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ORIGINAL ARTICLE

Hippocampal Contributions to the Large-Scale Episodic Memory Network Predict Vivid Visual Memories

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Abstract

A common approach in memory research is to isolate the function(s) of individual brain regions, such as the hippocampus, without addressing how those regions interact with the larger network. To investigate the properties of the hippocampus embedded within large-scale networks, we used functional magnetic resonance imaging and graph theory to characterize complex hippocampal interactions during the active retrieval of vivid versus dim visual memories. The study yielded 4 main findings. First, the right hippocampus displayed greater communication efficiency with the network (shorter path length) and became a more convergent structure for information integration (higher centrality measures) for vivid than dim memories. Second, vivid minus dim differences in our graph theory measures of interest were greater in magnitude for the right hippocampus than for any other region in the 90-region network. Moreover, the right hippocampus significantly reorganized its set of direct connections from dim to vivid memory retrieval. Finally, beyond the hippocampus, communication throughout the whole-brain network was more efficient (shorter global path length) for vivid than dim memories. In sum, our findings illustrate how multivariate network analyses can be used to investigate the roles of specific regions within the large-scale network, while also accounting for global network changes.

Key words: declarative memory, functional magnetic resonance imaging, graph theory, medial temporal lobes, recall

Introduction

Although the vast majority of studies on the neural bases of "episodic memory" (declarative memory for personally experienced, context-specific events) have focused on the contributions of specific brain regions, such as the hippocampus, it is generally accepted that no single region can support episodic memory unless it interacts with other components of the large-scale memory network. The properties of large-scale networks can be investigated by applying multivariate analytic methods, such as graph theory, to brain connectivity data collected from functional magnetic resonance imaging (fMRI). Complex network analyses using graph theory provide the means to reliably quantify properties of brain networks with a small number of neurobiologically meaningful measures that capture the interactions between all brain regions simultaneously (Bullmore and Sporns 2009; Rubinov and Sporns 2010). Yet, most complex network analyses have focused on global measures of resting-state networks rather than on the contributions of specific regions in task-related networks. The current large-scale network study provides a unique contribution to this literature by focusing primarily on the role of a specific brain region, the hippocampus, within the context of the whole-brain network supporting vivid episodic memory retrieval.

The contributions of the hippocampus to episodic memory have been the focus of thousands of lesion, electrophysiology,

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drug, and neuroimaging studies with both animals and humans. Lesion studies have provided clear evidence for the devastating effects of hippocampal damage on episodic memory, and functional neuroimaging studies with healthy adults have reliably shown greater hippocampal activity for successful than unsuccessful episodic retrieval and for rich than impoverished episodic memories (Eichenbaum et al. 2007; Skinner and Fernandes 2007; Spaniol et al. 2009; Kim 2015). The hippocampus is hypothesized to bind incoming information from different neocortical regions, to store integrated event representations, and to allow access to cortical memory traces during retrieval (Alvarez and Squire 1994; McClelland et al. 1995; Teyler and Rudy 2007; Danker and Anderson 2010; Ritchey et al. 2013). During these processes, the hippocampus is assumed to interact very closely not only with regions storing representations but also with frontal, parietal, cingulate, and basal ganglia regions involved in a variety of attention, control, working memory, and decision-making processes. Consistent with these assumptions, functional neuroimaging studies have shown that all these regions are coactivated with the hippocampus during episodic encoding and retrieval tasks (Cabeza and Nyberg 2000; Cabeza et al. 2008; Spaniol et al. 2009; Rugg and Vilberg 2013; Kim 2013). Even though all these regions are assumed to operate together as a complex large-scale network, existing functional connectivity studies of episodic memory have typically focused only on the relationship between a particular pair of regions, such as the interaction between the hippocampus and the prefrontal cortex (e.g., Schott et al. 2013; Wing et al. 2013). Only recently have researchers begun to use task-related functional connectivity analyses to investigate changes across larger sets of memory-related brain regions (Schedlbauer et al. 2014; King et al. 2015).

