Individual differences in cognitive style and strategy predict similarities in the patterns of brain activity between individuals

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A B S T R A C T

Neuroimaging is being used increasingly to make inferences about an individual. Yet, those inferences are often confounded by the fact that topographical patterns of task-related brain activity can vary greatly from person to person. This study examined two factors that may contribute to the variability across individuals in a memory retrieval task: individual differences in cognitive style and individual differences in encoding strategy. Cognitive style was probed using a battery of assessments focused on the individual’s tendency to visualize or verbalize written material. Encoding strategy was probed using a series of questions designed to assess typical strategies that an individual might utilize when trying to remember a list of words. Similarity in brain activity was assessed by cross-correlating individual t-statistic maps contrasting the BOLD response during retrieval to the BOLD response during fixation. Individual differences in cognitive style and encoding strategy accounted for a significant portion of the variance in similarity. This was true above and beyond individual differences in anatomy and memory performance. These results demonstrate the need for a multidimensional approach in the use of fMRI to make inferences about an individual.

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Introduction

One of the goals of neuroergonomics is to use neuroscientific tools to understand the individual mind at work in a naturalistic...
environment (Parasuraman and Wilson, 2008). But the use of functional magnetic resonance imaging (fMRI) to make an inference about an individual is particularly challenging (see Parasuraman and Jiang, this issue). Imagine a situation in which an institution (e.g., a court of law) seeks to use neuroimaging to establish the veracity of an individual’s memory. They have a template based on hundreds of individuals for what that individual’s pattern of brain activity should look like for a true memory. Yet, the individual in question has a very different pattern of brain activity. Are they to conclude that the individual must not be experiencing a true memory? The veracity of the memory is only one dimension that may explain why this individual’s pattern of brain activity is so different from the other individuals. For example, there may have been fundamental differences in the individual’s cognitive style that significantly affected their pattern of activity as well. If neuroimaging will be used to make an inference about an individual, then multiple dimensions in which individuals may differ must be considered.

We have shown previously that the topographical pattern of brain activity underlying a memory retrieval task can vary greatly from individual to individual, sometimes with little to no overlap in significant activations between individuals (Miller et al., 2002; Miller et al., 2009). However, despite that extensive variability, the individual patterns of brain activity are relatively consistent over time (Miller et al., 2002; Miller et al., 2009; for review of fMRI reliability, see Bennett and Miller, 2010), suggesting that differences in the patterns of brain activity are due to systematic differences in individual characteristics and are not due to random measurement error (see Fig. 1). In order to effectively use fMRI to infer unique aspects of the individual mind, it is necessary to untangle the critical factors that can vary the individual patterns of brain activity. In this study, we examine whether individual differences in strategy and cognitive style can account for the degree of similarity between any two individual patterns of brain activity during a retrieval task.

Using neuroscience methods to gain insight into the individual mind is a common goal among many institutions, including education (Byrnes, 2001; Posner and Rothbart, 2005), the military (National Research Council, 2008), and courts of law (Brown and Murphy, 2010). Implicit in the goals of these institutions is the ability to make judgments about an individual based on neuroscientific data collected from a group of individuals. This goal is often incompatible with the general scientific goal to make an inference about a general phenomenon that applies to a population by averaging data across individuals (Faigman, 2010). For fMRI in particular, this demand to average data across individuals is compounded by the fact that the signal-to-noise ratio (SNR) of the BOLD signal is very low (Friston et al., 1999) and that false positives due to the low SNR are far too common (Bennett et al., 2010). Yet, as acquisition devices and analytical tools for fMRI become more and more sophisticated, increasing effort is being made to infer unique aspects of the individual based on the group data.

A critical question remains within functional neuroimaging: do the results of a group analysis accurately represent the individuals that make up that group? Many studies have concluded that it does not (Heun et al., 2000; Machielsen et al., 2000; McGonigle et al., 2000; Miller et al., 2002; Feredoes and Postle, 2007; Seghier et al., 2008; Miller et al., 2009; Seghier and Price, 2009; Parasuraman and Jiang, this issue). For example, we found that the observed variations in functional brain activity across the whole brain during a simple recognition task were extensive, with some individuals activating mostly prefrontal regions while others activated mostly parietal regions (Miller et al., 2002; Miller et al., 2009). This was in contrast to the group analysis, which prominently showed both regions to be equally active. Are there quantifiable factors that might help to explain this effect? We found indirect evidence in a recent study that some variations in the degree of brain activity similarity between individuals during a memory retrieval task may be due to individual

![Fig. 1. Two participants from two scanning sessions held months apart representing the cross-correlation of unthresholded t-maps (retrieval – baseline) across subjects (average inter-individual correlation across all subjects = .224) and sessions (average intra-individual correlation across all subjects = .482). Each r-value represents the degree of similarity between individual t-statistic map volumes, i.e., the higher the r, the more similar the pattern of brain activity. The depiction of t-statistic maps is thresholded (p < .001 uncorrected) for visualization purposes only (adapted from Miller et al., 2009).](image)
differences in strategy (Miller et al., 2009). That is, the larger the difference in decision criterion the more dissimilar the two patterns of brain activity. However, a criterion measure is not a direct measure of memory strategy. Therefore, in this study we directly measure individual differences in cognitive style and strategy and test whether or not these differences can account for a significant portion of the variance in the similarity of brain activity between individuals.

