Research Report

Frontopolar cortex mediates abstract integration in analogy

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ABSTRACT

Integration of abstractly similar relations during analogical reasoning was investigated using functional magnetic resonance imaging. Activation elicited by an analogical reasoning task that required both complex working memory and integration of abstractly similar relations was compared to activation elicited by a non-analogical task that required complex working memory in the absence of abstract relational integration. A left-sided region of the frontal pole of the brain (BA 9/10) was selectively active for the abstract relational integration component of analogical reasoning. Analogical reasoning also engaged a left-sided network of parieto-frontal regions. Activity in this network during analogical reasoning is hypothesized to reflect categorical alignment of individual component terms that make up analogies. This parieto-frontal network was also engaged by the complex control task, which involved explicit categorization, but not by a simpler control task, which did not involve categorization. We hypothesize that frontopolar cortex mediates abstract relational integration in complex reasoning while parieto-frontal regions mediate working memory processes, including manipulation of terms for the purpose of categorical alignment, that facilitate this integration.

1. Introduction

Analogical reasoning is a complex form of reasoning in which concepts from one situation are mapped onto another situation resulting in new inferences and explanations. More specifically, an analogy is a mapping between the abstract structure of one situation and the abstract structure of another situation. Analogical reasoning, such as the reasoning involved in comprehending the analogy, "The atom is like the solar system," is a relational form of reasoning that is essential for learning, understanding our environment, and generating novel ideas (Dunbar and Blanchette, 2001; Gentner, 1999; Holyoak, 2005). Analogical comprehension has been regarded as a key component of intelligence (Sternberg, 1977), inductive reasoning (Holyoak and Thagard, 1995), and everyday dis-

course (Blanchette and Dunbar, 2002). Like all forms of reasoning, analogical reasoning involves a complex array of cognitive processes. Two processes that are central to analogy are manipulation of component terms in working memory and integration of relations in order to abstract a schema for the whole analogy (Holyoak, 2005). Here, using fMRI, we investigate the neural correlates of abstract relational integration in analogical thinking while keeping constant the demand for manipulation of component terms in working memory.

Starting with Milner's research on concept attainment in frontal lobe patients (Milner, 1963), neuroscientific research on complex human reasoning has shown that reasoning involves brain-based mechanisms for temporary maintenance of information as well as manipulation of this information. Temporary maintenance and manipulation of information are

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thought to be primary functions of working memory (Baddeley and Hitch, 1974; Curtis and D'Esposito, 2003; Owen, 1997). Disentangling working memory processes from other cognitive components of reasoning has become an important issue for cognitive neuroscience. For example, researchers have sought to isolate working memory processes such as goal-directed maintenance (Boroojerdi et al., 2001; Koechlin et al., 1999; Ruff et al., 2003; Wharton et al., 2000), attentional switching (Koechlin et al., 1999), and inhibiting distractor interference (Kroger et al., 2002). These investigations have revealed that working memory is a key component of the reasoning process. Furthermore, each of these studies identified reasoning processes mediated by prefrontal cortex (PFC) that are cognitively and neuroanatomically distinct from working memory processes.

1.1. Cognitive and neural underpinnings of analogical reasoning

Analogical reasoning is a form of relational reasoning in that it requires understanding how terms, and the relations between terms, are related to each other (Holyoak, 2005). In processing an analogy, a reasoner must first identify the relations that are present within each of the items/situations being compared; that is, the reasoner must be able to see how component elements relate to each other within each item/situation. These relations within items/situations have been called conventionalized semantic relations (Gentner, 1998) because they usually refer to a conventional way in which two things are related to each other. For example, in the analogy, "The atom is like the solar system," there is a conventionalized semantic relation between component elements of the atom (i.e., electrons revolve around the nucleus), and there is a conventionalized semantic relation between component elements of the solar system (i.e., planets revolve around the sun).

Additionally, in order to successfully appreciate an analogy, a reasoner must comprehend that the two conventionalized semantic relations both represent the same abstract relation. In the example analogy, a reasoner must comprehend that the two conventionalized semantic relations both represent the

abstract relation, *revolves around*. Gentner (2000) delineates, in computational terms, that the abstract relations that tie analogies together are higher-order relations in that they take other, lower-order relations (e.g., conventionalized semantic relations) as arguments. As noted by Blanchette and Dunbar (2000), these higher-order relations are abstract in that they do not depend on the specific surface-level properties of the elements of the analogy. Rather, they are similarities at the level of underlying structure. Thus, they can be abstracted from or applied to any item/situation within which the component elements are related to each other in a similar way.

Noting that abstractly similar relations are present within two different items/situations is a key component of analogical thought. This process, known as analogical mapping, requires more than simply identifying conventionalized semantic relations within each item/situation. Analogical mapping also involves an alignment process whereby the component elements of one item/situation are aligned one-to-one with corresponding elements of the other item/situation (Gentner, 1983; Holyoak and Thagard, 1997).

Recently, we have identified categorization as a potential mechanism underlying this alignment process in analogy (Green et al., in press). Specifically, using four-word stimuli, we provided evidence that mapping one item/situation onto another involves grouping component terms into categories. We have suggested that category relations facilitate appropriate one-to-one alignment of component terms between two items/situations. For example, in the solar system analogy, planets and electrons are grouped together in the category, *satellites*, and sun and nucleus are grouped together in the category *orbited objects*.

In addition to our recent empirical findings (Green et al., in press), connections between categorization and analogical reasoning have been suggested by previous models of categorical alignment (Bassok et al., 1998; Wisniewski and Bassok, 1999), and previous accounts of analogical mapping (Hess, 1966; Holyoak and Thagard, 1997; Sternberg, 1977). Bassok and colleagues (Bassok et al., 1998, Wisniewski and Bassok, 1999) have demonstrated that categorically related items such as apples and oranges can be readily compared
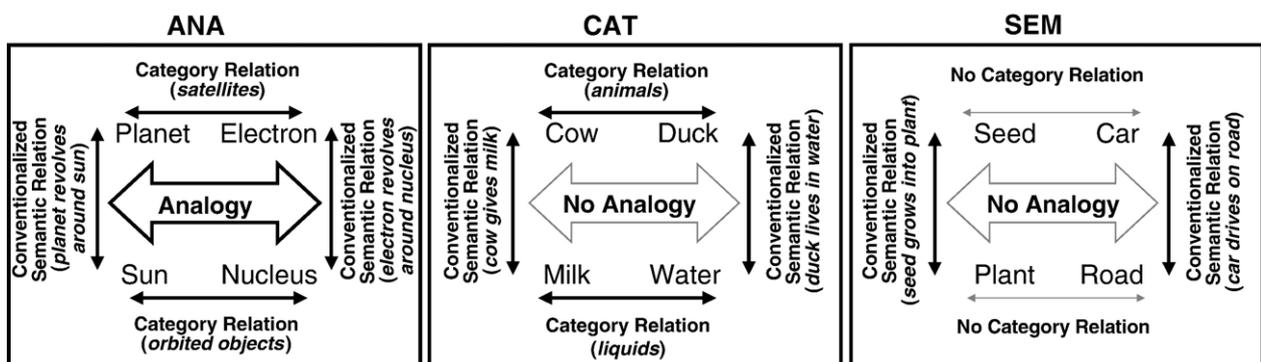

