

The Neural Bases of Strategy and Skill in Sentence–Picture Verification

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This experiment used functional Magnetic Resonance Imaging to examine the relation between individual differences in cognitive skill and the amount of cortical activation engendered by two strategies (linguistic vs. visual–spatial) in a sentence–picture verification task. The verbal strategy produced more activation in language-related cortical regions (e.g., Broca’s area), whereas the visual–spatial strategy produced more activation in regions that have been implicated in visual–spatial reasoning (e.g., parietal cortex). These relations were also modulated by individual differences in cognitive skill: Individuals with better verbal skills (as measured by the reading span test) had less activation in Broca’s area when they used the verbal strategy. Similarly, individuals with better visual–spatial skills (as measured by the Vandenberg, 1971, mental rotation test) had less activation in the left parietal cortex when they used the visual–spatial strategy. These results indicate that language and visual–spatial processing are supported by partially separable networks of cortical regions and suggests one basis for strategy selection: the minimization of cognitive workload. © 2000 Academic Press

Human cognition includes at least two processing modes: linguistic and visual–spatial. With the recent advent of neuroimaging techniques, it is now possible to examine the cortical systems that support these modes of processing and to understand how their behavioral characteristics relate to their neural substrates. To explore these issues, we present an experiment in which participants were taught to do a single task using either a verbal strategy or a visual–spatial strategy. One objective was to examine the relation between the strategies (i.e., cognitive routines) and their underlying patterns of cortical activation using functional magnetic resonance imaging (fMRI). In doing

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so, we were able to build on existing data which suggested partial separation between the cortical systems responsible for linguistic processing and those responsible for visual-spatial processing. A second objective was to examine how the strategy-related differences in cortical activity are modulated by individual differences in cognitive skill. This second goal brings together a hypothesis about the correlates of individual differences with some recent insights gained from neuroimaging (Just & Carpenter, 1992; Just, Carpenter, & Keller, 1996a). Before describing the individual-differences component of the research, however, we first describe the task, the cognitive processes underlying each strategy, and the cortical mechanisms believed to be implicated in linguistic and visual-spatial processing.

A paradigm that has been useful in contrasting these two modes of processing is the sentence-picture verification task. On each trial, participants read a sentence describing the spatial arrangement of two objects (e.g., *It is not true that the star is above the plus*) and then indicate whether a subsequent picture agrees with (e.g., a plus above a star) or falsifies (e.g., a star above a plus) the sentence. Typically, people are faster and more accurate making judgments about affirmative sentences (e.g., *It is true that . . .*) than negative sentences (e.g., *It is not true that . . .*). However, this variable, sentence polarity, also interacts with truth-value, so that true affirmative sentences are easier than false affirmative sentences, but true negative sentences are more difficult than false negative sentences (Clark & Chase, 1972; Glucksberg, Trabasso, & Wald, 1973; Trabasso, Rollins, & Shaughnessy, 1971).

The general finding that increasing the linguistic complexity of the sentences tends to make the sentence-picture verification more difficult suggests that people use a verbal strategy to do the task (Carpenter & Just, 1975). In this strategy, the sentence is first read so that its meaning can be represented in some type of linguistic, proposition-based format, such as: (*Not (Star above Plus)*). This representation is then maintained through active rehearsal until the picture is presented. Because the sentence and picture have to be represented in compatible formats to be compared, the picture is encoded in the same proposition-based format. For example, the person may first check which symbol is in the "above" position and then construct a representation around this item, such as: (*Star above Plus*). The components of the two representations are then compared, one at a time, starting with the items. In our example, this would initially lead to a match as the items and their spatial relation are compared, but then a mismatch after the negation is encountered in the sentence representation but not the picture representation.

Although the verbal strategy accounts for the linguistic complexity effects, people with better visual-spatial reasoning ability tended to use a visual-imagery strategy, in which the sentence is first translated into a visual-spatial format so that it can then be compared to the picture (MacLeod, Hunt, & Mathews, 1978). To the extent that the format is visual-spatial, those features

of the sentence that would otherwise contribute to linguistic complexity and affect the ease of comprehension have little or no effect on the comparison process. In other words, by converting a negative sentence (e.g., *It is not true that the star is above the plus*) into a mental image (e.g., of a plus above a star), the comparison process remains relatively unaffected by negation. Because sentence–picture mismatches require more time to verify than matches, the individuals that used the visual-imagery strategy still showed an effect of truth-value (i.e., whether the sentences were true or false). However, these same individuals did not show the effect of linguistic complexity (i.e., polarity) nor the Polarity \times Truth-Value interaction, both of which are indicative of the verbal strategy.

Additional evidence for the distinction between the verbal and visual-imagery strategies was obtained by explicitly training people to use both verbal and visual-imagery sentence–picture verification strategies; as predicted, the Polarity \times Truth-Value interaction was absent when the participants used the visual-imagery strategy but present when they used the verbal strategy (Mathews, Hunt, & MacLeod, 1980). These results indicate that the effects of linguistic complexity can be attenuated by explicit instructions to do the task using visual imagery (Glushko & Cooper, 1978). However, participants can also be discouraged from using visual imagery. By including trials in which the sentences (e.g., *It is not true that the star is above the plus*) might be true of more than one picture (e.g., a plus above a star or a star above a dollar sign), participants will be less likely to use mental imagery because this strategy will result in erroneous “no” responses whenever the picture is true of the sentence but mismatches the mental image (Kroll & Corrigan, 1981).

It is important to emphasize that, although the verbal strategy is an extension of natural language comprehension, it also entails the encoding, maintenance, and evaluation of visual–spatial information. That is, the pictures must be translated into a proposition-based format, and the meanings of the spatial terms (i.e., *above* and *below*) may be represented in visual–spatial or analog-based codes. Likewise, although visual imagery is the main component of the visual–spatial strategy, it also involves the encoding and comprehension of linguistic information, in that each sentence has to be read and understood to generate a mental image from the sentence. The fact that the two strategies share many of the same processes indicates that the linguistic system must communicate with the visual–spatial system. It also suggests that, although different cortical networks may mediate each strategy, the networks are likely to share components and thus be only partially separable. Because one of our objectives was to analyze the relations among the cortical systems mediating linguistic versus visual–spatial processing, we focused on those cortical regions that are primarily engaged by language processing or visual–spatial processing: the inferior frontal, posterior superior temporal, and parietal regions. Although it would have been informative to examine

the inferior temporal cortex (because it too has been implicated in visual imagery; D'Esposito et al., 1997; Kosslyn et al., 1993, Expt. 2; Smith & Jonides, 1995), this region was not included in our analyses because we could not scan the entire cortex. Several regions (e.g., frontal eye fields) were also excluded because there was no a priori reason to suspect their preferential involvement in one or the other strategy. Finally, because the control of strategies is associated with the dorsolateral prefrontal cortex, our scans included this region. The left inferior frontal cortex includes Broca's area, an important cortical center of language processing. A second major language region, Wernicke's area, is situated within the left posterior superior temporal cortex. Although these areas were traditionally thought to mediate language production and reception, respectively, this view has recently been challenged (Blumstein, 1995). There is now evidence using a number of neuroimaging methods that both regions are engaged by a wide variety of language tasks. Broca's area is activated by production tasks, such as generating words (Bookheimer et al., 1997) and sentences (Müller et al., 1997), and by receptive tasks, such as reading words (Binder et al., 1997) and sentences (Bavelier et al., 1997; Just et al., 1996b) and listening to words (Binder et al., 1997), sentences (Caplan, Alpert, & Waters, 1999; Schlosser, Aoyagi, Fulbright, Gore, & McCarthy, 1998; Stromswold, Caplan, Alpert, & Rauch, 1996), and short passages (Dehaene et al., 1997). Wernicke's area is activated by many of the same tasks: generating words, reading words and sentences, and listening to sentences and short passages.

These findings have led to much speculation about the functional roles of both language areas. For example, Mesulam (1990, 1998) has suggested that Broca's area tends to favor the articulatory-syntactic aspects of language processing, leaving the lexical-semantic processing for Wernicke's area. Broca's area may also correspond to the articulatory part of the articulatory-phonological loop (Baddeley, 1986, 1995) because it is apparently involved in the active maintenance of verbal information (Dehaene et al., 1997; Schlosser et al., 1998; Smith & Jonides, 1995; Stromswold et al., 1996). However, irrespective of their exact functional roles, it is clear that both areas perform many of the computations that are needed for language processing. Therefore, to the extent that a verbal strategy depends upon language processing, that strategy should engage one or both of these areas.

The role of the parietal cortex is less well defined (or perhaps more diverse), but it is thought to perform many of the computations that are necessary to reason about spatial relations (Mesulam, 1998). For example, several recent neuroimaging experiments have demonstrated that the parietal cortex is activated when people mentally rotate alphanumeric characters (Alivisatos & Petrides, 1997) and objects (Carpenter, Just, Keller, Eddy, & Thulborn, 1999). Parietal activation is also found when the spatial locations and identities of several different figures are maintained for a short time (Smith & Jonides, 1995). The latter result suggests another role of the parietal cortex:

the abstraction and maintenance of visuoimaginal information. This conjecture is supported by several results. For example, parietal activity has been found when people mentally write Japanese phonograms (Sugishita, Takayama, Shiono, Yoshikawa, & Takahashi, 1996). Parietal activity was also found when people superimposed imaginary block letters onto grids and then indicated whether the letters occluded certain grid positions (Kosslyn et al., 1993, Expt. 2). All of these results, then, suggest that the parietal cortex performs many of the computations that support visual-spatial reasoning. To the extent that this is correct, and to the extent that such computations are central to the visual-spatial strategy, the visual-spatial strategy should engage the parietal cortex.

Finally, the dorsolateral prefrontal cortex, or DLPFC, has been implicated in executive cognitive functions, such as planning and evaluating sequences of behavior, maintaining information in an active state, and inhibiting routine but contextually inappropriate responses (Cohen et al., 1997; D'Esposito et al., 1995; Eslinger, 1996; Pennington, 1997). Furthermore, because the region is thought to regulate other cognitive processes, it should play an important role in both language (Bavelier et al., 1997; Binder et al., 1997; Gabrieli, Poldrack, & Desmond, 1998; Müller et al., 1997) and visual-spatial imagery (Belger et al., 1998; Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Courtney, Ungerleider, Keil, & Haxby, 1997; Kosslyn et al., 1993; Prabhakaran, Smith, Desmond, Glover, & Gabrieli, 1997). Because the sentence-picture verification strategies were complex and involved many of the executive functions related to language and visual-spatial reasoning, we expected cortical activation in the DLPFC.