A powerful approach for investigating the operation of large-scale brain networks, such as the one supporting episodic memory, is to analyze functional connectivity data using multivariate analytic methods, such as graph theory. Most large-scale network analyses have provided valuable insights into the topology of resting-state networks (e.g., Dosenbach et al. 2007; Hayasaka and Laurienti 2010; Power et al. 2010; Vogel et al. 2013), but those resting-state networks do not necessarily match network architecture during specific cognitive tasks (e.g., Bassett et al. 2011; Moussa et al. 2011; Rzucidlo et al. 2013; Cao et al. 2014; Meunier et al. 2014; Moussa et al. 2014; Stanley et al. 2014; Braun et al. 2015). The topological properties of brain networks do not remain static and fixed. Depending upon the demands on the system, there are continuously changing patterns of functional interactions between regions, circuits, and systems in the brain (Sporns 2013). Furthermore, most of these large-scale network analyses have focused on global network properties rather than on the contributions of specific brain regions to the network, and hence, their findings have been somewhat disconnected from the main body of research on the functions of these regions. To address these issues, we applied graph theory measures to functional connectivity data during an episodic memory retrieval task, focusing in particular on how the contributions of the hippocampus to the large-scale network are related to the vividness of visual memories.

The behavioral paradigm we investigated, which is depicted in Figure 1, had 4 phases. First, participants encoded a series of labeled scenes (e.g., barn, tunnel) by rating the representativeness of each photo. Second, participants underwent a resting-state scan. Third, participants recalled the previously viewed scenes in response to their labels, rating the vividness of their memories (from 1 to 4). Finally, participants performed a forced-choice scene recognition test outside the scanner, in which they discriminated between each viewed scene and 3 similar distractors. Postscan recognition accuracy and confidence increased with in-scan vividness ratings, indicating that these ratings provide a valid measure of memory quality. In the current study, we focused on functional connectivity using graph theory measures during scene recall in order to identify network differences between "vivid memories" (ratings 3–4) and "dim memories" (ratings 1–2).

We investigated 4 main questions. First, "how do complex patterns of hippocampal interactions with the rest of the network change for the retrieval of vivid versus dim memories?" To answer this question, we measured vivid minus dim differences in 4 nodal measures: path length, degree centrality, page rank centrality, and leverage centrality. "Path length" measures the efficiency with which information can flow between any 2 nodes in the network and is computed as the average of the shortest paths between a node and every other node in the network. Shorter path lengths promote functional integration by allowing communication between any 2 network nodes with few intermediate steps, thereby reducing the effects of noise and signal degradation (Rubinov and Sporns 2010; Sporns 2013). Centrality measures index the convergence and joint processing of distributed information at central, influential nodes, and can be defined by diverse criteria. "Degree centrality" identifies nodes with many connections to other nodes in the network. "Page rank centrality" identifies nodes that are connected to nodes that are themselves central within the network. Finally, "leverage centrality" identifies nodes that are connected to more nodes than their immediate

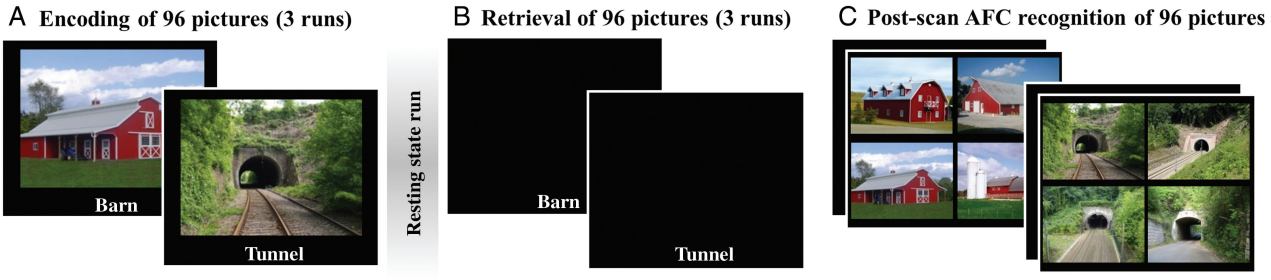

Figure 1. Figure 1 provides an overview of the experimental design. The same design was presented in Wing et al. (2015). (A) During encoding, pictures of scenes were presented to participants with a descriptive label while participants judged image composition. (B) At retrieval, only the descriptive labels for previously encoded scenes were presented. Participants rated how detailed (vivid) their memory was for the corresponding picture on a 4-point scale. (C) After the scan, all scenes from encoding were presented in a forced-choice recognition task that included 3 similar scene exemplars. Participants chose the specific image they believed was presented at encoding and then rated their confidence on a 4-point scale.

neighbors. We predicted that the hippocampus would display a shorter path length and become a more central, influential node to support the convergence of information in facilitating vivid memory retrieval, thereby confirming the assumption that hippocampal contributions to the episodic retrieval network have a significant impact on retrieval success.

