

# Shared and Distinct Contributions of Rostrolateral Prefrontal Cortex to Analogical Reasoning and Episodic Memory Retrieval

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**Abstract:** Rostrolateral prefrontal cortex (RLPFC) is widely appreciated to support higher cognitive functions, including analogical reasoning and episodic memory retrieval. However, these tasks have typically been studied in isolation, and thus it is unclear whether they involve common or distinct RLPFC mechanisms. Here, we introduce a novel functional magnetic resonance imaging (fMRI) task paradigm to compare brain activity during reasoning and memory tasks while holding bottom-up perceptual stimulation and response demands constant. Univariate analyses on fMRI data from twenty participants identified a large swath of left lateral prefrontal cortex, including RLPFC, that showed common engagement on reasoning trials with valid analogies and memory trials with accurately retrieved source details. Despite broadly overlapping recruitment, multi-voxel activity patterns within left RLPFC reliably differentiated these two trial types, highlighting the presence of at least partially distinct information processing modes. Functional connectivity analyses demonstrated that while left RLPFC showed consistent coupling with the fronto-parietal control network across tasks, its coupling with other cortical areas varied in a task-dependent manner. During the memory task, this region strengthened its connectivity with the default mode and memory retrieval networks, whereas during the reasoning task it coupled more strongly with a nearby left prefrontal region (BA 45) associated with semantic processing, as well as with a superior parietal region associated with visuospatial processing. Taken together, these data suggest a domain-general role for left RLPFC in monitoring and/or integrating task-relevant knowledge representations and showcase how its function cannot solely be attributed to episodic memory or analogical reasoning computations. *Hum Brain Mapp* 00:000–000, 2015. © 2015 Wiley Periodicals, Inc.

**Key words:** source memory; relational integration; semantic; multivariate pattern classification; decoding; functional connectivity; network analysis; rostral prefrontal cortex

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## INTRODUCTION

Rostrolateral prefrontal cortex (RLPFC) is thought to support the highest level and most abstract forms of cognitive control and decision-making, given its position at the apex of a putative rostrocaudal prefrontal hierarchy [Badre and D'Esposito, 2009; Koechlin and Hyafil, 2007; Ramnani and Owen, 2004]. This anterior-most segment of the frontal lobe, also referred to as frontopolar cortex, is generally considered to encompass lateral sections of Brodmann's area (BA) 10, although its definition is often broadened to include immediately neighboring aspects of BAs 9, 46, and 47 [e.g., Christoff and Gabrieli, 2000; Wendelken, et al., 2012]. Functional magnetic resonance imaging (fMRI) studies have reported RLPFC activations across a range of tasks requiring various high-level cognitive processes, including relational integration in analogical reasoning [Bunge, et al., 2005; Cho, et al., 2010; Green, et al., 2006, 2010; Krawczyk, et al., 2011; Watson and Chatterjee, 2012; Wendelken, et al., 2008b], initiating episodic memory search and evaluating retrieved contextual details [Lepage, et al., 2000; Ranganath, et al., 2000; Reynolds, et al., 2006; Simons, et al., 2005, 2008], task-set implementation and cognitive branching [Badre and D'Esposito, 2007; Charron and Koechlin, 2010; Koechlin and Hyafil, 2007; Koechlin, et al., 1999; Sakai and Passingham, 2002, 2006], storing situationally contingent intentions in the service of prospective memory [Beck, et al., 2014; Burgess, et al., 2011; Gilbert, 2011; Momennejad and Haynes, 2012], making counterfactual inferences that facilitate hypothesis-testing [Donoso, et al., 2014], and regulating the shifting between externally-oriented and internally oriented attentional states [Burgess, et al., 2007; Gilbert, et al., 2005]. Many of these high-level cognitive operations are intimately related to one another and likely constitute alternative conceptual framings of the same underlying phenomena. The involvement of RLPFC across a such a diverse array of cognitive task paradigms (for a meta-analysis, see [Gilbert, et al., 2006]) thus begs the question of whether there are core computations shared across these paradigms, or whether anatomically circumscribed RLPFC subregions mediate distinct processes that only appear to be overlapping when one takes a bird's-eye view of the literature. Because many anterior prefrontal regions can be labeled as RLPFC, and because few studies have attempted to directly compare RLPFC involvement across different cognitive domains, such as memory and reasoning, it has been challenging to know whether the RLPFC effects that have been reported in these respective literatures are related to each other in a meaningful way. One previous study by Reynolds et al. [2006] jointly examined episodic retrieval and relational integration processes and found that these cognitive functions appeared to be supported by distinct RLPFC foci, although they did identify a right-lateralized RLPFC region that showed sensitivity to both retrieval and integration demands.

In the memory literature, RLPFC has been consistently implicated in episodic retrieval processes. Early positron

emission tomography research showed that common RLPFC regions were engaged across four distinct memory retrieval tasks [Lepage, et al., 2000]. The authors theorized that RLPFC supports the enactment of a so-called "retrieval mode," involving the tonic specification of an internally-oriented attentional state in which one's goal is to search one's memory for relevant episodic content. Further research, using fMRI, confirmed that RLPFC is recruited in a temporally sustained manner during blocks of episodic retrieval trials, with the degree of activation modulated by the demands for cognitive control [Velanova, et al., 2003]. By incorporating a mixed block/event-related design, this study was also able to identify a separate RLPFC cluster that showed transient recruitment during trials with successful retrieval outcomes. Other studies have emphasized a role for RLPFC in the specification of retrieval strategies to recover specific contextual details about a past experience and/or the monitoring of the retrieved content [Dobbins and Han, 2006; Dobbins and Wagner, 2005; Ranganath, et al., 2000; Reynolds, et al., 2006; Simons, et al., 2005, 2008]. In meta-analyses of episodic retrieval, RLPFC consistently emerged as a core locus of activation [Cabeza and Nyberg, 2000; Gilbert, et al., 2006; Wagner, et al., 2005].

In the reasoning literature, a number of fMRI studies have demonstrated a role for RLPFC in relational reasoning, independent of task domain [for review, see Vendetti and Bunge, 2014]. One early study presented participants with visuospatial reasoning problems adapted from the Raven's progressive matrices test and found that RLPFC was preferentially activated on trials where two relations needed to be simultaneously considered and integrated [Christoff, et al., 2001]. A later study using word stimuli reported elevated RLPFC activity on trials where participants had to solve propositional analogies (requiring the comparison of two first-order semantics relationships) relative to trials that only demanded decisions about a single first-order semantic relationship [Bunge, et al., 2005]. Although such findings might point one to the conclusion that RLPFC engagement is simply proportional to the cognitive demands of the task, carefully designed follow-up experiments have demonstrated that RLPFC activity cannot be attributed to task difficulty alone, but rather seems to track the complexity of the relational processing [Wendelken, et al., 2008a, b] and/or the degree of representational abstractness [Christoff, et al., 2009]. In these studies, difficulty levels were either matched across conditions, or else it was the case that the most difficult condition was not the one that elicited the greatest RLPFC activity. Other work has ruled out an interpretation of RLPFC activity as being attributable to demands for interference resolution. In a study involving pairs of cartoon characters that either matched or mismatched on specific perceptual attributes, RLPFC was activated when an increasing number of visual characteristics needed to be compared but not when a visual characteristic needed to be inhibited [Cho, et al., 2010]. Further work has suggested that distinct RLPFC subregions may be preferentially recruited during

separate phases of the analogical reasoning process, such as generating structured representations of the stimuli and performing the mapping/comparison process [Krawczyk, et al., 2010; Volle, et al., 2010]. And it has been argued that left RLPFC is specifically involved in the abstract integration of multiple relationships [Bunge, et al., 2009].

Clearly, RLPFC is recruited for both reasoning and memory processes, but how distinct are the functional roles for RLPFC regions in these two cognitive domains? One approach that has yielded some clues into the neuro-cognitive mechanisms supported by RLPFC has been to examine which brain regions RLPFC communicates with as individuals perform goal-oriented operations requiring the retrieval of task-specific content. RLPFC regions appear capable of flexibly adjusting their functional connectivity with distinct posterior brain regions depending on the goals of the task at hand. For instance, one study found that left RLPFC preferentially interacted with different task-specific processing areas in left frontal cortex according to whether one's task-set required preparation for an upcoming phonological task or semantic task [Sakai and Passingham, 2006]. In a study of relational reasoning, Wendelken et al. [2012] found that the strength of coupling between left RLPFC and brain regions involved in either visuospatial or semantic processing is modulated based on the type of relations participants must consider to make their judgments. Although RLPFC can exhibit functional coupling with a range of content-specific processing regions, this area is thought to be a critical node in a core network sometimes referred to as the frontoparietal control network (FPCN) [Dosenbach, et al., 2007; Power, et al., 2011]. Indeed, RLPFC is often used as the "seed" region to identify the FPCN; this is typically done by looking for voxels throughout the brain whose spontaneous fluctuations in low-frequency blood-oxygen-level-dependent (BOLD) signal are correlated with those of the seed during the undirected resting-state [Power, et al., 2011; Shirer, et al., 2012; Vincent, et al., 2008]. This was further verified by a meta-analysis examining co-activation of RLPFC areas, showing that they tend to co-activate with FPCN areas [Gilbert, et al., 2010].