One of our main predictions, then, was that each strategy should engender more cortical activity in those regions that support the type of processing (language vs. visual imagery) that the strategy draws upon. Thus, the verbal strategy should generate more activation than the visual-imagery strategy in Broca's and Wernicke's areas, and the visual-imagery strategy should generate more activation than the verbal strategy in the parietal regions, resulting in an interaction between strategies and cortical regions. Furthermore, if the strategies do engender different patterns of cortical activation, then it should be possible to determine which strategy a person is using by examining their cortical activation. (This implies that, in the context of our task, fMRI-measured cortical activation can be used to "read" minds.)

A second focus of this article concerns individual differences in language and visual-spatial skills and the prediction that the amount of cortical activation generated by the strategies in their respective regions should be modulated by individual differences in the cognitive skill that supports the strategy. As verbal skill increases, the amount of cortical activation that is engendered by the verbal strategy in the language areas should decrease; a similar pattern should also hold for visual-spatial skill and parietal cortex activation. The theoretical rationale for these predictions stems from the

capacity-constrained view of working memory (Just & Carpenter, 1992; Just et al., 1996a) and some recent insights gained from neuroimaging (Carpenter et al., 1999; Just et al., 1996b).

Within the capacity-constrained framework, working memory for any given cognitive process, such as language comprehension, corresponds to the cortical systems that are involved in the active maintenance and processing of information, as well as the resources that support the system. The efficiency of neural systems is thus affected by several factors, including the brain's neurochemistry, the integrity of its cortical structure, the topographic distribution of its networks, and the strategies that it employs (Parks et al., 1989). Because this definition refers to a collection of physical systems that do computational work, working memory is subject to the same constraint as other physical systems: It can only do so much work per unit of time. Moreover, because the amount of work that can be done is limited by resource availability, some of the variation in cognitive ability can be construed as being due to individual differences in the amount of resources that are available to do the skill-related work.

For example, there is considerable behavioral evidence that many aspects of language processing differ systematically between college students having higher versus lower language skill (as measured by psychometric tests). Many of these regularities have been explained by the capacity-constrained theory of working memory (Carpenter, Miyake, & Just, 1995; Haarmann, Just, & Carpenter, 1997; Miyake, Carpenter, & Just, 1994). In the context of the theory, "resource" refers to a hypothetical construct that supports cognitive computations, such as accessing the meaning of words and parsing syntactic structures.

The present experiment further refines the capacity-constrained view of working memory and the theoretical notion of resources by examining the neural correlates of the resources. This is possible because recent neuroimaging research has demonstrated that the amount of cortical activation within a given region increases as the computational demands that are placed on the region increase. For example, in language comprehension, the volume of fMRI-measured cortical activation in both Broca's and Wernicke's areas increases with linguistic complexity (Just et al., 1996b). Similarly, in mental rotation, parietal cortex activation increases as the angular disparity between the two objects increases (Carpenter et al., 1999). These findings indicate that as a task becomes more difficult, it places additional computational demands on the cortical regions underlying task performance and hence elicits more fMRI-measured activation. Following this logic, individuals with above-average verbal skill should have more verbal working memory resources available to execute the verbal strategy, causing the strategy to consume a smaller proportion of the resource pool and hence to engender relatively less cortical activation in the language regions. Indeed, there is some evidence supporting this hypothesis: Several PET studies have reported neg-

ative correlations between psychometrically measured skills and the volume of cortical activation produced by tasks that draw upon these skills (Haier et al., 1988; Parks et al., 1988, 1989).

Our general procedure was similar to Mathews et al.'s (1980): First, participants were taught to do the sentence–picture verification task using both the verbal and the visual-imagery strategies. fMRI was then used to determine whether each strategy engendered a different pattern of cortical activation in areas that are known to play a role in language and visual–spatial imagery, namely, the inferior frontal, posterior superior temporal, parietal, and dorsolateral prefrontal regions. Specifically, we examined how the strategies influenced the volume and intensity of the cortical activation within these regions. Finally, we evaluated the relations between the amount of strategy-related cortical activation and our participants' performance on two psychometric tests: one measuring verbal ability and the other measuring visual–spatial reasoning ability.

METHOD

The primary task was to indicate (by pressing the appropriate response button) whether a sentence described a subsequent picture. On each trial, a sentence describing the spatial arrangement of two objects (e.g., *It is not true that the star is above the plus*) was presented in the center of the screen and remained visible until either of two response buttons was pressed. The sentence was then replaced by a picture that either agreed with (e.g., a plus above a star) or falsified (e.g., a star above a plus) the sentence. The participant responded by pressing the true (right) or the false (left) button. Response latencies and error rates were collected. The time between the presentation of the sentence and the first button press will be referred to as the sentence-comprehension latency. The time between the presentation of the picture and the second button press will be referred to as the picture-verification latency.

The experiment consisted of two sessions. During the training session, participants were instructed how to use (and given practice using) the two strategies. Participants were familiarized with the fMRI scanner, the general scanning procedures, and the sentence–picture verification task prior to being scanned. Participants also completed two psychometric tests: the mental rotation test of Vandenberg (1971) measured visual–spatial skill and the reading span test of Daneman and Carpenter (1980) measured verbal skill. During the test session, participants performed the verification task (alternating between strategies, as described below) while in the fMRI scanner.

Participants. Twelve right-handed native English speakers (5 males and 7 females) aged 21.5 ± 4.8 years ($M \pm SD$; range = 18–31) from the Carnegie Mellon University community (10 undergraduates and 2 postdoctoral research assistants) participated in the experiment. All of the participants gave informed consent that was approved by the University of Pittsburgh and Carnegie Mellon Institutional Review Boards. Two additional participants were excluded after the practice session because they were not able to use the visual-imagery strategy, as indicated by the participants during postpractice debriefing and by the presence of linguistic complexity effects in their picture-verification response latencies. Data from two additional participants were also excluded due to excessive out-of-plane head movement during scanning.

Psychometric tests. The Vandenberg (1971) mental rotation test was administered to 11 participants. Each trial of the test required participants to first examine a Shepard–Metzler (1971) figure and then examine four more figures and indicate which two of these four were rotated variants of the first figure (as opposed to mirror-image isomers). Participants had 3

min to complete 30 such trials. The test has been shown to measure visual-spatial ability (Just & Carpenter, 1985).

The Daneman and Carpenter (1980) reading span test was administered to 10 of 12 participants. The test required participants to simultaneously read aloud sentences and attempt to remember the last word of each sentence. The number of sentences that had to be read was gradually incremented until the participant failed to recall one or more of the sentence-final words on 50% of the trials. At this point, the number of words recalled was defined as that participant's reading span. Because this task requires participants to both actively maintain and process verbal information, the reading span provides an index of verbal working memory resources (Carpenter & Just, 1989; Just & Carpenter, 1992) and hence verbal skill.

Experimental paradigm. The order in which the two strategies were learned by the participants was alternated across participants. The strategy instructions were similar to those used by Mathews et al. (1980). The critical part of the verbal strategy instructions were

. . . Quickly read each sentence when it is presented. Don't try to form a mental image of the objects in the sentence, but instead look at the sentence only long enough to remember it until the picture is presented . . . After the picture appears, decide whether or not the sentence that you are remembering describes the picture. . . .

The critical part of the visual-imagery strategy instructions was.

. . . Carefully read each sentence and form a mental image of the objects in the sentence and their arrangement . . . After the picture appears, compare the picture to your mental image. . . .

During the training session, participants read one of the two sets of instructions and then practiced using the appropriate strategy by completing 36 practice trials, presented in six 6-trial blocks. Participants then read the other set of instructions and completed a second set of 36 practice trials using the other strategy. (The order in which participants practiced the two strategies was counterbalanced across participants.) Finally, the participants completed a third set of 36 practice trials in which a visual cue (VERBAL or VISUAL-IMAGERY) indicated which strategy was to be used during each 6-trial block. The training session was completed on an IBM-compatible personal computer.

During the test session, the sentences and pictures were projected onto a transparent screen that was suspended from the upper surface of the scanner bore. The test session consisted of 288 trials that were also presented in 48 6-trial blocks. Each block was separated by a 6-s rest period in which participants fixated a crosshair (+) that was displayed in the center of the screen. Sixteen additional 30-s rest periods were included to provide a baseline measure of cortical activation. The images collected during the rest periods and the first 6 sec of each epoch were discarded to accommodate the rise and fall of the hemodynamic response (Bandettini, Wong, Hinks, Tokofsky, & Hyde, 1992). A visual cue (VERBAL or VISUAL-IMAGERY) indicated which strategy was to be used during each block of trials.

Because the experiment contained many fewer practice trials than Mathews et al.'s (1980) experiment (54 vs. 192 per strategy, respectively), our participants may have had some difficulty using one of the strategies and/or switching from one strategy to the other. Consequently, our experiment may underestimate any difference between the two strategies with respect to fMRI-measured cortical activity because it may include trials in which the wrong strategy was used. We attempted to curb this problem by minimizing the number of times that participants had to change strategies so that they would have sufficient time to become accustomed to using one strategy before switching to the other. Thus, participants only had to switch between the two strategies twice; the verbal strategy was used during trials 1-72 and 217-288, and the imagery strategy was used during trials 72-144 and 145-216.

Each block of trials contained six affirmative or negative sentences, of which four were

true and two were false. All of the sentences combined two objects (from the set: plus, +; star, *; and dollar, \$) and one spatial relation (above; below). The experiment included all possible permutations of object pairs and relations. The two types of blocks (affirmative vs. negative) and the different sentences within each block were arranged into a single random sequence of trials that was presented to all of the participants.