Brain activity during a recognition memory task is a useful platform to study individual variability for two reasons: (1) the tremendous amount of previous research conducted on the relationship between recognition memory and fronto-parietal regions and (2) the widespread and distributed nature of the activity underlying the task (Miller and Van Horn, 2007). Many of the fronto-parietal regions implicated in recognition memory are known to underlie cognitive processes peripheral to the actual retrieval process (Shimamura, 1995; Fletcher et al., 1998; Moscovitch and Winocur, 2002). One potential implication of this distributed architecture is that one and the same behavioral outcome—such as an “old” response on a recognition test—could be the result of information processing and neural circuitry that are distinct to the individual but vary across individuals.

There is considerable evidence that individuals engage in a variety of strategies during the encoding phase of a standard recognition memory task (Stoff and Eagle, 1971; Battig, 1975; Weinstein et al., 1979; Paivio, 1983; Reder, 1987; Graf and Birt, 1996) and that individual differences in strategy can modulate the BOLD activity in certain brain regions (Savage et al., 2001; Casasanto et al., 2002; Speer et al., 2003; Kondo et al., 2005; Tsukiura et al., 2005). One notable study by Kirchhoff and Buckner (2006) identified the various strategies people adopt during the unconstrained encoding of an unrelated pairs of pictures. They found that verbal elaboration correlated with activity in prefrontal regions associated with controlled verbal processing, while visual inspection correlated with activity in the extrastriate cortex known to be involved in higher-order visual processing. These findings suggest that different encoding strategies may recruit different brain regions, even though the memory performance is similar between the two strategies. While the Kirchhoff and Buckner (2006) study showed how different encoding strategies can recruit different brain regions during the encoding phase, we investigated how different encoding strategies may account for the similarity in brain activity during the retrieval phase. One of the classic principles of episodic memory, the encoding specificity principle, states that encoding operations are directly related to retrieval operations (Tulving and Thomson, 1973). This relationship is illustrated by the fact that differences in encoding strategies can have a direct effect on the brain activity that occurs during retrieval (Raposo et al., 2009; Kirchhoff, 2009). From this evidence, we hypothesize that individual differences in encoding strategy will account for a significant portion of the variance that is observed in the similarity of brain activity between individuals during a retrieval task.

Aside from the particular strategy that an individual may choose to engage in during a memory task, individuals may also have a particular style of thinking or a preferred set of cognitive operations that could affect their pattern of brain activity. For example, the visualizer–verbalizer dimension of cognitive style is based on the idea that some people (who could be called visualizers) are better at processing visual material, whereas other people (who could be called verbalizers) are better at processing verbal material (Mayer and Massa, 2003; Massa and Mayer, 2006). Although individual differences in the tendency to engage in visual or verbal processing has little relationship to memory recall (Richardson, 1978, 1998) and the search for research-based attributes that may interact with instructional methods has had a somewhat disappointing history (Cronbach and Snow, 1977; Pashler et al., 2009; Sternberg and Zhang, 2001; Zhang and Sternberg, 2009), differences in cognitive style may still be pertinent to the issue of individual differences in brain activity during a retrieval task. The likelihood of involvement of any particular process and its underlying brain region may depend a great deal on the processing style of the individual. In other words, a visualizer and verbalizer may not necessarily differ in performance on learning outcome tests but may have highly distinct patterns of regional brain activity during learning (i.e., encoding) and retrieval that achieve the same level of performance. There is evidence suggesting that this may well be the case. Two recent studies by Kozhevnikov et al. (2002) and Kozhevnikov et al. (2005) attempted to clarify and revise the visualizer–verbalizer dimension and subsequently introduced two subtypes of visualizers: object visualizers who tended to focus on object properties such as shape and color and spatial visualizers who tended to focus on spatial properties such as location and spatial relations. A later fMRI study revealed that object visualizers activated more ventral regions of the visual processing stream while spatial visualizers activated more dorsal regions of the visual processing stream (Motes and Kozhevnikov, 2006). We hypothesize that differences in cognitive style may also be a significant contributor to the variability of the patterns of brain activity during a retrieval task.

In this study we test the hypothesis that individual differences in strategy and cognitive style will account for a significant portion of the variance in the similarity in the patterns of whole-brain activity between individuals during a memory retrieval task. To measure the variability in the patterns of brain activity across individuals we cross-correlate the unthresholded t-statistic maps contributed by each individual from the retrieval task (Miller et al., 2002; Miller et al., 2009). The more similar two individual patterns of brain activity, the higher the correlation value (see Fig. 1). Individuals were assessed on strategies and cognitive style after the fMRI scanning session using a battery of tests. In addition, strategy was implicitly manipulated within participants by varying the imageability of the word stimuli. If strategies and style depend to some degree on visualizing the word stimuli, then manipulating the imageability of the words should affect the predictability of those factors. We predict that individual differences in strategy and cognitive style will significantly account for inter-individual differences in brain activity above and beyond any factors attributable to individual differences in anatomy and memory performance.

Methods

Participants

A group of 50 participants (age 18–55, M = 25.8) were recruited from the undergraduate and graduate student population at University of California, Santa Barbara (UCSB) and were paid for their participation. Data from three participants was excluded due to excessive motion (1), scanner malfunction (1), or withdrawal from the study (1). Two more participants were excluded because they were left-handed. The remaining 45 participants were comprised of 22 men and 23 women. All participants gave informed consent as approved by the UCSB Institutional Review Board.

