

Neural Substrates of Fluid Reasoning: An fMRI Study of Neocortical Activation during Performance of the Raven's Progressive Matrices Test

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We examined brain activation, as measured by functional magnetic resonance imaging, during problem solving in seven young, healthy participants. Participants solved problems selected from the Raven's Progressive Matrices Test, a test known to predict performance on a wide range of reasoning tasks. In three conditions, participants solved problems requiring (1) analytic reasoning; (2) figural or visuospatial reasoning; or (3) simple pattern matching that served as a perceptual-motor control. Right frontal and bilateral parietal regions were activated more by figural than control problems. Bilateral frontal and left parietal, occipital, and temporal regions were activated more by analytic than figural problems. All of these regions were activated more by analytic than match problems. Many of these activations occurred in regions associated with working memory. Figural reasoning activated areas involved in spatial and object working memory. Analytic reasoning activated additional areas involved in verbal working memory and domain-independent associative and executive processes. These results suggest that fluid reasoning is mediated by a composite of working memory systems. © 1997 Academic Press

Some problems can be solved by direct application of long-term knowledge and practiced routines or *crystallized* knowledge (Cattell, 1963). For example, one can answer the question "What is the capital of France?" using crystallized knowledge. Novel problems, however, cannot be solved directly by referring to a store of long-term knowledge, but instead require analytic or *fluid reasoning*. There is evidence for a distinction between the psychological

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processes and the neural substrates that subserve fluid reasoning and crystallized knowledge. A psychometric literature documents individual differences that dissociate the psychological processes involved in fluid reasoning and crystallized knowledge (Cattell, 1963; Horn, 1985; Lohman, 1989). Normal aging disproportionately affects fluid relative to crystallized abilities (Salt-house, 1996). Neuropsychological studies have reported selective impairments of fluid abilities in patients with frontal-lobe lesions (Duncan, Burgess, & Emslie, 1995) or Parkinson's disease (Gabrieli, 1996).

Identification of the neural substrates of crystallized knowledge may be guided by the domain-specific nature of such knowledge. For example, there is evidence that crystallized long-term memory stores of the names of tools, animals, and people are represented in distinct left-hemisphere regions (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Martin, Wiggs, Ungerleider, & Haxby, 1996; Spitzer, Kwong, Kennedy, Rosen, & Belliveau, 1995). Working memory processes that sustain and manipulate task-relevant information are also domain specific. There is evidence for a right-hemisphere system mediating spatial working memory (Jonides, Smith, Koeppe, Awh, Minoshima, & Mintun, 1993) and separable left-hemisphere systems mediating verbal and object working memory (Smith, Jonides, Koeppe, Awh, Schumacher, & Minoshima, 1995; Smith, Jonides, & Koeppe, 1996a). Identification of the neural substrates of fluid reasoning, however, cannot be guided by domain specificity because such reasoning is, by definition, not domain specific. Fluid reasoning is "the ability to discriminate and perceive relations between any fundamentals, new or old" (Cattell, 1943).

The goal of the present study was to identify the neural substrates of fluid reasoning. Therefore, we imaged brain activation, as measured by functional magnetic resonance imaging (fMRI), while participants performed problems from the Raven's Progressive Matrices (RPM). The problems were taken from the Raven's Advanced Progressive Matrices (RAPM) (Raven, 1965) and sets C, D, and E of the Raven's Simple Progressive Matrices (RSPM) (Raven, 1976). The RPM is a widely used nonverbal test designed to be a culture-free measure of fluid reasoning that does not rely on crystallized knowledge. It is thought to provide an optimal measure of processes widely used in fluid reasoning. Snow, Kyllonen, and Marshalek (1984) demonstrated this property of the RPM in a multidimensional scaling analysis by which many tests were placed in a spatial configuration with closeness representing increased correlations among the tests. The RPM occupied a central position among all these tests (Fig. 1), indicating that it provided the optimal domain-independent measure of fluid reasoning processes relevant for many kinds of verbal, spatial, and mathematical problem solving.

To date, the Raven's task has been the subject of few imaging studies. A PET study using ¹⁸fluoro-2-deoxyglucose examined brain activation during RAPM performance (Haier, Siegel, Neuchterlein, Hazlett, Wu, Paek, Browning, and Buchsbaum, 1988). That study, which was designed to examine

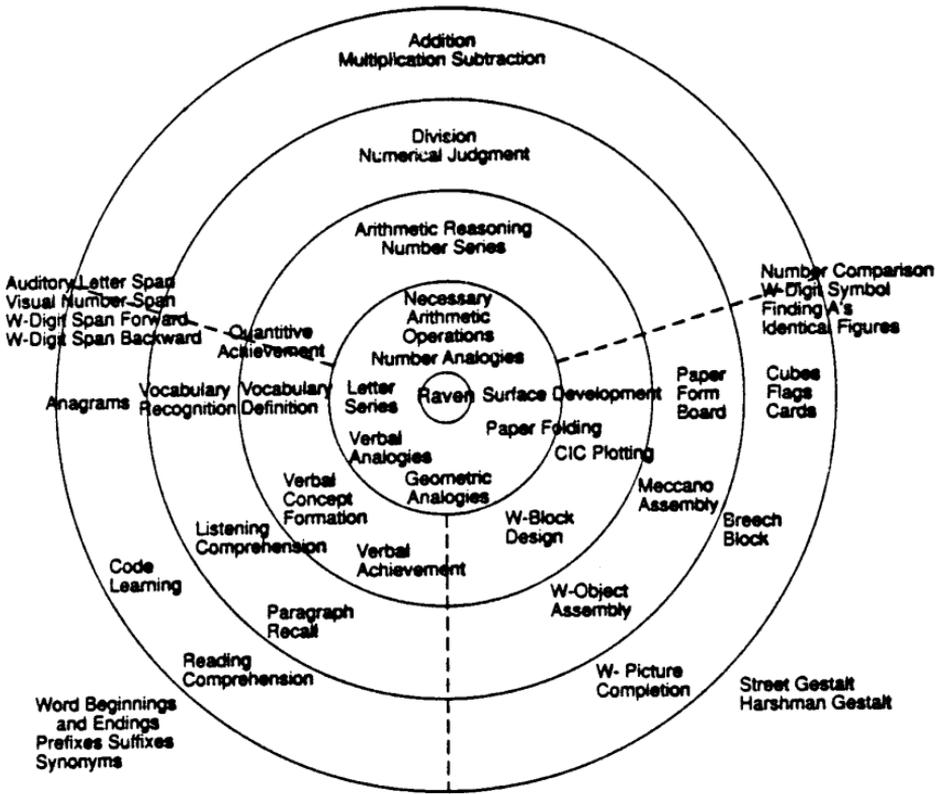


FIG. 1. A multidimensional scaling solution illustrating the intercorrelations among various ability tasks is shown in this idealized model. The Raven's task occupies the center of the model. Complex tasks such as Necessary Arithmetic operations and Verbal Analogies are shown to be near the Raven's task, indicating that performance on these tasks are highly correlated despite their differences in content. The subsequent contours contain tasks that show less correlation to the tasks near the center of the model and cluster more as a function of content area with separate clusters for figural, numerical, and verbal tasks. Tasks involving different content are separated by the dashed lines. (Reproduced, by permission, from *Advances in the Psychology of Human Intelligence* [p. 92] by R. E. Snow, P. C. Kyllonen, and B. Marshalek, 1984, Erlbaum, Hillsdale, NJ. Copyright 1984 by Erlbaum.)

individual differences, found that performance was correlated inversely with overall activation. That and other studies using the xenon 133 technique (Risberg, 1986; Berman, Illowsky, & Weinberger, 1988) have noted strong activation in the left parieto-occipital region during Raven's performance (but see Haier, 1993). These studies have a number of important limitations by current imaging standards including modest spatial and temporal resolution and an inability to compare multiple conditions within a subject in order to isolate cognitive factors of interest.