Although the sentence–picture verification task logically requires only two objects, three objects were used to discourage participants from using the imagery strategy during the verbal-strategy trials (Kroll & Corrigan, 1981). This was accomplished by including 24 trials in the verbal-strategy epochs that could not be answered correctly using the visual-imagery strategy. For example, given the sentence *It is not true that the star is above the plus*, the strategy of generating a mental image (of a star below a plus) and then attempting to match this image to a subsequent picture would result in a mismatch and an incorrect “no” response whenever the picture included a dollar sign. (This example was explained in the practice session instructions to emphasize the importance of using the correct strategy.)

fMRI procedure. fMRI provides a method of measuring changes in the blood oxygenation level by taking advantage of the natural paramagnetic properties of blood hemoglobin and does not require exogenous contrast agents (for a discussion of the BOLD or blood oxygenation level-dependent method, see Kwong et al., 1992; Ogawa et al., 1990). The activation that is measured by fMRI is thus an index of the oxygen level in the small capillaries that support local neuronal activity (for an introductory treatment of fMRI, see Cohen, Noll, & Schneider, 1993).

The study was conducted on a GE 3.0T scanner used in conjunction with a commercial birdcage, quadrature-drive radio-frequency whole-head coil. Fourteen oblique-axial images (5 mm thick, skipping 1 mm between slices) were selected to maximize the coverage of each participant’s cerebral cortex (see Fig. 1). An image of the MR signal intensity of each of the 14 slices was collected once per 3000-ms scan repetition time (TR). The images were collected using a gradient echo, resonant echo planar pulse sequence, with TE = 25 ms, 90° flip angle, and a 128 × 64 acquisition matrix with 3.125 × 3.125 × 5 mm voxels.



FIG. 1. A mid-sagittal structural image from a participant with lines superimposed to show the approximate prescription angle for the 14 oblique axial images.

Image preprocessing corrected for signal drift using FIASCO (Eddy, Fitzgerald, Genovese, Mockus, & Noll, 1996) and head motion using AIR (Woods, Cherry, & Mazziotta, 1992). Two of 14 slices (the superior- and inferior-most slices) also had to be discarded because of the AIR motion-correction algorithm. The means of the images corresponding to each of the 12 functional slices were registered to a high-resolution, T1-weighted structural volume scan of each participant. This volume scan was constructed from 124 3D SPGR axial images that were collected with TR = 25 ms, TE = 4 ms, 40° flip angle, and a 24 × 18 cm FOV, resulting in .9375 × .9375 × 1.5 mm voxels.

Regions of interest (ROIs) were defined using the parcellation scheme of Rademacher and his colleagues (Caviness, Meyer, Makris, & Kennedy, 1996; Rademacher, Galaburda, Kennedy, Filipek, & Caviness, 1992). This method uses limiting sulci and coronal planes (defined by anatomical landmarks) to segment cortical regions. For each participant, a mean of the functional images was coregistered to the structural volume scan, in parallel alignment with the anterior commissure–posterior commissure (AC–PC) line. The limiting sulci and other anatomical landmarks were then located by viewing the structural images simultaneously in the three orthogonal planes, and the ROIs were defined by manually tracing the regions onto the axial image of each functional slice (this procedure was completed by the first author).

Because language and visual–spatial reasoning are the product of large-scale cortical networks (Mesulam, 1990, 1998), the fMRI analyses focused on four ROIs (see Fig. 2) containing the following areas (defined by Caviness et al., 1996). The inferior frontal ROI included the inferior frontal gyrus [F3t and F3o; or Brodmann's areas (BA) 44 and 45]. The superior temporal ROI included the superior (T1a and T1p; or BA 22) and middle (T2a, T2p, and TO2; or BA 21, 22, and 37) temporal gyri. The parietal ROI included the superior parietal lobule (SPL; or BA 5 and 7), posterior supramarginal gyrus (SGp; or BA 40), and angular gyrus (AG; or BA 39). Finally, the DLPFC corresponds to the middle frontal gyrus (F2; or BA 6, 8, 9, and 46), except superior to the inferior frontal sulcus, where the two posterior-most voxels were excluded to avoid counting any activation that may have been due to the supplementary motor area. Both hemispheres were examined because the right homologues of many cortical areas

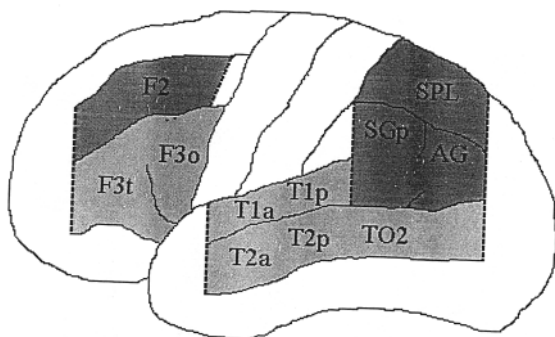


FIG. 2. The Rademacher et al. (1992) parcellation scheme. The inferior frontal ROI (region of interest) corresponds to the inferior frontal gyrus (F3t and F3o, in the nomenclature of Caviness et al., 1996; or Brodmann's area [BA] 44 and 45). The superior temporal ROI includes the superior (T1a and T1p; or BA 22) and middle (T2a, T2p, and TO2; or BA 21, 22, and 37) temporal gyri. The parietal ROI included the superior parietal lobule (SPL; or BA 5 and 7), posterior supramarginal gyrus (SGp; or BA 40), and angular gyrus (AG; or BA 39). Finally, the dorsolateral prefrontal cortex, or DLPFC, corresponds to the middle frontal gyrus (F2; or BA 6, 8, 9, and 46), excluding the two most posterior voxels from image slices superior to the inferior frontal sulcus.

have been shown to be activated by the same type of computational processing as their left counterparts (Just et al., 1996b).

fMRI Data Analysis. Because the sentence–picture verification trials were self-paced, participants completed the trials at different rates. This fact, in conjunction with our focus on between-strategy differences in cortical activation, made it necessary to equate both the number of epochs and the number of images collected while each strategy was being used. This was done for each participant by first yoking the epochs across the two strategies by number of images (i.e., the verbal-strategy epoch containing the most images was paired with the imagery-strategy epoch with the most images, then the epochs containing the next largest number of images from each strategy were paired, and so on). Next, the epochs that could not be yoked (because of an unequal number of epochs across strategies) were removed, and the longest epochs in each pair were then truncated (images at the ends of the epochs were removed). This procedure resulted in 19.5 ± 3.5 epochs ($M \pm SD$; range = 14–24) and 119.7 ± 19.1 images ($M \pm SD$; range = 84–149) per strategy. Although this procedure does not control for individual differences (e.g., skilled participants may have completed more trials and hence more epochs—but perhaps with fewer images per epoch—than less skilled individuals), it was nonetheless used because it did not require a priori assumptions about the relation between individual differences in skill and image acquisition rate and because it preserved the maximal amount of data per participant. (These issues will be raised again in the section on individual differences.)

Two steps were taken to insure that the fMRI-measured activation was due to changes in cortical microvascular activity rather than changes in the blood-flow rate of larger vessels. First, the activation maps that were defined by the ROIs corresponded to gray matter and not to the spaces normally occupied by cerebrospinal fluid or large blood vessels. The distribution of activation was thus confined to a discrete volume in the image space that did not correspond to the known drainage pattern of large veins. Second, to reduce the influence of large blood vessels, any voxel that showed an excessively large percentage of change in signal intensity (greater than 6.2%) was excluded from the analyses.

fMRI-measured activation was quantified in two ways. First, the difference between each voxel's activation in each strategy condition and the baseline condition was used to construct distributions of t values within each ROI. Voxels having activation values that exceeded their baseline values by a certain amount (as determined by a t test with $t > 8$) were then counted, and the mean number of activated voxels within each ROI was calculated for each condition. (Although a t value of 8 is conservative, t values of 6 and 7 gave the same qualitative patterns of cortical activation.) The second measure was the mean percentage of increase in the amplitude of activation relative to the baseline condition for those voxels included in the first measure.

RESULTS AND DISCUSSION

fMRI results. Figure 3 illustrates the general results by showing the pattern of thresholded fMRI-measured activation (indicated by the black voxels) superimposed on structural images for a pair of image slices in one participant. As Fig. 3 shows, each strategy engendered a different pattern of cortical activation; the verbal strategy produced more activation than the visual-imagery strategy in the left inferior frontal region, but the visual-imagery strategy produced more activation than the verbal strategy in the parietal regions, especially in the left hemisphere. Because our main prediction concerned the interaction between strategies and cortical regions, the activation was examined using analysis of variance (ANOVA) with ROI (parietal vs.

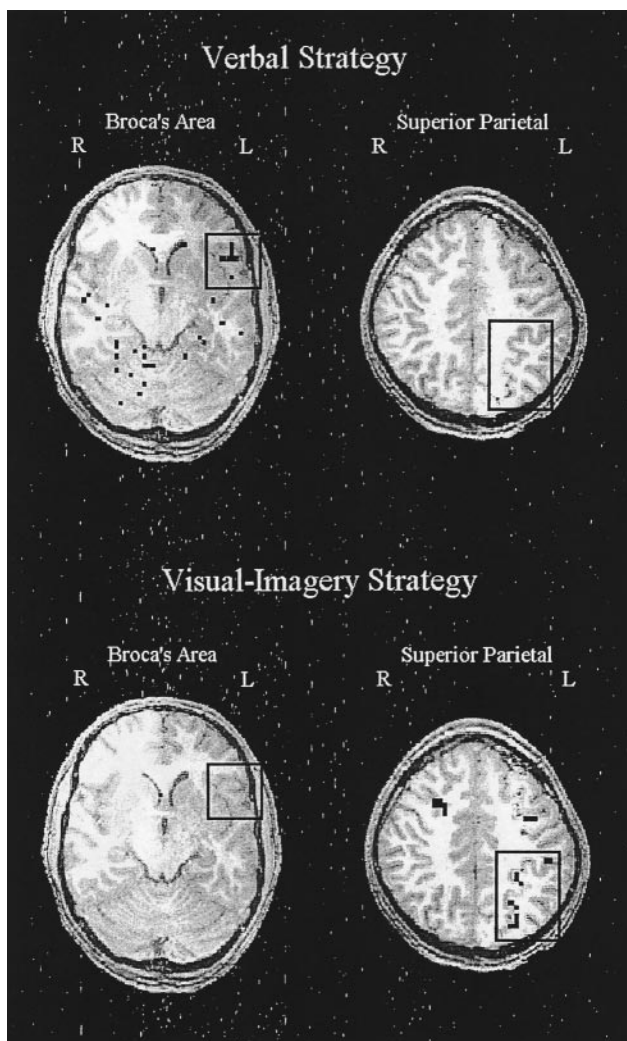


FIG. 3. The patterns of cortical activation in two image slices (slices 3 and 12 in Fig. 1) that are engendered by the verbal strategy (top) and visual-imagery strategy (bottom) in a single participant. In both panels, the left side of the brain is shown on the right and vice versa. The left images show the approximate location that includes part of Broca's area. The right images show the approximate location that includes part of the left parietal region. Voxels that are significantly more activated ($t > 8$) by either strategy than in the baseline condition are shown in black. As the figure shows, the verbal strategy produced more cortical activation than the visual-imagery strategy in Broca's area, but the visual-imagery strategy produced more activation than the verbal strategy in the parietal regions. The figure also shows that the verbal strategy produced activation in the bilateral superior temporal regions and cerebellum (posterior to Broca's area in the top left image), and that the visual-imagery strategy resulted in frontal eye-field activation (anterior to the parietal region in the bottom right image). The same pattern of activation volume (with more noise) was observed when lower t value thresholds ($t > 6$ and $t > 7$) were used to select activated voxels.