Fig. 1 – Schematic representations of stimuli. Stimuli in the ANA condition (left) involved two conventionalized semantic relations, two categorical relations, and constituted an overall analogical relation (planet is to sun as electron is to nucleus). Stimuli in the CAT condition (center) involved two conventionalized semantic relations and two categorical relations but did not constitute an overall analogical relation (cow is not to milk as duck is to water). Stimuli in the SEM condition (right) involved two conventionalized semantic relations but did not involve categorical relations or constitute an overall analogical relation.

because category co-membership makes them easier to mentally align with each other. Holyoak and Thagard (1997) have observed that "mapped elements… are typically similar but not identical" (p. 6). These authors provide the example of a military analogy wherein Saddam and Hitler are both members of the category, *leaders*, and invade and occupy are both members of the category, *acts of war*. Several other researchers have also suggested that analogies and categories may be importantly related (Bowdle and Gentner, 2005; Gentner, 1998; Gentner and Markman, 1997; Gick and Holyoak, 1983; Hummel and Holyoak, 2003). However, with the exception of Green et al. (in press), previous accounts have not addressed categorization as a *means* by which analogical mapping is accomplished, rather these accounts have addressed categorization only as a potential *end* result of analogical mapping. Thus, the role of categorization as a mechanism for accomplishing analogical mapping has not been clearly delineated.

Turning now to the neural underpinnings of analogy (a form of relational reasoning), convergent evidence has come from neuropsychological and neuroimaging research. Neuropsychological investigations of reasoning in patient populations have found specific deficits in relational integration of terms concurrent with damage to prefrontal cortex (Boroojerdi et al., 2001; Morrison et al., 2004; Waltz et al., 1999). In addition, recent neuroimaging research, using visuo-spatial stimuli, has specifically implicated left anterior prefrontal cortex in tasks demanding relational reasoning (Christoff et al., 2001; Kroger et al., 2002; Wharton et al., 2000). Taken together, these data clearly delineate the prominent role that frontal cortex, specifically left anterior prefrontal cortex, plays in the kind of relational thinking that underlies analogy.

Recently, Bunge et al. (2005) used four-word analogies to investigate the neural substrates of analogical thinking. Four-word analogies (also referred to as verbal proportional analogies) are word sets composed of two word-pairs such as 'Hand:Glove + Foot:Sock' (hand is to glove as foot is to sock). Bunge and colleagues presented four-word sets to a group of participants who were instructed to indicate whether each set constituted a true analogy. In the Bunge et al. (2005) experiment, subjects saw the first word-pair (e.g., Hand: Glove) and determined whether there was a conventionalized semantic relation between the two terms of this word-pair. The second word-pair (e.g., Foot:Sock) was presented afterwards. In the interim between the two word-pairs, subjects received one of two cues. Subjects were either cued to simply judge whether a conventionalized semantic relation was present within the second word-pair (no analogy condition), or to judge whether the two word-pairs represented abstractly similar relations (analogy condition). These authors were able to dissociate semantic retrieval of individual relations (no analogy condition) from subsequent processes of manipulating and integrating these relations (analogy condition). Retrieval of semantic information preferentially activated
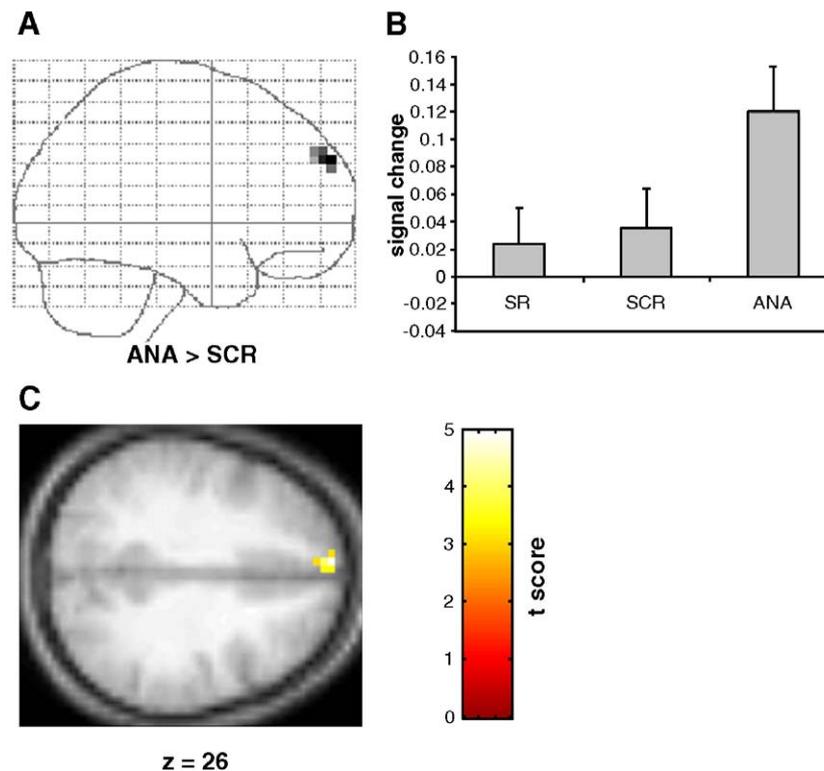

Fig. 2 – Recruitment of frontopolar cortex during analogical reasoning. Activity in frontopolar cortex was significantly greater ($P < 0.05$, corrected) for the analogical task (ANA) than for the non-analogical (CAT) control task. A) A glass brain rendering illustrates that a cluster of voxels in frontopolar cortex was the only cluster in the brain that exceeded the statistical threshold ($P < 0.005$ at a voxel extent greater than 10) in the ANA > CAT contrast. B) Peak activity averaged across all voxels within a spherical ROI ($r = 8$ mm, centered on the peak voxel from the ANA > CAT contrast) only differed significantly from baseline in the ANA condition. C) An axial slice rendering ($z = 26$) shows the location of the active voxels in frontopolar cortex.

anterior left inferior PFC (aLIPC), whereas determining abstract similarity between the two word-pairs preferentially activated left frontopolar cortex.