Evidence from the neuropsychological literature suggests a possible hemispheric asymmetry in brain regions that are involved in RAPM performance,

although the evidence is far from conclusive. Several researchers report that patients with left-hemisphere lesions perform worse than those with right-hemisphere lesions, but some report the opposite finding, and yet others report no hemispheric differences (reviewed in Berker & Smith, 1988; Villardita, 1985). The disparate results may reflect confounding variables such as neglect and aphasia. In one study designed to control the effects of neglect and aphasia, Villardita (1985) administered the Coloured Progressive Matrices Test (CPM, an easier version of the RAPM) to patients with either left- or right-hemisphere damage. Additionally, he classified problems according to whether they required perceptual or more conceptual, analytic thinking. Nonaphasic patients with right-hemisphere damage performed worse than nonaphasic patients with left-hemisphere damage on problems requiring perceptual operations, but patients with left-hemisphere damage performed worse than patients with right-hemisphere damage on problems requiring conceptual thinking or analytic reasoning. This suggests possible hemispheric asymmetries in brain regions employed in performing reasoning tasks that are to a large extent visuospatial or analytic in nature. Failure to analyze performance as a function of problem type (perceptual or conceptual) may have added to the inconclusive results of previous studies.

In addition to this hemispheric asymmetry in performance, there is evidence for different consequences of anterior and posterior lesions on RAPM performance. Berker and Smith (1988) suggested that failure to distinguish between anterior and posterior lesions has clouded the examination of hemispheric differences. They administered the CPM to 57 patients with focal lesions and found no difference in performance for patients with left versus right lesions. However, anterior lesions proved less damaging to performance than posterior lesions and, furthermore, they found evidence that the right posterior region was most important for CPM performance. In contrast to the more difficult RAPM, the CPM is composed mostly of problems that are visuospatial rather than analytic as distinguished by Villardita (1985). Because right-hemisphere lesions disproportionately hindered performance on visuospatial problems in his study, it is predictable that right-hemisphere patients would fare worse than left-hemisphere patients when administered the entire CPM test. This could explain the finding that right posterior lesions most affected performance. The Berker and Smith and Villardita studies suggest performance on the RAPM may be mediated differentially by the anterior and posterior regions and by the left and right hemispheres, and further, that results may crucially depend on classification of the problems as those stressing visuospatial versus analytic processing.

The distinction between RAPM problems that require an analytic reasoning strategy versus a visuo-perceptual or figural strategy has been advanced by other researchers on psychological grounds. Hunt (1975) differentiated problems which were solvable using a "Gestalt algorithm" and problems which were solvable using an "analytic algorithm." According to Hunt, the Gestalt

algorithm uses the operations of visual perception (such as continuation or superimposition), while the analytic algorithm applies logical operations to features contained within elements of the problem. Carpenter, Just, and Shell (1990) categorized problems systematically according to the number and type of rules required to solve the problems. Some rule types invoked mostly perceptual algorithms (Gestalt reasoning), while other rule types invoked more adaptive algorithms for solving novel problems (analytic reasoning).

To capitalize on the apparent neurological and psychological distinctions between problem types, we adapted three types of problems from the RPM (Fig. 2). "Figural" problems required mostly visuospatial analysis to determine the correct answer and corresponded to one rule type distinguished by Carpenter *et al.* (1990). These problems were chosen to require minimal analytic reasoning. "Analytic" problems required abstract/analytic reasoning and could not be solved by figural analysis alone. "Match" problems were included as a perceptual-motor control and required matching identical figures without figural or analytic reasoning.

These three types of problems were used in three separate comparisons (scans) with each participant. Activation in the analytic/match task was thought to identify all cortical areas involved in performing the Raven's task beyond the perceptual-motor demands of task performance. Activation in the figural/match scan was thought to identify cortical regions involved selectively in figural reasoning because no analytic reasoning was required. Activation in the analytic/figural scan was thought to identify cortical regions involved selectively in analytic reasoning with the assumption that both analytic and figural problems would involve figural processing, but that only analytic problems would demand the induction of abstract relations, strategy shifting or planning, and goal management or central executive control of assembly processes.

We had three main hypotheses. First, based on evidence from lesion studies, it was hypothesized that greater left-hemisphere activation would occur during analytic relative to figural problem solving, and that greater right-hemisphere activation would occur during figural problem solving relative to the perceptual-motor control task. Second, also based on lesion evidence, it was hypothesized that frontal activation would be linked more closely to analytic than to figural problem-solving.

The third hypothesis was motivated by a broad spectrum of behavioral studies reporting a close relation between working memory span or capacity and the Raven's task. Studies have found strong correlations between working memory and Raven's performance in aging, Parkinson's disease, development and in individual differences within an age span. Statistically controlling for age-related decline in working memory accounts for much of the age-related decline in Raven's performance (Gabrieli, 1996; Salt-house, 1993). Similarly, statistical control for reduced working memory span in Parkinson's patients virtually eliminates their deficit on the Raven's

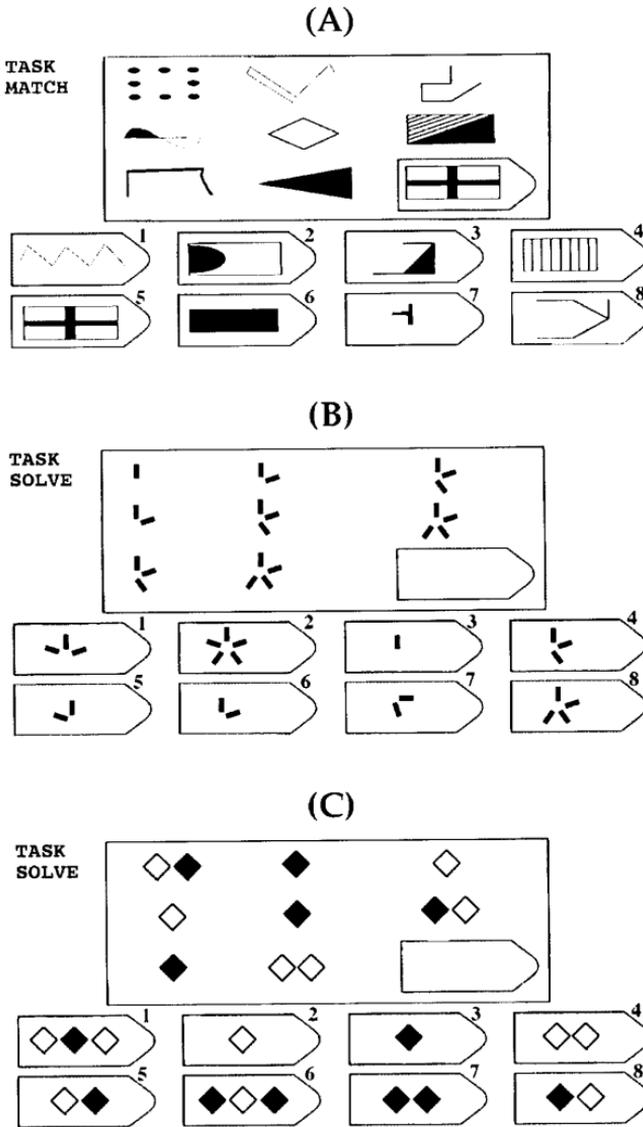


FIG. 2. Examples of problem types used in the experiment: (A) Match problem: Participants were instructed to select one of the eight response alternatives that matched the bottom right pattern. (B) Figural problem and (C) analytic problem: Participants were instructed to use the eight patterns in the upper array to determine which one of the eight response alternatives should appear in the bottom right position.

task relative to age-matched healthy people (Gabrieli, 1996). Much of the childhood developmental improvement in performance on the Raven's task is accounted for by improvement in working memory, and furthermore, when the effects of age are statistically controlled there remains a substan-

tial correlation between Raven's performance and working memory (Fry & Hale, 1996). Kyllonen and Christal (1990) found high correlations between working memory and reasoning in their behavioral studies which led them to conclude that "reasoning ability is nothing more than working memory capacity." Therefore, it was also hypothesized that some of the same regions activated during domain-specific verbal, spatial, and object working memory tasks (Jonides et al., 1993; Smith et al., 1995, 1996a, 1996b) would also be activated during the RPM task.