inferior frontal vs. superior temporal vs. DLPFC), laterality (left vs. right), and strategy (verbal vs. visual imagery) as within-subject factors.

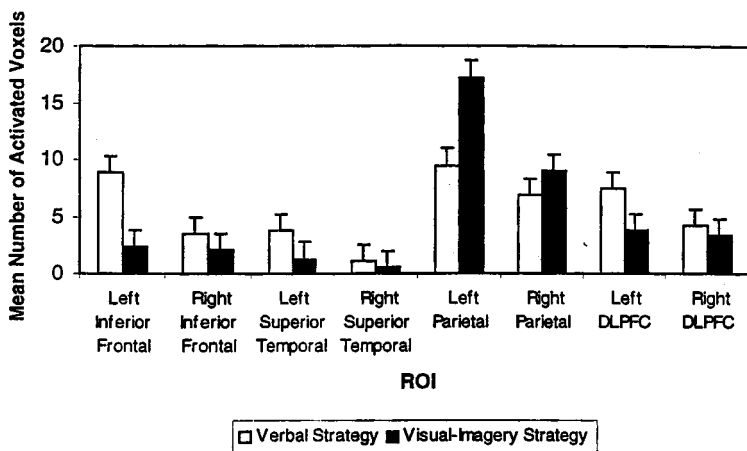
The top panel of Fig. 4 shows the mean number of activated voxels generated by each strategy in each ROI. As predicted, the verbal strategy produced more activation in the inferior frontal and posterior superior temporal ROIs, or classic language areas. In contrast, the visual-imagery strategy produced more activation in the parietal ROIs. The contrasting effects of the two strategies on the activation volume in the different regions resulted in an interaction between strategy and ROI, $F(3, 33) = 4.69, p < .01$. The bottom panel of Figure 4 collapses across the left inferior frontal and superior temporal ROIs (language regions) and the left and right parietal ROIs (visual-spatial regions) to show the total volume of cortical activation in the two main networks and graphically illustrates the predicted interaction between strategy and region.

The top panel of Fig. 4 suggests that the left hemisphere produced more activation ($M = 6.69$ voxels) than the right ($M = 3.82$ voxels), $F(1, 33) = 4.01, p < .08$. This left lateralization was expected for the verbal strategy because language has been traditionally associated with the left perisylvian region (Caplan, 1992). That the right homologues of the language regions also played a role (albeit much attenuated) in the verbal strategy is consistent with other reports of right-hemisphere homologue activation, particularly with difficult language tasks (Just et al., 1996b). Less expected was the finding that the visual-imagery strategy produced more left- than right-side parietal activation. This suggests that the left parietal region is more closely tied to the traditional language areas. It also suggests that both strategies share many component processes. For example, both strategies entail the processing of orthographic forms, which engenders activation of the angular gyrus of the left parietal ROI (Horwitz, Rumsey, & Donohue, 1998).

Although the dissociation between strategies and cortical regions is not complete, the patterns of cortical activation can be discriminated to reliably identify the strategy being used. That is, given a participant's fMRI data in each strategy, one can identify which data correspond to each strategy. One way of doing this is to count the number of activated voxels in two regions, Broca's area and the left parietal cortex, and then subtract the latter from the former. This difference should be larger for the verbal than visual-imagery strategy because the verbal strategy tends to activate Broca's area, whereas the visual-imagery strategy tends to activate the left parietal cortex. In fact, this simple procedure correctly identifies the strategies used for 10 of 12 (83%) participants in our experiment and thus provides a way to determine how an individual goes about doing the sentence-picture verification task by examining brain activation.

Finally, as Fig. 4 indicates, the differential effects of the two strategies were most pronounced in the left parietal and inferior frontal ROIs, resulting in a marginally reliable Strategy \times ROI \times Laterality interaction,

(A.)



(B.)

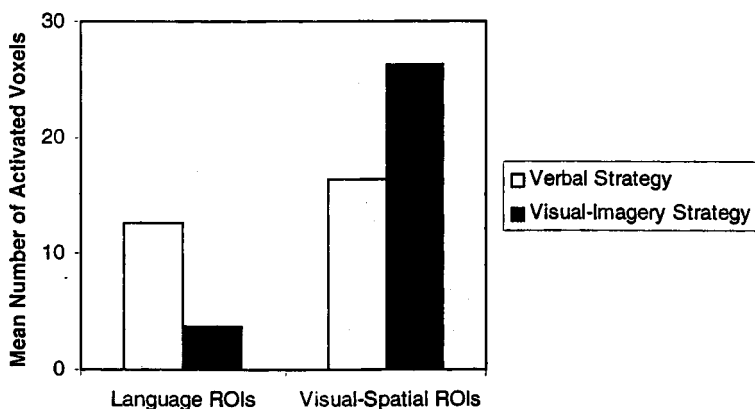


FIG. 4. (A) The mean volume of activation in the left and right inferior frontal, superior temporal, and parietal, and DLPFC ROIs (regions of interest) as a function of strategy (verbal vs. visual imagery) and (B) the mean volume of activation collapsed across the language areas (left inferior frontal and superior temporal ROIs) and the visual-spatial reasoning areas (left and right parietal ROIs) are shown. The predicted Strategy \times ROI interaction is clearly evident in B: The verbal strategy produced more activation than the visual-imagery strategy in the language regions, but the visual-imagery strategy produced more activation than the verbal strategy in the visual-spatial regions.

$F(3, 33) = 2.56, p < .08$. There was also a reliable effect of ROI, $F(1, 33) = 9.24, p < .0001$, with the most activation in the parietal ROIs and the least activation in the superior temporal ROIs. There were no other significant main effects or interactions; specific region-by-region analyses are reported below.

Inferior frontal ROIs. The left inferior frontal ROI, which includes Broca's area, is one of the major language-processing regions and has frequently been shown to be activated during language production (Bookheimer et al., 1997; Müller et al., 1997). Consequently, to the extent that the verbal strategy entails the generation and/or rehearsal of proposition-based codes, the verbal strategy would be expected to produce more cortical activation in Broca's area than would the visual-spatial strategy. To evaluate the effect of strategy within each ROI, additional ANOVAs evaluated strategy and laterality as within-subject factors. The marginally reliable interaction between strategy and laterality [$F(1, 11) = 4.50, p < .06$] was supported by planned contrasts, which showed more activation in this area for the verbal strategy than the visual-imagery strategy on the left side [$t(11) = 1.93, p < .05$], but not on the right side ($t < 1$). Neither the main effect of strategy nor that of laterality was reliable (both F s < 2.8).

Finally, separate one-way ANOVAs evaluated the percentage of change in signal intensity over baseline within each ROI with the within-subject factors of strategy and laterality. These analyses showed more activation in Broca's area for the verbal strategy than for the visual-imagery strategy, $F(1, 8) = 6.26, p < .05$, as can be seen in Fig. 5. Planned contrasts indicated

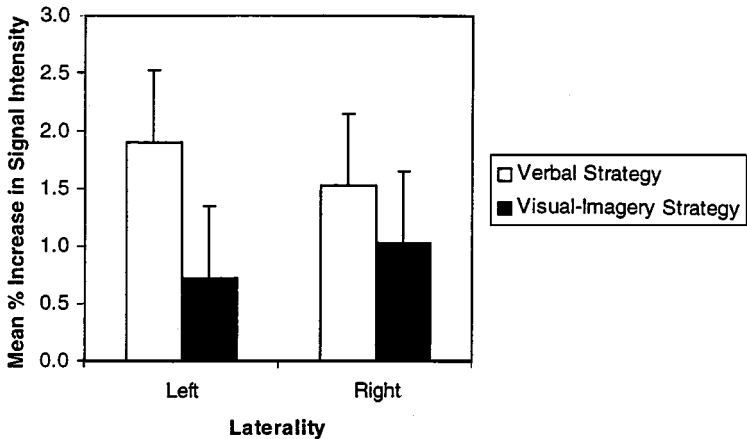


FIG. 5. Mean percentage increase in the signal intensity of the activated voxels in the left and right inferior frontal regions, as a function of strategy (verbal vs. visual imagery). The verbal strategy increased the signal intensity more than the visual-imagery strategy, especially in the left hemisphere.

that the verbal strategy caused the signal to increase more than the visual-imagery strategy in the left hemisphere [$t(8) = 3.01, p < .01$], but not the right ($t < 1$), although neither the main effect of laterality nor its interaction with strategy were significant (both F s < 1). Thus, both the activation volume and its increase in signal intensity indicate that Broca's area is differentially engaged by the two strategies.