The present investigation adopted this distinction between semantic retrieval and the subsequent processing that brings the pieces of an analogy together as a whole. The focus of the present investigation was on parsing this subsequent processing. Specifically, we were interested in distinguishing working memory processes (i.e., maintenance and manipulation of individual terms and relations in working memory) from abstract relational integration of multiple relations in order to form a single higher-order relation. By controlling for the relevant working memory demands, we sought to determine whether abstract relational integration could be isolated from the working memory processes that facilitate analogical reasoning. We also sought to determine whether cortical activity during analogical reasoning expresses a pattern consistent with our previous finding (Green et al., in press) that the manipulation of component terms in working memory during analogical reasoning involves categorizing these terms.

1.2. The approach of the present investigation

In the present investigation, we examined analogical reasoning using stimuli that were sets of four words. We varied the tasks that the subjects were required to perform with these words. In all conditions subjects responded *True* or *False*. Subjects were instructed to respond *True* if all the relations explicitly delineated for the condition were present, and to respond *False* if one or more of these relations was not present. All stimuli were previously determined *True* or *False* for their respective conditions with >90% agreement through pilot testing among a separate group of 27 participants. The different conditions are schematically represented in Fig. 1. In the Analogy condition (ANA), subjects saw four-word sets such as 'Planet:Sun + Electron:Nucleus' arranged in a rectangle

as in Fig. 1. In *True* four-term analogies, a conventionalized semantic relation was present between the two terms of the word-pair on the left (planet revolves around sun) and an analogous conventionalized semantic relation was present between the two terms of the word-pair on the right (electron revolves around nucleus). Subjects responded *True* if the four-word set included two conventionalized semantic relations (left and right word-pairs), and if the left and right word-pairs, taken together, constituted an analogy.

In the ANA condition, no category relations were explicitly delineated. However, as noted above, previous research with four-term analogies (Green et al., in press) has suggested that categorization is a necessary mechanism sub-serving analogical mapping. Thus, we designed the ANA condition based on the premise that evaluating four-word analogies would involve grouping component terms into categories. For example, in Fig. 1, both planet and electron can be grouped into the category, *satellites*, and both sun and nucleus can be grouped into the category, *orbited objects*.

In order to control for the working memory demands of analogical reasoning, we devised a non-analogical control task, called CAT, to mimic the number and kind of relations present in an analogy. In the CAT condition, subjects saw four-word sets such as 'Duck:Water + Cow:Milk.' In this example, a conventionalized semantic relation exists between the terms of the word-pair on the left (duck swims in water) and a conventionalized semantic relation exists between the terms of the word-pair on the right (cow gives milk). At a categorical level, duck and cow are both *farm animals*, and milk and water are both *liquids*. Thus, as in four-term analogies, there are two conventionalized semantic relations and two categorical relations. However, unlike four-term analogies, there is no analogical relation (i.e., duck is not to water as cow is to milk). This is because the two conventionalized semantic relations do not have the requisite abstract similarity. Subjects were not instructed to look for analogical relations in the CAT condition.
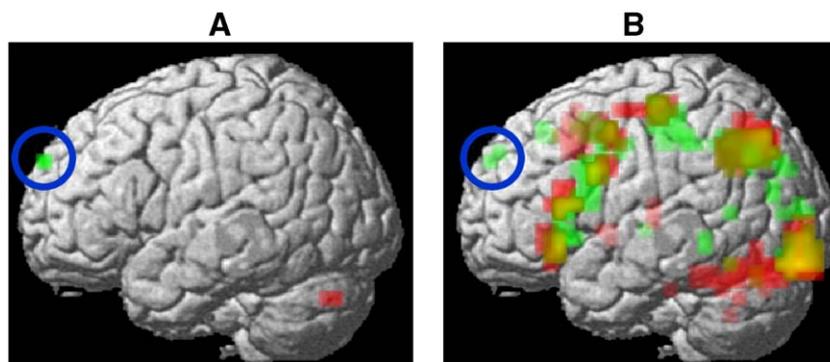

Fig. 3 – **Discrete and overlapping task-related activity. Analyses were undertaken to explore differences and similarities in the location and extent of cortical recruitment during the ANA and CAT tasks. A) To demonstrate the degree to which the ANA task preferentially recruited frontopolar cortex relative to the CAT task, the ANA > CAT and CAT > ANA contrasts are shown at a highly conservative threshold of $P < 0.0005$. Areas depicted in green were more active for analogies (ANA) than for items in the non-analogical control task (CAT). An area (blue circle) in left frontopolar cortex (BA 9) was the global maximum of activation in the ANA > CAT contrast. Areas depicted in red were more active for the CAT task than for analogies. B) To highlight the degree to which the ANA and CAT tasks recruited a common parieto-frontal network, both conditions are shown contrasted with the SEM condition at a less conservative threshold of $P < 0.005$. Areas depicted in green represent the results of the ANA > SEM contrast. Areas depicted in red represent the results of the CAT > SEM contrast. Yellow represents the overlap of the results of these two contrasts. The same frontopolar region identified in the ANA > CAT contrast was yielded by the ANA > SEM contrast but not by the CAT > SEM contrast (blue circle).**

Table 1 – Activation of frontopolar cortex						
Contrast	$t_{(at\ maxima)}$	$p_{uncorrected}$	Talairach coordinates			Cluster size
			x	y	z	no. voxels
ANA > CAT	4.96	<.005 [*]	−8	60	26	12
ANA > SEM	3.74	<.005	−8	60	26	2
[*] Significant after small volume correction (SVC).						

Subjects responded *True* if two conventionalized semantic relations (left and right word-pairs) and two categorical relations (top and bottom word-pairs) were present.

A third condition, called SEM, only involved conventionalized semantic relations. In this condition subjects were instructed to respond *True* if conventionalized semantic relations existed within the left and right word-pairs. This task neither involved assessing whether an overall analogy was present nor whether any category relations were present. Accordingly, this condition involved fewer working memory demands than the ANA and CAT conditions. The SEM condition was devised to facilitate our examination of categorization in analogical reasoning. Specifically, by comparing analogical reasoning (ANA) to two control tasks, one of which involved categorization (CAT) and one of which did not (SEM), we sought to test our hypothesis that categorization contributes to the working memory manipulations involved in analogical reasoning.