Although patterns of correlated resting-state BOLD fluctuations can be used to subdivide the brain into a set of discrete networks, these networks dynamically interact with one another during cognitive tasks. For instance, the FPCN has been found to show strong functional coupling with either the default mode network (DMN) or the dorsal attention network (DAN) depending on whether the task context requires orienting one's attention towards internally generated information or external information in the environment, which are the respective cognitive domains associated with these brain networks [Spreng, et al., 2010]. The ability of RLPFC (and its associated FPCN structures) to flexibly interact with distinct neural systems depending on task goals may be one important factor in understanding its common engagement across such a wide range of higher cognitive processes.

We designed the present fMRI study in an effort to further elucidate the nature of the RLPFC involvement in memory and reasoning. By having the same cohort of subjects perform closely matched tasks of episodic memory retrieval and verbal analogical reasoning during the same scanning session, our experiment offers a unique opportunity to evaluate the degree to which common and/or distinct RLPFC regions are engaged during these two cognitive domains. Our use of a mixed block/event-related design allows us to separately model transient recruitment in response to the information processing demands posed by individual trials and temporally-sustained processes [Petersen and Dubis, 2012]. We predicted that transient effects would dominate in RLPFC, as many prior memory and reasoning studies have reported trial type-specific activation here. To the degree that overlapping RLPFC activations are observed across the memory and reasoning tasks, we can use multivariate classification techniques [Rissman and Wagner, 2012; Tong and Pratte, 2012] to examine whether the underlying BOLD activity patterns nonetheless contain subtle markers of task-set identity, indicating sensitivity to the distinct computational demands of two tasks. We also aimed to examine whether the functional connectivity profiles of commonly engaged RLPFC regions show task-dependent changes that might be emblematic of the different types of mental representations that RLPFC must access and operate upon to accomplish the goals for the respective tasks.

## MATERIALS AND METHODS

### Participants

Twenty-two participants were recruited from UCLA and the surrounding community. Written informed consent was obtained in accordance with procedures approved by the UCLA Institutional Review Board, and participants received monetary compensation. Two participants were scanned and then excluded from analysis because of excessive head motion that led to data distortion and restricted brain coverage. The average age of the remaining 20 participants (10 females) was 21.1 years old (range: 19–25). All participants were right-handed native English speakers with normal or corrected-to-normal visual acuity and no history of mental illness, drug and alcohol dependence, or MRI contraindications.

### Cognitive Tasks

During the fMRI experiment, participants alternated between performing three distinct cognitive tasks: analogical reasoning, episodic memory retrieval, and visuospatial perception. Although the reasoning and memory tasks were of principle interest to us, the perception task was included as a comparison condition. We designed this task such that it shared the same stimulus characteristics and response demands as the other two tasks, yet did not require participants to engage in abstract thinking or operate on internally-generated representations. All three tasks

were structured such that on each trial participants viewed four words simultaneously displayed in the four quadrants of the screen. The tasks differed only with respect to the decision that participants had to make about a given 4-word array. Participants were informed that each task would have four response options and that they would use their right hand to indicate their response, with digits 2–5 corresponding to options 1–4. All words used in the experiment were trial unique and drawn from a set of 1,184 words, comprised of both concrete nouns (e.g., lobster) and abstract nouns (e.g., ethics). This set was divided into three separate word lists, and the assignment of lists to the three task conditions was counterbalanced across participants so as to eliminate the possibility that group-level differences in brain activity across tasks could be attributed to differences in the characteristics of the particular set of words appearing in each task.

Each block began with a task-set cue indicating which task should be performed on the ensuing four trials. The letter “R” cued the Reasoning task. Participants were to evaluate the top word-pair and bottom word-pair of each 4-word array to decide whether or not the two word-pairs had an analogical relationship. Analogical relationships—defined as the two word-pairs sharing the same “A is to B” semantic relationship—were present on 50% of trials. If participants believed that the two word-pairs did not constitute a valid analogy, they were to specify how many semantic relationships were present (non-analogy trials contained two, one, or zero semantic relationships in equal proportion). The four response options were: (1) Valid Analogical Relationship, (2) Two Valid Semantic Relationships, (3) One Valid Semantic Relationship, (4) No Semantic Relationships.

When cued to perform the Memory task with the task-set cue “M”, the participants’ task was to evaluate each 4-word array and determine whether one of the words had been previously encountered during an earlier memory encoding session, and if so, to indicate their recollection of the source context of the recognized word. The memory encoding session took place one day prior to MRI scanning and involved the presentation of a series of 80 words on a computer display. Each word was preceded by a 3 s cue, instructing participants to either visualize themselves interacting with the word’s referent (“Self” cue) or visualize somebody else interacting with the word’s referent (“Other” cue). Participants were allotted 10 s to generate a memorable visualization, followed by a 3 s interval before the next cue appeared. Participants were informed that they would later be tested on their memory for the words and their associated visualization conditions (i.e., the source context). During the scanned Memory task, each trial included a maximum of one previously studied word appearing at a random location in the 4-word array, but 25% of trials consisted of all novel words. Note that participants did not have to specify which of the four words they remembered, but only whether they had a memory

for one of the four words. The four response options were: (1) Remember One of the Words from SELF Context, (2) Remember One of the Words from OTHER Context, (3) Recognize One Of The Words, But Don’t Recall Source, (4) All Words Are Novel.

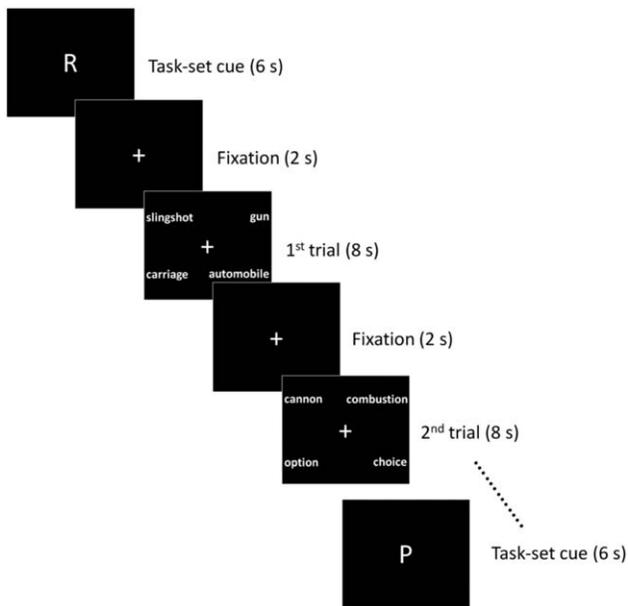
When cued to perform the Perception task with the task-set cue “P”, participants judged which of the four words contained the greatest number of straight lines in its printed form. Response options for this task included: (1) Top Left Word has the Most Straight Lines, (2) Bottom Left Word has the Most Straight Lines, (3) Bottom Right Word has the Most Straight Lines, (4) Top Right Word has the Most Straight Lines. The main function of this task was to serve as a baseline comparison for the Reasoning and Memory tasks, since like the other two tasks, it also required careful analysis of the word array and the indication of one of four potential responses. However, unlike the other two tasks, performance depended largely on perceptual processing of the low-level features of the word stimuli rather than evaluation of internally retrieved representations (i.e., semantic knowledge in the Reasoning tasks or episodic content in the Memory task).

## Experimental Procedure

The experiment consisted of two sessions on consecutive days. On the first day, participants received a detailed overview of the three cognitive tasks that they would be performing during the next day’s scanning session. The participants then completed the memory encoding task (described above). Following this encoding session, further instruction was provided on the four response options associated with each task and participants began a computerized training regimen to help them gain fluency with the buttons that were mapped to each response option. Once they demonstrated mastery of the button mappings, participants performed one practice run of each of the three tasks. None of the stimuli used in this practice session were reused during the fMRI scanning session.

On the second day, participants underwent MRI scanning as they alternated between performing the Reasoning, Memory, and Perception tasks. Data were collected across eight scanning runs, each comprised of nine 52 s blocks (3 blocks of each task). The ordering of these blocks was counterbalanced with the constraint that two blocks of the same cognitive task were never presented in sequence. Each block began with a task-set cue (6 s) followed by a fixation cross (2 s). Participants then performed four trials of the specified task. Each trial consisted of a 4-word stimulus array (8 s) during which time participants were to evaluate the stimuli and indicate their response. A 2 s fixation interval followed each trial, with an additional 4 s following the fourth trial of each block (Fig. 1). Across the entire experiment, participants completed a total of 288 trials (96 trials of each task).