METHOD

Participants

Seven right-handed Stanford University graduate students, three men and four women, with a mean age of 26 years (range, 23–30 years) participated in this study. Each participant provided a written consent approved by the Institutional Review Board at Stanford University.

Materials

Each problem was adapted from the RAPM (Raven, 1965) and RSPM (Raven, 1976) and consisted of a 3×3 matrix of figures arrayed and organized according to certain rules with the bottom right figure missing. Below the matrix were eight choice figures, of which only one belonged in the missing position of the above array according to rules that could be determined both across columns and down rows. The stimuli were created by scanning the images from the RSPM and RAPM and then modifying them for presentation in the fMRI scanner. Three types of problems were created (Fig. 2).

Figural problems were chosen from the "Quantitative Pairwise Progression" rule type provided by Carpenter et al. (1990) which refers to a "quantitative increment or decrement between adjacent entries in an attribute such as size, position, or number." These problems could all be solved with simple visuospatial analyses and were selected to require minimal analytic reasoning.

Analytic problems were chosen from different rule sets (Distribution of 3, Distribution of 2, Addition, Subtraction, combinations of these) provided by Carpenter et al. (1990) which require more than pairwise comparison of one attribute across columns or rows. These problems could not be solved by figural analysis, but required analytic reasoning based on formal operations or rules applied to sets and subsets of element features. For example, Distribution of 3 problems have three different "values of a categorical attribute" distributed across a row or down a column (Carpenter et al., 1990).

Match problems were designed to control for perceptual input and motor output in the figural and analytic reasoning tasks. Match problems consisted of nine random figures unrelated by any rules. Unlike the figural and analytic problems, a figure was present in the bottom right position and one of the eight response alternatives was identical to that figure.

Procedure

Imaging was performed with a 1.5T whole-body MRI scanner (General Electric Medical Systems Signa, Rev. 5.5). For functional imaging, two 5-in. diameter local receive coils were used for signal reception. Head movement was minimized using a bite bar formed with each participant's dental impression. A T2* sensitive gradient echo spiral sequence (Noll, Cohen, Meyer, & Schneider, 1995), which is relatively insensitive to cardiac pulsatility motion artifacts (Glover & Lee, 1995), was used for functional imaging with parameters of TR = 900 ms, TE = 40 ms, and flip angle = 65°. Four interleaves were obtained for each image with an acquisition time (sampling interval) of 2.88 s per image. T1-weighted, flow compensated spin-warp anatomy images (TR = 500 ms; minimum TE) were acquired for all sections that received functional

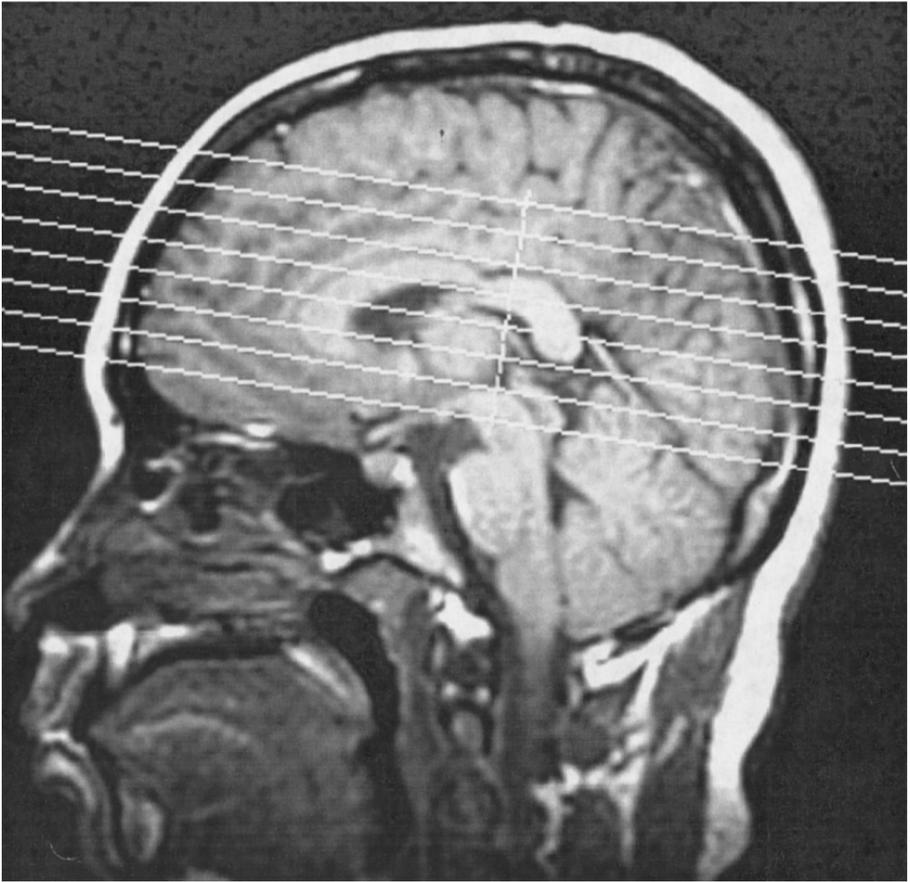


FIG. 3. The location of eight axial slices analyzed in this study are depicted as white lines on a sagittal localizer.

scans, and voxels found to be significantly activated during the functional scan were overlaid on these structural images. Eight 6-mm-thick slices were acquired in the horizontal plane of the Talairach and Tournoux atlas (1988) starting from 7.5 mm below the anterior-commissure (AC)–posterior commissure (PC) line, with a 1.5-mm interslice interval (Fig. 3).

Stimuli were generated from a computer and back-projected onto a screen located above the participant's neck via a magnet-compatible projector. Visual images were viewed from a mirror mounted above the participant's head. Each participant performed three scans: an analytic/match scan, a figural/match scan, and an analytic/figural scan. In each scan, there were 12 problems, with 6 of one kind and 6 of the other kind presented in alternation. Each problem was presented for 30 s. For figural and analytic problems, participants had to identify which of the eight choice figures belonged in the missing position according to rules derived from rows or columns of the figures in the array. Above figural and analytic problems, participants saw the instruction "Task Solve." For match problems, participants had to identify which of the eight choice figures was identical to the bottom right figure. Above match problems, participants saw the instruction "Task Match."

In the last 5 s, one choice was highlighted and participants responded by squeezing a squeeze

ball in their right hand only if that choice was correct. Half the highlighted choices were correct answers and half were incorrect answers. The order of the three scans was rotated across participants. Within each scan, the order of the problem kinds (e.g., analytic/match versus match/analytic) was alternated across participants.

fMRI Analysis

Image analysis was performed off-line by transferring the raw data to a Sun SparcStation. A gridding algorithm was employed to resample the raw data into a Cartesian matrix prior to processing with 2d FFT. Once individual images were reconstructed, time series of each pixel were obtained and correlation methods that take advantage of periodically oscillating paradigms were used to analyze functional activation (Friston, Jezzard, & Turner, 1994). Because a considerable amount of artifactual signal that occurred over time was due to events that were random with respect to the timing of the activation paradigm (e.g., pulsatile effects from blood, CSF, or brain movement), correlations of the pixel responses over time with a reference function that represents the time of the expected activation (based upon the timing of stimulus presentation) were used to remove artifacts (Bandettini, Jesmanowicz, Wong, & Hyde, 1993; Lee, Glover, & Meyer, 1995). As described by Friston, Jezzard, and Turner (1994), the reference function was computed by convolving a square wave at the task frequency with a data-derived estimate of the hemodynamic response function. The frequency of the square wave was computed from the number of task cycles divided by the total time of the experiment. One task cycle consisted of a control block and an experimental block each of equal duration. There were six cycles presented over a 360-s scan (frequency ~ 0.0166 Hz). Correlations between the reference function and the pixel response time series were computed and normalized (see Friston et al., 1994).