Stimuli

Participants completed two study–test sessions, the order of which was counterbalanced across participants. In one session, participants were presented lists of highly imageable, concrete nouns, while the other session presented less imageable, abstract nouns. Words were chosen to be 4–12 letters in length. High-imageability words had imageability scores greater than one standard deviation above the mean on the MRC Psycholinguistic Database Imageability rating (Coltheart, 1981) while low-imageability words were chosen to be greater than 1 SD below the mean. Within each study-test session the word order was randomized. Whether the word was old or new was also counterbalanced across participants.
Behavioral paradigm

This experiment employed an event-related fMRI design and included two study–test sessions—one for the low-imageability words and the other for the high-imageability words. Each study session consisted of 106 words that were presented for 2 s each. These study word trials were randomly intermixed with eighty 2-s fixation trials (‘+’). During the study session participants were simply instructed to try and learn the words for a later memory test. There was a 10-min interval between study and test phases. During this time, structural imaging scans (first high-resolution T1 MPRAGE and then diffusion tensor imaging scans) were collected. The test sessions consisted of 318 events: 212 test words (50% studied and 50% new) and 106 fixation trials, again randomly intermixed. Participants were instructed to respond with their index finger if an item was studied (i.e., “old”) and with middle finger if the item was new. Responses were collected using a MR-compatible button box held in the right hand. Once the scanning portion of the experiment was complete, participants completed an assessment of their cognitive style and strategies.

Assessments of cognitive style and strategy

Cognitive style was assessed using a visualizer–verbalizer test battery. This consisted of (1) a participant questionnaire on Verbal–Spatial Ability Rating and Verbal–Visual Style Rating (Mayer and Massa, 2003); (2) the Card Rotation Test (Ekstrom et al., 1976); (3) the Paper Folding Test (Ekstrom et al., 1976); (4) a Vocabulary Test (18 items adapted from the Vocabulary scale of the Armed Services Vocational Aptitude Battery (ASVAB) as selected from a test preparation book (Hogan and Cannon, 2007); (5) the Verbalizer–Visualizer Questionnaire (VVQ; Richardson, 1977); (6) the Santa Barbara Learning Style Questionnaire (Mayer and Massa, 2003); and (7) the Object–Spatial Imagery Questionnaire (Blajenkova et al., 2006). The results from the Visualizer–Verbalizer test battery data were submitted to a factor analysis using Principle Components Analysis and VARIMAX rotation to yield four orthogonal factors that are related to visualizing and verbalizing tendencies. Factors were interpreted and named based on the weightings of each of the measures. Prior research has been conducted showing the relationship of these scales to visualizing and verbalizing cognitive styles (Mayer and Massa, 2003; Massa and Mayer, 2006). Factor scores were then computed for each participant from the linear combinations of scale scores.

Cognitive encoding strategies were measured using a strategy questionnaire adapted from Kirchhoff and Buckner (2006). Although this questionnaire is meant to probe the strategies used during the study phase of the experiment, those encoding strategies would be related to the strategies and processes utilized during retrieval as well (Tulving and Thomson, 1973). This questionnaire consisted of 10 strategy descriptions (e.g., “Repeated the words to yourself” or “Formed a picture of the word in your mind”) and instructed the participant to rate on a 5-point scale how often they used each strategy during the study phase (see Appendix for a sample of the Questionnaire). A separate questionnaire was used for the set of high-imageability words and the set of low-imageability words. As in the analysis above, the ratings were submitted to a Principle Components Analysis and VARIMAX rotation to yield four components with eigenvalues greater than 1.0.

After the scanning was complete, in addition to the questionnaire, cognitive strategy was probed by simply asking the participants their memory strategy. Questions were asked regarding the first set of words, the second set of words, whether there was a difference when studying the two sets of words, and how they made a decision as to whether the word was studied or not. The participants answered these questions through free response. These responses were then categorized as either verbal or visual by three blind raters (50% agreement across all three raters and 87% agreement across two raters). One of the authors then mediated any disagreements using the general rule that any indication of visual imagery would be coded as visual.

Functional MRI data acquisition

Functional images were acquired with gradient-recalled echo-planar imaging (TR = 2000 ms, TE = 30 ms, RF flip angle = 90°, gradient-echo pulse sequence, 33 contiguous axial slices at 3.0 mm thick with a 0.5 mm slice gap, and an in-plane resolution of 64 × 64 pixels in a FOV of 192 cm, producing voxels of 3 mm × 3 mm × 3 mm) on a 3 T Siemens Trio MRI scanner equipped with high-performance gradients. Each BOLD run was preceded by four scans to allow for steady-state magnetization to be approached. In addition to the functional scans, a high-resolution T1-weighted structural image was acquired using a 3-D SPGR pulse sequence (TR = 25 ms, TE = 6 ms, RF flip angle = 25°, bandwidth = 15.6 kHz, voxel size = 0.9375 mm × 1.25 mm × 1.2 mm). Diffusion-weighted MRI data were acquired using a diffusion weighted, single-shot spin-echo, echo-planar sequence (TR = 9022 msec; TE = 91 msec; flip angle = 90°; slice thickness = 2.0 mm; number of slices = 70 (axial); FOV = 240 mm; matrix size = 128 × 128; acquisition time = 5:24 min). Diffusion weighting (b-value = 1000 s/mm²) was applied along 32 directions with one additional reference image acquired having no diffusion weighting (b-value = 0 s/mm²). Foam padding was used to minimize head motion.