Second, "how do the changes in hippocampal network properties from dim to vivid memory retrieval compare to the changes in other network nodes?" Even if there are stark shifts in hippocampal network properties from dim to vivid memory retrieval, it is possible that many other nodes in the network are changing in more dramatic ways. To address this issue, we computed the aforementioned 4 nodal measures for all nodes in the network. Memory theories generally assume that the hippocampus is a "bottleneck" or "convergence zone" in the episodic memory network because it integrates information from several different brain regions, each with particular functions related to memory retrieval (Damasio 1989; Moll and Miikkulainen 1997; Mišić et al. 2014). Thus, we predicted that when comparing dim to vivid memories, the hippocampus would show the most substantial changes in path length and centrality measures compared with all other regions in the network. Several other graph theory analyses of resting-sate connectivity data (Buckner et al. 2009; Tomasi and Volkow 2010) did not find the hippocampus among the most central, influential network nodes, or among the nodes occupying critical positions along shortest paths in the network. It remains possible, however, that hippocampal function in the context of larger networks is most sensitive to memory differences that are observed within the same memory task, rather than in resting-state networks. As such, we were interested in investigating network properties capturing the "relative shift"—i.e., how the hippocampus relates to the rest of the network—between dim to vivid memory retrieval.

Third, "to what extent does the hippocampus reorganize its set of direct (first step) connections from dim to vivid memory retrieval?" Even though shifts in multivariate hippocampal network properties can only be explained in full by appealing to the entire network architecture, one can ask whether those shifts are better explained by (1) a substantial reorganization of connectivity strengths for first step (direct) connections or (2) a substantial reorganization of connectivity patterns beyond first-step connections (indirect connections). To investigate this question, we calculated the extent to which first-step connections reorganize themselves for each and every node between dim and vivid retrieval networks using the novel "first-step reorganization" measure. If, in fact, a network node exhibits a substantial change in first-step reorganization between networks, we can reasonably conclude that changes in its set of direct connections are at least partly accounting for observed changes in path length, page rank centrality, and leverage centrality. In contrast, if a network node changes minimally in first-step reorganization between networks, then any observed significant changes in path length, page rank centrality, and leverage centrality for that node are primarily due to changes in indirect connectivity taking place elsewhere in the network.

Finally, "do properties of the entire episodic retrieval network change from dim to vivid memory retrieval, and are these changes driven by the hippocampus?" As noted before, most large-scale network analyses of functional neuroimaging data have focused on global network measures rather than on the operation of individual brain regions. Although these analyses focus on the role of the hippocampus, we believe that investigating the network properties of this region alone is insufficient to fully explain the neural basis of episodic memory. Even if our predictions about the role of the hippocampus within the episodic retrieval networks are confirmed, we assume that many other regions contribute to memory vividness. Thus, to assess global network changes in the efficiency with which information can be integrated in the network, we calculated the normalized average path length for the entire brain network. We predicted that the network as a whole would facilitate more efficient global communication (shorter global path length) for vivid than dim memory retrieval. And even after removing the hippocampus from the network, we predicted that we would find significant global network differences between vivid and dim memories in the remaining nodes.

Methods

Participants

Twenty-two participants completed the experiment. One participant, who lacked functional data due to a technical error, was excluded from these analyses. All analyses were performed with the remaining 21 participants (12 female, age range: 18–30, M = 23.5, standard deviation [SD] = 3.0). Participants were healthy, right-handed, fluent English speakers with normal or corrected-to-normal vision. Written informed consent was obtained from each participant in accordance with a protocol approved by the Duke University Institutional Review Board.

Behavioral Methods

The behavioral paradigm is depicted in Figure 1. Before beginning the scan, participants completed a short practice session so that they were familiar with the instructions at each phase of the study. The scan session contained 3 encoding runs, a resting-state run, and 3 retrieval runs (analyses comparing spatial patterns of activation across encoding and retrieval were reported in Wing et al. 2015). Stimuli consisted of the pictures of 96 nameable outdoor and indoor scenes, and the corresponding verbal labels (e.g., "island," "concert hall"). During 3 encoding runs, each scene and its label were presented for 4 s, and participants rated how well the picture matched the label. During 3 retrieval runs, each label was presented alone. Participants tried to recall the corresponding picture in as much detail as possible and then rated the amount of detail (vividness) in the image they generated from 1 (little or no detail) to 4 (highly detailed). For the purpose of the present network analyses, trials with responses of 1–2 were classified as "dim memory" trials, and trials with responses of 3–4 as "vivid memory" trials. During both encoding and retrieval, the 8-s intertrial intervals were filled by an active baseline task in which participants made even/odd judgments in response to randomly presented digits ranging from 1 to 9.