Because Broca's area is one of the classic language-processing regions, its involvement in the verbal strategy was expected. On the other hand, the processes that are executed in this region have not been completely identified. One hypothesis is that it is involved in language generation, including the rehearsal processes that are thought to be instantiated by Baddeley's (1986, 1995) articulatory-phonological loop (Dehaene et al., 1997; Schlosser et al., 1998; Smith & Jonides, 1995; Stromswold et al., 1996). If so, then the activation produced by the verbal strategy may reflect the generation and rehearsal processes that are necessary to read a sentence and maintain the sequence of propositional codes representing its elements until a picture appears. That the visual-imagery strategy produced some activation is consistent with the conjecture that linguistic codes are processed in order to generate images from sentences. However, the fact that the visual-imagery strategy produced less activation than the verbal strategy suggests that, with the visual-imagery strategy, the linguistic codes were not being rehearsed.

Superior temporal ROIs. The left posterior superior temporal ROI includes Wernicke's area, another major language processing region that has been implicated in the interpretive processes associated with language comprehension (Caplan, 1992; Dehaene et al., 1997; Müller et al., 1997; Schlosser et al., 1998). For this reason, the region was expected to show more activation with the verbal strategy than the visual-spatial strategy. Although this trend was apparent, the overall volume of activation was comparatively small ($M = 1.44$ voxels), and neither the main effect of strategy nor its interaction with laterality were reliable (F s < 3.2). The activation was significantly higher on the left than on the right [$F(1, 11) = 9.09, p < .05$], however, and planned contrasts indicated that these strategy-related differences in the activation volume were reliable on the left [$t(11) = 1.83, p < .05$], but only marginally reliable on the right [$t(11) = 1.54, p < .08$]. Finally, although Fig. 6 indicates that the mean percentage of increase in the signal intensity of these ROIs showed a tendency to be greater for the verbal strategy, these trends were not statistically reliable by either ANOVA (all F s < 3.1) or planned contrasts (both t s < 1.3).

Because both strategies involve many verbal components (e.g., accessing the meanings of words), we expected cortical activation in this region, especially in the left hemisphere. The results clearly support this prediction. On the other hand, it is also clear that the volume of activation in this region is markedly less than those for the inferior frontal ROIs and much less than those in other sentence comprehension studies that have been conducted in

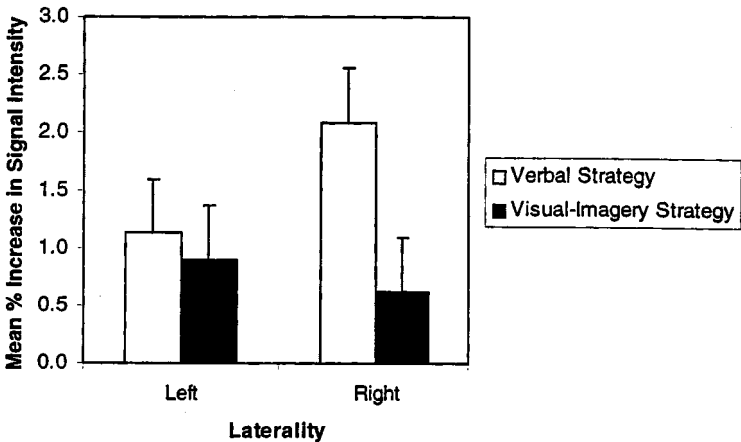


FIG. 6. Mean percentage of increase in the signal intensity of the activated voxels in the left and right superior temporal regions, as a function of strategy (verbal vs. visual imagery). Although the verbal strategy increased the signal intensity more than the visual-imagery strategy (especially in the right hemisphere), this trend was not statistically reliable.

our lab (e.g., Just et al., 1996b). A possible explanation for the relatively low levels of activation is that the repeated use of the same symbols and prepositions across the study decreased the role of interpretive processes per se. This hypothesis is currently being tested.

Parietal ROIs. The parietal cortex is thought to perform many of the computations that support visual-spatial reasoning (Carpenter et al., 1999; Smith & Jonides, 1995). Because the visual-spatial strategy is more dependent upon these processes than is the verbal strategy, we expected the former strategy to produce more parietal activation than the latter. This prediction was supported: Planned contrasts indicated that the strategy-related difference in the volume of activation was reliable on the left side [$t(11) = 2.07$, $p < .05$] and not the right ($t < 1$), although neither the main effect of strategy nor its interaction with laterality were statistically reliable (both F s < 2.7). There was also considerably more left- than right-side activation, as supported by a marginally reliable laterality effect, $F(1, 22) = 3.70$, $p < .08$. Finally, although Fig. 7 indicates that the strategy-related increase in signal intensity was also more pronounced with the visual-spatial strategy than the verbal strategy on the left side, these trends were not statistically reliable (all F s < 1.5). However, planned contrasts did suggest that the visual-spatial strategy increased the signal intensity more than the verbal strategy in the left hemisphere [$t(11) = 1.62$, $p < .07$] but not the right ($t < 1$).

The finding that the strategy-related effect on parietal activation was more pronounced on the left side is surprising because other visual-spatial reasoning tasks, such as mental rotation of objects, result in bilateral parietal activa-

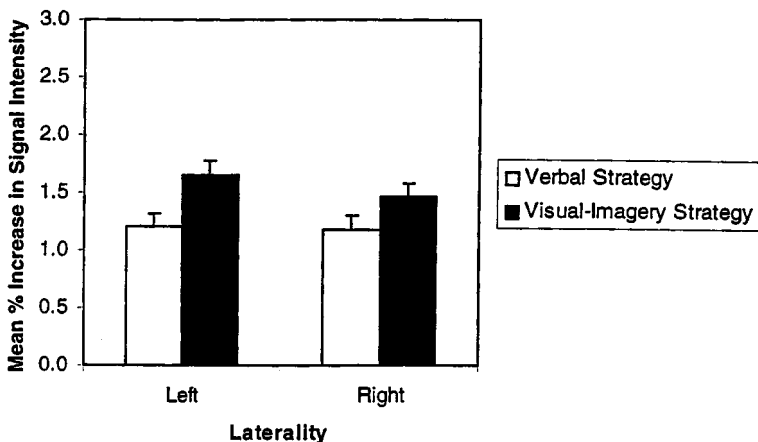


FIG. 7. Mean percentage of increase in the signal intensity of the activated voxels in the left and right parietal regions, as a function of strategy (verbal vs. visual imagery). The visual-spatial strategy increased the signal intensity more than the verbal strategy, especially in the left hemisphere.

tion (Carpenter et al., 1999). One reason for this discrepancy is that the sentence-picture verification task, unlike mental rotation of objects, involves word recognition, which activates the left angular gyrus of the left parietal cortex (Horwitz et al., 1998). Because language plays such a ubiquitous role in the functional life of the left hemisphere, its lateralization may “spill over” into other left-hemisphere areas, allowing them to take on secondary language-processing roles. This hypothesis is supported by several results showing that language tasks produce cortical activation in left hemispheric regions which are conjectured to have primary functional roles other than language processing (e.g., the left hippocampal region, which has been implicated in memory for verbal materials; Kopelman, Stevens, Foli, & Grasby, 1998).

Another explanation is that the left parietal cortex may be important for the visual representation of patterns that lend themselves to being verbally described. This interpretation is supported by several findings: First, more cortical activation is found along the left than right intraparietal sulcus when participants imagine the orthographic forms of Japanese phonograms (Sugishita et al., 1996). Likewise, the mental rotation of alphanumeric characters leads to more left- than right-side parietal activation (Alivisatos & Petrides, 1997), as does imagining letters (Kosslyn et al., 1993). Finally, the task of maintaining the identity of abstract (but highly regular and hence easy to describe) figures produces more activation in the left than right parietal cortex (Smith & Jonides, 1995).

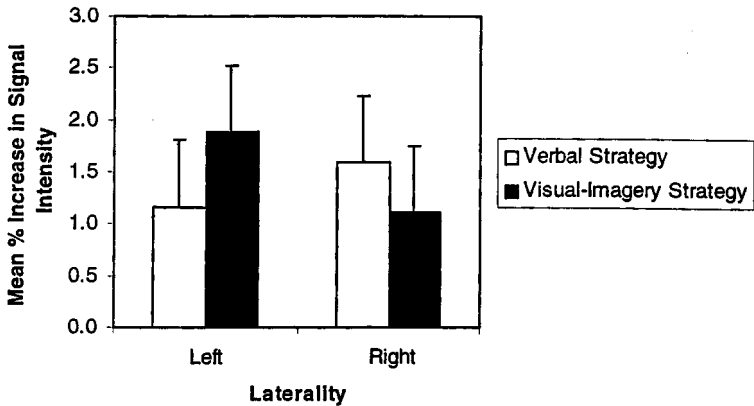


FIG. 8. Mean percentage of increase in the signal intensity of the activated voxels in the left and right DLPFC regions, as a function of strategy (verbal vs. visual imagery). Both strategies caused comparable increases in the signal intensity in both hemispheres.

DLPFC ROIs. The dorsolateral prefrontal cortex (DLPFC) is thought to support the executive cognitive functions, such as planning and evaluating complex sequences of behavior, maintaining information in an active state, and inhibiting context-inappropriate responses (Cohen et al., 1997; Mesulam, 1998; Pennington, 1997). Because the sentence–picture verification strategies involve complex sequences of behavior, and are thus dependent upon many of these executive functions, we expected cortical activation in the DLPFC. As Fig. 4 shows, both strategies engendered cortical activation in this region. An ANOVA confirmed that neither strategy nor laterality nor their interaction was reliable (all $F_s < 1$). Figure 8 shows the strategy-related increases in signal intensity. Again, neither strategy nor laterality nor their interaction was reliable (all $F_s < 1$), and planned contrasts showed that the strategies increased the signal intensity by comparable amounts in both hemispheres (both $t_s < 1.1$).

That both strategies produced more cortical activation in DLPFC ($M = 4.73$ voxels) than the superior temporal regions ($M = 1.69$ voxels) indicates that the DLPFC plays an important role in the verification task; however, the exact nature of this role is not known.

Behavioral results. The behavioral data indicate that the participants followed instructions and used the strategies at the appropriate times. The patterns of sentence-comprehension and picture-verification latencies are similar to those that have been used to distinguish between the two strategies in previous experiments (MacLeod et al., 1978; Mathews et al., 1980).