Functional MRI data analysis

Initial data preprocessing utilized SPM5 (Welcome Department of Cognitive Neurology, London, UK) for slice acquisition correction, motion correction, coregistration, and spatial normalization. The spatially normalized scans were then smoothed with an 8 mm FWHM isotropic Gaussian kernel to accommodate anatomical differences across participants. Statistical analysis was conducted using customized Matlab scripts implementing a standard least-squares voxel-wise general linear model, as described in Cuerin and Miller (2009). There were 10 separate parameters to model each 2-s post-stimulus time point up to 20 s (Ollinger et al., 2001). This unique set of 10 parameters was utilized for each trial type: old–high imageable, new–high imageable, old–low imageable, new–low imageable. To contrast responses between trial types, we calculated the mean of the 2nd, 3rd, and 4th time points of the estimated event-related response. In addition to the parameters already discussed, parameters were included to model linear drift within each session and the session-specific means. The critical contrast used for the individual variability analysis was retrieval greater than fixation for both the high-imageability condition and the low-imageability condition. The r-statistic maps from these contrasts that were input into the cross-correlation analysis were unthresholded so that a particular result would not be determined by the setting of an arbitrary threshold (see Miller et al., 2009). The thresholds used for Fig. 2 are for visualization purposes only.

Diffusion tensor imaging (DTI) analysis

All analyses were carried out using the SPM Tools diffusion toolbox as implemented in SPM5 (http://sourceforge.net/apps/trac/spmtools/). For preprocessing, diffusion-weighted images were motion-corrected and coregistered to the high-resolution T1-weighted image, which we spatially normalized to the MNI template brain. The resulting normalization parameters were subsequently applied to the diffusion-weighted images, reorienting the gradient directions accordingly. Following preprocessing, second-order diffusion tensors and fractional anisotropy (FA) values were established using the standard multiple regression approach. Individual FA images reflect the coherence of water diffusion on a voxel-by-voxel basis.

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Individual variability analysis

To quantify the variability in individual patterns of brain activity across the whole brain or across particular regions the unthresholded t-statistic map image volumes were cross-correlated across participants. This was done separately for each imageability condition. If one takes a three-dimensional volume of continuous values in each voxel and correlates that volume with another three-dimensional volume of continuous values in the same voxel matrix and atlas space then the result will be a single correlation value that represents the similarity between two volumes (see Miller et al., 2009, for a discussion of the method). A mask generated during the group analysis of all 45 participants was used so that only voxels with a signal intensity value for every participant were included in the analysis. The cross-correlation of 45 individual t-statistic maps produced 990 observations of unique pairings between different individuals. The resulting correlation values were then submitted to a multivariate hierarchical regression analysis with 60 predictor variables. Each factor was entered into the regression equation as part of a set of factors based on their theoretical relevance (see Table 1). Each set of factors is described below in the order that they were entered into the regression equation. It was critical to enter cognitive style and strategy after the other variables so that any relationship between them and the correlation values could not be attributed to differences in another characteristic.

1. Procedural was a single factor representing the presentation order (high- or low-imageability blocks first), coded as 0 for same and 1 for different. This was considered a nuisance variable and therefore it was entered first.
2. Demographics included variables for the similarity in age and sex. Differences in the similarity of brain activity could be attributed to differences in age and/or sex of the individuals, so this factor was entered next.
3. Anatomy included a cross-correlation of each individual’s normalized high-resolution anatomical (mprage) image and of each individual’s normalized diffusion tensor image (FA). Similar to the demographics factors, any differences in the similarity of brain activity could be attributed to structural differences in anatomy as measured by a high-resolution T1 scan or by DTI. Therefore, this factor was entered next.
4. Performance was represented by the difference between the individuals’ measures in $d'$ and in criterion. Any of the predicted differences in similarity of brain activity that could be accounted for by differences in cognitive style and strategy could be attributed instead to differences in memory performance. Therefore, it was necessary to account for these factors prior to entering in the sets having to do with cognitive style and strategy.
5. Encoding Strategy was represented by five variables. The first variable represented the categorization of the individual’s response to the open-ended strategy question, coded as 0 for same and 1 for different across the two study sessions. The prediction was that different strategies will have lower correlations. Strategy was further represented by the four factor scores from the strategy questionnaire. The four factors represented four different strategies for high-imageability words (verbal, visual, categorization, and
Results

The unique variance (standardized betas) contributed by each factor in the prediction of the degree of similarity in the patterns of brain activity between individuals during a memory retrieval task.