Immediately after exiting the scanner, participants completed a 4-alternative forced-choice recognition test assessing memory for all 96 pictures. Each trial had 2 phases. First, the target picture and 3 distractor pictures for the same label were presented in different quadrants of the computer screen. Participants selected the picture they believed they saw in the scanner. During the second phase of each recognition trial, participants used a 4-point scale to rate how confident they were in the preceding recognition decision (1 = guess, 4 = very confident).

MRI Scanning and Image Preprocessing

Imaging data were collected using a 3 T GE scanner. Following a localizer scan, functional images were acquired using a SENSE spiral-in sequence (time repetition = 2000ms, time echo = 30 ms, field of view = 24 cm, 34 oblique slices with voxel dimensions of

3.75 × 3.75 × 3.8 mm). Functional data were collected during 6 task runs of equal length during the performance of the memory task described above. A resting-state scan lasting for 5 minutes was collected following the third run but was not used in the current analyses. Stimuli were projected onto a mirror at the back of the scanner bore, and responses were recorded using a 4-button fiber optic response box. Scanner noise was reduced with ear plugs, and head motion was minimized with foam pads. A high-resolution anatomical image (96 axial slices parallel to the anterior commissure-posterior commissure plane with voxel dimensions of 0.9 × 0.9 × 1.9 mm) was collected following functional scanning. Our preprocessing procedure mirrored that of Fornito et al. (2011), who have published data on a β series derived network analysis. Briefly, using SPM8 software (www.fil.ion.ucl.ac.uk/spm) and custom MATLAB scripts, all data were high-pass filtered, motion corrected, and each individual's brain map was registered to standard MNI space.

Functional Brain Network Construction

To create episodic retrieval networks, we used a β time series analysis (Rissman et al. 2004), which assumes that 2 regions are functionally coupled during a task if the activity of both regions is significantly correlated across trials (Fornito et al. 2011; Schedlbauer et al. 2014). Each β value reflected the fit shape of the hemodynamic response evoked by a given trial during the retrieval phase of the procedure. These observed β values were then sorted in accordance with level of detail scores reported by participants during each trial of the retrieval condition. β Values obtained during trials for which participants reported high levels of detail with which they could remember the specific picture (ratings of 3 and 4) were concatenated to generate a β series for networks of vivid memory retrieval; β values obtained during trials for which participants reported low levels of detail with which they could remember the specific picture (ratings of 1 and 2) were concatenated to generate a β series for dim memory retrieval.

Networks can be represented as graphs, which consist of a set of nodes together with pairwise relationships between those nodes (edges). In these functional brain networks, each node represented a discrete brain region, and edges represented measured correlations between pairs of nodes. To measure functional connectivity among all regions simultaneously, the brain was first parcellated into 90 discrete anatomical regions of interest (45 ROIs in each hemisphere) defined in accordance with the automated anatomical labeling (AAL) atlas (Tzourio-Mazoyer et al. 2002). A commonly used nodal parcellation scheme in functional brain network analyses is this AAL template (Stanley et al. 2013), which parcellates the cortex and subcortical structures by identifying gyral and sulcal boundaries. Each anatomical ROI from the atlas served as a network node. Pairwise Pearson correlations between regional mean beta series were computed to generate {90 × 90} functional connectivity matrices, or adjacency matrices, with the correlation coefficients representing functional connectivity strength between nodes. These correlations between regional beta series reflected correlated variations in evoked hemodynamic responses within vivid and dim retrieval networks, respectively. The matrices were not thresholded, and each complete matrix served as an undirected, weighted graph (Rubinov and Sporns 2011). Adjacency matrices (averaged across subjects for display purposes only) for dim and vivid memory retrieval conditions are presented in Figure 2.