In order to construct the three word lists that were counterbalanced across subjects, we first generated three



**Figure 1.**

Schematic depiction of task paradigm. Each block starts with a task-set cue (R, M, or P) indicating which task should be performed during the upcoming four trials. Trials consist of 4-word arrays, and participants have 8 s to indicate a response. All events were separated by a brief fixation interval. After a four-trial block ends, a new block with a different task-set begins. In this example, the first trial represents a valid analogy and the second trial features two non-analogous semantic relationships.

independent versions of the Reasoning task. This involved creating 144 analogy trials and 144 non-analogy trials, with each trial consisting of a 4-word array. A trial was deemed to be a non-analogy if no reasonable second-order relationship existed between the upper and lower word pairs. Similarly, a word pair was deemed as having no semantic relationship if it contained no clear first-order relationship between the two words. We calculated first-order and pairwise semantic distance ratings for each trial using latent semantic analysis (<http://www.lsa.colorado.edu>; for a full review of this procedure, see [Green, et al., 2010]), and we divided the 288 trials into three lists of 96 trials each, equating for semantic distance in each list. For any given participant, one of these lists would be used for the Reasoning task, and the words from the remaining two lists would be used to populate the Memory and Perception tasks. To do this, words were sorted by length, with the middle 50% of words assigned to the Perception task and the short and long words assigned to the Memory task. We tested that the average word length in each task was matched within one letter for each list. Within the Memory task list, 75% of the words were randomly selected to be studied in the memory encoding task and were randomly assigned to the “Self” or “Other” source condition. Each memory retrieval trial was created by ran-

domly assigning words to the four quadrants of the screen; thus, no analogical relationships were present on these trials. Words allocated for the Perception task were assessed for how many straight lines were present in each of the words (all words appeared in lowercase letters in Geneva font). This was achieved by counting the number of straight lines in each letter (e.g., “j” has one straight line and “m” has 3 straight lines). We then generated experimental trials (4-word arrays) by ensuring that the word with the greatest number of straight lines had at least two more straight lines than the next best answer and that the second best answer had at least one more straight line than the third best answer.

### MRI Data Acquisition and fMRI Preprocessing

Whole-brain imaging was conducted on a Siemens 3.0 T TIM Trio MRI scanner at the Staglin IMHRO Center for Cognitive Neuroscience at UCLA. Functional images were collected using a T2\*-weighted echoplanar imaging (EPI) sequence (TR = 2.0 s; TE = 30 ms; flip angle = 75°; FoV = 19.2 cm, voxel resolution = 3.0 × 3.0 × 3.7 mm). Each functional volume consisted of 33 axial slices acquired in a temporally interleaved sequence. Functional data were collected across eight runs of 239 volumes each. The three initial volumes from each run were discarded to allow for T1 stabilization. A field map image was obtained to facilitate subsequent unwarping of anterior frontotemporal regions that are prone to susceptibility-induced distortion. To aid in spatial registration of the functional data, a coplanar T2-weighted anatomical image was also collected, along with a high-resolution (1 mm<sup>3</sup>) magnetization prepared rapid gradient echo (MPRAGE) T1-weighted image.

Image preprocessing and univariate fMRI analysis were performed with SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>). Functional images were corrected for differences in slice acquisition timing, unwarped based on the voxel-displacement field map to correct for distortions in static magnetic field, and motion-corrected using a six-parameter rigid-body realignment procedure. Image coregistration involved a two-part procedure where the coplanar anatomical image was registered to the mean functional image and the MPRAGE was registered to the coplanar anatomical. The MPRAGE was then segmented into gray matter, white matter, and cerebrospinal fluid (CSF), and the gray matter image was warped to the SPM8 MNI grey matter template. The resulting nonlinear warping parameters were in turn applied to the functional images, which were resampled to 3 mm isotropic voxels and then smoothed with a 6 mm full width at half maximum Gaussian kernel.

### Univariate fMRI Analysis

At the subject-level, fMRI data were analyzed using the general linear model (GLM) framework with a mixed block/event-related design [Visscher, et al., 2003]. The GLM included

transient effects regressors for each event type of interest; separate regressors were used to model correctly performed trials and error trials. Events were modeled as variable duration boxcars with the durations specified based on each trial's response time. Additional regressors were included to model the 6 s task-set cues that preceded each block. Sustained effects were modeled as 38 s boxcars beginning at the onset of the first trial and ending at the offset of the fourth trial of each task block. Task-related regressors were all convolved with a canonical hemodynamic response function. Several covariates of no interest were also entered into the model, including run means, 6-direction head movement parameters, and a variable number of stick-function regressors corresponding to artifact-prone volumes to censor from analysis. Censored volumes were flagged using ArtRepair (<http://www.cibsr.stanford.edu/tools/human-brain-project/artrepair-software.html>) as having translational movements exceeding 2 mm and/or global signal changes exceeding 6 SD from the mean. Serial autocorrelation and low-frequency drifts were accounted for using a first-order autoregressive model and a high-pass filter of 0.0042 Hz (cutoff period = 236 s, corresponding to half the duration of a scanning run). At the group-level, random effects  $t$  tests for contrasts of interest were performed on each voxel within a 50,162-voxel brain mask, which excluded white matter, ventricles, and any voxels not shared by all participants. Using FMRISTAT (<http://www.math.mcgill.ca/keith/fmri-stat/>) to model the null hypothesis distribution as Gaussian random field taking into account the image smoothness and the search space [Worsley, et al., 2004], it was determined that the combination of a voxel-level threshold of  $t > 3.17$  ( $P < 0.005$ , two-tailed) and a cluster extent requirement of  $486 \text{ mm}^3$  (18 voxels) was sufficient to correct for multiple comparisons at the  $P < 0.05$  level. This was the common minimum statistical threshold that was used for all whole-brain analyses. For the univariate analyses contrasting Memory and/or Reasoning activity against Perception activity, we adopted a more stringent voxel-level threshold of  $t > 4.19$  ( $P < 0.0005$ , two-tailed) while maintaining the 18 voxel extent requirement (use of a lower threshold in these contrasts would result in excessively diffuse activation throughout much of the brain). The Reasoning and Memory tasks were directly compared with the Perception task to subtract out the effects of perceptual processing and response demands. Specifically, transient effects parameter estimates from correct Perception trials were subtracted from correct source retrieval trials (Memory task) and correct valid analogy trials (Reasoning task). To aid in visualization of the resulting data, volumetric maps were projected onto the left and right hemisphere inflated PALS cortical surface templates using Caret software [Van Essen, 2005].

### Multivoxel Pattern Analysis

fMRI data were further analyzed with multivoxel pattern analysis (MVPA) to identify regions whose BOLD activity patterns could reliably differentiate trials from the Memory and Reasoning tasks. Specifically, we adopted a spherical

searchlight mapping approach [Kriegeskorte, et al., 2006], in which a multivariate classifier model is trained and tested using only information represented within a small spherical cluster of voxels, with this process then being repeated thousands of times until the "searchlight" has been centered at every possible brain location. Since each searchlight contains the central voxels and its surrounding neighbors (here defined as any voxels within a 3-voxel radius of the center), it inherently contains some overlapping information with searchlights centered nearby, making this approach useful for mapping the spatial distribution of locally diagnostic information throughout the brain. This analysis was implemented using the Princeton MVPA toolbox (<https://www.code.google.com/p/princeton-mvpa-toolbox/>) and custom MATLAB code. For each trial, preprocessed but unsmoothed BOLD images corresponding to the 3rd, 4th, and 5th TRs following stimulus onset were averaged, yielding trial-specific brain activity maps ("patterns"). These three TRs (reflecting BOLD activity levels measured 4–10 s postonset) were chosen a priori based on our intuitions regarding the temporal evolution of the hemodynamic response; we confirmed that these TRs were appropriate for MVPA decoding during our initial piloting. Also, owing to recent concerns about the susceptibility of searchlight MVPA to pick up on brain signals that scale with subtle, yet consistent, response time (RT) differences between conditions [Todd, et al., 2013], we pre-emptively removed the effects of RT from each voxel's activity on a trial-by-trial basis with linear regression. Searchlight MVPA was then performed on the residuals. For each searchlight sphere, we trained a Gaussian Naïve Bayes (GNB) classifier algorithm to discriminate correct valid analogy trials from correct source memory trials. For participants who did not have equal numbers of trials in each condition, a random subset of trials from the more plentiful condition were randomly selected for exclusion prior to classification; in this way, the trial counts from the two conditions were always balanced. The average number of Reasoning and Memory trials included in this analysis was 29.10 per class (range: 10–40). The accuracy of the classifier, determined by a within-subjects 10-fold cross-validation procedure (i.e., using 90% of the available trials for training and the remaining 10% of the trials for testing in each cross-validation fold), was assigned to the voxel in the center of that sphere. This entire process was repeated 10 times for each participant to minimize the effects of random trial balancing. Group-level  $t$ -maps were generated by comparing the mean area under the curve (AUC) classification estimate for each voxel against a null-hypothesis value of 0.5 (for a thorough description of AUC, which is similar to classification accuracy, see Rissman et al. [2010]). The resulting maps were stringently thresholded using a whole-brain Bonferroni correction for multiple comparisons ( $t > 6.73$ ) to aid in visualization of the peak effects.

