

Functional-Anatomic Correlates of Individual Differences in Memory

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Summary

Memory abilities differ greatly across individuals. To explore a source of these differences, we characterized the varied strategies people adopt during unconstrained encoding. Participants intentionally encoded object pairs during functional MRI. Principal components analysis applied to a strategy questionnaire revealed that participants variably used four main strategies to aid learning. Individuals' use of verbal elaboration and visual inspection strategies independently correlated with their memory performance. Verbal elaboration correlated with activity in a network of regions that included prefrontal regions associated with controlled verbal processing, while visual inspection correlated with activity in a network of regions that included an extrastriate region associated with object processing. Activity in regions associated with use of these strategies was also correlated with memory performance. This study reveals functional-anatomic correlates of verbal and perceptual strategies that are variably used by individuals during encoding. These strategies engage distinct brain regions and may separately influence memory performance.

Introduction

Memory abilities differ greatly across individuals. While it is recognized that multiple factors can affect individuals' memory performance, including their cognitive abilities (e.g., IQ, working memory capacity), past experiences, and strategy use, relatively little is known about the functional-anatomic differences across individuals that relate to memory performance. Individual differences in episodic memory (for reviews see Bors and MacLeod, 1996; Habib et al., 2000), and in particular the strategies adopted during intentional encoding (Boltwood and Blick, 1970; Martin et al., 1965; McDaniel and Kearney, 1984; Richardson, 1978; Stoff and Eagle,

1971), provide a rich source of variation to begin such an exploration. The present study explored individual differences in encoding strategy use and their relationship to memory performance and brain activity.

Insights into the types of strategies that individuals adopt during unconstrained intentional encoding have come from self-reports of strategy use (for review see Richardson, 1998). Various self-report methods have been used, including having individuals answer open-ended questions concerning their strategy use (Eagle, 1967; Pressley and Levin, 1977; Roberts, 1968; Stoff and Eagle, 1971), describe how they attempted to learn each item (Martin et al., 1965; Reed, 1918), indicate which type of strategy they used to learn each item from a list of possible strategies (Dunlosky and Hertzog, 2001; Paivio and Yuille, 1969; Paivio et al., 1966; Richardson, 1978, 1998), indicate overall which strategies they used from a list of possible strategies (Camp et al., 1983; Zivian and Darjes, 1983), and rate how often they used specific strategies with multiple-item rating scales (McDaniel and Kearney, 1984; Paivio and Yuille, 1969; Shaughnessy, 1981). Several types of encoding strategies have been reported, including strategies based on verbal elaboration, visual imagery, and rote repetition (Boltwood and Blick, 1970; Paivio and Yuille, 1969; Roberts, 1968; Yarmey and Csapo, 1968). There is a great deal of variability in the types of encoding strategies that different individuals report using (Boltwood and Blick, 1970; McDaniel and Kearney, 1984). Individuals who report using complex, elaborative encoding strategies have been shown to have better memory for verbal stimuli than individuals who report using relatively simple encoding strategies (Camp et al., 1983; Geiselman et al., 1982; Martin et al., 1965; Shaughnessy, 1981). In addition, Richardson (1978) found a significant correlation between self-reported use of a visual imagery strategy during encoding and individuals' memory for verbal paired associations.

While the majority of functional neuroimaging studies of episodic memory have only examined group activity patterns, significant between-participant variability in activity patterns has been reported (Heun et al., 2000; Machielsen et al., 2000; Miller et al., 2002). Regional activity during encoding (Alkire et al., 1998; Cahill et al., 1996; Canli et al., 1999; Casasanto et al., 2002) and retrieval (Nyberg et al., 1996; Tulving et al., 1999) has been shown to correlate with participants' memory performance. Between-participant variability in functional activation patterns may arise, in part, from differences in encoding and retrieval strategies (Casasanto et al., 2002; Heun et al., 2000; Miller et al., 2002; Savage et al., 2001). Consistent with this possibility, an event-related brain potential (ERP) study found differences in a frontal-positive slow wave component of the ERP between individuals who reported using simple rote strategies versus those who reported using more elaborative strategies during intentional encoding (Karis et al., 1984).

Motivated by these prior studies, the present study characterized individual differences in memory encoding strategies, examined their effect on memory

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Figure 1. Examples of the Interacting Object Pair Images Studied during Intentional Encoding

Participants were instructed to carefully study each image in anticipation of an unspecified memory test. No other instructions were provided, allowing individuals to adopt their own encoding strategies.

performance, and explored their functional-anatomic correlates. Participants intentionally encoded images of interacting object pairs (Figure 1) during functional magnetic resonance imaging (fMRI). This task allowed participants maximal flexibility in adopting encoding strategies, including strategies based on verbal elaboration and visual-perceptual analysis. Following the scan session, a memory retrieval test was given that assessed whether participants remembered the object associations. In a final phase, participants completed a questionnaire that assessed their use of encoding strategies. This procedure allowed exploration of the relationship between individual differences in reported strategy use and individual differences in memory performance and regional brain activity during intentional encoding.

Results

Overview

Analyses were conducted in five major steps. First, participants' responses on the strategy questionnaire were examined using principal components analysis to identify the main types of strategies that participants used to encode the object pairs. Second, the resulting strategy component scores were correlated with the proportion of object associations that each participant remem-

bered to determine which strategies, if any, were associated with variation in memory performance. Individuals' use of two of these strategies was correlated with their memory performance. Third, the functional-anatomic correlates of these two strategies were explored in the imaging data using hypothesis-driven regions of interest. Fourth, the functional-anatomic correlates of these strategies were further investigated with whole-brain exploratory analyses to identify additional regions that were associated with use of these strategies. Finally, the activity patterns of regions associated with use of these effective encoding strategies were analyzed to determine whether they also predicted individual differences in memory performance.

Strategy Use Correlates with Memory Performance

The central goal of this study was to examine individual differences in strategy use during intentional encoding. Participants answered a strategy questionnaire after intentional encoding of object pairs. Mean ratings for the ten questions are presented in Table 1. Participants reported using strategies involving studying the physical appearance and arrangements of the objects and mental imagery the most, and strategies involving coding the beginning letter of the object names and constructing sentences the least. In order to formally identify the main strategies that participants used to encode the object pairs, a principal components analysis with Varimax rotation was performed on the strategy use ratings. Four components with eigenvalues greater than 1 were identified that together accounted for 66% of variance (Table 1). Because each of these components was associated with a plausible, intuitive strategy, they were labeled with these strategies. Although useful as heuristics, these labels are tentative descriptions.

The first component, associated with *verbal elaboration*, accounted for 28% of variance in strategy use ratings before rotation. It had high loadings on the "used the starting letter of the names of the objects" (question 6) and "constructed sentences that described what you physically saw in the pictures" (question 7) strategies. The second component, associated with *mental imagery*, accounted for an additional 14% of variance in strategy use ratings. It had a high positive

Table 1. Mean Use Ratings and Rotated Component Loadings for the Questions on the Strategy Questionnaire

Questions	Rating	Components			
		Verbal Elaboration	Mental Imagery	Visual Inspection	Memory Retrieval
1. Studied the colors and/or the orientations of the objects	3.7	0.22	0.11	<u>0.70</u>	0.12
2. Studied how the objects were physically arranged in relationship to each other	4.1	-0.05	-0.08	<u>0.79</u>	0.01
3. Used the living/nonliving status of the objects	2.4	-0.08	-0.15	0.08	<u>0.87</u>
4. Used prior personal memories associated with the objects	2.4	0.34	0.23	0.08	<u>0.75</u>
5. Said the names of each object to yourself	3.2	0.37	-0.67	-0.20	-0.22
6. Used the starting letter of the names of the objects	1.5	<u>0.85</u>	0.02	0.00	0.03
7. Constructed sentences that described what you physically saw in the pictures	2.0	<u>0.79</u>	0.09	0.29	0.19
8. Constructed weird/silly sentences	2.2	0.28	0.45	0.31	-0.07
9. Constructed stories that explained what was occurring in the picture	2.1	0.20	0.39	0.51	0.37
10. Used mental imagery	3.8	0.15	<u>0.86</u>	-0.16	-0.07
Explained Variance (%)		18	16	16	16