<table>
<thead>
<tr>
<th></th>
<th>High imageability</th>
<th>Low imageability</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Whole Frontal Parietal Tempo Occip.</td>
<td>Whole Frontal Parietal Tempo Occip.</td>
</tr>
<tr>
<td>Procedural</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Order</td>
<td>-.015 -.002 -.022 -003 -.005</td>
<td>-.028 -.022 -.029 -.031 -.005</td>
</tr>
<tr>
<td>Demographics</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age</td>
<td>-.042 .080 -.016 -.120* -.004</td>
<td>-.100* -.116* -.078 -.012 -.118*</td>
</tr>
<tr>
<td>Sex</td>
<td>.019 -.009 .037 .030 .013</td>
<td>.005 .001 .057 .014 -.016</td>
</tr>
<tr>
<td>Anatomy</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MPRAGE</td>
<td>.100 .010 .017 .032 .100</td>
<td>.123* .017 .058 .080 .118*</td>
</tr>
<tr>
<td>DTI (FA)</td>
<td>.281* .205* .152* .284* .256*</td>
<td>.407* .351* .247* .412* .170*</td>
</tr>
<tr>
<td>Performance</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Memory (d')</td>
<td>-.006 -.010 -.013 -.015 -.020</td>
<td>-.005 .039 .020 -.052 -.032</td>
</tr>
<tr>
<td>Criterion</td>
<td>-.060 -.004 .082 -.115* -.023</td>
<td>-.037 -.052 .067 -.063 -.011</td>
</tr>
<tr>
<td>Encoding strategy*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open-ended</td>
<td>-.009 .005 .043 -.018 -.002</td>
<td>-.130* -.168* .112* .029 .071</td>
</tr>
<tr>
<td>Verbal</td>
<td>-.100 -.073 -.066 -.147* -.061</td>
<td>-.068 -.106* -.091 -.013 -.005</td>
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<tr>
<td>Visual</td>
<td>-.044 .021 .051 .111 .161*</td>
<td>-.171* -.180* -.199* -.059 -.160*</td>
</tr>
<tr>
<td>Categorical</td>
<td>-.065 -.141* -.036 .055 .115*</td>
<td>-.176* -.205* -.181* -.102* -.072</td>
</tr>
<tr>
<td>Rote/Elaborate</td>
<td>.106* -.129* .070 .064 .048</td>
<td>.107* .096 .105 .092 .033</td>
</tr>
<tr>
<td>Cognitive style</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Verbal</td>
<td>.016 -.029 .033 .047 .100</td>
<td>.052 .005 .046 .065 .159*</td>
</tr>
<tr>
<td>Visual</td>
<td>-.130* -.129* -.131* -.174* -.024</td>
<td>-.020 -.004 .000 -.057 .027</td>
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<tr>
<td>Imagem</td>
<td>-.081 -.016 -.158* -.114* -.019</td>
<td>-.112* .023 -.105* -.114* -.130*</td>
</tr>
<tr>
<td>Spatial</td>
<td>-.025 -.032 -.055 -.020 .040</td>
<td>-.040 -.101 -.067 -.076 .002</td>
</tr>
</tbody>
</table>

Beta values in bold type are significant at the p < .01 level, and those with an * are significant at the p < .001 level. The five factors were determined separately for the high and low imageability conditions, but those factors with a similar intuitive label were included in the same row (see Supplemental Materials).

rote memorization) and four different strategies for low-imageability words (verbal, visual, categorization, and elaboration) (see Supplemental Material). Only the factor scores relevant to the high-imageability words were entered into the equation with brain activity associated with the high-imageability condition, and vice versa. The prediction was the bigger the difference in factor scores, the lower the correlation.

6. Cognitive Style was represented by the four factors derived from the battery of visualizing–verbalizing tests. The four factors represented four different cognitive styles: verbal, visual, imagery, and spatial (see Supplemental Material). The prediction was the bigger the difference in factor scores, the lower the correlation. The set of cognitive style factors was entered after the set of strategy factors for arbitrary reasons, and the order of these two sets had little effect on the results (indicating little shared variance between the two sets).

7. Individual Residuals represented 44 dummy variables, each one representing whether or not a particular individual was a part of the correlation pair. As reported in Miller et al. (2009), some individuals are more deviant from the group than others in their patterns of brain activity. It was necessary to enter these variables last because some of the differences between individuals were expected to be captured by the variables previously entered, but there could be differences in certain characteristics that we have not captured. These variables were meant to illustrate unique aspects of individuals that have yet to be represented.

Results

Behavioral analysis

A signal detection analysis was separately conducted on the results of the recognition test for the high-imageability words and the low-imageability words. Using a repeated-measures ANOVA we found that memory accuracy, or d', was significantly higher for the high-imageability words (1.51) than the low-imageability words (0.84) (F(1,44) = 81.25, MSE = .123, p < .001), while criterion, C, was not significantly different between the high-imageability words (0.13) (F(1,44) = 1.80, MSE = .029, n.s.).

Details of the results of the factor analysis for both cognitive style and strategy are contained in the Supplemental Material. In brief, the results from the battery of visualizing and verbalizing tests loaded onto four strategy factors that we labeled based on an intuitive evaluation of the component scores as verbal (Factor 1), visual (Factor 2), imagery (Factor 3), and spatial (Factor 4). The results from the strategy questionnaire similarly loaded onto four factors for the both the high-imageability and the low-imageability words labeled as verbal (Factor 1), visual (Factor 3 for high imageability and Factor 2 for the low imageability), categorical (Factor 2 for high imageability and Factor 3 for the low imageability), rote memory for high-imageability words (Factor 4) and elaboration for low-imageability words (Factor 4).

Correlation tests (with alpha at .05) showed that individual differences in the visualizing and verbalizing style factor scores had no significant relationship with memory (d') in either the high imagery cognition or the low imagery condition. Some of the strategy factors did have a significant relationship to d', but only in the high imagery condition. The visual strategy factor (Factor 3) in the high imagery condition strongly correlated with memory performance (d'); r = .446, p < .002. In contrast, the rote strategy factor (Factor 4) had a negative effect on memory performance: r = -.407, p < .006. Since the words used in the high imagery condition were those that were highly imageable, it makes sense that a visual strategy may benefit long-term memory performance.