Graph Theory Measures

Path Length

Path length measures the overall capacity for efficient information transfer across a network. From each weighted graph, 2 global network measures were computed: weighted characteristic path length (L^w_{net}) and the normalized weighted characteristic path length (λ). Both L^w_{net} and λ were calculated individually for each node and subsequently averaged over the entirety of the graph. The path length values computed for each individual node (L^w_i) were also used in our analyses. The path length between nodes v_i and v_j is defined as the sum of the edge lengths along the path where each edge's length is obtained by computing the reciprocal of the edge weight $1/W_{ij}$, such that the weighted shortest path L^w_{ij} between nodes v_i and v_j is the length of the shortest path between the nodes. L^w_{net} is then computed by measuring the shortest path lengths between all nodes in the network:

$$L^w_{net} = \frac{1}{\frac{1}{N(N-1)}\sum_{i=1}^{N}\sum_{j\neq i}^{N}\frac{1}{L^w_{ij}}}$$

where N is the number of nodes in the network. The average L^w_{net} reflects the global integration of a network. Short path lengths

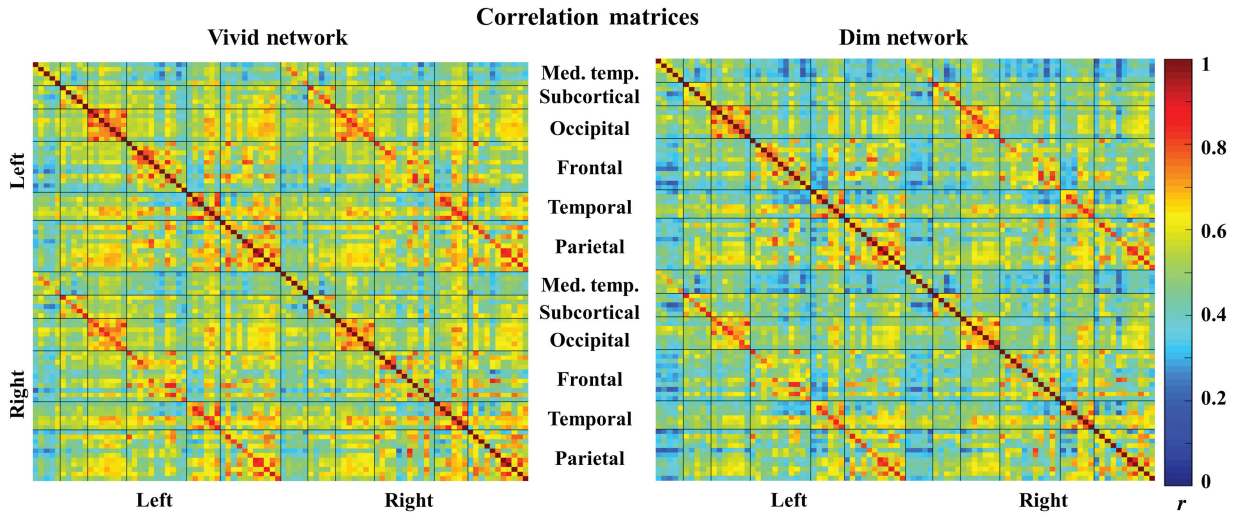

Figure 2. Average (across subjects) adjacency matrices derived from β series correlations are presented for dim and vivid retrieval conditions and split by hemisphere (right and left). For ease of visualization, regions of interest are ordered in accordance with the procedure implemented by Salvador et al. (2005).

ensure that information quickly and easily spreads throughout the network, making efficient distributed and parallel information processing possible. Link lengths are inversely related to link weights, as large weights typically represent strong associations between nodes (Rubinov and Sporns 2010, 2011).

Normalized Path Length

In order to normalize the computed values of L^w_{net} for differences in overall connection strength between vivid and dim memories, we randomly rewired each observed network. Network randomization was performed by randomly rewiring edges an average of 10 times for each full network. This randomization procedure was accomplished a total of 100 times for each corresponding real network, and the path lengths were computed for each random network. Then, the mean path length was computed for all 100 networks, and the mean of the mean path length for the 100 networks was computed to serve as L^w_{rand} in the calculation of λ:

$$\lambda = \frac{L^w_{net}}{L^w_{rand}}$$

L^w_{net} and λ provide summary statistics estimating global integration properties of an entire network. As such, these measures should be used in conjunction with other measures that provide further information regarding localized shifts in network topology.