To obtain composite maps of activation over all participants, average functional activation maps were created by transforming each section from each subject to a corresponding standardized horizontal section (Talairach & Tournoux, 1988) at the same distance rostral to the AC (Desmond, Sum, Wagner, Demb, Shear, Glover, Gabrieli, & Morell, 1995). This transformation was done individually for all horizontal sections. Following transformation, the average z value for each pixel in a section was computed across participants and voxels that reached a statistical threshold of $p < .01$ or lower were displayed on each map. To identify foci of activation, the following algorithm was used. For each pixel in the functional map whose activation exceeded threshold, a recursive procedure was used to identify all neighboring voxels (eight surrounding voxels). When a neighboring pixel was found, the recursive algorithm in turn found other neighbors until no more neighbors could be identified. The set of all voxels that resulted from the recursive search were defined as a cluster. Each cluster was then characterized by the number of voxels it contained, the location of the maximum focus of activity in the cluster, the mean and maximum activations associated with the voxels in the cluster, and the regions that the cluster encompassed.

RESULTS

Behavioral Performance

Scores were percentage of correct responses (Table 1). Participants performed perfectly on the match problems ($M = 100\%$), slightly less well on the figural problems ($M = 92.9\%$), and least well on the analytic problems ($M = 73.9\%$). Performance on each problem type did not differ significantly across scans. Therefore, scores for each problem type were combined across scans and examined in a repeated-measures analysis of variance (ANOVA). Scores differed significantly for the three problem types, $F(2,6) = 8.81$, $p < .01$. Participants performed significantly better on match than analytic prob-

TABLE 1
Performance (Percentage Correct) on the Raven's Problems

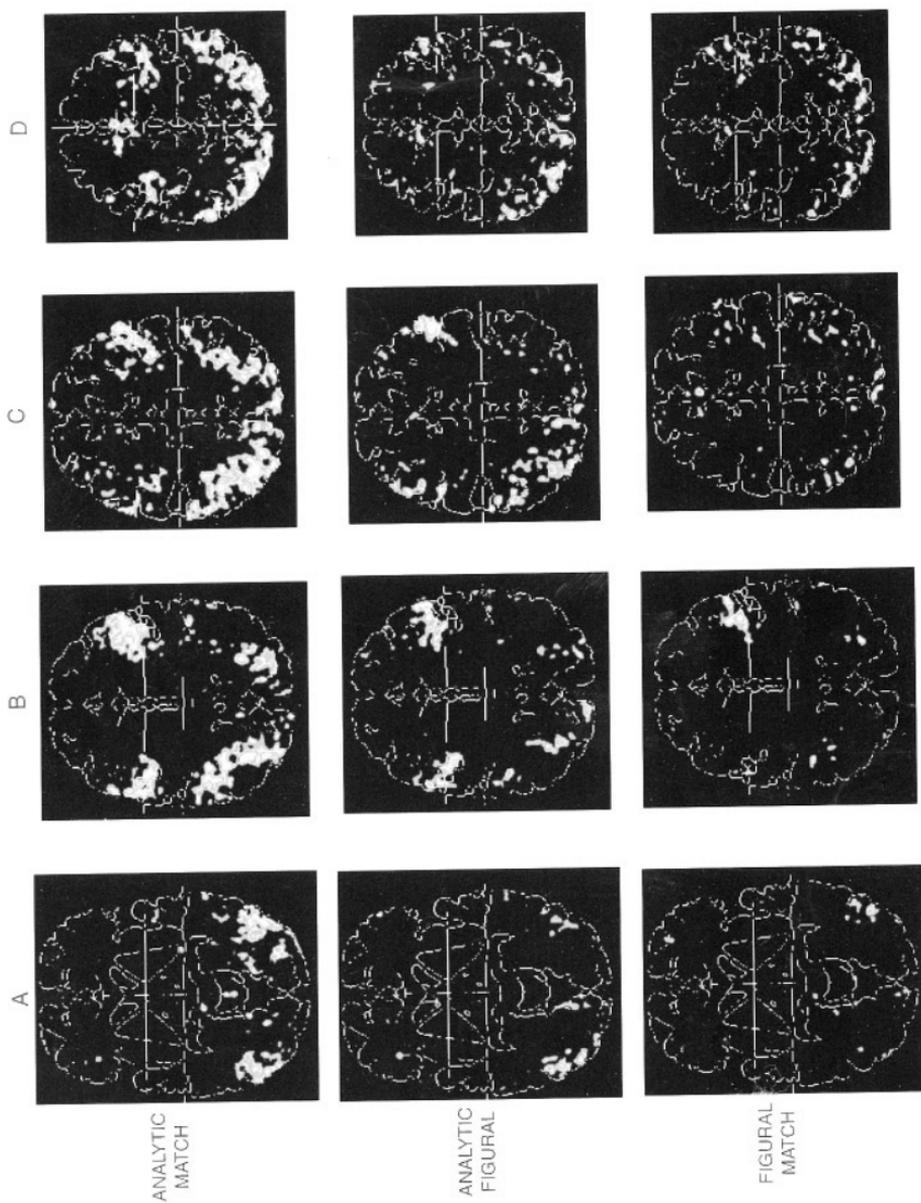
Scan	Problem type		
	Match	Figural	Analytic
Figural/match			
<i>M</i>	100	95.3	—
<i>SD</i>	0	12.5	—
Analytic/match			
<i>M</i>	100	—	71.6
<i>SD</i>	0	—	20.9
Figural/analytic			
<i>M</i>	—	90.4	76.1
<i>SD</i>	—	13.1	21.1

lems, $t(6) = 3.35$, $p < .01$ (one-tailed) and on match than figural problems, $t(6) = 2.72$, $p < .05$. They tended to perform better on figural than analytic problems, $t(6) = 1.87$, $p < .06$.

fMRI Scans

The analytic/match scan yielded a number of cortical activations that were all greater for analytic than for match problems (Fig. 4). Major foci of activity that expanded across a minimum of three slices occurred bilaterally in the middle and inferior frontal gyri, premotor regions (Brodmann areas 6, 9, 44, 45, and 46), and in the right rostrolateral prefrontal region (area 10). Extensive activation also occurred in the superior and inferior parietal regions, and in supramarginal and angular gyri (areas 7, 39, and 40). Occipital activation occurred in the precuneus and in lingual, medial, and superior occipital gyri (areas 7, 18, and 19). Activation occurred bilaterally in the inferior and middle

FIG. 4. Statistical parametric maps (SPMs) of three comparisons: Analytic vs match (top row), analytic vs figural (middle row), and figural vs match tasks (bottom row). Each column depicts activation from the same section. Sections A, B, C, and D (Talarach & Tournoux, 1988) correspond to slices 1 (4 mm below AC-PC plane), 6 (32 mm above AC-PC), 7 (40 mm above AC-PC), and 8 (50 mm above AC-PC) in Fig. 3. Functional maps are normalized and scaled with the lowest significant correlation magnitudes appearing in violet/blue and the highest in bright yellow/white. The left side of the image corresponds to the left side of the brain. Section A depicts temporal and occipital areas at bottom and frontal area at top. Sections B, C, and D depict parietal and occipital areas at bottom and frontal area at top. The analytic/match comparison reveals bilateral activation in frontal, parietal, occipital (B–D), and temporal lobes (A). The analytic/figural comparison shows activation lateralized to left parietal, temporal, and occipital lobes (A–D) and bilateral activation in frontal lobes (B–C). The figural/match comparison reveals a major focus of activation in the right frontal lobe (B) and minor foci of activation in bilateral parietal and occipital lobes (B–D) and right temporal lobe (A).



temporal gyri (areas 19, 21, and 37). Minor foci of activity were seen bilaterally in the anterior cingulate (area 32).