Based on the cognitive demands of each or our tasks, we made specific predictions regarding neural activity associated with these tasks. We predicted that the analogical reasoning task (ANA), which involved abstract relational integration, would engage left frontopolar cortex because of this region's apparent role in abstract relational integration (Boroojerdi et al., 2001, Bunge et al., 2005; Goel et al., 1997). Critically, if analogical reasoning involves abstract relational integration that is distinct from maintenance and manipulation of lower-order relations in working memory, then left frontopolar cortex should be preferentially recruited by the ANA task relative to the control task matched for working memory (CAT). Conversely, in brain regions other than frontopolar cortex, we hypothesized that activation elicited by the ANA task would be highly similar to that elicited by the CAT task. A comparison of the neural activation associated with these two tasks outside of frontopolar cortex was intended to provide an index of the extent to which the CAT task was successful in mimicking the demands (other than abstract relational integration) of the ANA task.

Because the CAT task involved both identifying conventionalized semantic relations and categorization of terms, while the SEM task only involved identifying conventionalized semantic relations, we predicted that the CAT task would preferentially recruit parieto-frontal regions associated with semantic categorization (Aizenstein et al., 2000; Elliott et al., 1999; Grossman et al., 2002; Koenig et al., 2005; Patalano et al., 2001) relative to the SEM task. Additionally, if analogical reasoning involves working memory manipulations for the purpose of categorizing terms, then the brain regions preferentially recruited by the CAT task relative to the SEM task should also be preferentially recruited by the ANA task relative to the SEM task.

Our specific predictions are consistent with the theoretical framework of functional organization in prefrontal cortex provided by Christoff and Gabrieli (2000). These authors have hypothesized a rostro-caudal hierarchy of prefrontal function such that rostral regions mediate abstract processing of the cognitive products of more caudal regions. In addition, Ramnani and Owen (2004) have specifically argued that frontopolar cortex mediates abstract relational integration of information produced at more caudal cortical regions. As noted above, research on abstract reasoning is consistent with this hypothesis as it has strongly implicated frontopolar cortex in tasks involving abstract reasoning (Boroojerdi et al., 2001; Bunge et al., 2003, 2005; Goel et al., 1997; Strange et al., 2001; Wagner et al., 2001). Our prediction that abstract relational integration in the ANA task would recruit more rostral areas of prefrontal cortex (i.e., frontopolar cortex) than the CAT or SEM tasks is consistent with the proposed rostro-causal hierarchy of prefrontal function.

2. Results

The 14 participants whose data were retained for analysis performed at a mean response accuracy level of 92.86% for the three conditions (SEM 95.36%, CAT 92.02%, ANA 91.19%). Data analyses were restricted to trials for which the correct response was *True*. Effect size estimates for the behavioral analyses were computed using partial η^2.

2.1. Behavioral results

There was no significant effect of condition on response accuracy ($F < 1$). For each subject, RTs < 300 ms or >3 standard deviations above the mean, were considered outliers and were omitted from further behavioral analyses. Outliers constituted fewer than 2% of responses. Mean RTs for *True* trials in the three conditions were SEM 2902.02 ms, CAT 4132.83 ms, and ANA 3893.59 ms.[1] Analysis of variance revealed a significant main effect of condition on reaction time $F(2,26) = 49.57$, $MSE = 240586.59$, $P < 0.001$, $\eta^2 = 0.65$. Follow up analyses revealed that this effect was due to significantly longer RTs for both ANA and CAT than for SEM $t(27) = 7.53$, $SE = 101.61$ and $t(27) = 12.11$, $SE = 131.64$ respectively, both P values <0.001. RTs for CAT were slightly longer than for ANA but this difference was not significant $t(27) = 1.54$, $SE = 153.02$, $P = 0.14$.

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[1] Mean reaction times for foils (SEM 3124.63 ms, CAT 4040.50 ms, ANA 4084.30 ms) did not differ significantly from reaction times for *True* trials in any condition.

Table 2 – ROI activation by task

Anatomical region	BA	ANA > SEM	CAT > SEM	Talairach coordinates			Cluster size
		t	t	x	y	z	no. voxels
Left inferior frontal cortex	6/9/44	4.72	2.73	−51	9	25	18
	9/45	N.S.	2.80	−48	20	21	18
Left pre-central gyrus	6	N.S.	3.34	−36	−5	52	6
Left inferior parietal cortex	40	3.45	4.19	−36	−53	36	9
Left superior parietal cortex	7	3.60	3.62	−36	−64	44	9
Right posterior parietal cortex	7/39	4.21	3.02	28	−72	33	10

Note. All reported *t* values are significant at $P < 0.05$ corrected (using a Bonferroni correction for the number of clusters in the ALL > BASELINE contrast).

2.2. fMRI results

When the ANA condition was contrasted with the CAT condition (Fig. 2), significantly greater activation ($t(13) = 4.96$, $P < 0.005_{uncorrected}$) was observed for the ANA condition in left frontopolar cortex (superior frontal gyrus, BA 9/10). Activation in this area represented the global maximum activation for this contrast[2] (Fig. 2a). Due to the a priori hypothesis regarding the involvement of left frontopolar cortex in analogical reasoning mentioned above, a small volume correction (SVC) was performed based on the anatomical localization of frontopolar cortex described by Fletcher and Henson (2001). This result was found to be significant following the SVC ($P < 0.05_{corrected}$). Notably, the opposite contrast did not reveal any cortical activity that was significantly greater in the CAT task than the ANA task (Fig. 3a).

In the ANA > SEM contrast (see Table 1 and Fig. 3b), the same region of left frontopolar cortex identified in the ANA > CAT contrast again showed preferential recruitment for the ANA task ($t(13) = 3.74$, $P < 0.005_{uncorrected}$; this activation was not significant following the small volume correction). Only in the ANA task did the peak activity of this frontopolar cluster differ significantly from baseline (Fig. 2b). Talairach coordinates and voxel extents for the frontopolar activations are reported in Table 1.

