	Center of Mass (MNI space)			Cluster Extent (mm ³)	Mean ALE Score
	X	Y	Z		
1	-54	-38	0	2248	2.997398615
2	-50	20	14	1840	2.411432981
3	-6	-76	-32	1168	2.755334377
4	-18	6	-4	1016	2.47303915
5	-46	44	-4	928	1.907864809
6	16	10	-6	768	2.219819307
7	32	-58	-32	760	2.22034359
8	-44	16	42	688	1.848007679
9	-48	-62	38	432	2.081069469
10	-8	6	44	248	1.883606553
11	-8	28	44	216	1.80697155
12	-52	24	-6	80	1.819324493
13	24	-60	46	48	1.733970284
14	8	12	54	32	1.815988064
15	-8	-90	-4	32	1.730034351
16	-20	-64	48	16	1.735799193
17	-14	-88	-8	16	1.734013796

c) Visuospatial Problem Solving Meta-Analysis: Cluster Results

Cluster	Center of Mass (MNI space)			Cluster Extent (mm ³)	Mean ALE Score
	X	Y	Z		
1	-22	-48	-8	2648	2.875540972
2	26	-44	-8	2128	3.413183212
3	14	-70	44	2000	2.023887396
4	16	-50	10	1840	3.255892754
5	-14	-56	10	1408	2.71631217
6	-10	-60	44	1176	2.350823879
7	52	32	24	576	2.226128817
8	22	0	56	544	1.922692895
9	-22	-10	54	472	1.992258668
10	40	26	38	288	2.014489889
11	44	-50	50	232	1.95740664
12	28	20	-6	144	1.769598603
13	-4	-66	58	96	1.929203629
14	-12	-72	34	72	1.777338266
15	-28	16	10	48	1.747480989
16	-24	14	62	16	1.708054066

Table 6.**Problem Demand Meta-Analysis: Cluster Results**

Cluster	Center of Mass (MNI space)			Cluster Extent (mm ³)	Mean ALE Score
	X	Y	Z		
1	2	20	46	8000	4.666377414
2	46	18	30	6048	4.15580997
3	-30	-62	46	5888	3.862501404
4	-46	18	30	5488	3.90340326
5	-48	42	-4	2952	3.816493092
6	-26	-2	56	2008	4.388107072
7	30	-60	48	1960	3.703304083
8	-32	20	-2	1712	4.010184277
9	34	24	-6	1496	3.495624957