Individual variability analysis1

Between-subject variability

The extreme difference in the patterns of brain activity between individuals is evident in Figs. 2 and 3. The findings replicate our previous studies (Miller et al., 2002; Miller et al., 2009) in that the average correlation between high-imageability and low-imageability words within the same participant (.626) was significantly higher than the average correlation between high-imageability and low-imageability words between different participants (.341) (F(1,2023) = 312.15, MSE = .011, p < .001). There was also a difference in variability

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1 Although the focus of this study was on the variability of brain activity during the retrieval phase of the task, we did have data on the brain activity during the encoding phase as well. However, the fMRI data for the encoding phase turned out to possess a much lower SNR relative to the retrieval phase (the average correlation between participants for encoding was .185 compared to .358 for retrieval). This was most likely due to the fact that only half as many trials were collected during the study phase. Any inferences that could be drawn about the differences in variability between encoding and retrieval (e.g., differences in encoding strategy were a significant factor for the variability in brain activity during retrieval but not during encoding) would be confounded by the differences in the number of trials.

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between the imageability conditions, with the average correlation of low-imageability words (.371) being significantly higher than the average correlation of high-imageability words (.346) ($F(1,990)=56.96, \text{MSE}=.005, p<.001$).

Hierarchical regression analyses—whole brain

The results are summarized in Fig. 4 (which collapses the results across imageability conditions) and Table 1 (which lists the standardized betas for each factor). For high-imageability words, the full model accounted for 79.3% of the variance in correlation values across pairs of whole-brain patterns of activity. The model first takes into account the differences in the order of the conditions (procedural), which was not significant ($R^2$ change = .000, $F(1,988) = 0.05, \text{n.s.}$); then differences in demographics ($R^2$ change = .006, $F(2,986) = 3.09, p = .046$); differences in anatomy ($R^2$ change = .108, $F(2,984) = 59.83, p < .001$); and differences in performance ($R^2$ change = .006, $F(2,982) = 2.46, \text{n.s.}$). Above and beyond those differences, differences in strategy were significantly related to the variability ($R^2$ change = .023, $F(5,977) = 5.16, p<.001$). Above and beyond differences in strategy and other characteristics, differences in cognitive style were also significantly related to the variability ($R^2$ change = .017, $F(4,973) = 6.63, p<.001$). Finally, another 44.5% of the variance in correlation values could be accounted for by the dummy variables coding for each individual ($R^2$ change = .445, $F(44,929) = 53.23, p<.001$).

Hierarchical regression analyses—separate brain regions

An identical analysis as the one used for the whole brain was conducted separately for the cortices of each of the lobes. Masks for each lobe were generated using the Wake Forest Pickatlas Matlab toolbox (Maldjian et al., 2003). The results for each lobe were very similar to the whole brain, with the differences summarized in Fig. 4 and Table 1 with the standardized betas for each factor listed. One of the notable differences between the lobes was in the low-imageability condition except that anatomy and strategy differences accounted for a much larger portion of the variance in the correlation values. Again, the model first takes into account the differences in the order of the conditions (procedural), which was not significant ($R^2$ change = .002, $F(1,988) = 1.63, \text{n.s.}$); then differences in demographics ($R^2$ change = .012, $F(2,986) = 6.13, p = .002$); differences in anatomy ($R^2$ change = .252, $F(2,984) = 168.72, p < .001$); and differences in performance ($R^2$ change = .002, $F(2,982) = 1.22, \text{n.s.}$). Above and beyond those differences, differences in strategy were significantly related to the variability ($R^2$ change = .094, $F(5,977) = 28.75, p < .001$). Above and beyond differences in strategy and other characteristics, differences in cognitive style were also significantly related to the variability ($R^2$ change = .017, $F(4,973) = 6.63, p<.001$). Finally, another 44.5% of the variance in correlation values could be accounted for by the dummy variables coding for each individual ($R^2$ change = .445, $F(44,929) = 53.23, p<.001$).

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frontal and parietal lobes than in the temporal and occipital lobes. Another notable difference between the lobes was in the high-imageability condition, in which cognitive style differences (i.e., differences in the general tendency of cognitive style regardless of the particular set of words) had a stronger relationship to variability in the parietal and temporal lobes than in the frontal and occipital lobes.

Most of the direct effects reported in Table 1 were in the expected direction. The direct effects represent the unique variance of each of the factors derived from the regression equation prior to entering the individual residuals. Some of the notable relationships include the following: the bigger the difference in age, the lower the correlation values (i.e., the more variable), particularly in the low-imageability condition, while the difference in sex had no relationship to correlation values in either condition. As for anatomy, differences in white matter integrity as measured by the FA maps were a much stronger factor than overall differences in anatomy as measured by the high-resolution T1 MPRAGE. The more similar the white matter maps, the more similar the functional maps for every lobe in both conditions. This was clearly the strongest factor in every analysis. Differences in performance had little relationship to variability, except for criterion differences in the temporal lobe in the high-imageability condition.