Rating values indicate mean ratings of how often participants used a strategy (1 = never, 5 = always). Component values indicate component loadings. High positive component loadings are underlined. Explained variance is for the rotated solution.

loading on the “used mental imagery” (question 10) strategy. This component also had a high negative loading on the “said the names of each object to yourself” (question 5) strategy, which represents an object-naming strategy. The opposite signs of the strategies related to this component suggest that participants who used a mental imagery strategy were unlikely to use an object-naming strategy, and vice versa. The third component, associated with *visual inspection*, accounted for another 13% of variance in strategy use ratings. It had high positive loadings on the “studied the colors and/or the orientations of the objects” (question 1) and “studied how the objects were physically arranged in relationship to each other” (question 2) strategies. The fourth component, associated with *memory retrieval*, accounted for an additional 11% of variance in strategy use ratings. It had high positive loadings on the “used the living/nonliving status of the objects” (question 3) and “used prior personal memories associated with the objects” (question 4) strategies. This component appears to correspond to use of a memory retrieval strategy that relies on both semantic, meaning-based memory (e.g., attributes that would allow one to categorize the object as living) and episodic memory (i.e., prior personal memories).

Having identified four main types of encoding strategies, we next asked whether variation in use of these strategies predicted individuals’ memory performance. Associative memory performance was tested outside of the scanner by having participants draw lines between objects that they thought were paired together during the scan session and indicate their confidence in their pairings by making “definitely paired,” “probably paired,” or “guess paired” confidence judgments (see the [Experimental Procedures](#) section for method details). Overall, participants were able to correctly pair 45% (standard error of the mean [SEM] = 4%) of the studied object associations on the associative retrieval test (range 9%–97%). They made an average of 36 (SEM = 4) correct “definitely paired” responses, 10 (SEM = 1) correct “probably paired” responses, and 8 (SEM = 1) correct “guess paired” responses on the associative memory test out of a total of 120 object pairs. Participants were correct 82% of the time (SEM = 4%) when they made “definitely paired” responses, 38% of the time (SEM = 5%) when they made “probably paired” responses, and 20% of the time (SEM = 2%) when they made “guess paired” responses. The relationship between participants’ component scores for the four strategies and the proportion of object associations that they remembered (correct “definitely paired” and “probably paired” trials) was examined using bivariate correlation analyses. Participants’ verbal elaboration ($r = 0.45$, $p < 0.05$) and visual inspection ($r = 0.44$, $p < 0.05$) strategy scores were significantly correlated with their ability to retrieve object associations successfully (Figure 2). In contrast, participants’ mental imagery ($r = -0.20$, $p > 0.1$) and memory retrieval ($r = -0.05$, $p > 0.1$) strategy scores were not significantly correlated with their ability to retrieve object associations successfully.

These analyses of the self-reported strategy data identified four main types of strategies that are used variably by participants during memory encoding. Greater use of verbal elaboration and visual inspection

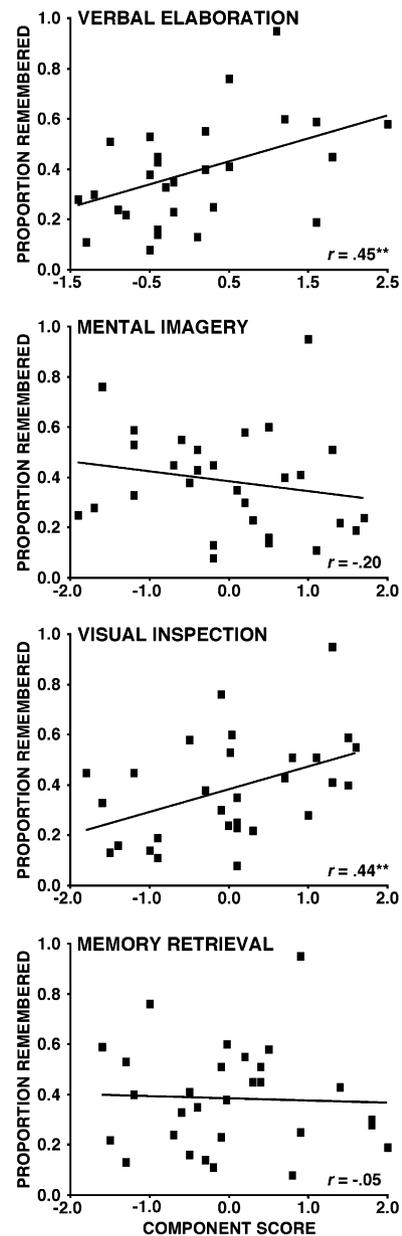


Figure 2. Individuals’ Use of Verbal Elaboration and Visual Inspection Encoding Strategies Was Correlated with the Proportion of Object Associations that They Remembered

Participants’ verbal elaboration and visual inspection strategy scores were positively correlated with their memory performance. Participants’ visual imagery and memory retrieval strategy scores were not significantly correlated with their memory performance (** $p < 0.05$).

strategies was associated with better memory performance.

Use of Multiple Encoding Strategies Enhances Memory Performance

All participants reported using multiple encoding strategies at least “sometimes” on the strategy questionnaire (range from 3 to 9, mean 6). In addition, participants who reported using the most encoding strategies remembered the most object associations ($r = 0.40$, $p < 0.05$).

Motivated by these observations, the effects of using multiple encoding strategies were explored further.

Following orthogonalization of the strategy components during the principal components analysis, a participant's component score for one strategy was not correlated with his/her component score for another strategy. Multiple regression analysis revealed that together, use of the verbal elaboration and visual inspection strategies accounted for 40% of variance in participants' memory performance. There was not a significant interaction between the effects of these strategies on variance in memory performance. Therefore, the verbal elaboration and visual inspection strategies had independent, additive effects on memory performance.

Use of Verbal and Visual Encoding Strategies Correlates with Activity in Distinct Brain Regions Associated with Verbal and Visual Processing

Hypothesis-driven analyses were performed to determine if use of the verbal elaboration and visual inspection strategies was correlated with regional brain activity, and if so, whether regional differences existed. For this analysis, a priori regions of interest were selected from prior verbal and visual processing studies conducted in our laboratory. As noted in the **Experimental Procedures** section, these regions were defined independently of the present data.

Participants' use of the verbal elaboration strategy during intentional encoding was predicted to correlate with their activity in prefrontal regions previously associated with verbal elaboration. Specifically, left prefrontal regions along the inferior prefrontal gyrus, including those near Brodmann's area (BA) 45/47 and BA 6/44, have been repeatedly associated with controlled verbal processing, including semantic elaboration and phonological processing (Demb et al., 1995; Gold and Buckner, 2002; McDermott et al., 2003; Petersen et al., 1988; Wagner et al., 2001). Moreover, the activity patterns of the specific prefrontal regions selected for examination here (based on Konishi et al., 2001) have previously been found to be associated with effective memorization (Logan et al., 2002). Based on these prior observations, activity during intentional encoding in these prefrontal regions was predicted to correlate with reported use of the verbal elaboration strategy but not with reported use of the visual inspection strategy. Consistent with this prediction, verbal elaboration strategy scores were positively correlated with activity during intentional encoding in left BA 45/47 ($r = 0.37$, $p < 0.05$) and showed a trend for a positive correlation in left BA 6/44 ($r = 0.33$, $p < 0.1$; Figure 3). In contrast, visual inspection strategy scores were not significantly correlated with activity during intentional encoding in these regions (BA 45/47: $r = 0.06$, $p > 0.1$; BA 6/44: $r = 0.14$, $p > 0.1$). Multiple regression analyses demonstrated that use of the visual inspection strategy did not make a significant unique contribution to the explanation of variance in percent signal change in these regions. There were also no significant interactions between the type of strategy used and brain activity in these regions (all p values > 0.1).