### Defining Regions of Interest (ROIs)

The region of peak decoding accuracy in RLPFC was identified from the searchlight MVPA analysis and was used to

generate a spherical ROI (6 mm radius), which was then used as the seed in the task-related functional connectivity analysis described below. The sphere radius of 6 mm, which is twice the voxel width, was chosen to replicate that used in McLaren et al.'s [2012] paper introducing the generalized psychophysiological interactions approach. The anatomical localization of this region was assessed by querying the Harvard-Oxford Atlas [Kennedy, et al., 1998] for the probability of it being in the frontal pole.

### Task-Related Functional Connectivity Analysis

In order to assess the task-dependent connectivity of our RLPFC seed ROI, fMRI data were analyzed using the generalized psychophysiological interactions (gPPI) toolbox (<http://www.nitrc.org/projects/gppi>) [McLaren, et al., 2012]. This is done by performing multiple regression in the GLM framework with the constituent regressors being: (1) the physiology of the seed region (i.e., its BOLD timeseries), (2) the psychological regressors from the task (i.e., the sustained effects model, which coded for the onsets and duration of each task block), and (3) a psychophysiological interaction (PPI) term representing the interaction between the physiological and psychological regressors. The same regressors of no interest included in the univariate GLM were also included in the gPPI GLM. The sustained effects model was chosen instead of the transient effects model due to the increased power afforded by using all timepoints within each block. However, it was confirmed that re-running the gPPI analysis with the transient effects model produced nearly identical results. Task-dependent connectivity maps, based on the PPI regressor parameter estimates from each condition, were generated for each participant and subjected to group-level random effects *t*-tests. Contrast maps that compared condition-specific connectivity versus baseline (i.e., a null hypothesis value of 0) were stringently thresholded at the whole-brain Bonferroni level ( $t > 6.73$ ) to aid in visualization of peak effects. Contrast maps that directly compared functional connectivity between tasks were thresholded at our standard minimum threshold ( $t > 3.17$ ; cluster extent  $\geq 18$  voxels).

### Seed-to-Network Connectivity Profiling

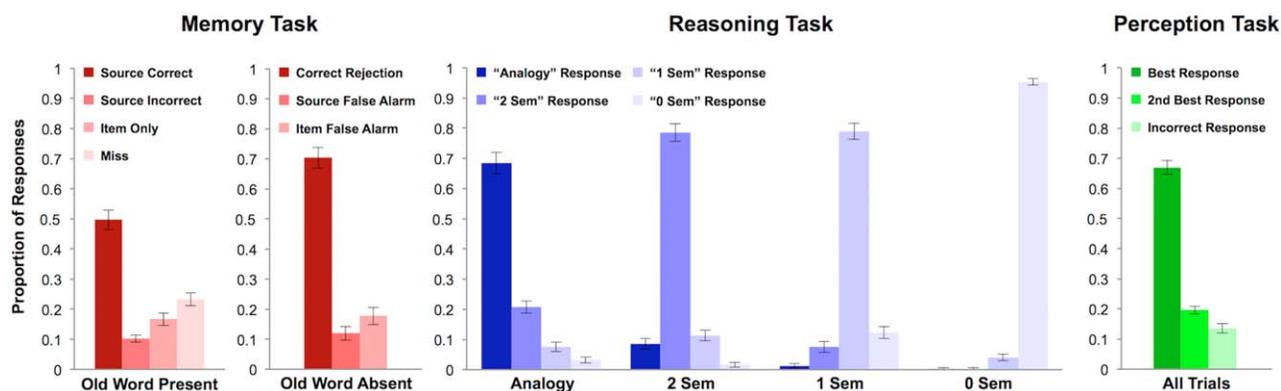
To quantify the strength of each seed ROI's coupling with distinct brain networks, we extracted connectivity parameter estimates from 264 individual nodes throughout the brain (each defined as a 5 mm radius sphere); the coordinates of these nodes were reported in a recent study that used resting-state connectivity and meta-analytic data to identify dissociable functional networks [Power, et al., 2011]. We chose to adopt the same 5 mm radius spheres used in that study in order to precisely replicate the networks and maintain sufficient distance between nearby spheres. Based on the nature of our tasks and our a priori

hypotheses regarding their network connectivity profile, we chose to focus our analyses on 6 of the networks defined by that study: FPCN, DMN, DAN, salience network (SN), memory retrieval network (MRN), and visual network (VN). The relevance of the FPCN, DMN, and DAN has been discussed above. The SN was included due to its important role in coordinating attention towards salient stimuli and its interaction with brain networks involved in cognitive control [Menon and Uddin, 2010; Seeley, et al., 2007]. The MRN and VN were included due to their respective roles in the retrieval of memory and visual processing of task stimuli [Power, et al., 2011]. The nodes in these 6 networks constituted 148 of the 264 total regions. Each subject's connectivity parameter estimates were averaged across nodes within each network, and group-level effects were analyzed using repeated measures multivariate ANOVAs and *post hoc* simple effects comparisons with Šidák correction for multiple comparisons.

## RESULTS

### Behavioral Analysis

Response distributions for all three tasks are plotted in Figure 2, demonstrating that participants performed the three tasks accurately, with error responses following a predictable pattern for each task. In the Memory task, the overall hit rate was significantly higher than the overall false alarm rate ( $t(19) = 12.76$ ,  $P < 0.001$ ), and the source memory hit rate (i.e., probability of indicating the correct source, given an attempt to report the source) was significantly higher than the source false alarm rate ( $t(19) = 10.40$ ,  $P < 0.001$ ). Although participants only indicated having a memory for the source context on 60.00% of Old Word Present trials, when they did so they were highly accurate, selecting the correct source 82.34% of the time. In the Reasoning task, the hit rate for valid analogy trials was significantly higher than the false alarm rate (i.e., calling a non-valid analogy "valid") ( $t(19) = 16.93$ ,  $P < 0.001$ ). Overall accuracy (pooled across trial types) did not significantly differ between the Memory task and the Reasoning task (76.36% vs. 75.12%;  $P = 0.69$ ). In our tabulation of overall accuracy for the Memory task, hits (including trials where participants reported recognition of an old word but either could not recall or incorrectly recalled its source context) and correct rejections (responding that "All Words are Novel" on Old Word Absent trials) were scored as correct responses, and misses (responding "All Words are Novel" on Old Word Present trials) and false alarms (reporting a memory on Old Word Absent trials) were scored as incorrect responses. For the Reasoning task, correct trials were those in which participants properly indicated whether the word array contained a valid analogy, 2 semantic relations, 1 semantic relation, or 0 semantic relations. Finally, in the Perception task, the probability of participants correctly reporting the word with the greatest number of straight



**Figure 2.**

Distribution of behavioral responses for the Memory, Reasoning, and Perception tasks. For the Memory task, trial types are split up according to whether the 4-word probe array contained a word that had been studied (Old Word Present) or whether all four words were novel (Old Word Absent). For the Reasoning task, trials are split up according to whether the 4-word array included a Valid Analogy, 2 Semantic Relations, 1 Semantic Rela-

tion, or No Semantic Relations. For the Perception task, data from all trials are analyzed according to whether participants correctly indicated which word contained the greatest number of straight lines (Best Response), or whether they produced a suboptimal response that was either the close runner-up (2nd Best Response) or one of the other two words (Incorrect Response).

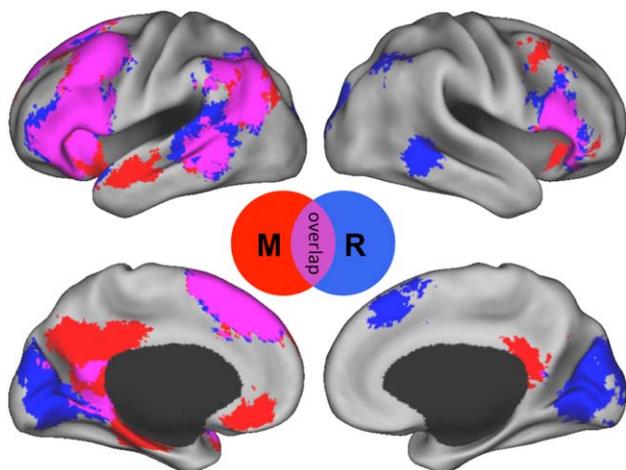
lines was significantly greater than the probability of reporting the word with the second highest straight line count ( $t(19) = 13.86, P < 0.001$ ). Participants' overall accuracy on the Perception task (66.89%) was somewhat lower than their overall accuracy for the other tasks (vs. Memory task:  $t(19) = 3.54, P = 0.002$ ; vs. Reasoning task:  $t(19) = 3.21, P = 0.005$ ). However, in designing the Perception task as a control condition, our aim was merely to engage participants with a challenging perceptual decision task, and thus we cared predominantly about participants' mental effort (reflected in their RTs) rather than their success *per se*.