The critical factors were in the set labeled cognitive style or the set labeled strategy. While most of the direct effects for these factors were in the predicted direction, a few factors were surprising. For example, three factors had significant effects in the direction opposite from the expected one (positive betas): differences in verbal tendency in the occipital lobe, differences in the open-ended query about strategy in the low-imageability condition in the frontal and parietal lobe, and differences in the fourth strategy factor across several regions. In these cases, the standardized beta was positive indicating that the bigger the difference between the two individuals the more similar their patterns of brain activity. However, this may be due to the imbalance in the number of individuals within each of these categories. For example, in the low-imageability condition, most of the participants utilized a verbal strategy. Only five individuals maintained a visual strategy. Yet, for all five of these participants, the average correlation between them and the rest of the participants was higher than the overall average, i.e., these five individuals happened to be more like the group than most of the other individuals. Therefore, due to the low number of individuals and the characteristics of this group, the difference in strategy factor is biased towards being more similar to the group than maybe would be represented if we had a larger sample.

Most of the significant factors in these sets were in the predicted direction (negative betas). That is, the more two individuals were different in their strategy and cognitive style, the moe the individuals were different in their patterns of brain activity. One critical factor was the tendency to visualize, which was the main target in manipulating the imageability of the words. As shown in Table 1, the bigger the difference in the tendency to visualize the lower the correlation value, but only in the high-imageability condition and not in the low-imageability condition as predicted. While, in general, cognitive style factors seemed to play a slightly larger role in the high-imageability condition, strategy factors clearly played a larger role in the low-imageability condition and most notably in the frontal and parietal regions. Differences in the two strongest strategy factors (verbal and visual strategies) were strongly related to variability in the low-imageability condition in the frontal and parietal lobes but not in the high-imageability condition. Interestingly, differences in the visual strategy factor scores were significantly related to memory performance (‘d’) in the high imagery condition but not the low imagery condition, while differences in the same factor scores were significantly related to similarity in brain activity in the low imagery condition but not the high imagery condition.

Discussion

What makes the pattern of brain activity so similar for two individuals and, yet, so different for another two individuals? We found, as predicted, that individual differences in cognitive style and encoding strategy during a memory retrieval task were significant.
factors in explaining this variability. For example, the more different two individuals were in their tendency to visualize highly imageable word stimuli, the more different their two patterns of brain activity were across the whole brain. Further, we found that the relationship between differences in cognitive style and strategy and differences in the similarity of brain activity was significantly affected by implicit manipulations of strategy, in this case, manipulating the imageability of the word stimuli.

We defined strategy as a specific set of cognitive operations that an individual utilized to better encode certain word stimuli, such as forming an image of the word in their mind or using the word in a sentence. We found participants used a combination of operations or strategies during a particular block of trials. Thus, certain strategies tended to group together, depending on the imageability condition and that those groupings (factors) could be intuitively identified as visual, verbal, or otherwise (see Supplemental Material). Likewise, we defined cognitive style as a specific set of cognitive processes that may be similar to the cognitive operations engaged by specific strategies, but we defined them separately because they represent general processing tendencies by the individual that are not necessarily a direct or explicit strategy, like the tendency to visualize written material. A number of visualizing–verbalizing test batteries were completed by the participants and the results of those tests also tended to group together into intuitively identifiable factors, like visual tendency or verbal tendency. While the two sets of factors, cognitive style and strategy, may have engaged similar processes, they accounted for unique proportions of the variance in the similarity of brain activity. In the analysis of the whole brain, both sets of factors together accounted for 8.0% of the variance in the similarity of brain activity, while less than 0.3% of the variance was shared between the two sets. Each set of factors was a significant and unique predictor of similarity in brain activity.

It should be noted that not just any difference between individuals could be related to the similarity in their patterns of brain activity. For example, whether or not the two individuals were the same sex had no effect on their brain similarity. Also, the difference in age between the two individuals had no relationship to similarity in brain activity in the high-imageability condition, but it did have a significant relationship in the low-imageability condition. We also found that differences in memory performance had little relationship to differences in the similarity of brain activity. Even though differences in memorability (d’) are known to modulate the activity in key brain regions (Nyberg et al., 1996; Tulving et al., 1999; Kirchhoff, 2009), it appears to have little relationship to differences in the topography of brain activity across large regions.

In our previous study we found that correlations of spatially normalized high-resolution anatomical images were not related to correlations of functional brain activity (Miller et al., 2009). We surmised, though, that finer measures of anatomical differences might eventually prove to be related. In the current study, we found that the correlations of the high-resolution MPRAGE images were significantly related to the correlations of functional brain activity across the whole brain, but the effect was inconsistent across different cortical regions. It was significant in the occipital lobe, but not in the frontal, parietal or temporal lobes.

Still, not all differences in anatomy were so weakly related to differences in functional brain activity. Clearly one of the strongest factors overall was the difference in white matter integrity as measured by fractional anisotropy. The effect was significant across every region of the brain, but it was strongest in the temporal cortex (with standardized betas as high as .412). The study of individual differences in white matter connectivity has been of great interest across neuroscience (Wolbers et al., 2006; Boorman et al., 2007; Niogi et al., 2010; Tomassini et al., 2011) and this finding is consistent with that literature demonstrating the greater the difference in white matter integrity between two individuals the bigger the difference in task-related functional brain activity. Although the degree of similarity between individual DTI images seemed to have little relationship to differences in actual memory performance, it clearly had a significant impact on the similarity of brain activity underlying memory performance. This would suggest that similar memory performance on a recognition test could be associated with very different patterns of brain activity, and that individual differences in white matter connectivity plays a major role in that variance.