Left extrastriate regions BA 19/37 and BA 20 have been associated with object-level perceptual and image retrieval processes (Denys et al., 2004; Grill-Spector et al., 2000; Ishai et al., 2000; Malach et al., 1995;

Wheeler and Buckner, 2003; Wheeler et al., 2000). Left BA 19/37 is located at the junction of the occipital and temporal lobes, in the vicinity of the anterior occipital sulcus. Left BA 20 is in anterior fusiform cortex. Activity in these regions during intentional encoding was predicted to correlate with reported use of the visual inspection strategy, but not with reported use of the verbal elaboration strategy. Consistent with this prediction, activity in left BA 19/37 was positively correlated with visual inspection strategy scores ($r = 0.38$, $p < 0.05$) but not with verbal elaboration strategy scores ($r = 0.01$, $p > 0.1$; Figure 3). Activity in left BA 20 was not significantly correlated with either visual inspection ($r = 0.08$, $p > 0.1$) or verbal elaboration ($r = 0.08$, $p > 0.1$) strategy scores. Multiple regression analyses demonstrated that use of the verbal elaboration strategy did not make a significant unique contribution to the explanation of variance in percent signal change in left BA 19/37, and there also was not a significant strategy use interaction (all p values > 0.1).

Taken together, the results of these hypothesis-driven regional analyses demonstrate that use of the verbal elaboration encoding strategy was selectively correlated with activity in prefrontal regions associated with controlled verbal processing, while use of the visual inspection encoding strategy was selectively correlated with activity in an extrastriate region associated with object processing.

Whole-Brain Exploration

The above analyses provide a powerful, unbiased exploration of the correlation between regional brain activity and individuals' reported strategy use. To complement these targeted analyses, whole-brain exploratory analyses were also performed to examine whether activity in additional brain regions was correlated with use of the verbal elaboration and/or visual inspection strategies, and to further explore whether use of these strategies was associated with distinct functional-anatomic networks.

Consistent with the findings of the hypothesis-driven regional analyses above, the exploratory analyses demonstrated significant correlations between activity in left inferior prefrontal cortex (BA 45: $r = 0.53$, BA 44: $r = 0.67$) and verbal elaboration strategy scores, but not visual inspection strategy scores (BA 45: $r = -0.09$, $p > 0.1$; BA 44: $r = 0.09$, $p > 0.1$) (Figure 4 and Table 2). Multiple regression analyses demonstrated that use of the visual inspection strategy did not make a significant unique contribution to the explanation of variance in percent signal change in these regions. There were also no significant interactions between the type of strategy used and brain activity in these regions (all p values > 0.1). Also consistent with the hypothesis-driven regional analyses, activity during intentional encoding in left extrastriate cortex was significantly correlated with use of the visual inspection strategy (BA 19/37, $r = 0.67$) but not with use of the verbal elaboration strategy ($r = 0.01$, $p > 0.1$). A multiple regression analysis demonstrated that use of the verbal elaboration strategy did not make a significant unique contribution to the explanation of variance in percent signal change in this region, and also, there was not a significant strategy use interaction (all p values > 0.1). These correlation values

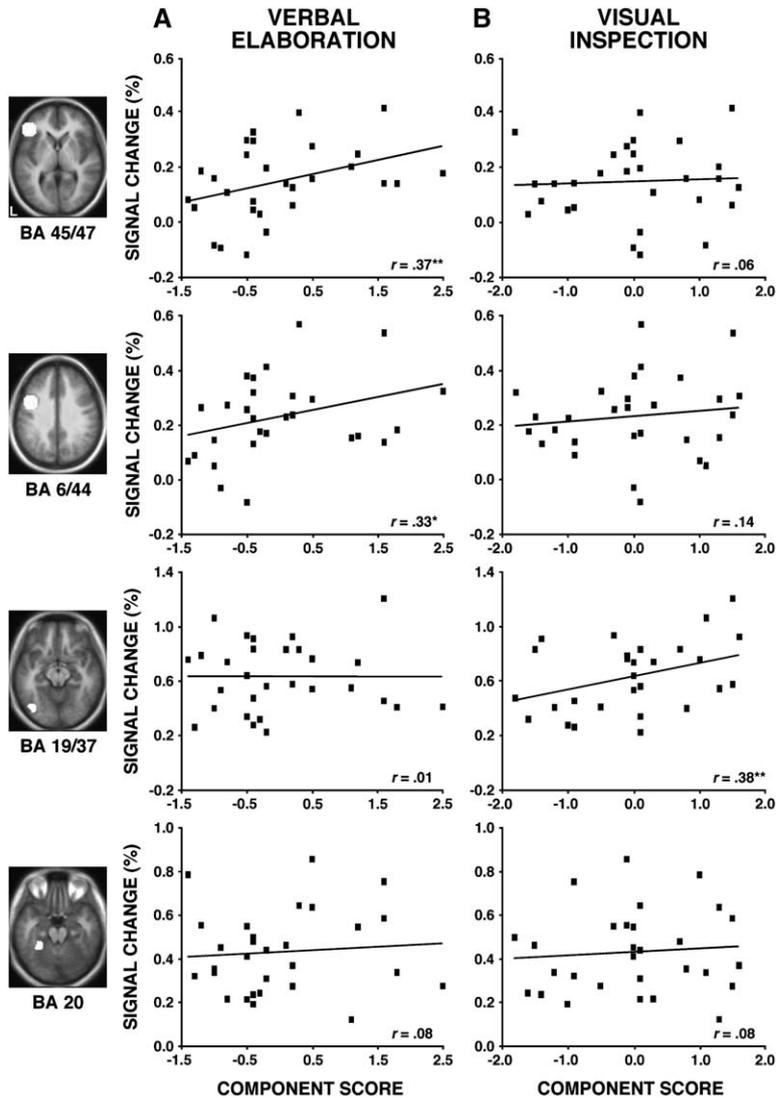


Figure 3. Hypothesis-Driven Regional Analyses Demonstrated that Use of Verbal Elaboration and Visual Inspection Encoding Strategies Was Correlated with Brain Activity in Distinct Regions Associated with Verbal and Visual Processing

(A) Participants' verbal elaboration strategy scores were selectively correlated with their brain activity during intentional encoding in left inferior prefrontal regions (at or near BA 45/47 and BA 6/44) associated with controlled verbal processing.

(B) In contrast, participants' visual inspection strategy scores were selectively correlated with their brain activity during intentional encoding in a left extrastriate region (at or near BA 19/37) associated with object processing. Brodmann's area labels should be considered approximate and are referenced to the Talairach and Tournoux (1988) atlas (* $p < 0.1$, ** $p < 0.05$).

reflect those determined within regions selected based on the present data and are thus maximized. Such a procedure is common in the literature, and the convergence between the hypothesis-driven analyses and the voxel-based, whole-brain exploration bolsters confidence in the findings.

Additional regions were identified in the whole-brain exploratory analyses that provide candidates for future study (Table 2). We describe these for thoroughness, but report them with less confidence because they were not identified based on a priori hypotheses. Significant correlations between verbal elaboration strategy scores and activity in right anterior prefrontal cortex (BA 9/10), a region at or near the supplementary motor area (BA 6), left middle temporal cortex (BA 21), right extrastriate cortex (BA 18), and the right cerebellum were found. There were also significant correlations between visual inspection strategy scores and activity in a left extrastriate region (BA 18) distinct from that tested in the a priori hypotheses, as well as activity in right anterior prefrontal cortex (BA 9/10), right inferior prefrontal cortex (BA 44), left middle occipital cortex (BA 19), and parietal cortex (BA 7/19) bilaterally.

Taken together, these whole-brain exploratory analyses are consistent with the results of the hypothesis-driven analyses above that revealed distinct functional-anatomic correlates of verbal elaboration and visual inspection strategies in left inferior prefrontal and extrastriate cortex. These analyses also provide multiple targets for further study.