The figural/match scan yielded activations that were greater for figural than match problems (Fig. 4). In contrast to the analytic–match activations, figural/match activations were fewer, less pronounced when occurring in the same region, and lateralized to the right hemisphere in all except parietal regions. The largest focus of activity was seen in the right middle frontal gyrus (areas 9 and 46). Other regions of activation in the right hemisphere included anterior cingulate (area 32), superior and inferior parietal gyri (areas 7 and 40), the inferior temporal gyrus (area 37), and the precuneus (areas 7 and 19). Left-hemisphere activation was seen in the inferior and superior parietal regions (areas 7 and 40).

The analytic/figural scan yielded activations that were greater for Analytic than figural problems (Fig. 4). Bilateral activation was seen in the middle and inferior frontal gyri and premotor regions (areas 6, 9, 44, 45, and 46). The posterior cortex showed asymmetrically greater activity in left than right superior parietal, inferior parietal, angular, and supramarginal gyri (areas 7, 39, and 40), inferior and middle temporal gyri (areas 37, 21, and 19), and in precuneus and medial occipital gyri (areas 18, 19, and 37).

DISCUSSION

Fluid reasoning invoked by RPM performance yielded fMRI activation of an extensive, but specific, network of cortical regions. The analytic/match comparison revealed activations associated with fluid reasoning in bilateral frontal, parietal, temporal, and occipital regions with only the parietal activation being lateralized to the left hemisphere. This network was differentiated into activations associated specifically with figural or analytic reasoning in the other scans. The figural/match comparison revealed predominantly right-hemisphere activations associated with figural reasoning in frontal, parietal, temporal, and occipital lobes. The analytic/figural scan revealed bilateral frontal activations and predominantly left-hemisphere parietal, temporal, and occipital activations associated with analytic reasoning. Most regions activated in the figural/match and analytic/figural scans were activated in the analytic/match scan. This suggests that both figural and analytic reasoning processes were recruited to solve analytic problems. These results are in accord with PET findings from Haier et al. (1988) in regard to activation of parieto-occipital regions during Raven's performance. The present study, however, also reveals major frontal activations associated with fluid reasoning, a finding consistent with specific impairment in fluid reasoning after frontal-lobe lesions (Duncan et al., 1995).

The present study has a number of limitations. One issue is the considerable difference in difficulty of match, figural, and analytic problems. Ideally, the time and amount of mental processing would approximate one another across conditions as did the perceptual and motor demands of the three conditions.

Such equivalence, however, may be logically impossible when comparing tasks that are aimed to differ greatly in their demands upon high-level reasoning. An alternative approach could involve more trials in the easier conditions. This could equate total mental processing time, but at a cost of mismatching perceptual and motor demands across conditions. An advantage to the present format is that problems were almost identical to those used widely in RPM studies, so they may be directly relevant to many studies of development, aging, individual differences, and diseases. A second issue is that technical limitations prevented scanning of the complete brain, and therefore we did not have the opportunity to examine activations in potentially relevant structures like the cerebellum. Furthermore, deep structures such as the basal ganglia and thalamus may be active but sufficiently distant from the surface coils that such activation may not have been measurable. These issues may be resolved in future PET or fMRI studies.

Relation to Lesion Effects on Fluid Reasoning

Villardita (1985) suggested that figural and analytic reasoning are disproportionately diminished after right-hemisphere or left-hemisphere lesions, respectively. The present findings are consistent with the lesion findings in that figural reasoning activated primarily a right-hemisphere network, whereas analytic reasoning invoked additional left frontal, parietal, occipital, and temporal activations. Both figural and analytic reasoning, however, yielded activations that were not restricted to right and left hemisphere regions. Figural reasoning yielded left parietal activations. Analytic reasoning yielded right frontal activations that extended well beyond those occurring during figural reasoning. In order to quantify these global impressions, the number of significant voxels of activation were summed separately for the two hemispheres during figural reasoning (figural/match scan) and during analytic reasoning (analytic/figural scan) (Fig. 5). Indeed, there was greater right than left hemisphere activation during figural reasoning and greater left than right hemisphere activation during analytic reasoning. Thus, lesion and imaging findings provide convergent evidence about dual hemispheric asymmetry for figural and analytic reasoning.

Lesion evidence also suggests a predominant role of posterior cortex in figural reasoning (Berker & Smith, 1988). In order to examine the correspondence between lesion and imaging findings, the number of significant voxels of activation were summed separately for the anterior cortex (frontal lobe) and posterior cortex (parietal, temporal, and occipital lobes) during figural reasoning (figural/match scan) and during analytic reasoning (analytic/figural scan) (Fig. 5). There was slightly greater posterior than anterior activation during figural reasoning, and substantially greater anterior than posterior activation during analytic reasoning. By these analyses, frontal cortex may have a particularly important, but not exclusive, role in analytic reasoning.

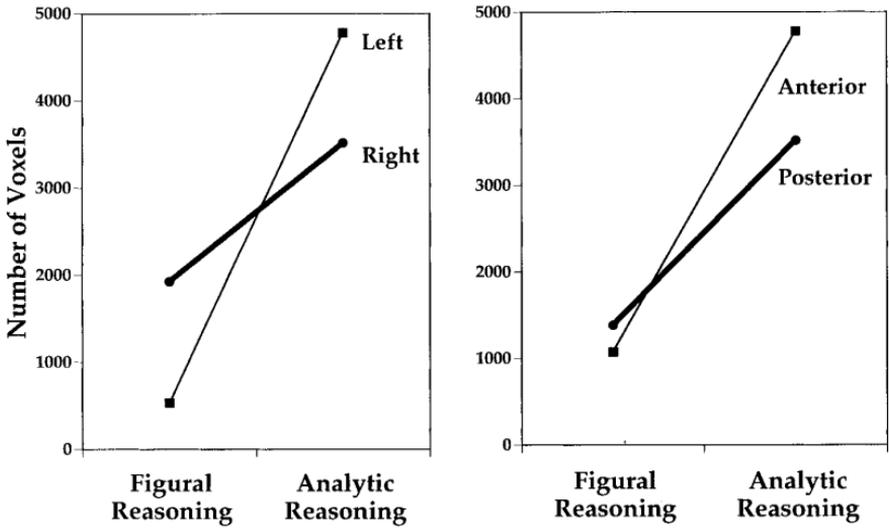


FIG. 5. Total number of significantly activated voxels ($p < .01$) during analytic reasoning and figural reasoning in left and right hemispheres (left panel) and in anterior (frontal) and posterior (temporal, parietal, occipital) regions (right panel). A double dissociation is shown with analytic reasoning yielding greater activation in the left than in the right hemisphere and figural reasoning yielding greater activation in the right than in the left hemisphere. A second double dissociation is shown with analytic reasoning yielding greater anterior than posterior activation, and figural reasoning yielding greater posterior than anterior activation.

Relations to Activations Associated with Working Memory

Activations associated with figural and analytic reasoning in the present study may be related to activations associated with working memory in PET and fMRI studies. Most of these studies operationalize working memory by comparing activations in two conditions that differ by the duration that information is held in mind, the amount of information that must be held in mind, or the degree to which information must be transformed. Further, most of these studies use relatively simple tasks and stimuli. These simple operationalizations of working memory are inspired by lesion and recording studies of monkeys from Goldman-Rakic (1987) and her colleagues identifying prefrontal regions that appear to hold or rehearse information in mind when that information is not perceptually available and, after a delay, will guide later action. Further, different prefrontal regions in the monkey appear to mediate different domains of working memory, such as spatial versus object working memory (Wilson, Fraser, O Scalaidhe, & Goldman-Rakic, 1993).