Sentence comprehension and sentence–picture verification latencies greater than 3 SD above the mean for a given participant (less than 1%) were

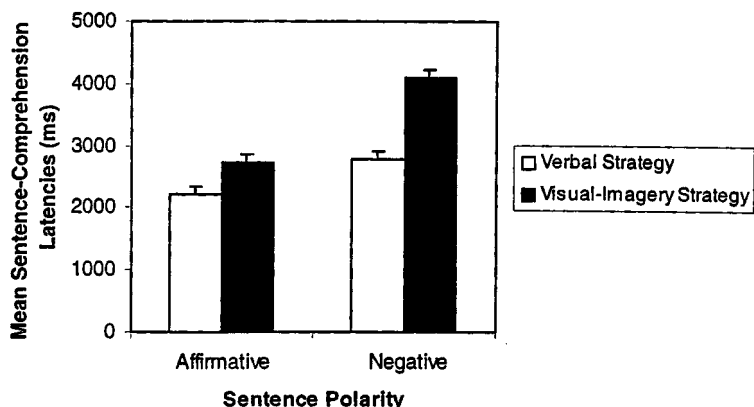


FIG. 9. Mean sentence-comprehension latencies (in milliseconds), as a function of strategy (verbal vs. visual imagery) and sentence polarity (affirmative vs. negative). Sentence comprehension was more rapid (a) with the verbal strategy than the visual imagery strategy and (b) with affirmative sentences than negative sentences. These two factors (strategy and polarity) also interacted.

truncated to avoid extreme values. The sentence comprehension latencies were then evaluated by ANOVA using strategy (verbal vs. visual imagery) and polarity (affirmative vs. negative) as within-subject factors. As shown in Fig. 9, the participants comprehended the sentences more rapidly when they used the verbal strategy ($M = 2467$ ms) than when they used the visual imagery strategy ($M = 3439$ ms), $F(1, 11) = 8.66$, $p < .05$. With the verbal strategy, the sentences had to be converted into proposition-based representations, which was comparatively easy because proposition-based representations are presumably similar to the verbatim wordings of the sentences. In contrast, the visual-spatial strategy required participants to read the sentence in a deeper, more labor-intensive fashion and translate its meaning into a mental image.

As Fig. 9 also shows, participants were faster reading affirmative sentences ($M = 2500$ ms) than negative sentences ($M = 3406$ ms), $F(1, 11) = 22.39$, $p < .0005$. This difference reflects the fact that the more linguistically complex, negative sentences are more difficult to process than the easier, affirmative sentences. The difference was exaggerated with the visual-spatial strategy because negative predicates had to be fully comprehended before visual images could be generated. This resulted in a Polarity \times Strategy interaction, $F(1, 11) = 9.21$, $p < .05$.

Figure 10 shows the picture-verification latencies, which were evaluated by ANOVA using strategy, polarity, and truth-value (true vs. false) as within-subject factors. As expected, with the verbal strategy, true affirmative sentences are easier than false affirmative sentences, but false negative sentences are easier than true negative sentences. With the visual-imagery strategy,

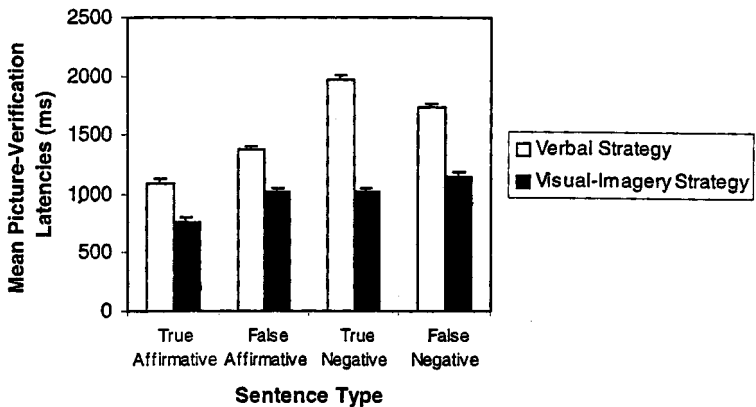


FIG. 10. Mean picture-verification latencies (in milliseconds) for correct responses, as a function of strategy (verbal vs. visual imagery), and sentence polarity (affirmative vs. negative) and truth-value (true vs. false). A Polarity \times Truth-Value interaction is evident in the verbal strategy data (the light bars), but absent in the visual-imagery strategy data (the dark bars).

however, the latencies are comparable for affirmative and negative sentences, and true sentences are faster than false sentences, irrespective of whether the sentence is affirmative or negative. This Strategy \times Polarity \times Truth-Value interaction [$F(1, 14) = 14.67, p < .005$] is the litmus test for distinguishing between the verbal and visual-spatial strategies (MacLeod et al., 1978; Mathews et al., 1980) and indicates that our participants were using each strategy as instructed.

Figure 10 indicates that participants were faster making judgments using the visual-spatial strategy ($M = 988$ ms) than the verbal strategy ($M = 1544$ ms), $F(1, 11) = 26.13, p < .005$. This difference may reflect the time that is required to generate proposition-based descriptions of the pictures in the case of the verbal strategy. Alternatively, this difference may indicate that the components of the visual image can be compared to those of the picture in parallel.

Figure 10 also shows that true sentences ($M = 1214$ ms) are easier than false sentences ($M = 1318$ ms), and affirmative sentences ($M = 1065$ ms) are easier than negative sentences ($M = 1467$ ms). Both main effects were statistically reliable [$F(1, 11) = 6.56, p < .05$; and $F(1, 11) = 51.41, p < .0001$, respectively], as was their interaction [$F(1, 11) = 18.10, p < .005$]. As already mentioned, however, the Polarity \times Truth-Value interaction is indicative of the verbal strategy, so that both variables (i.e., Polarity and Truth-Value) affected performance more with the verbal strategy than the visual-spatial strategy, giving reliable Strategy \times Polarity [$F(1, 11) = 14.17, p < .005$] and Strategy \times Truth-Value [$F(1, 11) = 13.54, p < .005$] interactions. These results indicate that, with the visual-spatial strategy, the process of converting the sentence into a visual image removes the

affirmative–negative difference and attenuates the true–false difference. (Of course, the benefit so gained ignores the cost that is initially associated with constructing the image.)

The overall mean error rate was extremely low ($M = .037$) and did not differ between the two strategies, $F < 2.5$. The participants did not trade accuracy for speed because the easier conditions (i.e., those with faster latencies) also had fewer errors. Participants made fewer errors with affirmative ($M = .022$) than negative ($M = .051$) sentences [$F(1, 11) = 6.83, p < .05$] and fewer errors with true ($M = .028$) than false ($M = .045$) sentences [$F(1, 11) = 5.75, p < .05$]. Finally, in the error data, none of the two- or three-way interactions were reliable in the analyses of strategy, polarity, and truth-value (all F s < 3.6).

In summary, our behavioral results replicate those of earlier experiments (MacLeod et al., 1978; Mathews et al., 1980) and indicate that the participants used the strategies as instructed. The different patterns of cortical activation generated by each strategy can be attributed to fact that the strategies differentially engaged the cortical systems supporting language and visual–spatial processing.

Individual differences. As mentioned under Method, individual differences in skill (or, more precisely, the trial completion rate) covaries with the number of images collected per participant, which could affect the statistical power underlying the selection of activated voxels. Because of this potential problem, the analyses of individual differences in skill that are reported in the upcoming sections were completed two ways: The first way was to use the data as reported thus far (i.e., the full data set); the second was to use the data after it had been truncated to equate for the number of epochs and images across both strategies and participants (i.e., the truncated data set).

The truncation procedure was as described previously, except that the epochs for each strategy were also yoked across participants, so that each participant contributes the same number of epochs (14) and images (49) per strategy. The number of baseline epochs (11) and images (66) were also equated across participants. Because of the overall reduction in the number of images in the truncated data set, the t value criterion for activated voxels had to be decreased (from $t > 8$ to $t > 6$) to allow for comparable numbers of activated voxels across the two sets of analyses. Although our analyses of the truncated data set may be conservative in that the truncation procedure removed much of the data, the fact that both sets of analyses produced such similar results suggests that the relations between skill and fMRI-measured cortical activation are robust. Thus, the relations reported in the next two sections are not likely to be due to the specific choice of criteria used to select activated voxels.

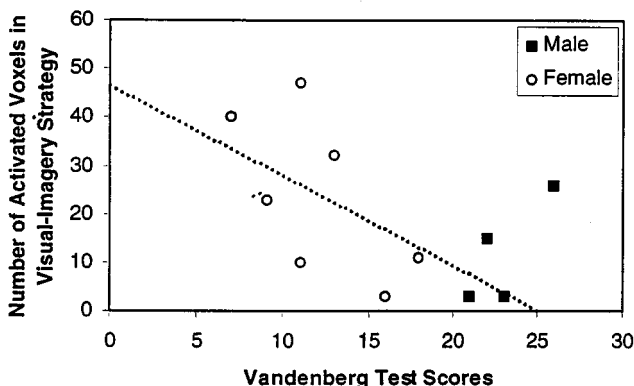
Visual–spatial skill. We predicted that our participants' Vandenberg (1971) mental rotation test scores would be negatively related to the activation volume generated by the visual–spatial strategy in the parietal region.

As expected, an analysis of the full data set indicated that mental rotation scores ($M = 16.1$, $SD = 6.35$, range = 7–26) were negatively related to the difference in activation volume between the visual-imagery and verbal strategies (i.e., visual-imagery strategy volume – verbal strategy volume) in both the left [$r = -0.68$, $t(9) = -2.77$, $p < .05$] and right [$r = -0.55$, $t(9) = -1.97$, $p < .05$] parietal ROIs and collapsed across laterality [$r = -0.66$, $t(9) = -2.65$, $p < .05$]. These results reflect facility in using the visual–spatial strategy because the mental rotation test scores were also negatively related to the amount of activation produced by the visual–spatial strategy (but not the verbal strategy) in the same parietal ROIs: left [$r = -0.78$, $t(9) = -3.74$, $p < .005$], right [$r = -0.55$, $t(9) = -1.97$, $p < .05$], and collapsed across laterality [$r = -0.73$, $t(9) = -3.21$, $p < .01$].