Activity in Regions Associated with Effective Encoding Strategies Correlates with Memory Performance

The above analyses demonstrate that individuals' use of verbal elaboration and visual inspection strategies correlates with their memory performance and regional brain activity during intentional encoding. These analyses imply, but do not demonstrate, that regional activity associated with encoding strategy use is also related to memory performance. To directly explore this possibility, we conducted post hoc analyses to determine whether activity in regions associated with use of effective encoding strategies is also correlated with subsequent memory performance. This relationship was tested in two ways using (1) hypothesis-driven regions

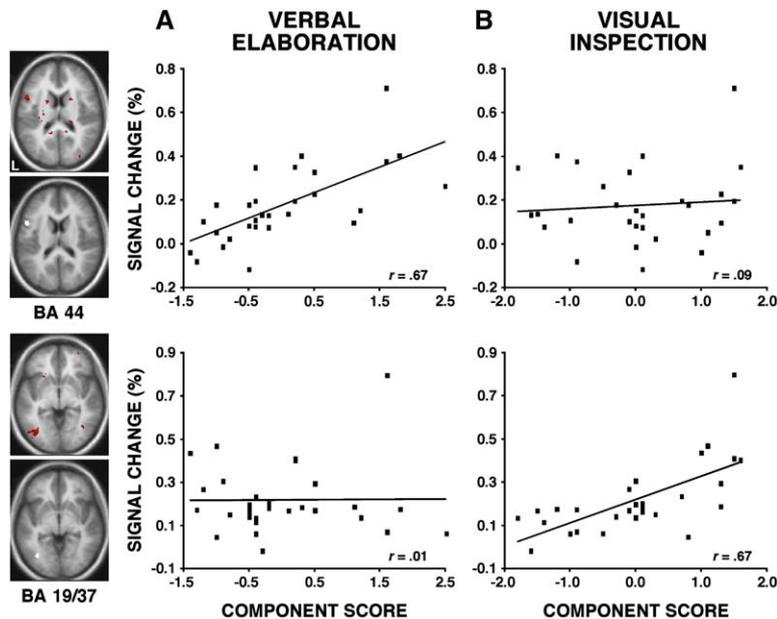


Figure 4. Exploratory Analyses of the Functional-Anatomic Correlates of Verbal Elaboration and Visual Inspection Encoding Strategies

Consistent with the findings of the hypothesis-driven regional analyses, (A) participants' verbal elaboration strategy scores were selectively correlated with their brain activity during intentional encoding in left inferior prefrontal cortex (at or near BA 44), and (B) participants' visual inspection strategy scores were selectively correlated with their brain activity during intentional encoding in left extrastriate cortex (at or near BA 19/37). The upper images for each region show voxels with positive correlations ($p < 0.01$, uncorrected) between activity during intentional encoding and verbal elaboration strategy scores (left BA 44) or visual inspection strategy scores (left BA 19/37). The lower images show the regions that were used to examine the relationship between activity during intentional encoding and strategy use in regional analyses.

and (2) regions generated from the exploratory analyses above. The exploratory regions have a benefit of increased power because of their definition within the present dataset.

Of the three hypothesis-driven regions associated with use of effective encoding strategies, left BA 45/47 showed a significant correlation between activity during intentional encoding and memory performance across participants ($r = 0.43$, $p < 0.05$; Figure 5). The correlation between activity during intentional encoding and memory performance failed to reach significance in the other hypothesis-driven regions. However, there were significant correlations between participants' activity during intentional encoding and their subsequent memory per-

formance within multiple regions identified from the exploratory analyses (Table 2), including regions in left inferior prefrontal (BA 44: $R = 0.40$, $p < 0.05$) and left middle occipital ($r = 0.41$, $p < 0.05$) cortex (Figure 6). Overall, these results demonstrate that activity associated with individuals' use of effective encoding strategies is also associated with their subsequent memory performance in many brain regions.

Discussion

Individuals differ in their memory abilities. While it is almost certain that a complex constellation of factors contributes to individual differences in memory

Table 2. Correlations between Regional Brain Activity during Intentional Encoding, Strategy Use, and Memory Performance

Region	BA	Talairach Coordinates			r_{VE}	r_{VI}	r_M
		x	y	z			
Verbal elaboration ^a							
Left inferior prefrontal	45	-51	28	5	0.53	-0.09	0.34*
Left inferior prefrontal	44	-51	8	17	0.67	0.09	0.40**
Right anterior prefrontal	9/10	5	53	15	-0.65	-0.08	-0.48***
Supplementary motor area	6	-6	-1	55	0.69	-0.04	0.37**
Left middle temporal	21	-47	-43	-2	0.60	-0.16	0.18
Right extrastriate	18	13	-92	-10	0.70	-0.03	0.35*
Right cerebellum		16	-82	-21	0.66	0.30	0.45**
Visual inspection ^b							
Left extrastriate	19/37	-34	-70	-4	0.01	0.67	0.21
Right inferior prefrontal	44	48	10	15	0.05	0.62	0.34*
Right anterior prefrontal	9/10	15	59	28	-0.01	0.61	0.31*
Left middle occipital	19	-48	-68	19	0.28	0.62	0.41**
Left extrastriate	18	-28	-89	1	0.06	0.57	0.23
Left parietal	7/19	-20	-71	46	0.03	0.58	0.23
Right parietal	7/19	35	-76	43	-0.09	0.65	0.15

BA: Brodmann's Area. r_{VE} : zero-order correlation between regional activity and verbal elaboration strategy scores. r_{VI} : zero-order correlation between regional activity and visual inspection strategy scores. r_M : zero-order correlation between regional activity and subsequent memory performance. * $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$.

^aVerbal elaboration regions were defined from a whole-brain, voxel-based analysis (threshold $p < 0.01$, uncorrected) of zero-order correlations between brain activity and verbal elaboration strategy scores.

^bVisual inspection regions were defined from a whole-brain, voxel-based analysis (threshold $p < 0.01$, uncorrected) of zero-order correlations between brain activity and visual inspection strategy scores.

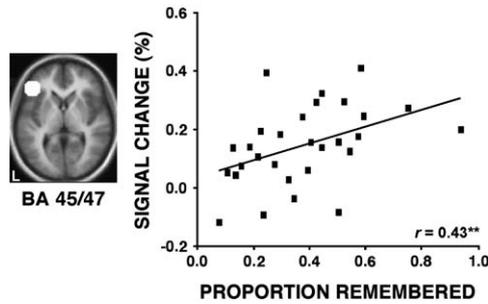


Figure 5. Individuals' Regional Brain Activity during Intentional Encoding Was Correlated with Their Subsequent Memory Performance

Participants' brain activity during intentional encoding in the left BA 45/47 a priori region of interest associated with use of the verbal elaboration strategy was significantly correlated with their subsequent memory performance (** $p < 0.05$).

performance and regional brain activity during memory formation, the present study provides evidence that a significant contributing factor is the nature of the encoding strategies that individuals adopt. Specifically, our analyses identified four distinct strategies that were variably adopted by participants during intentional encoding. Two strategies—verbal elaboration and visual inspection—showed evidence of separate contributions to memory performance and were associated with brain activity in distinct prefrontal and extrastriate regions during intentional encoding. Activity in regions associated with use of these effective encoding strategies was also correlated with individuals' memory performance. The implications of these results are discussed below.

Individual Differences in Use of Encoding Strategies

A main finding of the present study is that individuals differ in their use of strategies during unconstrained intentional encoding even under experimental conditions in which task instructions and studied items are held constant. Consistent with the results of prior behavioral studies (Boltwood and Blick, 1970; McDaniel and Kearney, 1984), there was considerable variation in strategy use across individuals as measured by the self-report questionnaire. Principal components analysis revealed that participants used four main strategies to encode the object pairs. Although the principal components analysis in the present study was conducted using a relatively small sample, the strategy components identified consisted of plausible, intuitive strategies: verbal elaboration, mental imagery, visual inspection, and memory retrieval. The vast majority of previous studies of strategy use during unconstrained intentional encoding have used verbal stimuli instead of pictorial stimuli (for an exception see Hasher et al., 1976). In these prior studies, first letter, sentence generation, visual imagery, and personal experience strategies similar to strategies that loaded highly onto the strategy components in the present study have been reported (e.g., Boltwood and Blick, 1970; Dunlosky and Hertzog, 2001), suggesting that people may use some of the same types of strategies to encode verbal and visuospatial stimuli.