We aimed to match the Memory, Reasoning, and Perception tasks as closely as possible to minimize potential confounds such as bottom-up perceptual input, number of response options, and RT. Mean ( $\pm$ SE) RTs were as follows: Memory = 5.04 s (.15), Reasoning = 4.72 s (.10), Perception 5.03 s (.19); the main effect of task, although trending, was not significant ( $F(2,18) = 3.45, P = 0.054$ ). Importantly, mean RTs for the two primary trial types of interest (correct source responses in the Memory task and correct valid analogy responses in the Reasoning task) did not significantly differ ( $t(19) = 1.06, P = 0.304$ ). When considering RTs to correctly performed Reasoning trials excluding valid analogies, the pattern of results was consistent with participants' use of a hierarchical process-of-elimination strategy. Specifically, trials with no semantic relations were faster than those with one semantic relation ( $t(19) = 3.78, P = 0.001$ ), which in turn were faster than those with two semantic relations ( $t(19) = 2.28, P = 0.034$ ). The fact that valid analogy trials showed RTs on par with one semantic relation trials ( $t(19) = 0.55, P = 0.59$ ) and faster than two semantic relations trials ( $t(19) = 2.79, P = 0.012$ ) suggests that participants terminated further processing once an analogy had

been confidently identified, but continued futilely searching for an analogical relationship on two semantic relations trials (and possibly also continued searching for another first-order relationship on one semantic relation trials). A complete reporting of RT data across tasks and trial types is provided in Supporting Information Table I.

### Univariate fMRI Analysis

Activation parameter estimates from successful source retrieval trials from the Memory task and successful valid analogy trials from the Reasoning task were each contrasted with successful trials from the Perception task in an effort to control for bottom-up perceptual input, word reading, and motor response demands (Fig. 3; Supporting Information Table II). Memory trials in which participants successfully indicated the source context engaged a broad set of prefrontal regions including ventrolateral PFC (VLPFC), dorsolateral PFC (DLPFC), ventromedial PFC, dorsomedial PFC (DMPFC), and insular cortex; although these activations were seen in both hemispheres, activation was stronger and more extensive in the left hemisphere. Additional activations were observed in left lateral temporal cortex, posterior cingulate cortex (PCC), precuneus, left angular gyrus, and left hippocampus. Reasoning trials in which participants successfully identified valid analogies engaged a largely overlapping set of prefrontal regions with a similar degree of left hemisphere bias. Additional activations were observed in bilateral lateral temporal cortex, angular gyrus, intraparietal sulcus (IPS), PCC, and early visual cortex. The common involvement of left lateral PFC, PCC, bilateral insula, and left angular gyrus suggests that both FPCN and DMN structures are utilized in these two tasks. We next



**Figure 3.**

Univariate BOLD activity during memory and reasoning. Regions exhibiting activation during Memory trials with correctly retrieved source details (red), Reasoning trials with correctly identified valid analogies (blue), or overlapping activity for both trial types (purple). Memory and Reasoning effects are shown relative to activity levels from the Perception task, which served as a common control condition and has been contrasted out of each map. Maps are thresholded at  $t > 4.19$  ( $P < 0.0005$ , two-tailed; cluster extent  $\geq 18$  voxels).

performed a direct contrast of successful source memory retrieval trials vs. successful valid analogy trials (Fig. 4a; Supporting Information Table II). The analysis revealed no significant differences in the left lateral PFC and only minimal differences in the bilateral inferior parietal lobule. However, analogy trials did show increased involvement in the right lateral PFC, early visual cortex, left lateral occipital cortex, right IPS, and bilateral lateral temporal cortex, while source retrieval showed greater activations in the precuneus, PCC, left insula, left angular gyrus, left medial temporal lobe, and anterior cingulate cortex.

### Multivoxel Pattern Analysis

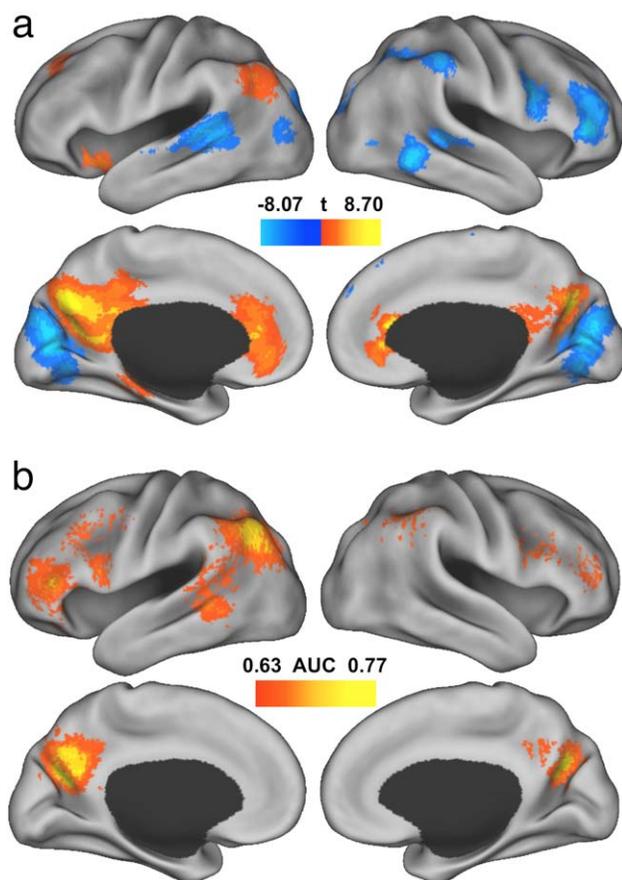
The striking overlap of left lateral PFC recruitment during source memory retrieval and solving valid analogies, along with the lack of significant univariate activity differences between these conditions throughout this large swath of cortex, seems to suggest that memory and reasoning engage common left PFC-mediated control processes. However, given the inherently distinct types of mental representations that must be accessed and integrated in order for one to recall the contextual source of a memory or to evaluate the validity of an abstract verbal analogy, it seems plausible that neural processing in left lateral PFC might be reconfigured in some subtle yet predictable way when performing these respective tasks. To examine this possibility, we conducted a searchlight

MVPA analysis, which can offer heightened sensitivity to detect condition-specific changes in local activity patterns, even when levels of mean BOLD activity are comparable across conditions.

As with the transient effects univariate contrast reported above, our searchlight MVPA analysis focused on the discriminability of Reasoning trials where participants correctly identified a valid analogy from Memory trials where they correctly reported the source context of a previously encountered item. This analysis revealed robust decoding performance throughout many brain areas. To identify the most consistently informative clusters within this map, we imposed secondary thresholding procedure requiring that at least 75% of participants showed decoding performance that surpassed a within-subject metric of significance at each sphere location (determined based on a binomial null hypothesis distribution, taking into account the number of trials included in the classification analysis for each subject [Pereira, et al., 2009]). For a voxel to be present in the resulting map, it thus was not only essential that decoding accuracy levels had low variance across subjects (yielding high  $t$  values) but also that the accuracy levels were significantly above chance in most individual subjects. The resulting map (Fig. 4b) showcased especially reliable decoding in left lateral PFC with a clearly demarcated peak in the posterior aspect of RLPFC. Other regions exhibiting reliable decoding included the left lateral temporal cortex, angular gyrus, and midline areas such as PCC and precuneus.

It is intriguing that some regions that showed significant univariate effects did not reach significance in the MVPA searchlight analysis. Such discrepancies between univariate and searchlight MVPA results are not uncommon and reflect the differential sensitivity of these techniques to distinct attributes of the BOLD data [Davis, et al., 2014; Jimura and Poldrack, 2012]. One possibility is that univariate effects in some regions were too variable at the level of individual trials to yield decoding accuracies surpassing our stringent thresholding procedure. Indeed, most of these regions do show some degree of Memory vs. Reasoning decoding at a more lenient threshold.

With any searchlight MVPA analysis there is always the possibility that classification performance in a given region might be heavily influenced by condition-specific differences in the mean activity level within that region rather than its local spatial pattern of activation. To assess the degree to which our decoding analysis was detecting information above and beyond that which could be gleaned from each sphere's mean signal, we ran a new searchlight analysis that forced the classifier to generate its predictions based only on a single feature for each sphere, its mean signal level. We then performed a paired  $t$  test between the pattern-based searchlight maps and the mean-of-sphere (MoS) based maps to identify which sphere locations showed significantly improved decoding when provided with the pattern information. Of the 905 significant voxels in our original searchlight map, 866 (96%) survived this test, and the mean



**Figure 4.**

Univariate and multivariate comparisons of memory and reasoning effects. (a) Random effects paired  $t$  test of univariate activity parameter estimates from correct source retrieval trials and correct valid analogy trials. Warm colors represent regions with significantly greater activity during memory and cool colors represent regions with significantly greater activity during reasoning; maps thresholded at  $P < 0.05$  (corrected). (b) Results of whole-brain searchlight-mapping MVPA, illustrating regions whose local BOLD patterns (within a 3-voxel radius sphere) could facilitate reliable classification of these two trial types. Voxel intensities represent the classifier's area under curve (AUC) at each sphere center; only effects achieving group-level significance at  $P < 0.05$  (whole-brain Bonferroni's corrected;  $t > 6.73$ ) and individual subject-level significance in at least 75% of subjects are depicted.

classification AUC across these 905 voxels diminished from AUC = 0.70 in the pattern-based analysis to AUC = 0.59 in the MoS analysis, indicating a marked advantage in decoding when the classifier was provided with multivariate pattern information.