In order to explore activity in regions outside of frontopolar cortex, an unbiased whole-brain region of interest (ROI) analysis was performed (results shown in Table 2). This analysis revealed that left inferior frontal cortex as well as superior and inferior parietal cortex were active for the ANA and the CAT tasks relative to the SEM control task. No ROIs were significantly active for the ANA > CAT contrast. Due to the nature of this ROI analysis, activity in frontopolar cortex would not be expected to emerge because of the unconventional hemodynamic response properties in that region of the brain, including a late onset and variable early dip in activity, as described by Schacter et al. (1997) and Buckner et al. (1998). Fig. 3b shows more clearly the overlap of activation between the ANA and CAT tasks relative to the SEM task. This comparison was a useful means of further exploring differences and

similarities in the location and extent of cortical recruitment during the ANA and CAT tasks beyond the constraints of the spherical ROIs. Consistent with the ROI analysis, this overlay reveals similar networks of activation for the ANA and CAT tasks involving parietal and prefrontal regions. Activity that did not emerge in the ROI analysis was observed the fusiform gyrus for both the ANA and CAT tasks relative to the SEM task. Notably, despite the overall similarity of activation for the ANA > SEM and CAT > SEM contrasts in most regions of the brain, the left frontopolar activation that is present in the ANA > SEM contrast is absent from the CAT > SEM contrast.

3. Discussion

3.1. Selective recruitment of frontopolar cortex by abstract relational integration

Investigations into the functional underpinnings of complex human reasoning have only recently been undertaken and many questions about the nature of complex reasoning have not yet been answered. One fundamental question is whether the mental integration of abstractly related items and relations comprises cognitive processes beyond holding and manipulating items and relations in working memory. To address this question, we used fMRI to compare an analogical reasoning task (ANA) to another complex verbal task (CAT) that required the same number and kind of semantic retrieval and working memory demands but did not involve abstract relational integration. Recall that CAT stimuli were designed such that the four words (and the four relations) could not be brought together to form a single valid analogical relation. For example, in the CAT stimulus represented in Fig. 1, there are two separate conventionalized semantic relations and two separate category relations, but the various terms and relations do not form a valid analogy (i.e., it is not true that Cow is to Milk as Duck is to Water). The CAT task elicited activation in several left frontal regions but not frontopolar cortex. The ANA task was the only task that elicited frontopolar activation. Indeed, the ANA task showed preferential recruitment of frontopolar cortex in direct comparisons with both the CAT and SEM control tasks (Fig. 3 and Table 1). This pattern of results specifically implicates the abstract relational integration component of analogy, rather than the working memory processes that subserve analogy, as the source of the observed frontopolar activation.

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[2] This same frontopolar region was significantly more active for *True* trials than for foils in the ANA condition ($t(13) = 3.43$, $P < 0.005_{uncorrected}$). Preferential recruitment of this region was not observed in any contrasts between *True* trials and foils in the SEM and CAT conditions.

This interpretation of the data is supported by behavioral and imaging manipulation checks built into the present paradigm in order to assess whether the design of our conditions was successful in keeping working memory demands constant between the ANA and CAT tasks. Behavioral data for the ANA and CAT tasks showed that reaction times and response accuracy were not significantly different between the two tasks. Reaction times for both the ANA and CAT tasks were significantly longer than for the SEM task, which was designed to place less demand on working memory. Considering our imaging data in the context of our behavioral data, it seems unlikely that the observed frontopolar activation in the ANA task reflects additional working memory demands. Reaction times were actually slightly shorter for the ANA task than the CAT task, yet frontopolar activity was yielded by the ANA > CAT contrast and no such activity was yielded by the CAT > ANA contrast (Fig. 3a). Furthermore, our imaging analyses indicate that the ANA and CAT tasks elicited highly similar patterns of cortical activation. Although both the ANA and CAT tasks recruited a large network of brain areas, the ANA > CAT contrast reveals that virtually no cortical area, other than the noted area of frontopolar cortex, was active during the ANA task but not the CAT task (Fig. 3a). The opposite contrast (CAT > ANA) also argues for the similarity of cognitive processes involved in these two tasks as this contrast yielded no significant cortical differences in the left hemisphere (Figs. 2a and 3a). The thorough extent to which the ANA and CAT tasks canceled each other out in these contrasts is especially noteworthy given the cognitive complexity of the tasks and the number of cortical areas they recruited. Moreover, when the ANA and CAT tasks were independently compared to the less demanding SEM task, these comparisons revealed highly similar patterns of activation (Fig. 3b and Table 2). The high degree of similarity between the ANA and CAT tasks is also demonstrated by the whole-brain ROI analysis, which revealed no significant differences in activated regions in a direct comparison between these two tasks. Taken together, these findings indicate that the CAT task was an appropriate control for the ANA task in that it successfully enabled us to distinguish other cognitive processes involved in complex reasoning (e.g., working memory manipulations) from the abstract relational integration component that we sought to identify.

Our findings regarding frontopolar cortex are supported by previous reasoning investigations that have observed frontopolar activation during tasks that involve abstract relational integration (Bunge et al., 2005; Goel et al., 1997; Prabhakaran et al., 1997; Reynolds et al., 2006). Recently, Reynolds et al. (2006) found that a region of left frontopolar cortex similar to the area identified in the present investigation was preferentially recruited for integration of internally represented information. This investigation compared a condition in which subjects made judgments about words (e.g., abstract vs. concrete) and then integrated these judgments to make a single response to a condition in which subjects made separate, non-integrated judgments. An investigation carried out by Prabhakaran et al. (1997) used sets of object picture matrices as stimuli in complex reasoning tasks. This study employed an analytic task that required abstract reasoning. This task was compared to another task that required mostly visuo-spatial analysis. Left prefrontal regions, including an

area of frontopolar cortex similar to the one identified in the present investigation, were only recruited by the analytic task. This indicates that the abstract reasoning necessary for the analytic task included frontopolar processes beyond the working memory demands of the visuo-spatial task. An investigation by Goel et al. (1997) provided further evidence implicating left frontopolar cortex in abstract relational integration. These authors compared induction to deduction using verbal stimuli. The deduction task used in this investigation placed greater demand on working memory than the induction task. Nonetheless, these authors observed greater activation for inductive reasoning in a region of left frontopolar cortex virtually identical to the region preferentially recruited by analogical reasoning in the present investigation. Integration of abstractly similar items or experiences was a key aspect of the induction task used by these authors but was not involved in the more demanding deduction task. Thus, the Goel et al. (1997) finding provides further support for the conclusion that frontopolar cortex is recruited for abstract relational integration independent of working memory demands.

The findings of the present research are also consistent with a body of work showing dissociable working memory and abstract reasoning performance as a function of cognitive aging. For example, Small et al. (1999) found that older individuals showed significant reductions in working memory performance across the lifespan, whereas age-related declines were not observed for tests of language, visual spatial reasoning, or abstract reasoning (see also Levitt et al., in press). Similarly, Gilinsky and Judd (1994) found that age-related changes in abstract reasoning were only minimally reduced when controlling for working memory measures, suggesting that working memory and abstract reasoning rely on dissociable underlying mechanisms.