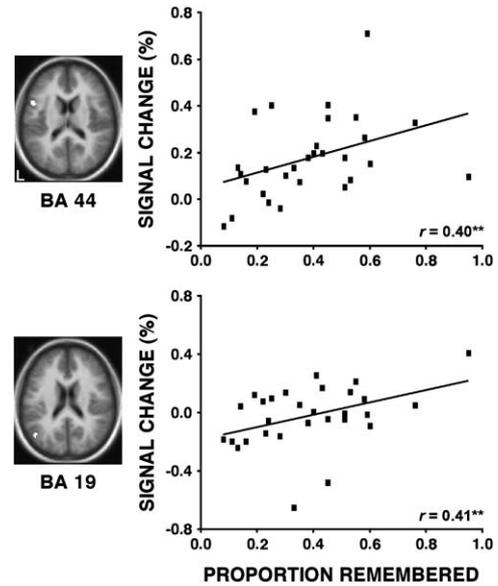


Figure 6. Individuals' Brain Activity during Intentional Encoding Was also Correlated with Their Subsequent Memory Performance in Regions Associated with Use of Effective Encoding Strategies Identified from Whole-Brain Exploratory Analyses

Participants' brain activity during intentional encoding was significantly correlated with their subsequent memory performance in a left inferior prefrontal region (at or near BA 44) associated with use of the verbal elaboration strategy and a left middle occipital region (at or near BA 19) associated with use of the visual inspection strategy. These regions were identified from whole-brain exploratory analyses of the neural correlates of these strategies (** $p < 0.05$).

Individual Differences in Strategy Use Are Associated with Memory Performance

Participants' use of two strategies—verbal elaboration and visual inspection—was correlated with their ability to successfully retrieve object associations in the present study. This suggests that individual variation in self-initiated strategy use is a significant contributor to individual variation in episodic memory abilities.

Participants' use of the mental imagery and memory retrieval strategies was not correlated with their memory performance in the present study. While mental imagery was not an effective encoding strategy in this study, Richardson (1978) found a significant correlation between individuals' reported use of a visual imagery strategy during intentional encoding and their memory for verbal paired associations. A possible explanation for the lack of a significant correlation between use of the mental imagery and memory retrieval strategies in this study and subsequent memory performance is that different stimulus materials and/or experimental procedures may encourage or discourage the use of certain strategies. For example, visual inspection may be a more effective encoding strategy than mental imagery for learning object associations because self-generated visual images may interfere with individuals' ability to process the visual properties of the objects. Also, the use of the living/non-living judgments during single object familiarization may have reduced the effectiveness of this strategy, which loaded highly onto the memory retrieval strategy component, for later use in the formation of associations between objects. Thus, our results suggest that verbal

elaboration and visual inspection are two strategies that can enhance associative memory, but should not be interpreted to imply that these are the only important strategy variants.

The results of the present study also demonstrated that individual participants use multiple strategies during intentional encoding (see also [McDaniel and Kearney, 1984](#); [Roberts, 1968](#)). Participants who reported using the most strategies on the strategy questionnaire remembered the most object associations (see also [Zivian and Darjes, 1983](#)). Furthermore, analysis of the effects of use of the verbal elaboration and visual inspection strategies did not reveal an interaction. These results suggest that use of multiple encoding strategies can augment memory performance, and that different encoding strategies can make independent, additive contributions to memory performance.

Use of Verbal Elaboration and Visual Inspection Strategies Is Associated with Activity in Distinct Brain Regions

The results of our hypothesis-driven and exploratory analyses demonstrated that activity during intentional encoding in left prefrontal cortex along the inferior prefrontal gyrus (at or near BA 45/47 and BA 6/44) was selectively correlated with use of the verbal elaboration strategy. These regions have consistently been implicated in successful memory encoding ([Buckner et al., 1999](#); [Fletcher and Henson, 2001](#); [Tulving et al., 1994](#)), presumably through their contributions to controlled verbal processing ([Demb et al., 1995](#); [Gold and Buckner, 2002](#); [McDermott et al., 2003](#); [Petersen et al., 1988](#); [Wagner et al., 2001](#)). In contrast, activity during intentional encoding in left occipital-temporal cortex (at or near BA 19/37) was selectively correlated with use of the visual inspection strategy, consistent with this strategy's reliance on the perception of visual object information ([Denys et al., 2004](#); [Grill-Spector et al., 2000](#); [Malach et al., 1995](#)). Several other regions also demonstrated significant zero-order correlations between strategy use and regional activity for only the verbal elaboration or the visual inspection strategy. Importantly, the results of our analyses of the neural correlates of the verbal elaboration and visual inspection strategies demonstrated that individual differences in use of these strategies can explain a significant amount of variation in functional activity across individuals within multiple brain regions.

Activity in Regions Associated with Effective Encoding Strategies Predicts Individual Differences in Memory Performance

Analyses of activity during intentional encoding in our hypothesis-driven and exploratory regions of interest demonstrated that the activity patterns of multiple brain regions associated with use of effective encoding strategies also predicted individual differences in memory performance. For example, activity in one of the a priori regions of interest in left inferior prefrontal cortex (BA 45/47) associated with use of the verbal elaboration strategy was significantly correlated with individuals' memory performance. Notably, this region has historically been associated with memory performance both within individuals (e.g., [Wagner et al., 1998](#); also see

[Figure S1 in the Supplemental Data](#)) and across experimental conditions (see [Fletcher and Henson, 2001](#); [Buckner et al., 1999](#) for reviews). The present results add to this literature by demonstrating that individual variation in activity in this region is associated with individual variation in use of a verbal encoding strategy and memory performance (see also [Alkire et al., 1998](#); [Canli et al., 1999](#); [Casasanto et al., 2002](#)). Our exploratory analyses revealed that activity in another left inferior prefrontal region (BA 44) associated with use of the verbal elaboration strategy was also correlated with individuals' subsequent memory performance. Interestingly, our exploratory analyses demonstrated that activity in a left middle occipital region (BA 19) associated with use of the visual inspection strategy was correlated with individuals' subsequent memory performance. Greater activity in the vicinity of left middle occipital cortex has been reported during viewing of intact versus scrambled objects ([Denys et al., 2004](#); [Grill-Spector et al., 2000](#)), which suggests that the left middle occipital region associated with individuals' use of the visual inspection strategy and their memory performance in the present study may play an active role in processing visual object information. Overall, our results suggest that individual differences in strategy use may be a significant contributor to individual differences in regional brain activity during intentional encoding that are associated with subsequent memory performance.

Implications for the Investigation of Individual Differences in Self-Initiated Strategy Use

The present study and several prior behavioral studies of unconstrained encoding strategy use have relied on retrospective self-reports. There are many potential reasons to be skeptical of self-report approaches (for review see [Richardson, 1998](#)). Potential problems include the difficulty in independently assessing self-report accuracy and validity and the delay between use of the strategies and participants' self-reports. For example, participants may forget which strategies they used, or may not even have awareness of important component processes. Biased reports could result from attempts to rationalize memory performance or to comply with the perceived aims of the experimenter.

Despite these concerns, the present study provides strong support for the validity of retrospective self-reports of encoding strategy use. First, individuals' reported use of the verbal elaboration and visual inspection encoding strategies was significantly correlated with their ability to retrieve object pair associations. Second, and perhaps of greater importance, participants' activity during intentional encoding in prefrontal regions hypothesized to play an important role in controlled verbal elaboration was selectively correlated with their reported use of the verbal elaboration strategy. In addition, participants' activity during intentional encoding in a ventral visual region hypothesized to play an important role in the perception and retrieval of object information was selectively correlated with their reported use of the visual inspection strategy. Thus, while aspects of strategy use may not have been tapped by the present methods, or even accessible for report by the participants, self-reported use of strategies did capture significant variation in memory performance and regional

brain activity. Retrospective self-reports of strategy use are a useful method for examining individual differences in self-initiated strategy use.