Given our interest in understanding the nature of prefrontal contributions to memory and reasoning, we next identified the locus of maximal decoding performance within the frontal lobe. The top-performing sphere was

localized to the posterior aspect of left RLPFC (MNI coordinates of central voxel:  $[-42, 42, 6]$ ; mean classification AUC = 0.71; group  $t$  value = 10.06). This region, which falls near the boundary of middle frontal gyrus and inferior frontal gyrus, constitutes the most caudal section of the lateral frontal pole [Kennedy, et al., 1998]; its RLPFC designation was assessed by cross-referencing the central coordinate against the Harvard–Oxford atlas, which assigns it a 68% probability of being “Frontal Pole” and only a 5% probability of being “Inferior Frontal Gyrus.”

To further explore this left RLPFC region's involvement, we defined a spherical ROI around the top-performing voxel and examined both its univariate activity profile and its functional connectivity profile. Univariate parameter estimates (Fig. 5a) revealed that this region showed activation that scaled both with the amount of mnemonic content retrieved on Memory task trials and with the amount of relational/semantic information accessed on Reasoning task trials. Specifically, during the Memory task, this region showed maximal activity on trials where participants reported remembering the source of a recognized item (regardless of whether this source report was accurate), marginally lower activity on trials where participants only reported item recognition (vs. correct source retrieval:  $t(19) = 1.94, P = 0.071$ ; vs. incorrect source retrieval:  $t(12) = 1.78, P = 0.10$ ), and substantially lower activity on Correct Rejection trials, where the participants correctly reported that no studied items were present (vs. item only recognition:  $t(16) = 3.30, P = 0.004$ ). Note that data from participants with fewer than five trials of any given trial type are excluded from the respective statistical contrasts. During the Reasoning task, this area showed maximal activity on trials where participants correctly reported the presence of a valid analogy or two semantic relations (with no significant difference between these trial types:  $t(19) = 0.37, P = 0.709$ ). Both of these trial types showed greater activity than trials with only one semantic relation (vs. analogy:  $t(19) = 3.05, P = 0.006$ ; vs. two semantic relations:  $t(19) = 3.12, P = 0.005$ ), and trials with one semantic relation elicited greater activity than trials with no semantic relations ( $t(19) = 3.81, P = 0.001$ ). When the event-related activity estimates from the Reasoning and Memory task were directly contrasted, correct valid analogy trials showed greater activity than correct source retrieval trials ( $t(19) = 2.55, P = 0.019$ ); an effect that only achieved significance in this ROI analysis but not in the whole-brain voxelwise contrast (e.g., Fig. 4a). Activity during correct source retrieval was comparable with that measured during one semantic relation trials ( $t(19) = 0.36, P = 0.722$ ). Additionally, 36 of 41 voxels in the left RLPFC ROI showed significant effects in the original searchlight analysis compared to MoS classification, showing that multivariate pattern information is critical for classifying between analogical reasoning and episodic memory retrieval in this region. Taken together, these data suggest that this left RLPFC region most strongly responds when participants

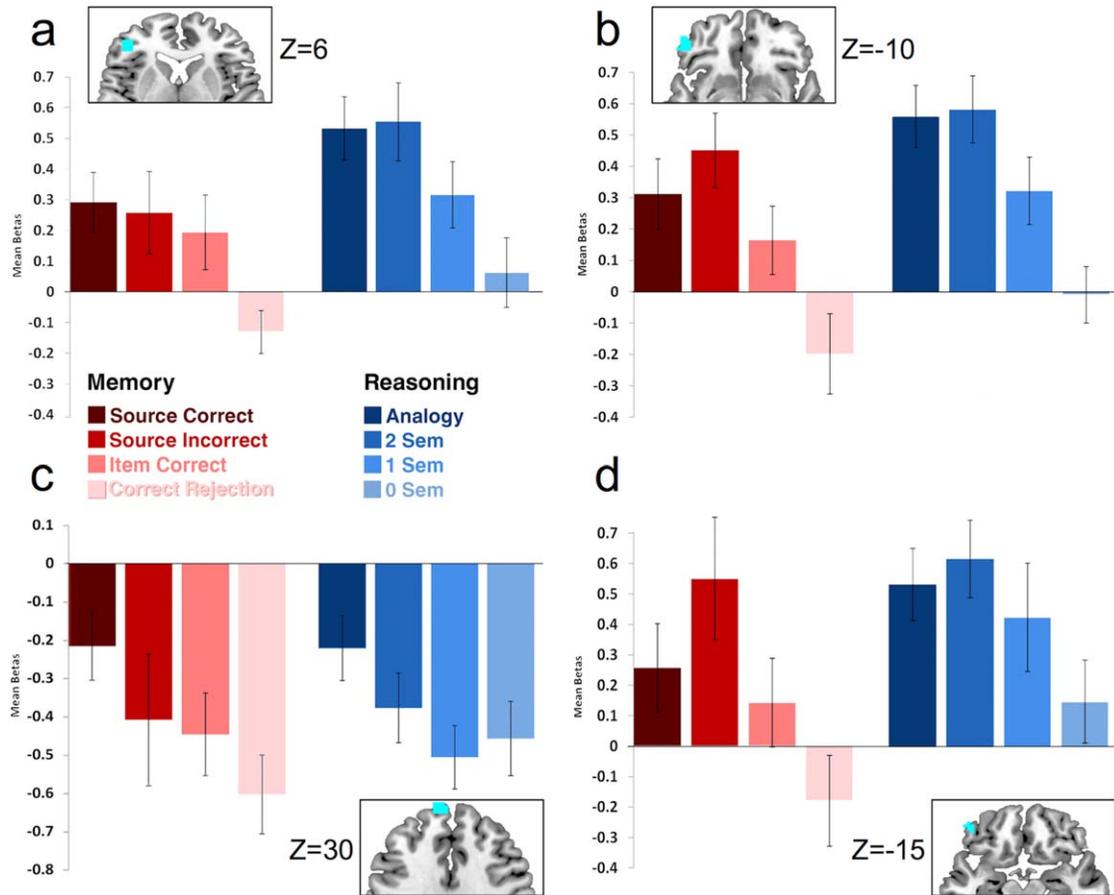


Figure 5.

Univariate activity parameter estimates extracted from our left RLPFC seed ROI and three additional ROIs derived from previous studies of analogical reasoning. All four ROIs exhibited trial type-dependent activity changes during both the Memory and Reasoning tasks, suggestive of functional contributions to both cognitive domains. Inlay images depict locations of ROIs (cyan clusters) on a template brain. (a) Our left RLPFC seed ROI, cen-

tered on the peak searchlight MVPA decoding effect; MNI coordinates:  $[-42, 42, 6]$ . (b) Left RLPFC ROI, defined based Cho et al. [2010]; MNI coordinates:  $[-50, 42, -10]$ . (c) Left dorsal frontopolar ROI, defined based Green et al. [2010]; MNI coordinates:  $[-8, 62, 30]$ . (d) Left RLPFC ROI, defined based Bunge et al. [2005]; MNI coordinates:  $[-42, 48, -15]$ .

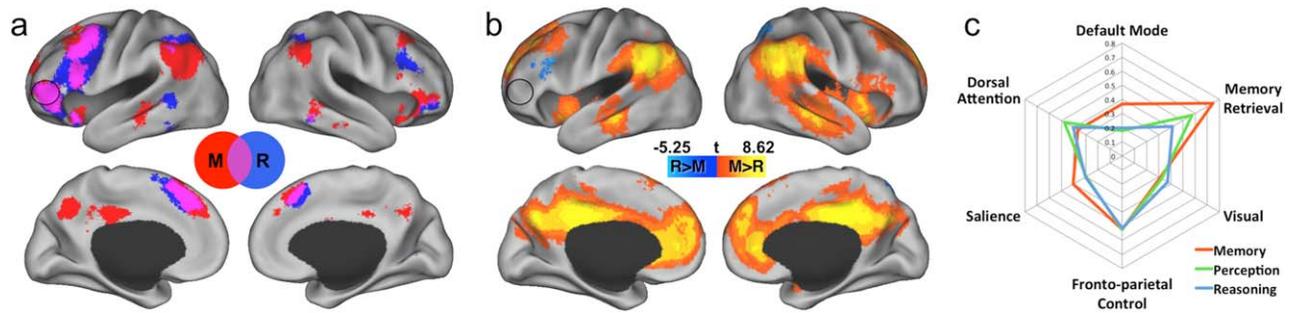
attempt to integrate two semantic relationships (whether or not these two relationships are ultimately found to constitute a valid analogy), but that this region also exhibits notable involvement in attempting to retrieve the contextual source of a verbal memory. In contrast, activity in this region during correctly performed Perception task trials did not reliably exceed the fixation baseline level ( $t = 0.66$ ,  $P = 0.516$ ).