From a developmental perspective, given the relatively late maturation of prefrontal cortical regions (Gogtay et al., 2004), our findings are also consistent with a body of evidence indicating a shift to more abstract relational integration during development (Chen et al., 1998; Gentner, 1988; Gentner and Medina, 1998; Gentner and Toupin, 1986; Halford, 1987). For example, Gentner (1988) observed that young children are capable of identifying superficial similarities between items (e.g., a sponge is like a cloud because they are both fluffy). However, adults tend to make and prefer more abstract connections that emphasize the relation of items to other items (e.g., a sponge is like a cloud because both items hold water and then release it). Similar results were obtained by Gentner and Toupin (1986) when they asked younger and older children to identify similarities between groups of story characters. Younger children noticed superficial similarities (e.g., a squirrel looks like a chipmunk), while older children made similarity judgments based on the relations between the characters. Comprehending the abstract similarity between dissimilarly instantiated relations may be a function of the maturation of prefrontal cortical regions including frontopolar cortex.

3.2. Parieto-frontal recruitment reflects categorization in analogical reasoning

The finding that the analogical task (ANA) and the explicitly categorical task (CAT) elicited highly similar patterns of

activation is consistent with our previous finding that analogical reasoning involves categorization (Green et al., in press). Specifically, the pattern of functional recruitment observed for the ANA and CAT tasks relative to the non-categorical SEM task appears to reflect working memory manipulations involved in categorization. This observation is supported by the fact that the parieto-frontal network engaged by both the ANA and CAT tasks has been specifically implicated in the strategic manipulation of items in working memory for the purpose of semantic categorization (Aizenstein et al., 2000; Elliott et al., 1999; Grossman et al., 2002; Koenig et al., 2005). Grossman and colleagues (Grossman et al., 2002; Koenig et al., 2005) asked subjects to perform a task that involved strategic manipulation of information in working memory for the purpose of categorizing written descriptions of objects and pictures of novel animals. Semantic categorization in these investigations engaged the same parieto-frontal network (including BAs 40, 6, and 44) that was preferentially engaged by the ANA and CAT tasks relative to the non-categorical SEM task in the present investigation. Aizenstein et al. (2000) observed recruitment of these same parieto-frontal regions when subjects categorized patterns of dots.

In addition to parieto-frontal areas specifically associated with semantic categorization, exploratory analysis within the present study also found that the CAT and ANA tasks both recruited fusiform cortex, which has been broadly implicated in tasks of categorical cognition (Chao et al., 1999; Haxby et al., 2001; Kanwisher, 2002; Tarr and Gauthier, 2000), including semantic categorization of verbally presented stimuli (Adams and Janata, 2002; Chao et al., 1999; Tarr and Gauthier, 2000). Although these data bear future clarification, these findings further suggests that both the ANA and CAT tasks involved categorization.

Recall that category relations were not explicitly delineated in the ANA task. Subjects were simply instructed to evaluate the four-word analogies. Thus, any categorization that subjects carried out during the ANA task seems to have been necessary to performing the analogical reasoning task. The suggestion that categorization is a critical mechanism for analogical mapping accords with our recent finding (Green et al., in press) that category relations are activated during analogical reasoning. Specifically, we found that category relations were primed as strongly in a four-word analogy task, in which subjects were not instructed to identify category relations, as in a four-word task in which subjects were explicitly instructed to identify category relations.

Previous accounts of analogical mapping have suggested alignment of terms that play similar roles (e.g., Bowdle and Gentner, 2005; Gentner, 1983; Gentner and Markman, 1997; Holyoak and Thagard, 1995, 1997; Hummel and Holyoak, 2003). However, these accounts have not argued for categorization as a mechanism for this alignment. Rather, previous models of analogical mapping have generally addressed categorization as an end result of determining that two items/situations are analogous. The LISA model described by Hummel and Holyoak (2003) predicts that forming an analogy between two or more items/situations will lead to the formation of a category based on the structured intersection of what these items/situations have in common. Specifically, the LISA model predicts that category relations will be formed between items/situations

within which component terms relate to each other in similar ways (e.g., two different kinds of chairs can be grouped into the category *chair* because there is a particular relation between legs and seat that is common to both chairs). Note that it is the whole items/situations, not the component terms, which are categorized in this model. Gentner and Markman (1997) have made the related argument that determining two items/situations to be analogously similar is an important criterion in deciding that the two items/situations are members of a common category. Categorization in this account also involves whole items/situations rather than component terms that make up each item/situation. Thus, these previous accounts of analogy describe categorization that can be said to occur at a macro level, rather than a micro level.

Our recent investigation of analogical reasoning (Green et al., in press) supported a different but non-conflicting hypothesis. Specifically, this research implicated categorization as a mechanism by which individual component terms are aligned subservient to analogical mapping–categorization at a micro level. This micro-level vs. macro-level distinction between our account and previous accounts of categorization in analogy also has implications as a means vs. ends distinction. Specifically, insofar as previous accounts of analogy have addressed categorization, they have treated categorization as the *end* result of analogical reasoning and have been concerned with the formation of categories between whole items/situations. We posit that categorization may also act as a *means* to analogical reasoning by subserving analogical mapping. Our account is concerned with category relations between the component elements of respective items/situations rather than category relations between whole items/situations.

The present investigation provides initial brain-based evidence consistent with our previous findings. Specifically, we have interpreted the imaging data obtained in the present investigation to implicate the parieto-frontal network recruited by the ANA and CAT tasks as the locus of categorization during analogical reasoning.