Experimental Procedures

Participants

Thirty-one right-handed, healthy young adults participated for payment. All had normal or corrected-to-normal vision and reported no significant neurological history. Data from 29 participants were included in behavioral and fMRI analyses (age range 18–31, mean age 22.3 yrs, 17 F). Data from two participants were excluded due to scanner malfunction or excessive movement. fMRI signal from only two out of three functional scans could be analyzed for another participant due to excessive movement during the final functional scan. Informed consent was provided in accordance with Washington University's Human Studies Committee guidelines.

Stimuli

Two hundred and forty color clip-art images of single objects were used as stimuli for the single object familiarization sequences and the post-scan associative memory test. Half depicted living things, and half depicted inanimate objects. The single objects were combined to construct 120 images of two interacting objects for use during the intentional encoding fMRI session (Figure 1). Unrelated objects were used to construct each image. Forty images depicted two living things, forty images depicted two nonliving things, and forty pictures depicted one living thing and one nonliving thing. Memory for the interacting images was tested during stimulus development. Object pairings that were almost always remembered or almost always forgotten were discarded to control for differences in the inherent memorability of the object pairings.

Single Object Familiarization

During a single object familiarization session immediately prior to the scan session, participants made living/nonliving judgments for images of single objects. Each object was shown centrally for 1500 ms and was followed by a fixation plus sign presented for 325 ms. Participants indicated their responses by making right-handed key presses on a PsyScope (Carnegie Mellon University, Pittsburgh, PA) button box. After making the living/nonliving decision for all 240 objects, participants made the same decision a second time for all objects (one participant was accidentally shown the objects an extra time prior to scanning). During the acquisition of the MP-RAGE anatomical sequence (see below), participants made living/nonliving judgments for all 240 objects one more time. The objects were shown in a different order during each familiarization sequence. Participants made the correct living/nonliving judgment on 98% of trials and took an average of 587 ms to indicate their responses. We familiarized participants with the individual objects that were later used in the object pairs prior to intentional encoding because we were primarily interested in investigating the neural correlates of the formation of memories for associations between objects instead of the formation of memories for individual objects in this study.

Intentional Encoding

Approximately 45 min after the single object familiarization sequence that occurred during the MP-RAGE anatomical scan (an unrelated language study with verbal stimuli was scanned during this time), participants intentionally encoded object pairs. During each of three functional scans, three blocks of fixation plus signs (23.6 s each) alternated with two blocks of interacting object-pair stimuli (94.4 s each). An additional 9.44 s of the fixation condition was acquired at the beginning of each scan to allow T1 magnetization to stabilize; data from these fixation trials were not analyzed. Twenty images of interacting object pairs were shown per stimulus block. Each object pair was shown for 4000 ms and was followed by a fixation plus sign presented for 720 ms. Participants were told to study each image carefully in anticipation of a later, unspecified memory test. Because this experiment used unconstrained intentional encoding instructions, brief interstimulus fixation plus signs of constant duration were used within blocks to encourage participants to

study each object pair for the same amount of time. Six different object-pair presentation orders were used across participants.

Post-Scan Associative Memory Test

After scanning (~10 min delay), participants' memory for the object associations was tested. Participants were given ten sheets of 11 × 17 inch paper. Two columns of 12 objects were on each sheet. One member of each pair was in the left column, and the other member of each pair was in the right column. Participants were instructed to draw lines between the objects that had been paired during scanning. They were instructed to draw a line from each object in the left column to an object in the right column so that each object had one line drawn to it. They indicated their confidence in their pairings by writing a letter next to each line. Participants put a D next to a line if they thought that the objects had definitely been paired during scanning, put a P next to a line if they thought that the objects had probably been paired, and put a G next to a line if they were just guessing that the objects had been paired. Two different randomized object orders were used across participants. Test sheets were constructed so that participants could not use object order, living/nonliving status, or size to determine which objects had been paired during scanning.

Strategy Questionnaire

After completing the associative memory test, participants completed a questionnaire on which they rated how often they had used each of ten possible strategies to study the images of object pairs: never, rarely, sometimes, usually, or always (Table 1). These ratings were then converted into numerical values using a five point scale (1 = never, 2 = rarely, 3 = sometimes, 4 = usually, 5 = always). The list of strategies was based on the literature and on participants' reports of strategy use during pilot testing.

fMRI Data Acquisition

Scanning was performed using a Siemens 1.5 Tesla Vision scanner (Erlangen, Germany). An Apple Power Macintosh G4 computer (Apple, Cupertino, CA) and PsyScope software (Cohen et al., 1993) controlled the stimulus display and recorded responses from a magnet-compatible, fiber-optic key press device interfaced with a PsyScope button box. An LCD projector displayed stimuli onto a screen at the head of the magnet bore. Participants viewed the stimuli using a mirror attached to the head coil. Foam pillows and a thermoplastic mask minimized head movement and headphones dampened scanner noise. High-resolution structural images (1 × 1 × 1.25 mm) were acquired using a sagittal T1-weighted MP-RAGE sequence (TR = 9.7 ms, TE = 4 ms, flip angle = 10°, TI = 20 ms, TD = 500 ms). Functional images were acquired using an asymmetric spin-echo echo-planar sequence sensitive to blood oxygen level-dependent (BOLD) contrast (T2*; TR = 2.36 s, TE = 37 ms). Three functional runs of 114 whole-brain (16 contiguous 8 mm axial slices oriented parallel to the AC-PC plane; 3.75 × 3.75 mm in-plane resolution) images were collected per participant. The first four images in each run were discarded to allow T1 magnetization to stabilize.

fMRI Data Analysis

fMRI data were preprocessed to remove noise and artifacts. Data were corrected for odd-even slice intensity differences and were motion-corrected using a rigid-body rotation and translation correction (Snyder, 1996). Slice timing differences were adjusted using sinc interpolation, and linear slope was removed on a voxel-by-voxel basis to correct for drift (Bandettini et al., 1993). Data were normalized to a mean magnitude value of 1000 and transformed into the stereotaxic atlas space of Talairach and Tournoux (1988) using 2 mm isotropic voxels (Maccotta et al., 2001). Functional data were analyzed using the general linear model implemented in an in-house analysis and display package (Miezin et al., 2000). Run mean and slope were coded as effects of no interest, and the data were smoothed using a two-voxel isotropic Hanning filter.

Principal Components Analysis

Principal components analysis was conducted to identify the major strategies used by participants to encode the object pairs. With this technique, we were able to determine whether more than one strategy question assessed use of the same type of underlying strategy.

If two strategy questions had high positive loadings on the same component, this would indicate that participants who reported using one of the strategies during intentional encoding tended to also report using the other strategy during intentional encoding. This pattern would suggest that these two strategy questions were likely to be assessing use of the same underlying strategy dimension. Also, if one strategy question had a high positive loading onto a component and another strategy question had a high negative loading onto a component, this would demonstrate that participants who tended to use the first strategy tended not to use the second strategy and vice versa.

Four components with eigenvalues greater than 1 were identified that accounted for a large amount of the variance in strategy use ratings (66%) in the principal components analysis. These components were rotated to simple structure with Varimax rotation. Component scores were calculated using a regression method implemented in SPSS 10 (SPSS Inc., Chicago, IL). Each of the four components identified were associated with a plausible, intuitive strategy, and they were therefore labeled with these strategies.

Analyses of the Relationship between Strategy Use and Memory Performance

Each participant's strategy component scores and the proportion of object associations that each participant correctly remembered (correct "definitely paired" and "probably paired" responses) were entered into Pearson Product Moment bivariate correlation analyses to test for associations between strategy use and memory performance. Two participants performed exceedingly well on the memory test (97% and 76% correct). Excluding these participants' associative memory scores from the correlation analyses had minimal effects on the results of these analyses, and therefore data from these participants were included in all of these analyses.

The relationship between the number of encoding strategies that participants used and their memory performance was examined by performing a bivariate correlation analysis to test for a significant correlation between the number of strategies that each participant reported using on the strategy questionnaire (ratings of "sometimes," "usually," or "always") and the proportion of object associations that each participant correctly remembered. A multiple regression analysis was also performed to investigate whether there was an interaction between the effects of using the verbal elaboration and visual inspection strategies on memory performance.