In addition to interrogating univariate activity levels within this MVPA-defined RLPFC ROI, we obtained activity parameter estimates from three additional ROIs defined based on peak foci reported by prior studies of analogical reasoning [Bunge, et al., 2005; Cho, et al., 2010; Green, et al., 2010]. Consistent with these prior reports, activity within each of these ROIs (Fig. 5b–d) showed reasoning-related effects in our data

set, such that activity was greater for reasoning trials necessitating the comparison between two semantic relationships (i.e., analogy and 2 semantic relations trials) than for trials with one or no semantic relationships (all  $P$ 's  $< 0.05$ ). Of particular interest, these three “reasoning-related” ROIs also showed clear memory-related effects in our study (e.g., significantly elevated activity during correct source retrieval trials relative to correct rejections, all  $P$ 's  $< 0.001$ ) suggesting the need for a broader interpretation of their functional role.

### Task-Related Functional Connectivity Analysis

We then performed a gPPI analysis to characterize task-dependent connectivity effects [Friston, et al., 1997;



**Figure 6.**

Task-dependent functional connectivity. Group-level  $t$ -maps representing the gPPI analysis depict regions showing significantly positive functional coupling with the RLPFC (a) seed during Memory (red) and Reasoning (blue), with overlapping effects shown in purple. This single-condition map is stringently thresholded at  $P < 0.05$  (whole-brain Bonferroni's corrected;  $t > 6.73$ ). A direct contrast between Memory and Reasoning is shown in

panel (b), with warm colors indicating Memory > Reasoning and cool colors indicating Reasoning > Memory. This contrast map is thresholded at  $P < 0.05$  (cluster corrected;  $t > 3.17$ ; extent  $\geq 18$  voxels). Mean network-level connectivity parameter estimates for the RLPFC seed (c) are represented on a radar plot, with data from the Perception task (green) included.

McLaren, et al., 2012] of the left RLPFC seed. A group-level map depicting regions that were significantly the word associated actually seems more appropriate with the RLPFC ROI during Memory, Reasoning, or both is presented in Figure 6a. The left RLPFC seed exhibited overlapping Memory and Reasoning connectivity effects in seed-adjacent left RLPFC areas, left VLPFC, left DLPFC, and DMPFC. Relative to the Memory task, the RLPFC seed's connectivity during the Reasoning task showed a broader spatial extent throughout left lateral PFC and exhibited unique regions of coupling in IPS, right DLPFC, and left lateral temporal cortex regions. A random effects paired  $t$  test between the Reasoning and Memory conditions (Fig. 6b), showed two significant clusters favoring Reasoning: one in left BA 45 (peak MNI coordinate:  $[-39, 23, 22]$ ), partially overlapping with putative Broca's area [Anwander, et al., 2007] and one in the right superior parietal lobule (peak MNI coordinate:  $[21, -70, 64]$ ); a Reasoning > Memory effect was also present in the homologous left parietal region, but this cluster did not survive correction for multiple comparisons. During the Memory task, the RLPFC seed showed unique task-dependent coupling with many regions, including bilateral angular gyrus, left lateral temporal cortex, PCC, precuneus, right RLPFC, and right DLPFC (Fig. 6a), with significant Memory > Reasoning effects emerging in all of these regions (Fig. 6b).

Although whole brain maps provide one assay of a seed's connectivity, it can be informative to more directly evaluate the degree to which specific brain networks—documented based on prior work—show functional coupling with each seed. To this end, network connectivity parameter estimates were extracted from six previously described brain networks [Power, et al., 2011], and the within-network means are presented in Figure 6c (note that the radar plot also includes estimates derived from the Perception task, to

allow for comparison). These within-network means were entered into a multivariate ANOVA with the factors of network and task, and *post hoc* simple effects comparisons were performed between the tasks for each network using the Šidák correction. This analysis revealed a significant main effect of network ( $F(5,15) = 21.53, P < 0.001$ ), while the main effect of task was trending ( $F(2,18) = 2.92, P = 0.080$ ). There was a highly significant network by task interaction ( $F(10,10) = 12.11, P < 0.001$ ). Simple effects comparisons showed that the RLPFC seed's connectivity with the DMN was significantly increased during Memory relative to Reasoning ( $t(19) = 4.59$ ) and relative to Perception ( $t(19) = 4.34$ ). The same was true for its coupling with the MRN, with a significant advantage seen for Memory over Reasoning ( $t(19) = 5.61$ ) and marginally significant advantage for Memory over Perception ( $t(19) = 3.37$ , critical  $t$  threshold = 3.42); although an apparent advantage exists for Perception over Reasoning, this effect was not significant ( $t(19) = 2.24$ ). The RLPFC seed also showed a significant boost in its connectivity with the SN during Memory relative to Perception ( $t(19) = 4.65$ ), but its connectivity with the DAN showed the reverse pattern, with a significant advantage for Perception over Memory ( $t(19) = 3.42$ ). At the network-level, the RLPFC seed did not show any preferential coupling with the assessed brain networks during Reasoning, relative to Memory and Perception. These network analyses showcase the ability of this RLPFC region to dynamically modulate its functional communication with distinct cortical networks in accordance with the processing demands posed by each task context (e.g., favoring coupling with the DMN and MRN during Memory, which requires an internally-oriented focus on one's episodic recollections, and favoring coupling with the DAN during Perception, which requires externally-oriented attention to low-level perceptual attributes of the stimuli).

## DISCUSSION

The present fMRI study used a novel experimental paradigm, coupled with multivariate data analytic tools, to characterize the functional contribution of RLPFC regions to higher cognition. We focused our investigation on two relatively complex cognitive processes—episodic source memory retrieval and analogical reasoning—since these tasks have been strongly associated with RLPFC function [Badre and D’Esposito, 2009; Gilbert, et al., 2006; Krawczyk, 2012; Ramnani and Owen, 2004; Vendetti and Bunge, 2014]. Our third cognitive task was closely matched to the other tasks with respect to its perceptual attributes and response demands yet did not require participants to access and integrate semantic or episodic knowledge. This provided a baseline from which to compare fMRI effects during memory and reasoning.

Our results revealed remarkable overlap of episodic memory-related activity (trials with correctly retrieved source details) and analogical reasoning-related activity (trials with correctly identified valid analogies) across a large swath of left lateral PFC. This finding of shared prefrontal involvement across tasks requiring seemingly distinct cognitive operations is consistent with prior demonstrations that common lateral prefrontal regions exhibit domain-general recruitment across a wide range of complex cognitive tasks [Duncan and Owen, 2000; Fedorenko, et al., 2013]. Although we found overlapping memory and reasoning effects in both left and right lateral PFC, the extent of recruitment was far broader in the left hemisphere, where it extended anteriorly into RLPFC. This left hemisphere dominance may reflect the verbal nature of our cognitive tasks.

Although our experiment is the first, to our knowledge, to directly compare brain activity during memory and reasoning tasks, our interest in the potential overlap of the RLPFC mechanisms that support these two cognitive processes is motivated by numerous prior studies that have independently identified similar RLPFC regions that activate either during episodic memory retrieval or analogical reasoning tasks [e.g., Bunge, et al., 2005; Cho, et al., 2010; Dobbins and Wagner, 2005; Ranganath, et al., 2000; Wendelken, et al., 2008b], in addition to Reynolds et al. [2006], which examined both retrieval and integration processes in the context of an episodic memory task. Considering the recent focus in the literature on the RLPFC mechanisms in relational reasoning, where RLPFC foci have been consistently and selectively linked to task conditions requiring relational integration [Krawczyk, 2012], we aimed to investigate whether these regions would show comparable effects in our data set. And, perhaps more importantly, our data set affords us the ability to also evaluate how these same regions respond during episodic memory retrieval. To this end, we defined ROIs based on peak coordinates reported in three prior studies; two left RLPFC foci were identified from analogical reasoning studies with verbal [Bunge, et al., 2005] or nonverbal stimuli [Cho, et al., 2010], and we also explored activity within a more anterior and dorsal prefrontal region that has been linked to verbal analogical reasoning [Green, et al., 2010].

Replicating prior work, all three areas generally activated more strongly for reasoning trials necessitating the comparison between two semantic relationships than for trials with one or no semantic relationships. But interestingly, activity in these very same regions also tracked aspects of episodic retrieval, such that trials where participants reported source retrieval (regardless of accuracy) showed greater activity than trials where participants correctly indicated that no studied items were present in the 4-word array. These data demonstrate that left RLPFC exhibits domain-general activity for both reasoning and memory across areas that have been recently considered to be primarily involved in relational integration processes.