The negative relations between visual–spatial skill and volume of parietal activation also held in analyses of the more conservative truncated data set (i.e., equated for epochs and images across strategies and participants): The negative correlations between mental rotation test scores and the activation volume differences (visual-imagery strategy–verbal strategy) were marginally reliable in the left [$r = -0.48$, $t(10) = 1.62$, $p = .070$], right [$r = -0.43$, $t(9) = 1.43$, $p = .093$], and bilateral [$r = -0.52$, $t(9) = 1.83$, $p = .051$] parietal ROIs. Likewise, mental rotation scores correlated negatively with activation volume in all three parietal ROIs [$r_s = -0.74$, -0.61 , and -0.70 for left, right, and bilateral ROIs, respectively; all $t_s > 2.29$, all $p_s < .05$]. Figure 11 shows the relations that were observed for each participant between mental rotation test scores and activation volume in the left (Fig. 11A) and right (Fig. 11B) parietal ROIs, with the truncated data set. As the best-fitting regression lines indicate, both relations were remarkably similar and were more pronounced for female ($r_s = -0.63$ and -0.68 for the left and right hemispheres, respectively) than male ($r_s = -0.37$ and 0 for the left and right hemispheres, respectively) participants. This final conclusion must remain speculative, however, due to the small sample sizes involved and because the range of scores is restricted with the males.

Verbal skill. We predicted a negative relation between our participants' reading spans and the volume of activation generated by the verbal strategy in the language ROIs. That is, because people with higher verbal ability have more resources at their disposal to do verbal tasks (Carpenter & Just, 1989; Carpenter et al., 1995; Haarmann et al., 1997; Miyake et al., 1994), the verbal strategy should consume a smaller proportion of those resources, producing less activation in language-related regions. As expected, with the full data set, reading span ($M = 3.5$, $SD = .86$, range = 2–5) was negatively related to the difference in activation volume between the verbal and visual-imagery strategies (i.e., verbal strategy volume–visual-imagery strategy volume) in the left inferior frontal ROI [$r = -0.59$; $t(8) = -2.08$, $p < .05$] and in the same ROI collapsed across laterality [$r = -0.62$; $t(8) = -2.24$, $p < .05$]. These results reflect differences in how facile the participants were at using

(A.)



(B.)

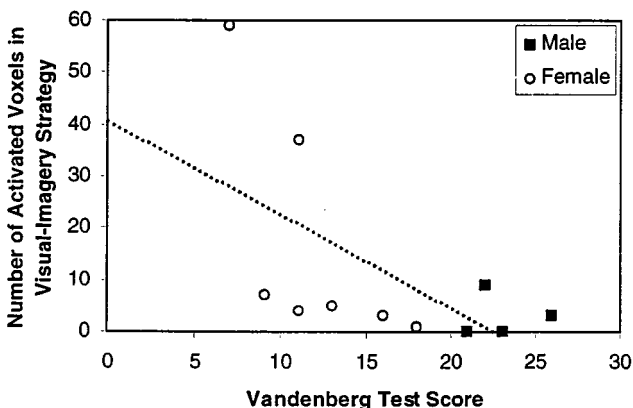
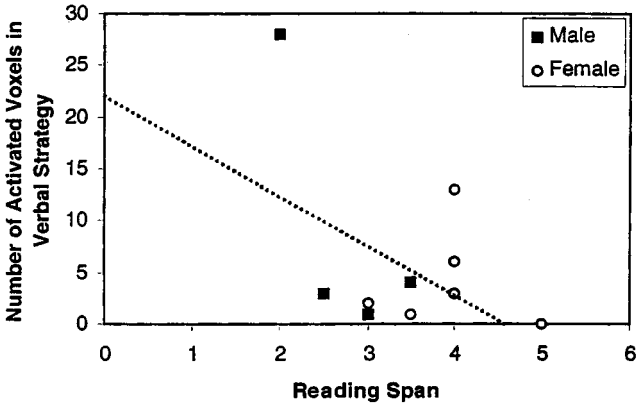


FIG. 11. The relation between visual-spatial skill (as measured by the Vandenberg, 1971, mental rotation task) and the volume of cortical activation generated in the left (A) and right (B) parietal regions of interest (ROIs), as a function of gender. The best-fitting regression lines (A: $y = 47.18 - 1.86x$; B: $y = 40.62 - 1.80x$) indicate that visual-spatial skill was negatively correlated with activation volume in both the left ($r = -0.74$) and right ($r = -0.61$) hemispheres.

the verbal strategy because reading span was also negatively related to the volume of activation generated by the verbal strategy (but not the visual-imagery strategy) in the same language-related regions: the left [$r = -0.54$, $t(8) = -1.83$, $p < .06$] and bilateral [$r = -0.50$, $t(8) = -1.62$, $p < .08$] inferior frontal ROIs.

Again, these relations held with the truncated data set: Reading span negatively correlated with the activation volume differences (verbal strategy-visual-imagery strategy) in left [$r = -0.54$, $t(8) = 1.80$, $p = .054$] and

(A.)



(B.)

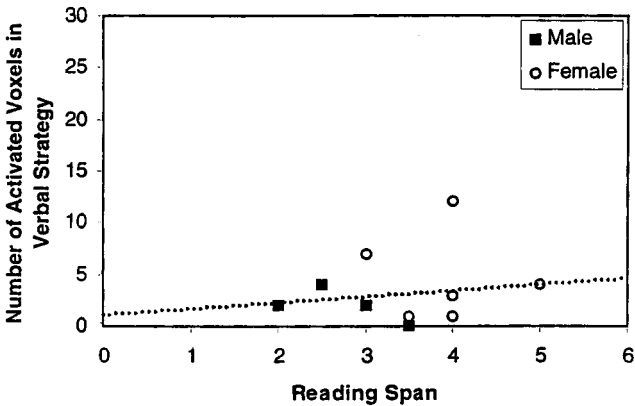


FIG. 12. The relation between individual differences in verbal skill (as measured by the Daneman and Carpenter, 1980, reading span task) and the volume of cortical activation generated in the left (A) and right (B) inferior frontal ROIs, as a function of gender. As the best-fitting regression lines (A: $y = 22.75 - 4.83x$; B: $y = 1.39 + 0.64x$) indicate, verbal skill was negatively correlated with activation volume in the left hemisphere ($r = -0.49$), but not the right ($r = 0.16$).

bilateral [$r = -0.63$, $t(8) = 2.30$, $p < .05$] inferior frontal ROIs. Likewise, the negative correlation between reading span and activation volume was marginally reliable in the left hemisphere, $r = -0.49$, $t(8) = 1.58$, $p < .08$. Figure 12 shows the relations observed for each participant between reading span and activation volume in the left (Fig. 12A) and right (Fig. 12B) inferior frontal ROIs, with the truncated data set.

Although the verbal skill is negatively related to activation volume in the

left, but not the right, hemisphere (as indicated by the best-fitting regression lines, which are negatively sloped in the left hemisphere and positively sloped in the right hemisphere), this asymmetry is largely due to one male participant. Consequently, any conclusion regarding the relationship between verbal skill and the volume of cortical activation engendered by the verbal strategy in Broca's area remains tentative. (However, it is worth pointing out that it is not likely that the large volume of activation displayed by this participant in the left inferior frontal ROI is spurious because the same participant showed little activation in the right hemisphere analog.)

Finally, the analysis of DLPFC was intended to assess if individual differences in verbal and/or visual-spatial skills are related to the amount of strategy-related activation in this region. Only one such relation was observed with the full data set: a negative correlation between reading span and the activation volume generated by the verbal strategy in the left DLPFC, $r = -0.62$, $t(8) = -2.22$, $p < .05$, meaning that more skilled individuals showed less fMRI-measured activation. However, this negative relation failed to reach statistical significance with the truncated data set ($r = -0.40$, $t < 1.3$). One possible reason for this result is that the left DLPFC is anatomically adjacent to Broca's area. The proximity of these two regions, in conjunction with the fact that both areas are similarly related to the verbal strategy, may indicate that the left DLPFC plays an important functional role in language processing. Indeed, this hypothesis has been suggested elsewhere to account for DLPFC activation with linguistic tasks (Bavelier et al., 1997; Binder et al., 1997; Gabrieli et al., 1998; Müller et al., 1997).

GENERAL DISCUSSION

The current study contrasted the patterns of cortical activation underlying two ubiquitous representational modes, linguistic and visual-spatial. The same task may give rise to significantly different patterns of activation depending upon the strategy used by the participant. In this section, we elaborate on the implications of this result, the pattern of individual differences, and the nature and role of strategies in relation to cognitive processes.

A major contribution of the study is to show that the two behavioral strategies, linguistic and visual-imaginal, correlate with partially differentiable patterns of fMRI-measured activation. The various cortical regions that show activation during each of the two strategies are hypothesized to be parts of the large-scale cortical and subcortical networks that subservise linguistic and visual-spatial processing, respectively. The hypothesis is that there are multiple regions that participate to a greater or lesser extent depending in part on the properties of the language comprehension task or the visual problem solving task, rather than a fixed set of regions that constitute each network. For example, the left inferior frontal region plays a particularly important role in the current verification task presumably because of the necessity to

maintain and rehearse the order of the sentence constituents (i.e., *star*, *plus*, and/or *dollar*). By contrast, the posterior superior and middle frontal gyri, which typically are highly activated in sentence comprehension tasks (e.g., Binder et al., 1997; Just et al., 1996b), activate to a much lesser degree in the current study. These lower levels of activation may be due to the small role of semantic interpretation in the current task (in which the lexical content is repeated) compared to other comprehension tasks (in which the sentences usually contain novel lexical content). Similarly, the nonnegligible involvement of the right hemisphere may partially reflect the difficulty of the task (Just et al., 1996b) and partially reflect the concrete visual referents of the sentences. Thus, the current results are consistent with the hypothesis that language comprehension is subserved by a flexible network of cortical regions and that the degree of involvement of these regions is partially dependent on the processing characteristics of the task. This stands in stark contrast to the implicit assumption that there are fixed networks for cognitive tasks that are as specialized as language comprehension.