Figural reasoning yielded predominantly right-hemisphere activations that correspond to a number of working memory activations associated with spatial location, object identity, and mental rotation. The largest activation occurred in the right middle frontal gyrus (Brodmann areas 9 and 46). These areas have been activated in working memory for the spatial location of irregular

nonverbal shapes, letters, and squares (McCarthy et al., 1994, 1996; Smith et al., 1996a). Right premotor activation seen in figural reasoning was also reported for working memory for the spatial location of dots (Jonides et al., 1993). Baker et al. (1996) found that a spatial delayed response task activated regions of the right dorsolateral prefrontal cortex, lateral premotor, anterior cingulate, and right inferior frontal cortex that were activated during figural reasoning in the present study. In a more complex task, Petrides, Alivisatos, Evans, & Meyer (1993a) compared activation in a visual association task with nonverbal materials where participants had to self-order a series of responses in one condition or make perceptually, externally guided responses in another condition. Self-ordered performance is more demanding of working memory because it must be guided by internally generated rather than externally perceived cues. Self-ordered performance yielded activation of the right middle frontal gyrus (areas 9 and 46). Thus, the largest area of activity invoked by figural reasoning in the present study appears to correspond to frontal-lobe activations found for nonverbal working memory tasks.

Figural reasoning also produced posterior activations in parietal, occipital, and temporal lobes. Parietal activations occurred bilaterally in inferior and superior parietal regions (areas 40 and 7). Area 40 in the left and right hemispheres, respectively, have been activated during object (Smith et al., 1995) or spatial location working memory tasks (Baker, Frith, Frackowiak, & Dolan, 1994; Jonides et al., 1993; Smith et al., 1995, 1996a). Superior parietal cortex, area 7, has been implicated both in the direction of visuospatial attention (Corbetta, Meizin, Dobmeyer, Shulman, & Petersen, 1991) and in visuospatial manipulations such as mental rotation (Cohen, Kosslyn, Breiter, Digirolamo, Thompson, Anderson, Bookheimer, Rosen, & Belliveau, 1996; Rypma, De Bell, Gabrieli, Prabhakaran, Zabinski, Desmond, & Glover, 1996a). In occipital regions, bilateral activation was seen in area 7 of precuneus and areas 18 and 19 of the right hemisphere. Other studies have shown the precuneus to be active in visual imagery (Fox, Fox, Raichle, & Burde, 1985; Roland, Eriksson, Stone, & Widen, 1987; Watson, Myers, Frackowiak, Hajnal, Woods, Mazziotta, Shipp, & Zeiki, 1993), and in representing shape and spatial location (Baker et al., 1994; Haxby, Grady, Horwitz, Ungerleider, Mishkin, Carson, Herscovitch, Shapiro, & Rapoport, 1991). Area 19 has shown activity during working memory for spatial location (Jonides et al., 1993; Smith et al., 1996a) and when participants are explicitly instructed to maintain visual images of simple forms (Kosslyn, Alpert, Thompson, Maljkovic, Weise, Chabris, Hamilton, Rauch, & Buonanno, 1993). The right-hemisphere asymmetry of occipital visual cortex may reflect the asymmetries of frontal and temporal activations. Temporal-lobe activation occurred only in the right inferior and middle gyri (areas 19, 21, and 37). The middle temporal gyrus appears involved in mental rotation (Cohen et al., 1996); interestingly, it is also activated by the perception of actual movement (Tootell, Reppas, Kwong, Malach, Born, & Brady, 1995). In the present study, the

right temporal lobe activations may reflect mental transformations involved in generating a candidate answer for the missing pattern. Thus, overall, posterior activations during figural reasoning were similar to those seen in the right hemisphere during the rehearsal and retention of spatial information in working memory. Additional right- and left-hemisphere activations may reflect the transformational demands (e.g., imagery and rotation) of figural reasoning that are not present in simple retention of visuospatial information.

Activations associated specifically with analytic reasoning may be compared and contrasted with those found for figural reasoning. In the frontal lobes, right-hemisphere activations observed during figural reasoning in the middle and inferior frontal gyri and in premotor regions were more expansive during analytic reasoning. This suggests that the same frontal regions involved in visuospatial working memory during figural reasoning were even more active during analytic reasoning with nonverbal figures. In addition, however, left-hemisphere activations were observed for analytic reasoning in the inferior (areas 44 and 45) and middle (areas 8, 9, 46) frontal gyri and premotor cortex (areas 6 and 44). A number of these left frontal areas are activated during verbal working memory for letters, digits, and phonological information, including premotor cortex and areas 6, 9, 44, and 46 (Paulesu, Frith, & Frackowiak, 1993; Petrides, Alivisatos, Meyer, & Evans, 1993b; Rypma, Gabrieli, Prabhakaran, & Desmond, 1996b; Smith et al., 1996a). In addition, areas 45 and 46 and perhaps area 8 may be involved in semantic or verbal working memory (Gabrieli, 1996; Raichle, Fiez, Videen, Macleod, Pardo, Fox, & Petersen, 1994). Thus, analytic reasoning activated a series of left frontal lobe regions associated with multiple kinds of verbal working memory.

In the temporal lobes, whereas figural reasoning resulted in right temporal activation, analytic reasoning resulted in left temporal activation of the middle and inferior temporal gyri (areas 19, 21, 37). Working memory for complex nonverbal objects results in left-hemisphere activation of area 37 (Smith et al., 1995). Figural reasoning yielded bilateral parietal activations, and so did analytic reasoning. The activations were nearly symmetric during figural reasoning, but, there was a strong left-hemisphere asymmetry in all parietal regions during analytic reasoning. Finally, in addition to right occipital areas activated by figural reasoning, left occipital areas (18, 19, and 37) were activated by analytic reasoning. As shown in Fig. 4, there was greater left than right posterior parieto-occipital activation in the analytic condition compared to the figural and match conditions; this result is in accord with previous studies (Risberg, 1986; Berman, 1988; Haier, 1988). Kosslyn (1994) proposed that the posterior parieto-occipital area in the left hemisphere is involved in forming categorical spatial relations. Such abstracted, categorical representations may be useful in analytic reasoning about Raven's figures. Thus, the activation in left-hemisphere posterior regions can be attributed to areas involved in object (area 40; Smith et al., 1995) and verbal (areas 7, 40; Paulesu et al., 1993; Petrides et al., 1993b; Smith et al.,

1996a) working memory tasks as well as additional higher-order associational areas involved in forming categorical spatial relations.

The activations observed in the analytic/match condition are largely a sum of the activations associated specifically with figural or analytic reasoning in the other two scans. In the above review, we have noted how many domain-specific working memory activations correspond to areas activated during RPM performance. There are, however, aspects of working memory that may not be linked specifically to verbal, object, or spatial domains. Rather, these areas may contribute to the direction and coordination of domain-specific working memory systems. The largest frontal-lobe activations in the present study occurred in dorsolateral and rostrolateral prefrontal regions (areas 9, 10, and 46). Previous imaging and lesion studies have posited that the rostral prefrontal area is involved in nonroutine selection of cognitive strategies, whereas the dorsolateral prefrontal area is involved in goal management or in representing intermediate problem states in visuospatial working memory. For example, a PET study of the Tower of London task reported increased activity in dorsolateral and rostrolateral prefrontal areas with increasing demands on goal management and planning (Baker, Rogers, Owen, Frith, Dolan, Frackowiak, & Robbins, 1996). Activation of the rostrolateral prefrontal cortex has been observed also in sequence learning paradigms that require planning, strategy shifting, and selection and evaluation of possible alternatives (Deiber, Passingham, Colebatch, Friston, Nixon, & Frackowiak, 1991; Jenkins, Brooks, Nixon, Frackowiak, & Passingham, 1994). D'Esposito, Detre, Alsop, Shin, Arlas, and Grossman (1995) reported bilateral activation of dorsolateral prefrontal areas 9 and 46 when participants had to perform two tasks at once; these activations were not present when either task was performed by itself. Therefore, these activations were thought to reflect executive components of working memory that coordinated dual task performance. Areas 9 and 46 also were activated when participants directed their own performance on a task relative to a control condition in which performance was instructed (Petrides et al., 1993a). Thus, fluid reasoning during RPM performance activated not only areas associated with rehearsing and storing domain-specific information, but also areas associated with the executive or self-initiated control of working memory systems.