The most striking factor, though, as depicted in Fig. 4, was the leftover amount of variability that could be attributed to specific individuals (some individuals were more deviant in their pattern of brain activity than others). For example, in the whole-brain analysis, the full model accounted for 81% of the variance in the similarity of brain activity, but only 27% of the variance could be attributed to unique characteristics of the individuals that we were able to identify, with the differences in cognitive style and strategy being two of those factors. That means that there was another 54% of the variance that was attributable to specific individual traits but that we have not been able to identify yet. This variability could conceivably be due to differences in cognition but also due to differences in personality, physiology, state of mind, and/or other factors, such as caffeine intake.

Though a large amount of variance remains unexplained, it is clear that differences in cognitive style and strategy are significant predictive factors. In previous studies and reports on brain activity associated with memory retrieval (Miller and Van Horn, 2007; Miller et al., 2009) we have proposed that differences in strategy could account for some of that variability. Episodic memory retrieval engages widespread regions throughout the cortex, and includes cognitive processes that might be peripheral to the actual retrieval of episodic information (Shimamura, 1995; Fletcher et al., 1998; Moscovitch and Winocur, 2002). A single “old” response on a recognition test could be accomplished along multiple processing routes through the brain, many of which may depend on the strategy of the individual. The Encoding Specificity Principle states that memory performance relies on the relationship between processes engaged during retrieval and the processes engaged during encoding (Tulving and Thomson, 1973). Previously, it has been shown that differences in encoding processes can have a direct effect on the brain activity that occurs during retrieval (Raposo et al., 2009; Kirchhoff, 2009). Indeed, we found that differences in encoding strategies had a significant relationship to the similarity in brain activity. This was particularly pronounced in the low-imageability condition relative to the high-imageability condition, which may be due to the increased demands on strategy for words that do not easily evoke a visual image. We also found that strategy differences had a larger effect in frontal and parietal regions than in temporal and occipital regions, which would be consistent with literature on memory strategies and those brain regions (Gershberg and Shimamura, 1995; Davachi et al., 2001; Savage et al., 2001; Crescentini et al., 2010). For example, previous studies with aging populations have suggested that as memory performance declines prefrontal and parietal cortex activations become more variable, suggesting that older individuals compensate for reduced memory by engaging in more strategic processing (Cabeza et al., 2002; Spreng et al., 2010).

Individual differences in cognitive style go back as far as the work of Paivio (1971, 1986), including a distinction between visualizers and verbalizers. Since that time, a great deal of effort has been put into assessing and categorizing those differences (Mayer and Massa, 2003; Sternberg and Zhang, 2001; Zhang and Sternberg, 2009). Yet, the practical effect of those distinctions on memory (Richardson, 1978, 1998) and on other research-based interventions has been largely absent (Massa and Mayer, 2006; Pashler et al., 2009). However, our results suggest that those distinctions in cognitive style are not without consequences. Individual differences in cognitive style can have a significant effect on the similarity of brain activity. In particular, we found that differences in visual style had a significant effect on similarity throughout the frontal, parietal and temporal lobes. As predicted, we found that this effect was evident for highly imageable
words but not for lowly imageable words. This suggests that knowledge about an individual's cognitive style may be necessary when evaluating the individual's pattern of brain activity, depending on the type of stimuli.

There are many methods to probe individual differences in brain activity, like correlating brain activity for a particular region with individual differences in behavior or separating individuals into distinct groups and comparing the activity between the two groups (for a brief review, see Miller and Van Horn, 2007). While these methods are useful and easy to visualize, they are examining correlations only along a single dimension. Our method explores multiple dimensions by utilizing a multivariate regression analysis to predict the correlation of functional t-statistic maps (i.e., the similarity in brain activity). We found that multiple factors predict similarity in brain activity during a memory retrieval task, including differences in age, normalized white matter integrity, and cognitive style and strategy.

The multidimensional quality of individual differences in brain activity could be a critical factor in achieving the goal of neuroergonomics to use neuroimaging to understand unique aspects that might inform the individual mind in the workplace. In the introduction, we presented an example in which the veracity of an individual's memory was questioned by the fact that the individual's pattern of brain activity was different than a typical pattern of activity for a true memory. However, the difference may have been due to other factors, like the individual's cognitive style or the strategy the individual used to retrieve the episode. In some extreme cases, the failure to consider the multiple factors that can drive differences in brain activity between individuals can have life or death consequences. For example, a recent court case grappled with the use of functional brain images as evidence of a defendant's past mental state (Brown and Murphy, 2010). In that case, a neuroscientist testified on the brain images of convicted child rapist and murderer Brian Dugan during the sentencing phase, arguing that the scans of Dugan were different enough from non-psychopath individuals and that this dissimilarity indicated that Dugan lacked the capacity to make normal moral decisions. This argument was intended to persuade jurors that Dugan's mental defect precluded the use of the death penalty. However, the difference in activity that was evident in Dugan's brain image may not be the result of diminished moral reasoning, but could be attributed to other potential differences, such as the difference in white matter integrity or cognitive style or personality. Our study indicates that any inference that can be made about an individual based on their pattern of brain activity must take into consideration the multiple factors that can contribute to the variations in that activity.

Variability is often considered a nuisance, leaving the study of individual variability in brain activity to the dustbin of statistical averaging. But the systematic nature of variations in brain activity between individuals offers a unique opportunity to fulfill one of the goals of neuroergonomics; to use neuroscience to understand unique aspects of the individual mind.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2011.05.060.

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