The fact that the same conclusion applies also to the systems mediating the visual–spatial strategy makes the significant point that these insights may represent general characteristics of the cortical processing systems. For example, the cortical regions activated in the current visual-imagery task overlap with (but are not identical to) the regions involved in another nonlinguistic imagery task, namely, the mental rotation of abstract three-dimensional forms (Carpenter et al., 1999). In mental rotation, the activation is more left–right symmetrical in the parietal region than left lateralized, as in the current task, perhaps due to the central role of the linguistic processes in generating the representations in the current task. Thus, the cortical system components that mediate both strategies show degrees of involvement that depend partially on the task's characteristics.

Because one of our goals was to discriminate between the cortical systems supporting language versus visual–spatial reasoning, we took several precautions to minimize any between-participants differences in how the task was performed and to ensure that participants used only the intended strategies. First, the task naturally lends itself to being done either verbally or visual–spatially because of the simplicity of the stimuli. Second, the instructions gave detailed descriptions of both strategies to make participants aware of both ways of doing the task and thereby differentiate between the two strategies. Also, participants practiced using both strategies. Finally, the participants' patterns of response times supported the hypothesis that, on average, they used the appropriate strategies. Moreover, the response times enabled us to select participants on the basis of their ability to appropriately select and execute the strategy. [Although this last precaution may limit the generalizability of our results, only two of 16, or 12.5%, of the participants that completed the practice sessions showed response time patterns that suggested that they were unable to use both strategies. This result is concordant with

Mathews et al.'s (1980) finding that it was difficult to identify the strategy that was used by 16% of their participants.]

Although our methodology allowed us to partially separate the language systems from the visual-spatial systems, it is important to note that neither the strategies nor the neural systems underlying the strategies are completely independent. The former claim is supported by the fact that the strategies share many of the same task components (e.g., reading sentences). The latter claim is supported by our finding that both strategies produced at least some cortical activation in all of the examined regions and produced comparable amounts of activation in some of those regions (e.g., superior temporal ROIs).

The involvement of the large-scale networks in a task such as sentence-picture verification may be expected given that the component processes, such as reading sentences, are themselves mediated by several functionally linked regions (Mesulam, 1998). Nonetheless, the results suggest that there is probably not a one-to-one correspondence between cognitive functions and cortical regions. Thus, previous failures to localize cognitive functions (for a review, see Cabeza & Nyberg, 1997) to specific cortical regions may not be failures per se, but may instead reflect an overly simplistic view of cortical organization. Instead, our results suggest that high-level cognitive tasks, such as sentence comprehension, are likely to reflect the highly orchestrated processing of several cortical regions.

A second contribution of the current study is to show that the fMRI-measured activation is correlated with behaviorally assessed cognitive skill in the two processing domains. Moreover, the direction of the correlation is consistent with a resource-based approach to cognition: More skilled individuals show less fMRI-measured activation than do less skilled individuals. Specifically, individual differences in language comprehension correlate with resource availability in the comprehension system; similarly, individual differences in visual-spatial reasoning correlate with resource availability in the visual-spatial system.

However, although the current study demonstrated a significant correlation between skill and the amount of activation in particular cortical regions, it would be a mistake to interpret these regions as being the sources of individual differences in general. On the contrary, the current study, in conjunction with other studies of individual differences, suggests that a fruitful approach is to consider the neural correlates of these cognitive skills at a systems level. The efficiency of a system depends not only on its components, but also on their interactions, so that, in general, the system's output cannot be reduced to the performance of a single process or a single cortical region.

This system-level analysis may explain how language comprehension, for example, can show similar behavioral modulations as a function of difficulty with different pathological conditions that have their primary effect on different neural substrates. For example, both individuals with Parkinson's Disease

and those with aphasia due to cortical infarct show impairments in comprehending complex sentences, presumably due to problems that, at some level, impair the overall system's performance (Karbe et al., 1989; Parks et al., 1989). The performance of individual neural regions and their ability to interact appropriately with other regions may provide overall limits that show up in parallel profiles of language comprehension performance.

One theory that is consistent with the current results is the capacity-constrained view of working memory (Just & Carpenter, 1992; Just et al., 1996a) and its corollary that individual differences in the availability of cognitive resources partially determine task difficulty. This theory has been operationalized in a cognitive architecture that is a hybrid of a production system and an activation-based connectionist system (Just & Carpenter, 1992; Haarmann et al., 1997). In this architecture, the productions reiteratively propagate "activation" from source elements to target elements. An important property of the architecture is that the activation capacity is constrained; there is a limit on the total amount of activation that can be propagated between elements and/or used to maintain the activation level of recently processed elements above threshold.

In the context of language comprehension, this capacity limitation results in a conjoint constraint on the processing and storage that are necessary for comprehension. One implication of this is that many performance differences among individuals can be related to differences in activation capacity, particularly if the activation demanded by a particular comprehension task is sufficient to exhaust the resources available to do the task. An important contribution of the current study is to provide a convergent measure of this resource consumption, specifically, a neurophysiological index. This experiment and others have shown that these resources have correlates in the physiological processes that support cortical activation. For example, in many tasks, activation volume is positively related to cognitive workload (Carpenter et al., 1999; Just et al., 1996b) and negatively related to the skills underlying the tasks (Haier et al., 1988; Parks et al., 1988, 1989). This study therefore ties the theoretical construct of processing resources (at the level of cognition) to its underlying neural substrate (cortical activation). That this relation holds for at least two domains—language and visual-spatial reasoning—suggests that it is a basic principle of cortical functioning.

The relation of cortical activation to individual differences also illuminates a general aspect of the task as an instantiation of cognitive strategies, namely, how strategies reflect a form of cognitive economics. Generally speaking, strategies are behavioral routines that are selected to facilitate completion of many high-level cognitive tasks. Strategies thus refer to "adaptive processing patterns" (Payne, Bettman, & Johnson, 1988, p. 541) or "procedures aimed at meeting particular goals" (Siegler, 1998, p. 92). Because resource-efficient strategies impart a smaller cognitive workload, they leave a larger proportion of the resources available, making task performance more rapid,

less prone to error, and less effortful. This being the case, then (with everything else being equal) people should prefer strategies that consume fewer resources because they facilitate task performance. For example, participants with above-average visual-spatial skills should prefer the visual-spatial strategy because, by using fewer resources, the strategy makes the sentence-picture comparisons easier. As discussed in the Introduction, this prediction has been supported (MacLeod et al., 1978; Mathews et al., 1980). An alternative experimental test of this prediction might involve biasing the verification task so that one strategy is easier to use than the other; for example, participants should prefer the visual-spatial strategy with difficult-to-describe pictures or prefer the verbal strategy when little time is allowed to read the sentences.

The existence of the two strategies for the same task gives rise to the question of how the particular performance comes to be organized. Given the ubiquity of the various component skills (e.g., reading, forming images), it is fair to assume that the strategies examined in this article are extensions of natural skills: language and visual-spatial reasoning. Indeed, it was this prerequisite knowledge that allowed the participants to walk into the laboratory and, with only minimal instruction, complete our experiment (Newell, 1991).

One possibility is that the prefrontal cortex (which has been implicated in many executive functions; Cohen et al., 1997; Mesulam, 1998; Pennington, 1997), helps to regulate the other cortical regions and to orchestrate their processing so that the computations that are necessary to do the verification task are appropriately coordinated. Because this may initially involve a considerable amount of planning, setting up and keeping track of goals and subgoals, and monitoring the outcomes of alternative computations or actions, this top-down strategy selection resembles problem solving (Newell, 1991). In this view, the prefrontal cortex is one component of a large-scale interacting set of networks (which include many other regions) that together support the processes required by various tasks.

With tasks like the current one, however, it is likely that the component processes are partially organized by the task itself. For example, on the first trial of the verification task, a participant may happen to read the sentence and form a mental image of its content and then compare this mental image to the picture to determine the correct response. Although the person in this example may not have been deliberately trying to use a particular strategy, their skills and knowledge, when combined with the momentary demands of the task, led to the development and use of the visual-spatial strategy (Hunt, 1978; Newell, 1991). One might also expect the person in the preceding example to use the strategy again if it leads to a correct response. This type of bottom-up strategy selection is analogous to biological evolution in that, with any given task, there is a pool of strategies (or component processes for assembling new strategies) that compete to execute the task and which

are selected and retained on the basis of their utility (Siegler, 1998). Note, however, that “utility” must be broadly defined to include many aspects of the task such as meeting time constraints (Payne et al., 1988), minimizing effort (Reder, 1987), satisfying curiosity and exploring new (and possibly better) strategies (Siegler, 1998), and following instructions (Reder, 1987). As a result, there are many determinants of strategy selection: information that is intrinsic to the task, expectations about task performance, pressure to perform the task rapidly and/or accurately, and explicit task instructions.

In the present experiment, strategy selection was mainly determined by instructions; a cue indicated which strategy was to be used during a given block of trials. The fact that the participants used the cues suggests that the participants were able to maintain the appropriate strategy in “set” and/or inhibit the inappropriate strategy (both of these functions probably involve the prefrontal cortex; Mesulam, 1998). However, participants undoubtedly monitored their own performance and adjusted their processing to compensate for momentary fluctuations in task demands (Payne et al., 1988). For example, because the verification task can be completed two ways, the participants may have sometimes switched to the inappropriate strategy to compensate for weak cognitive skills (or, conversely, to take advantage of strong cognitive skills). This again suggests why cognitive strategies are useful: They make task performance easier. Because cognitive strategies are behavioral routines, they may provide a way to organize and keep track of a task’s component processes, especially if the task is complex or the strategy is well practiced. This is beneficial because it allows participants to monitor their performance (Payne et al., 1988). It also provides organization, which facilitates learning (Baddeley, 1990). Finally, with extensive practice, the strategies (or their component processes) may become increasingly automated, so that the task demands less attention, freeing up additional computational resources.

In summary, then, the present experiment used fMRI and the known relation between cognitive workload and cortical activation to explore the relations between cognitive strategies and skills (on the one hand) and their underlying cortical regions (on the other). This endeavor was successful in that it revealed some of the neural correlates of strategy and skill (at least in the limited context of the sentence–picture verification task) and suggested how both factors are related to the availability of working memory resources. An analysis of these relations has offered some insight into the nature of cognitive strategies, especially with respect to how they are selected and why they are useful.

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