Conclusions

The present study provides a new and direct view of the neural network underlying a prized human ability: the fluid reasoning that allows people to solve novel problems. Figural reasoning (figural/match task) was associated with a network mediating domain-specific working memory for spatial and object information. Analytic reasoning (analytic/figural task) was associated with (1) the same right-hemisphere frontal and parietal regions; (2) additional left-hemisphere systems mediating domain-specific verbal, and object working memory and association areas involved in induction of categorical or

abstract visuospatial relations; and (3) frontal areas linked more closely with goal management and strategy shifting, planning, or executive control processes of working memory. The RPM task (analytic/match task) activated areas seen in both figural and analytic reasoning. Thus, RPM performance appears to activate many, if not all, domain-dependent and domain-independent working memory systems.

The characterization of a neural network for RPM as the sum of domain-dependent and domain-independent working memory systems may explain a number of findings. First, it explains why so many studies have found strong correlations between working memory and Raven's performance in aging, Parkinson's disease, development, and in individual differences within an age span (Fry & Hale, 1996; Gabrieli, 1996; Salthouse, 1993). In a number of these studies, measures of verbal working memory largely accounted for differences in Raven's performance. The present study shows that brain regions critical for verbal working memory are also powerfully engaged when reasoning analytically about nonverbal visual patterns. Thus, the present study suggests that strong links between working memory and fluid reasoning occur because the tasks measuring those processes are, in fact, measuring common neural systems.

Second, the present findings indicate why performance on the Raven's Progressive Matrices predicts performance so well for so many other tasks. Namely, performance on the Raven's Progressive Matrices reflects the status of numerous, perhaps almost all, working memory systems. For many laboratory tasks, only one or two of these systems may be invoked. For performance outside the laboratory, it may be more common that multiple working memory systems are relevant for performance. In either case, performance on the Raven's Progressive Matrices may provide a survey of working memory abilities that forecasts how well other tasks will be performed whether they require one, several, or all working memory systems.

REFERENCES

- Baker, S. C., Frith, C. D., Frackowiak, R. S. J., & Dolan, R. J. (1994). The neural substrate of active memory for shape and spatial location in man. *European Journal of Neuroscience*, **Suppl. 7**, 113.03.
- Baker, S. C., Rogers, R. D., Owen, A. M., Frith, C. D., Dolan, R. J., Frackowiak, R. S. J., & Robbins, T. W. (1996). Neural systems engaged by planning: a PET study of the Tower of London task. *Neuropsychologia*, **34**, 515–526.
- Bandettini, P. A., Jesmanowicz, A., Wong, E. C., & Hyde, J. S. (1993). Processing strategies for time-course data sets in functional MRI of the human brain. *Magnetic Resonance in Medicine*, **30**, 161–173.
- Berker, E., & Smith, A. (1988). Diaschisis, site, time and other factors in Raven performances of adults with focal cerebral lesions. *International Journal of Neuroscience*, **38**, 267–285.
- Berman, K. F., Illowsky, B. P., & Weinberger, D. R. (1988). Physiological dysfunction of dorso-lateral prefrontal cortex in schizophrenia. *Archives in General Psychiatry*, **45**, 616–622.
- Carpenter, P. A., Just, M. A., & Shell, P. (1990). What one intelligence test measures: A theoretical account of the processing in the Raven Progressive Matrices Test. *Psychological Review*, **97**, 404–431.

- Cattell, R. B. (1943). The measurement of adult intelligence. *Psychological Bulletin*, **40**, 153–193.
- Cattell, R. B. (1963). Theory of fluid and crystallized intelligence: A critical experiment. *Journal of Educational Psychology*, **54**, 1–22.
- Cohen, M. S., Kosslyn, S. M., Breiter, H. C., Digirolamo, W. L., Thompson, W. L., Anderson, A. K., Bookheimer, S. Y., Rosen, B. R., & Belliveau, J. W. (1996). Changes in cortical activity during mental rotation. A mapping study using functional MRI. *Brain*, **119**, 89–100.
- Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L., & Petersen, S. E. (1991). Selective and divided attention during visual discriminations of shape, color, and speed: Functional anatomy by positron emissions tomography. *Journal of Neuroscience*, **11**, 2383–2402.
- Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D., & Damasio, A. R. (1996). A neural basis for lexical retrieval. *Nature*, **380**, 499–505.
- Deiber, M. P., Passingham, R. E., Colebatch, J. G., Friston, K. J., Nixon, P. D., & Frackowiak, R. S. (1991). Cortical areas and the selection of movement: A study with positron emission tomography. *Experimental Brain Research*, **84**, 393–402.
- Desmond, J. E., Sum, J. M., Wagner, A. D., Demb, J. B., Shear, P. K., Glover, G. H., Gabrieli, J. D. E., & Morell, M. J. (1995). Functional MRI measurement of language lateralization in Wada-tested patients. *Brain*, **118**, 1411–1419.
- D'Esposito, M., Detre, J. A., Alsop, D. C., Shin, R. K., Atlas, S., & Grossman, M. (1995). The neural basis of the central executive system of working memory. *Nature*, **378**, 279–281.
- Duncan, J., Burgess, P., & Emslie, H. (1995). Fluid intelligence after frontal lobe lesions. *Neuropsychologia*, **33**, 261–268.
- Fox, P. T., Fox, J. N., Raichle, M. E., & Burde, R. M. (1985). The role of cerebral cortex in the generation of voluntary saccades: A positron emission tomographic study. *Journal of Neurophysiology*, **51**, 348–369.
- Friston, K. J., Jezzard, P., & Turner, R. (1994). Analysis of functional MRI time-series. *Human Brain Mapping*, **1**, 153–171.
- Fry, A., & Hale, S. (1996). Processing speed, working memory, and fluid intelligence: Evidence for a developmental cascade. *Psychological Science*, **7**, 237–241.
- Gabrieli, J. D. E. (1996). Memory systems analyses of mnemonic disorders in aging and age-related disease. *Proceedings of the National Academy of Sciences of the United States of America*, **93**, 13534–13540.
- Goldman-Rakic, P. S. (1987). Circuitry of primate prefrontal cortex and regulation of behavior by representational memory. In F. Plum (Ed.), *Handbook of physiology—The nervous system V* (pp. 373–417). New York: Oxford University Press.
- Glover, G. H., & Lee, A. T. (1995). Motion artifacts in fMRI: Comparison of 2DFT with PR and spiral scan methods. *Magnetic Resonance in Medicine*, **33**, 624–635.
- Haier, R. J., Siegel, B. V., Neuchterlein, K. H., Hazlett, E., Wu, J. C., Paek, J., Browning, H. L., & Buchsbaum, M. S. (1988). Cortical glucose metabolic rate correlates of abstract reasoning and attention studied with positron emission tomography. *Intelligence*, **12**, 199–217.
- Haier, R. J. (1993). Cerebral glucose metabolism and intelligence. In P. A. Vernon (Ed.), *Biological approaches to the study of human intelligence* (pp. 317–332). New Jersey: Ablex Publishing Corporation.
- Haxby, C. L., Grady, J. V., Horwitz, B., Ungerleider, L. G., Mishkin, M. M., Carson, R. E., Herscovitch, P., Shapiro, M. B., & Rapoport, S. I. (1991). Dissociation of object and spatial visual processing pathways in human extrastriate cortex. *Proceedings of the National Academy of Sciences of the United States of America*, **88**, 1621–1625.
- Horn, J. L. (1985). Remodeling old models of intelligence. In B. B. Wolman (Ed.), *Handbook of intelligence* (pp. 267–300). New York: Wiley.
- Hunt, E. (1975). Quote the raven? Nevermore! In L. W. Gregg (Ed.), *Knowledge and cognition* (pp. 129–158). Hillsdale: Erlbaum.
- Jenkins, I. H., Brooks, D. J., Nixon, P. D., Frackowiak, R. S. J., & Passingham, R. E. (1994).