This interpretation is open to question, but is grounded in the data and based on logical inference. Importantly, our interpretation does not hinge on the premise that recruitment of parieto-frontal regions is specific to categorization. It is clear from the literature that these areas are involved in a range of tasks (Duncan and Owen, 2000; Gold and Buckner, 2002). Nonetheless, previous research has established that these areas do mediate categorization (Aizenstein et al., 2000; Grossman et al., 2002; Koenig et al., 2005; Patalano et al., 2001). We can conclude that subjects performed categorization in the CAT task because they had to perform categorization in order to respond correctly and the accuracy level was very high (91.19%). Thus, there is good reason to believe that the categorization that occurred in the CAT task was mediated by parieto-frontal regions that were active for the CAT task. The parieto-frontal activity associated with the CAT task was highly similar to the parieto-frontal activity associated with the ANA task. The similarity is such that direct comparisons (ANA > CAT and CAT > ANA) cancel out all parieto-frontal activation (Fig. 3a). The argument that categorization accounts for at least some of what the ANA and CAT tasks have in common is strengthened by the fact that the overlap in

activation for these two tasks included concurrent recruitment of BAs 40, 6, and 44. Concurrent recruitment of BAs 40, 6, and 44 has been implicated in semantic categorization (Aizenstein et al., 2000; Grossman et al., 2002; Koenig et al., 2005). This activity was common to the ANA and CAT tasks even after activity associated with the SEM task (which did not involve categorization) was subtracted out in the ANA > SEM and CAT > SEM contrasts. This finding emerged from both the exploratory analysis (Fig. 3b) and the ROI analysis (Table 2).

Based on these data, and based on the behavioral evidence we have recently obtained implicating categorization in the process of analogical mapping (Green et al., in press), we have inferred that parieto-frontal activity during the ANA task reflects categorization. It is nonetheless important to consider the possibility that parieto-frontal activity may not have reflected categorization in the ANA task even if it did reflect categorization in the CAT task. Thus, while the present data provide initial brain-based evidence in support of our hypothesis concerning categorization in analogy, future research will be necessary in order to examine this issue more definitively.

3.3. A functional anatomical hierarchy of processing in prefrontal cortex during relational reasoning

Several researchers have sought to distinguish the roles of different prefrontal regions in complex cognitive tasks (e.g., Aron et al., 2004; Duncan and Owen, 2000). Petrides and colleagues (Petrides, 1994, 1995; Owen et al., 1996) proposed a two-stage model of working memory whereby ventrolateral PFC alone is recruited for retrieval and maintenance of a small number of items, but both ventrolateral PFC and dorsolateral PFC are recruited when maintenance and manipulation of information is required. Christoff and Gabrieli (2000) have suggested that this model be extended to represent a rostro-caudal hierarchy. In their hierarchical model, caudal regions of superior and inferior PFC are lower in the hierarchy. They mediate the monitoring and manipulation of externally generated information. More rostral areas of prefrontal cortex are higher in the hierarchy. They mediate processing of internally generated information produced at the lower (more caudal) regions of the hierarchy. Other researchers have also proposed models in which the division of labor in prefrontal cortex operates such that the most abstract cognition occurs at the most rostral regions (e.g., Bunge et al., 2005; Fincham et al., 2002; Koechlin et al., 2003). One such model was proposed by Fincham et al. (2002) based on Anderson's ACT-R (Adaptive Control of Thought–Rational) cognitive model (Anderson, 1990; Anderson and Lebiere, 1998). These authors demonstrated that DLPFC performs working memory subcomponents of planning in service of more abstract-level planning which, as these authors note, has been putatively localized to frontopolar regions (Christoff and Gabrieli, 2000; Koechlin et al., 1999).

In a recent review of data and theories concerning frontopolar cortex, Ramnani and Owen (2004) put forward a common theoretical framework for frontopolar function. These authors note that the extent of arborization of neurons in frontopolar cortex (number of dendritic spines per cell and spine density) is greater than in comparable areas of frontal cortex, while the density of cell bodies is substantially less. These authors suggest that this structure indicates an integrative function. Specifically, based on the functional brain imaging literature, these authors argue that frontopolar cortex mediates integration information received from more caudal areas of supramodal cortex. One of the major integrative functions that these authors ascribe to frontopolar cortex is abstract relational integration. Based on their theoretical framework, Ramnani and Owen (2004) predict that the process of integration itself should be reflected in frontopolar activity above and beyond the activity observed for processing the component elements to be integrated.

The data obtained in the present investigation provide empirical support for this theoretical prediction. The ANA and CAT tasks involved processing of similar component elements, however, only the ANA task required abstract relational integration of these elements. Consistent with the prediction of Ramnani and Owen (2004), the ANA task elicited activation in frontopolar cortex while the CAT task did not. Activation of relatively caudal areas of PFC in the present investigation also supports previous accounts of a hierarchical caudal-to-rostral progression in PFC information processing. Specifically, our data indicate that relatively caudal PFC regions, including the parieto-frontal network discussed above, mediate manipulation of information in working memory (possibly including alignment of corresponding terms based on category co-membership) and that the cognitive products of these relatively caudal regions provide the substrate for more abstract processing (relational integration) in frontopolar cortex.

As noted above, neither the CAT task nor the SEM task significantly engaged frontopolar cortex. These results suggest that activity in frontopolar cortex during the ANA task is not driven by task difficulty. The SEM task was not as difficult as the ANA task. The CAT task was at least as difficult as the ANA task and was much more difficult than the SEM task. Thus, task difficulty cannot explain the fact that SEM and CAT similarly failed to recruit this region or the fact that ANA recruited this region more strongly than SEM and CAT. The observed pattern of results indicates that it is the abstract relational integration component of the analogy task, rather than task difficulty, that resulted in the observed frontopolar recruitment. This finding is in accordance with evidence (reviewed in Christoff et al., 2001) that increasing task difficulty is not a sufficient explanation of prefrontal activation.

4. Conclusion

By experimentally controlling for manipulation of terms in working memory, the present investigation sought to isolate the neural signature of abstract relational integration in an analogical reasoning task. We identified a region at the frontal pole of the brain that is selectively active for the abstract relational integration component of analogical reasoning. Both analogical reasoning and a task of explicit categorization engaged a parieto-frontal network of regions previously associated with manipulation of information in working memory for the purpose of categorization. This finding provides initial brain-based evidence that categorization is a mechanism underlying analogical mapping. The present investigation also functionally delineates a cognitive and

anatomical processing hierarchy in left PFC from caudal to rostral. Specifically, caudal regions of left PFC, in conjunction with parietal regions, mediate working memory processes that provide the cognitive substrate for abstract relational integration at more rostral areas (frontopolar cortex). These findings provide new insight into complex reasoning and the processing of abstract representations. Complex reasoning about abstract information is among the capacities that make the human brain unique in terms of its function, just as highly developed frontal lobes–frontopolar cortex in particular–make the human brain unique in terms of its structure. It is perhaps not coincidental that the most advanced reaches of the evolved human brain should mediate function at the most advanced reaches of human cognition.