Hypothesis-Driven Analyses of the Relationship between Strategy Use and Regional Brain Activity

The relationship between individual variation in strategy use and individual variation in regional brain activity was examined by performing bivariate correlation analyses to test for significant correlations between participants' strategy component scores and magnitude estimates of their brain activity during intentional encoding in four a priori regions of interest. The magnitude estimates of activity during intentional encoding were referenced to the fixation condition and scaled to percent signal change. Two left inferior prefrontal regions of interest (BA 45/47: $-45, 29, 6$; BA 6/44: $-43, 3, 32$; coordinates reported reflect peak locations within the Talairach and Tournoux [1988] atlas) containing multiple voxels were identified from a meta-analysis of regions engaged during word and face encoding (Konishi et al., 2001). Two extrastriate regions of interest (left BA 19/37: $-36, -73, -12$; left BA 20: $-25, -37, -20$) containing multiple voxels were identified from a prior study in which these regions demonstrated greater activity in response to intact versus scrambled objects (L. Maccotta and R.L. Buckner, 2002, *J. Cogn. Neurosci.*, abstract). These regions have been used in previous studies from our laboratory (e.g., Logan et al., 2002; Wheeler and Buckner, 2004).

Hierarchical regression analyses were also performed to further examine the relationship between strategy use and activity during intentional encoding in these regions. The strategy that demonstrated a significant zero-order correlation between its use and activity within a region was entered in the first step in these analyses. In the second step, the other strategy was entered into the model to assess whether use of the second strategy explained a significant additional amount of variance in percent signal change in the region over and above the contribution of the first strategy. Finally, an inter-

action term (product of the component scores for the two strategies) was added to the model in the third step. This tested whether there was an interaction between the effects of use of the verbal elaboration and visual inspection strategies on brain activity.

Exploratory Analyses of the Relationship between Strategy Use and Regional Brain Activity

Whole-brain, exploratory analyses were conducted to test for correlations (Pearson Product Moment bivariate correlations) between brain activity during intentional encoding and verbal elaboration and visual inspection strategy scores in each voxel of the brain. Resulting *r* statistics were converted to *z* statistics and plotted over structural images created by averaging data from the 29 participants. The statistical significance criterion for these activation maps was set to $p < 0.01$, uncorrected for multiple comparisons. An automated algorithm identified activation peaks in these functional maps. Regions of interest were then grown that included all continuous voxels within 4 mm of an activation peak, masked by the appropriate functional activation map (threshold: $p < 0.01$, uncorrected). Bivariate correlation analyses were then performed within these regions of interest between magnitude estimates of individuals' brain activity during intentional encoding and their verbal elaboration and visual inspection strategy scores. Hierarchical multiple regression analyses were also performed to further examine the relationship between strategy use and activity during intentional encoding within these regions.

Analyses of the Relationship between Regional Brain Activity and Subsequent Memory Performance

Bivariate correlation analyses of activity during intentional encoding in the three a priori regions of interest (left BA 45/47, 6/44, and 19/37), whose activity was modulated by self-initiated use of effective encoding strategies (either the verbal elaboration strategy or the visual inspection strategy), were performed to determine whether individuals' activity in these regions was also correlated with their subsequent memory performance. The relationship between regional brain activity and subsequent memory performance was also examined using bivariate correlation analyses in the regions identified from the whole-brain exploratory analyses that demonstrated significant correlations between their activity during intentional encoding and use of the verbal elaboration or visual inspection strategies.

Supplemental Data

The Supplemental Data for this article can be found online at <http://www.neuron.org/cgi/content/full/51/2/263/DC1/>.

Acknowledgments

We thank Brian Gold, Kate O'Brien, and Tracy Wang for assistance with data collection and analysis. We also thank Neal Cohen, Martha Storandt, and David McCabe for helpful discussion and Avi Snyder and Mark McAvooy for development of MR analysis procedures. This research was supported by a W.M. Keck Fellowship (B.K.), the Howard Hughes Medical Institute, the James S. McDonnell Foundation Program in Cognitive Neuroscience, and the National Institute of Mental Health (MH57506).

Received: December 1, 2005

Revised: April 10, 2006

Accepted: June 1, 2006

Published: July 19, 2006

References

- Alkire, M.T., Haier, R.J., Fallon, J.H., and Cahill, L. (1998). Hippocampal, but not amygdala, activity at encoding correlates with long-term, free recall of nonemotional information. *Proc. Natl. Acad. Sci. USA* 95, 14506–14510.
- Bandettini, P.A., Jesmanowicz, A., Wong, E.C., and Hyde, J.S. (1993). Processing strategies for time-course data sets in functional MRI of the human brain. *Magn. Reson. Med.* 30, 161–173.
- Boltwood, C.E., and Blick, K.A. (1970). The delineation and application of three mnemonic techniques. *Psychon. Sci.* 20, 339–341.