- Motor sequence learning: A study with positron emission tomography. *Journal of Neuroscience*, **14**, 3774–3790.
- Jonides, J., Smith, E. E., Koeppe, R. A., Awh, E., Minoshima, S., & Mintun, M. A. (1993). Spatial working memory in humans as revealed by PET. *Nature*, **363**, 623–625.
- Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Maljkovic, V., Weise, S. B., Chabris, C. F., Hamilton, S. E., Rauch, S., & Buonanno, F. S. (1993). Visual mental imagery activates topographically organized visual cortex. *Journal of Cognitive Neuroscience*, **5**, 263–287.
- Kosslyn, S. M. (1994). *Image and brain: The resolution of the imagery debate*. Cambridge: Bradford Book.
- Kyllonen, P. C., & Christal, R. E. (1990). Reasoning ability is (little more than) working memory capacity?! *Intelligence*, **14**, 389–433.
- Lee, A. T., Glover, G. H., & Meyer, C. H. (1995). Discrimination of large venous vessels in time-course spiral blood-oxygen-level-dependent magnetic-resonance functional neuroimaging. *Magnetic Resonance in Medicine*, **33**, 745–754.
- Lohman, D. F. (1989). Human intelligence: An introduction to advances in theory and research. *Review of Educational Research*, **59**, 333–373.
- Martin, A., Wiggs, C. L., Ungerleider, L. G., & Haxby, J. V. (1996). Neural correlates of category-specific knowledge. *Nature*, **379**, 649–652.
- McCarthy, G., Puce, A., Constable, R. T., Krystal, J. H., Gore, J. C., & Goldman-Rakic, P. S. (1996). Activation of human prefrontal cortex during spatial and nonspatial working memory tasks measured by functional MRI. *Cerebral Cortex*, **6**, 600–611.
- McCarthy, G. M., Blamire, A. M., Puce, A., Nobbe, A. C., Bloch, G., Hyer, F., Goldman-Rakic, P., & Shulman, R. G. (1994). Functional magnetic resonance imaging of human prefrontal cortex activation during a spatial working memory task. *Proceedings of the National Academy of Sciences of the United States of America*, **91**, 8690–8694.
- Noll, D. C., Cohen, J. D., Meyer, C. H., & Schneider, W. (1995). Spiral k-space MRI of cortical activation. *Journal of Magnetic Resonance Imaging*, **5**, 49–56.
- Paulesu, E., Frith, C. D., & Frackowiak, R. S. J. (1993). The neural correlates of the verbal component of working memory. *Nature*, **362**, 342–345.
- Petrides, M., Alivisatos, B., Evans, A. C., & Meyer, E. (1993a). Dissociation of human mid-dorsolateral from posterior dorsolateral frontal cortex in memory processing. *Proceedings of the National Academy of Sciences of the United States of America*, **90**, 873–877.
- Petrides, M., Alivisatos, B., Meyer, E., & Evans, A. C. (1993b). Functional activation of the human frontal cortex during the performance of verbal working memory tasks. *Proceedings of the National Academy of Sciences of the United States of America*, **90**, 878–882.
- Raichle, M. E., Fiez, J. A., Videen, T. O., Macleod, A. K., Pardo, J. V., Fox, P. T., & Petersen, S. E. (1994). Practice-related changes in human brain functional anatomy during non-motor learning. *Cerebral Cortex*, **4**, 8–26.
- Raven, J. C. (1965). *Advanced progressive matrices: Sets I and II*. London: Lewis.
- Raven, J. C. (1976). *Standard progressive matrices: Sets A, B, C, D & E*. Oxford: Oxford Psychologists Press.
- Risberg, J. (1986). Regional cerebral blood flow in neuropsychology. *Neuropsychologia*, **24**, 135–140.
- Roland, P. E., Eriksson, L., Stone, E. S., & Widen, L. (1987). Does mental activity change the oxidative metabolism of the brain? *Journal of Neuroscience*, **7**, 2373–2389.
- Rypma, B., DeBell, M. A., Gabrieli, J. D. E., Prabhakaran, V., Zabinski, M. F., Desmond, J. E., & Glover, G. H. (1996a). *Functional MRI studies of mental rotation and object identification processes*. Paper presented at the 26th Annual Meeting of the Society for Neuroscience, Washington, DC.
- Rypma, B., Gabrieli, J. D. E., Prabhakaran, V., & Desmond, J. E. (1996b). *fMRI of working memory and aging*. Poster presented at the 37th Annual Meeting of the Psychonomic Society, Chicago, IL.

- Salthouse, T. A. (1993). Influence of working memory on adult age differences in matrix reasoning. *British Journal of Psychology*, **84**, 171–179.
- Salthouse, T. A. (1996). The processing-speed theory of adult age differences in cognition. *Psychological Review*, **103**, 403–428.
- Smith, E. E., Jonides, J., & Koeppel, R. A. (1996a). Dissociating verbal and spatial working memory using PET. *Cerebral Cortex*, **6**, 11–20.
- Smith, E. E., Jonides, J., Koeppel, R. A., Awh, E., Schumacher, E. H., & Minoshima, S. (1995). Spatial versus object working memory: PET investigations. *Journal of Cognitive Neuroscience*, **7**, 337–356.
- Smith, J. A. L., Rypma, B., Prabhakaran, V., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1996b). *A functional MRI study of working memory central executive*. Poster presented at the 26th Annual Meeting of the Society for Neuroscience, Washington, DC.
- Snow, R. E., Kyllonen, C. P., & Marshalek, B. (1984). The topography of ability and learning correlations. In R. J. Sternberg (Ed.), *Advances in the psychology of human intelligence* (pp. 47–103). Hillsdale, NJ: Erlbaum.
- Spitzer, M., Kwong, K. K., Kennedy, W., Rosen, B. R., & Belliveau, J. W. (1995). Category-specific brain activation in fMRI during picture naming. *Neuroreport*, **6**, 2109–2112.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. Stuttgart: Thieme.
- Tootell, R. B., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., & Brady, T. J. (1995). Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *Journal of Neuroscience*, **15**, 3215–3230.
- Villardita, C. (1985). Raven's colored progressive matrices and intellectual impairment in patients with focal brain damage. *Cortex*, **21**, 627–634.
- Watson, J. D., Myers, R., Frackowiak, R. S., Hajnal, J. V., Woods, R. P., Mazziotta, J. C., Shipp, S., & Zeiki, S. (1993). Area V5 of the human brain: Evidence from a combined study using positron emission tomography and magnetic resonance imaging. *Cerebral Cortex*, **3**, 79–94.
- Wilson, F. A. W., Fraser, A. W., O'Scalaidhe, S. P., & Goldman-Rakic, P. S. (1993). Dissociation of object and spatial processing domains in primate prefrontal cortex. *Science*, **260**, 1955–1957.

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