In striking contrast to left RLPFC, which showed comparable activation during analogical reasoning and episodic memory retrieval, its right hemisphere homologue showed a strong preference for reasoning. The involvement of right RLPFC in reasoning is consistent with many prior relational reasoning studies that have reported bilateral RLPFC effects [Cho, et al., 2010; Christoff, et al., 2001, 2003; Watson and Chatterjee, 2012; Wendelken, et al., 2012, 2008b]. In one prior effort to understand the differential contributions of left and right RLPFC, Bunge et al. [2009] concluded that only left RLPFC met their stringent criteria for a role in relational integration, whereas right RLPFC showed activity that scaled with task complexity in a graded manner, but was not selective for relational integration. Right RLPFC areas have also been implicated in attentional switching and subgoal processing [Braver and Bongiolatti, 2002; Braver, et al., 2003; Gilbert, et al., 2005], so it is possible that these types of cognitive control processes may be the mechanism through which right RLPFC provides auxiliary support to left RLPFC in analogical reasoning tasks.

Although only right hemisphere prefrontal regions emerged as significant in our univariate contrast of reasoning vs. memory trials, we wanted to explore the possibility that left prefrontal regions also show differential neural responses across these two tasks, but in a manner that was perhaps too subtle to be detected by the simple assessment of mean BOLD signal levels. To this end, we used a whole brain searchlight MVPA approach to identify regions whose local BOLD activity patterns were sufficiently distinct so as to facilitate accurate classification of whether a given trial was involved in reasoning or memory operations. We specifically focused on trials from each task that constituted the pinnacle of successful information processing in their respective domains. Specifically, we trained our classifier to discriminate reasoning trials with correctly identified valid analogies from memory trials with correctly reported source contexts. Perhaps unsurprisingly, this analysis revealed significant decoding effects in right RLPFC, putatively driven by this region’s differential univariate engagement between tasks. More noteworthy was our finding that even stronger decoding effects were observed in left-lateralized prefrontal regions, with the peak effect emerging in RLPFC. The fact that local activity patterns within left RLPFC are reliably

dissociable during memory and reasoning trials, despite roughly comparable activity levels, could reflect that this region is performing similar cognitive control processes (e.g., relational integration/comparison) on distinct forms of information that it gains access to via its functional communication with content-representing regions. In other words, RLPFC activity patterns may be modulated by the nature of the inputs that this area is receiving (e.g., semantic vs. episodic knowledge representations). Alternatively, the dissociable BOLD patterns in RLPFC could be indicative of underlying neural codes that are linked to the engagement of distinct cognitive control processes. According to this view, a subtle reconfiguration of RLPFC activity may reflect the specification and enactment of domain-specific task goals, or the implementation of distinct computations performed on activated knowledge representations. In the reasoning task, participants must assess the second-order relationship of two first-order relationships, whereas in the memory task they must evaluate the relationship between a present stimulus and a past experience. With respect to the latter, it is plausible that participants arrive at their episodic source judgments by quickly generating a mental image of themselves and/or someone else interacting with the recognized item (i.e., re-simulating the encoding task) and then assessing the relative familiarity of the resulting mental image(s). The nature of this episodic comparison process shares fundamental elements with the relational comparison process inherent in analogical reasoning, perhaps explaining the shared left RLPFC recruitment. Yet differences in specific types of representations being compared and the dissociable neural networks providing this information may account for the decodable RLPFC activity patterns uniquely associated with each task.

We reasoned that a thorough assessment of how rostral prefrontal regions communicate with other brain networks during different cognitive states might offer additional insight into the nature of their functional contributions. To this end, we examined the task-dependent connectivity profile of the RLPFC node that emerged in our analysis of trial-type specific MVPA decoding. This RLPFC seed showed pronounced differences in the strength and anatomical distribution of its connectivity across these two tasks. Specifically, during the Memory task the RLPFC seed's coupling with the DMN, MRN, and SN was significantly elevated above the level observed during the Reasoning and Perception tasks. We hypothesize that RLPFC plays a role in monitoring and integrating self-referential episodic source details represented within DMN and MRN regions. RLPFC's heightened coupling with the SN during Memory was a less expected finding. Although this network is thought to be involved in the bottom-up monitoring of salient environmental stimuli, this network may also help facilitate the orienting of one's attention towards salient episodic information retrieved from memory [Ciarumelli, et al., 2008; Menon and Uddin, 2010]. Also somewhat surprising was the fact that none of our six networks-of-interest showed stronger coupling with the

RLPFC seed during Reasoning than in Memory or Perception. However, in a mapwise contrast two individual brain regions did show reliably stronger coupling during Reasoning. One of these areas was a left lateral prefrontal region (BA 45) that was posterior and dorsal to the seed, putatively corresponding to Broca's area. We suspect that this region likely contributes to controlled semantic retrieval demands [e.g., Bunge, et al., 2005; Goldberg, et al., 2007; Wagner, et al., 2001] posed by the Reasoning task. The other area was a superior parietal lobe region potentially involved in the top-down attentional demands of the task, which could include rapid shifting of attention between the word pairs and visuospatial imagery of the analogical relationships (e.g., a useful strategy for solving some of the analogies, e.g., "jacket: zipper:: wound: suture"). The task-dependent flexibility of the RLPFC seed's coupling was further illustrated by the finding that it showed significantly heightened coupling with the DAN during the Perception task, relative to the Memory task (its advantage over Reasoning was not significant). Thus, when the task demands exclusively required externally-focused visuospatial attention to facilitate the goal of identifying which word's printed form contained the greatest number of straight lines, the RLPFC region strengthened its connectivity with the brain network whose functions are most well-aligned with the information processing demands of the Perception task. Thus, the task-dependent connectivity analysis demonstrates that RLPFC can flexibly adjust its coupling with distinct brain regions and networks to enact task goals in all three tasks.

Given the diversity of functional roles that prior studies have ascribed to this RLPFC area, it is challenging to specify what overarching principles may best account for the present data. It is likely that there is considerable functional heterogeneity within RLPFC, and additional experimentation and meta-analytical investigations may help elucidate the contributions of distinct subregions. That said, we believe that our findings points to at least one common theme. A common left-lateralized posterior RLPFC area appears to play a particularly important role whenever two or more highly structured representations (e.g., semantic relationships, episodic memory traces, etc.) need to be compared or integrated. That this area showed overlapping engagement across two very different cognitive tasks suggests that its functional contribution should not be characterized in terms of memory retrieval or analogical reasoning-related processes, per se, but rather by a more general role in operating upon two or more retrieved declarative knowledge representations in the service of an impending decision. This account of the role of RLPFC in analogical reasoning and episodic memory retrieval is consistent with the mechanisms described by Bunge and Wendelken [2009] in these task contexts. The ubiquitous involvement of RLPFC across such a diverse array of cognitive paradigms in the fMRI literature is likely due to this region's ability to flexibly interact with whichever posterior regions/networks process and represent information relevant to one's current behavioral goals.

It is important to note that the left RLPFC region highlighted in our analyses falls at the posterior aspect of the territory that can be fairly referred to as “rostral” PFC. This relatively posterior localization raises the question of how our findings relate to prior work concerning RLPFC contributions to higher cognition. Although the central coordinate of our region of interest is approximately 1 cm anterior to the peak RLPFC focus identified by Koechlin et al. [2003] as being responsible for the most abstract form of task-set control, our region is approximately 1 cm posterior to the RLPFC area that Badre and D’Esposito [2007] implicated as the apex of the control hierarchy. Our region is also 1 cm posterior to foci reported in some prior studies of episodic retrieval [e.g., Dobbins and Wagner, 2005] and relational reasoning [e.g., Christoff, et al., 2001]. That said, many other studies of memory and reasoning have used the label “rostral PFC,” “anterior PFC,” or “frontal pole” to refer to foci whose y-coordinates, like that of our present RLPFC ROI, fall between +40 and +42 [e.g., Cho, et al., 2010; Krawczyk, et al., 2010; Kroger, et al., 2002; Ranganath, et al., 2000; Wendelken, et al., 2008b]. Further work will be needed to better characterize the differential functional contributions of more anterior RLPFC regions, such as those that fall squarely within BA10, versus more posterior RLPFC regions, such as those featured in our study, which fall near the boundary of BA10 and BAs 46 and 47.

More work will also be needed to clarify whether the left RLPFC region identified in our study is preferentially engaged by verbal tasks, such as the tasks used in our experiment, or whether its seemingly domain-general properties extend to other information processing modalities. To this end, future experiments should compare memory and reasoning tasks that use visuospatial stimuli or auditory stimuli. Although it may be challenging to design nonverbal memory and reasoning task paradigms that appropriately equate the level of bottom-up perceptual stimulation across tasks, such studies could provide additional insight into the relative contributions of left and right hemisphere RLPFC regions. Furthermore, fMRI studies with superior temporal resolution and/or the use of effective connectivity modeling techniques may help better characterize the timing of RLPFC involvement relative to information processing operations occurring in other prefrontal and posterior cortical regions. Such work could also shed light on which regions communicate directly with RLPFC and which apparent interactions are mediated through one or more intermediate relays. Finally, the use of targeted brain stimulation techniques, such as transcranial magnetic stimulation or transcranial direct current stimulation, could valuably weigh in on the still unspecified causal relationship between RLPFC function and memory and reasoning task performance.

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