- Bors, D.A., and MacLeod, C.M. (1996). Individual differences in memory. In *Memory: Handbook of Perception and Cognition*, E.L. Bjork and R.A. Bjork, eds. (San Diego: Academic Press, Inc.), pp. 411–441.
- Buckner, R.L., Kelley, W.M., and Petersen, S.E. (1999). Frontal cortex contributes to human memory formation. *Nat. Neurosci.* 2, 311–314.
- Cahill, L., Haier, R.J., Fallon, J., Alkire, M.T., Tang, C., Keator, D., Wu, J., and McGaugh, J.L. (1996). Amygdala activity at encoding correlated with long-term, free recall of emotional information. *Proc. Natl. Acad. Sci. USA* 93, 8016–8021.
- Camp, C.J., Markley, R.P., and Kramer, J.J. (1983). Naive mnemonics: what the “do-nothing” control group does. *Am. J. Psychol.* 96, 503–511.
- Canli, T., Zhao, Z., Desmond, J.E., Glover, G., and Gabrieli, J.D.E. (1999). fMRI identifies a network of structures correlated with retention of positive and negative emotional memory. *Psychobiology* 27, 441–452.
- Casasanto, D.J., Killgore, W.D.S., Maldjian, J.A., Glosser, G., Alsop, D.C., Cooke, A.M., Grossman, M., and Detre, J.A. (2002). Neural correlates of successful and unsuccessful verbal memory encoding. *Brain Lang.* 80, 287–295.
- Cohen, J.D., MacWhinney, R.C., Flatt, M., and Provost, J. (1993). An interactive graphic system for designing and controlling experiments in the psychology laboratory using Macintosh computers. *Behav. Res. Methods Instrum. Comput.* 25, 257–271.
- Demb, J.B., Desmond, J.E., Wagner, A.D., Vaidya, C.J., Glover, G.H., and Gabrieli, J.D.E. (1995). Semantic encoding and retrieval in the left inferior prefrontal cortex: a functional MRI study of task difficulty and process specificity. *J. Neurosci.* 15, 5870–5878.
- Denys, K., Vanduffel, W., Fize, D., Nelissen, K., Peuskens, H., Van Essen, D., and Orban, G.A. (2004). The processing of visual shape in the cerebral cortex of human and nonhuman primates: a functional magnetic resonance imaging study. *J. Neurosci.* 24, 2551–2565.
- Dunlosky, J., and Hertzog, C. (2001). Measuring strategy production during associative learning: the relative utility of concurrent versus retrospective reports. *Mem. Cognit.* 29, 247–253.
- Eagle, M.N. (1967). The effect of learning strategies upon free recall. *Am. J. Psychol.* 80, 421–425.
- Fletcher, P.C., and Henson, R.N.A. (2001). Frontal lobes and human memory: insights from functional neuroimaging. *Brain* 124, 849–881.
- Geiselman, R.E., Woodward, J.A., and Beatty, J. (1982). Individual differences in verbal memory performance: a test of alternative information-processing models. *J. Exp. Psychol. Gen.* 111, 109–134.
- Gold, B.T., and Buckner, R.L. (2002). Common prefrontal regions co-activate with dissociable posterior regions during controlled semantic and phonological tasks. *Neuron* 35, 803–812.
- Grill-Spector, K., Kushnir, T., Hendler, T., and Malach, R. (2000). The dynamics of object-selective activation correlate with recognition performance in humans. *Nat. Neurosci.* 3, 837–843.
- Habib, R., McIntosh, A.R., and Tulving, E. (2000). Individual differences in the functional neuroanatomy of verbal discrimination learning revealed by positron emission tomography. *Acta Psychol. (Amst.)* 105, 141–157.
- Hasher, L., Riebmman, B., and Wren, F. (1976). Imagery and the retention of free-recall learning. *J. Exp. Psychol. [Hum Learn]* 2, 172–181.
- Heun, R., Jessen, F., Klose, U., Erb, M., Granath, D.O., Freymann, N., and Grodd, W. (2000). Interindividual variation of cerebral activation during encoding and retrieval of words. *Eur. Psychiatry* 15, 470–479.
- Ishai, A., Ungerleider, L.G., and Haxby, J.V. (2000). Distributed neural systems for the generation of visual images. *Neuron* 28, 979–990.
- Karis, D., Fabiani, M., and Donchin, E. (1984). “P300” and memory: individual differences in the von Restorff effect. *Cognit. Psychol.* 16, 177–216.
- Konishi, S., Donaldson, D.I., and Buckner, R.L. (2001). Transient activation during block transition. *Neuroimage* 13, 364–374.
- Logan, J.M., Sanders, A.L., Snyder, A.Z., Morris, J.C., and Buckner, R.L. (2002). Under-recruitment and nonselective recruitment: dissociable neural mechanisms associated with aging. *Neuron* 33, 827–840.
- Maccotta, L., Zacks, J.M., and Buckner, R.L. (2001). Rapid self-paced event-related functional MRI: feasibility and implications of stimulus-versus response-locked timing. *Neuroimage* 14, 1105–1121.
- Machielsen, W.C.M., Rombouts, S.A.R.B., Barkhof, F., Scheltens, P., and Witter, M.P. (2000). fMRI of visual encoding: reproducibility of activation. *Hum. Brain Mapp.* 9, 156–164.
- Malach, R., Reppas, J.B., Benson, R.R., Kwong, K.K., Jiang, H., Kennedy, W.A., Ledden, P.J., Brady, T.J., Rosen, B.R., and Tootell, R.B.H. (1995). Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. *Proc. Natl. Acad. Sci. USA* 92, 8135–8139.
- Martin, C.J., Boersma, F.J., and Cox, D.L. (1965). A classification of associative strategies in paired-associate learning. *Psychon. Sci.* 3, 455–456.
- McDaniel, M.A., and Kearney, E.M. (1984). Optimal learning strategies and their spontaneous use: the importance of task-appropriate processing. *Mem. Cognit.* 12, 361–373.
- McDermott, K.B., Petersen, S.E., Watson, J.M., and Ojemann, J.G. (2003). A procedure for identifying regions preferentially activated by attention to semantic and phonological relations using functional magnetic resonance imaging. *Neuropsychologia* 41, 293–303.
- Miezin, F.M., Maccotta, L., Ollinger, J.M., Petersen, S.E., and Buckner, R.L. (2000). Characterizing the hemodynamic response: effects of presentation rate, sampling procedure, and the possibility of ordering brain activity based on relative timing. *Neuroimage* 11, 735–759.
- Miller, M.B., Van Horn, J.D., Wolford, G.L., Handy, T.C., Valsangkar-Smyth, M., Inati, S., Grafton, S., and Gazzaniga, M. (2002). Extensive individual differences in brain activations associated with episodic retrieval are reliable over time. *J. Cogn. Neurosci.* 14, 1200–1214.
- Nyberg, L., McIntosh, A.R., Houle, S., Nilsson, L.G., and Tulving, E. (1996). Activation of medial temporal structures during episodic memory retrieval. *Nature* 380, 715–717.
- Paivio, A., and Yuille, J.C. (1969). Changes in associative strategies and paired-associate learning over trials as a function of word imagery and type of learning set. *J. Exp. Psychol.* 79, 458–463.
- Paivio, A., Yuille, J.C., and Smythe, P.C. (1966). Stimulus and response abstractness, imagery, and meaningfulness, and reported mediators in paired-associate learning. *Can. J. Psychol.* 20, 362–377.
- Petersen, S.E., Fox, P.T., Posner, M.I., Mintun, M., and Raichle, M.E. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* 337, 585–589.
- Pressley, M., and Levin, J.R. (1977). Developmental differences in subjects’ associative-learning strategies and performance: assessing a hypothesis. *J. Exp. Child Psychol.* 24, 431–439.
- Reed, H.B. (1918). Associative aids: I. their relations to learning, retention, and other associations. *Psychol. Rev.* 25, 128–155.
- Richardson, J.T.E. (1978). Reported mediators and individual differences in mental imagery. *Mem. Cognit.* 6, 376–378.
- Richardson, J.T.E. (1998). The availability and effectiveness of reported mediators in associative learning: a historical review and an experimental investigation. *Psychon. Bull. Rev.* 5, 597–614.
- Roberts, W.A. (1968). Alphabetic coding and individual differences in modes of organization in free-recall learning. *Am. J. Psychol.* 81, 433–438.
- Savage, C.R., Deckersbach, T., Heckers, S., Wagner, A.D., Schacter, D.L., Alpert, N.M., Fischman, A.J., and Rauch, S.L. (2001). Prefrontal regions supporting spontaneous and directed application of verbal learning strategies: evidence from PET. *Brain* 124, 219–231.
- Shaughnessy, J.J. (1981). Memory monitoring accuracy and modification of rehearsal strategies. *J. Verbal Learn. Verbal Behav.* 20, 216–230.
- Snyder, A.Z. (1996). Difference image versus ratio image error function forms in PET-PET realignment. In *Quantification of Brain Function Using PET*, D. Bailey and T. Jones, eds. (San Diego: Academic Press, Inc.), pp. 131–137.
- Stoff, D.M., and Eagle, M.N. (1971). The relationship among reported strategies, presentation rate, and verbal ability and their effects on free recall learning. *J. Exp. Psychol.* 87, 423–428.

- Talairach, J., and Tournoux, P. (1988). *Co-Planar Stereotaxic Atlas of the Human Brain* (New York: Thieme Medical Publishers, Inc.).
- Tulving, E., Kapur, S., Craik, F.I., Moscovitch, M., and Houle, S. (1994). Hemispheric encoding/retrieval asymmetry in episodic memory: positron emission tomography findings. *Proc. Natl. Acad. Sci. USA* *91*, 2016–2020.
- Tulving, E., Habib, R., Nyberg, L., Lepage, M., and McIntosh, A.R. (1999). Positron emission tomography correlations in and beyond medial temporal lobes. *Hippocampus* *9*, 71–82.
- Wagner, A.D., Schacter, D.L., Rotte, M., Koutstaal, W., Maril, A., Dale, A.M., Rosen, B.R., and Buckner, R.L. (1998). Building memories: remembering and forgetting of verbal experiences as predicted by brain activity. *Science* *281*, 1188–1191.
- Wagner, A.D., Pare-Blagoev, E.J., Clark, J., and Poldrack, R.A. (2001). Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron* *31*, 329–338.
- Wheeler, M.E., and Buckner, R.L. (2003). Functional dissociation among components of remembering: control, perceived oldness, and content. *J. Neurosci.* *23*, 3869–3880.
- Wheeler, M.E., and Buckner, R.L. (2004). Functional-anatomic correlates of remembering and knowing. *Neuroimage* *21*, 1337–1349.
- Wheeler, M.E., Petersen, S.E., and Buckner, R.L. (2000). Memory's echo: vivid remembering reactivates sensory-specific cortex. *Proc. Natl. Acad. Sci. USA* *97*, 11125–11129.
- Yarmey, A.D., and Csapo, K.G. (1968). Imaginal and verbal mediation instructions and stimulus attributes in paired-associate learning. *Psychol. Rec.* *18*, 191–199.
- Zivian, M.T., and Darjes, R.W. (1983). Free recall by in-school and out-of-school adults: performance and metamemory. *Dev. Psychol.* *19*, 513–520.