5. Experimental procedures

5.1. Participants

Eighteen participants (9 females and 9 males, mean age = 22.5 years) took part in the fMRI study and were paid $20. Four participants (2 males, 2 females) were eliminated from subsequent analysis due to severe motion throughout the scanning session or poor behavioral task performance (<90%). All participants were right-handed, reported no significant abnormal neurological history and had normal or corrected-to-normal visual acuity. Informed written consent was obtained from all participants prior to the experiment in accordance with the guidelines established by the Committee for the Protection of Human Subjects at Dartmouth College.

5.2. Design and apparatus

Data were acquired in six event-related functional runs. Each run consisted of trials of one of the three conditions (two consecutive runs for each condition). The order in which the conditions (SEM, CAT, and ANA) were presented was counterbalanced. Each run consisted of 30 trials (15 True and 15 False) and lasted 8 minutes and 24 seconds. Each trial was 9 seconds in duration. Fixations lasting one, two, three, or four TRs were inserted randomly between trials with the constraint that all trials were preceded and followed by at least one fixation. Visual stimuli were generated using a G4 PowerBook computer running PsyScope 2.5.1 software (Cohen et al., 1993). Stimuli were projected to participants with an Epson (model ELP-7000) LCD projector onto a screen positioned at the head end of the bore. Participants viewed the screen through a mirror mounted on the head coil. Cushions were used to minimize head movement.

5.3. Materials and procedures

The three conditions presented were Semantic Relations (SEM), Semantic and Categorical Relations (CAT), and Analogy (ANA). Stimuli in each condition were a set of four words presented such that a 15 cm by 6 cm rectangle was formed by the midpoints of the four words subtending approximately 7.5° of visual angle (see Fig. 1 for a schematic representation). A fixation cross appeared at the center of this rectangle at the same position where it appeared during periods of fixation only. Thus, the fixation cross did not disappear or vary during functional scanning. For all trials, subjects responded True or False by pressing a button with either the index or middle finger of their right hand.

In the SEM condition, subjects judged whether a conventionalized semantic relation existed between the two words on the left and whether a conventionalized semantic relation existed between the two words on the right. A conventionalized semantic relation was defined to exist when there was "a common sense way in which two things often do, or easily could, have to do with each other." Foils in the SEM condition were four-word sets in which either the left or right word-pair did not represent a conventionalized semantic relation. In the CAT condition, subjects judged whether conventionalized semantic relations were present within the left and right word-pairs, as in the SEM condition. In addition, they judged whether the two words on the top were co-members of a category and whether the two words on the bottom were co-members of a category. Foils in the CAT condition were four-word sets in which either the left or right word-pair did not represent a conventionalized semantic relation or in which either the top or bottom word-pair did not represent a category relation. In the ANA condition, subjects judged whether conventionalized semantic relations were present within the left and right word-pairs, as in the SEM and CAT conditions. In addition, subjects judged whether the left word-pair and the right word-pair were analogous to each other. That is, did the two conventionalized semantic relations, taken together, constitute an analogy? Foils in the ANA condition were four-word sets in which either the left or right word-pair did not represent a conventionalized semantic relation or in which the two word-pairs did not constitute analogous relations. In all conditions, foils constituted 50% of trials. In each condition, subjects were instructed to indicate that a trial was True if all the relations explicitly delineated for that condition were present in the trial. If one or more of these relations was not present, subjects were instructed to indicate that the trial was False.

The first run of each condition was preceded by an instructional and practice session that included seven practice trials. A diagram was presented using labeled arrows to represent the relations to be judged in each condition. All words were singular nouns and were controlled for mean word length, number of syllables, word frequency, and concreteness within and across conditions using the MRC Psycholinguistic Database (Wilson, 1988). All stimuli were pilot tested with a separate group of 27 participants. Only stimuli that were judged with 90% agreement or higher were used in the subsequent behavioral and fMRI investigations.

5.4. fMRI image acquisition

Imaging was performed on a 1.5 Tesla whole body scanner (General Electric Medical Systems Signa, Milwaukee, Wisconsin) with a standard head coil. Anatomical images were acquired using a high-resolution 3-D spoiled gradient recovery sequence (SPGR; 124 sagittal slices, TE = 6 ms, TR = 25 ms, flip angle = 25°, voxel size = 1 × 1 × 1.2 mm). Functional images were collected in runs using a gradient spin-echo

echo-planar sequence sensitive to BOLD contrast (T2*) (TR = 3000 ms, T2* echo time = 35 ms, flip angle = 90°, 3.75 × 3.75 mm in-plane resolution). During each functional run, 168 sets of axial images (25 slices; 5.5-mm slice thickness, 1 mm skip between slices) were acquired allowing complete brain coverage.

5.5. Statistical image analysis

All data were analyzed using the general linear model for event-related designs in SPM99 software (Wellcome Department of Cognitive Neurology, London, UK; Friston et al., 1995). For each functional run, data were preprocessed to remove sources of noise and artifact. Functional data were realigned within and across runs to correct for head movement using a six parameter, rigid body alignment technique (Kiebel et al., 1997; Woods et al., 1998) and coregistered with each participant's anatomical data. Functional data were then transformed into a standard anatomical space (3 mm isotropic voxels) based on the ICBM 152 brain template (Montreal Neurological Institute), which approximates Talairach and Tournoux (1988) atlas space using higher order polynomial functions, then non-linear basis functions (Ashburner and Friston, 1999). Normalized data were then spatially smoothed (8 mm full-width-at-half-maximum) using a Gaussian kernel in order to optimize signal-to-noise (Skudlarski et al., 1999) and meet the assumptions of Gaussian random field theory (Worsley and Friston, 1995). Analyses took place at two levels: formation of statistical images and regional analysis of hemodynamic responses. For each participant, a general linear model (Friston et al., 1998), incorporating task effects and covariates of no interest (a session mean, a linear trend, and six movement parameters derived from realignment corrections) was used to compute weighted parameter estimates (β) and t-contrast images for each comparison at each voxel.

Following these analyses, a separate whole-brain ROI analysis was conducted. To calculate signal intensities in an unbiased manner, spherical ROIs ($r = 6$ mm) were defined based on peaks identified in a whole-brain mean t image (excluding cerebellum) that was created by comparing all active tasks to the baseline fixation task (averaged across all subjects). In this way, each task (ANA, CAT, and SEM) contributed equally to the generation of ROIs. Only clusters that were active at a threshold of $P < 0.001$ with a voxel extent greater than 5 were included in this analysis. For each subject, Signal intensities for each ROI were calculated separately for each subject and each condition and then examined statistically using paired-samples t tests. Results of this analysis are shown in Table 2.

Acknowledgments

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