Degree Centrality

Degree centrality in weighted networks measures the overall strength of a node's connections in terms of the total summed weights of their connections.

$$DC^w_i = \sum_j^N w_{ij}$$

where w_{ij} represents the weighted adjacency matrix in which $w_{ij} > 0$ if v_i is connected to v_j, and the value given to the link is the weight of the connection. Nodes with a high-degree centrality directly interact with many other nodes in the network, are likely to be highly influential over the behavior of the network, and play a critical role in the flow of information or resources throughout the network. While degree centrality often identifies critical network elements, a highly essential node in the brain network may not necessarily have ubiquitous connections to other nodes in the network as assumed by degree centrality; thus, degree centrality should be used in conjunction with other centrality metrics to fully grasp the influence of a given node in a network.

Page Rank Centrality

Page rank centrality, a variant of eigenvector centrality ideal for small networks, is unique in that it considers the centrality of the immediate neighbors of node v_i in computing the centrality of v_i itself (van den Heuvel and Sporns 2013). Although eigenvector centrality has been used more widely in complex brain network analyses, the distributions of centrality scores for page rank centrality tend to follow a normal distribution unlike eigenvector centrality scores (Zuo et al. 2012), making page rank centrality more amenable to standard statistical analyses. Much like degree centrality, page rank centrality favors nodes strongly connected with many other network nodes. In contrast to degree centrality, it favors nodes that are connected to nodes that are themselves central within the network. Because of this recursive property, page rank centrality captures information regarding global features of the graph. Recent work has shown that page rank centrality is able to identify certain brain regions that are not as widely connected throughout the brain but are connected with key hubs (Zuo et al. 2012). This allows those nodes with high page rank centrality to integrate information throughout the entire network efficiently and effectively in relatively few steps. Mathematically, page rank centrality is defined as the stationary distribution achieved by instantiating a Markov chain on a graph, meaning that the page rank centrality of v_i is proportional to the number of steps spent at v_i as a result of that process (Ding et al. 2009). For ease of interpretation, page rank centrality in binary, unweighted networks is standardly defined as

$$PRC_i = (1-d)\frac{1}{N} + d\sum_{i=1}^{k}\frac{PR(p_i)}{L(p_i)}$$

where $p_1, p_2, \ldots p_N$ are the nodes under consideration, $PR(p_i)$ is the set of nodes that link to p_i, $L(p_i)$ is the number of connections for node p_i, and d is the damping factor. This equation is easily generalizable to weighted graphs (Ding et al. 2009; Rubinov and Sporns 2010). The page rank index is modified by the addition of a damping factor, d, which specifies the fraction of time that a random walker will transition to one of its neighboring nodes in order to handle walking traps on graphs (Boldi et al. 2009). It is standard for the damping value to be set at $d = 0.85$, the value used in the present study. One limitation of the page rank centrality measure is that it fails to account for the disparity in the degree of a node with respect to its neighbors, which has important implications depending upon the network's assortativity, or the tendency for nodes to be connected to other nodes of a similar degree more often than would be expected by chance alone (Joyce et al. 2010). We included in our analyses the recently developed measure of leverage centrality, which is able to overcome this limitation inherent in the calculation of page rank centrality.

Leverage Centrality

Leverage centrality considers the degree of a node, v_i, relative to its neighbors by identifying nodes in the network that are connected to more (or fewer) nodes than their immediate neighbors (Joyce et al. 2010).

$$LC^w_i = \frac{1}{k_i}\sum_{N_i}\frac{k_i - k_j}{k_i + k_j}$$

where k_i is the degree (summed strength) of node v_i. Nodes with high leverage centrality tend to be more connected to nodes of lower degree, whereas nodes with low leverage centrality tend to be more connected to nodes of higher degree. Lower leverage centrality indicates that a node tends to be more connected to nodes of a higher degree than itself; higher leverage centrality indicates that a node tends to be more connected to nodes of a lower degree than itself. Leverage centrality is unique from other centrality measures in that it does not assume serial transportation of information, but rather allows for parallel information processing, which is fundamentally characteristic of certain systems such as the brain.

Nodal Reorganization of First-Step Connections

The above nodal measures are dependent upon the entire set of connections between all network nodes (with the exception of degree centrality, which relies only on first-step connections). That is, these functional brain networks are interdependent, nonlinear systems. Even though stark shifts in nodal network properties can only be explained in full by appealing to the entire

network architecture, these shifts can only occur because of (1) the reorganization of connectivity strengths for the set of first-step (direct) connections and/or (2) the reorganization of connectivity patterns beyond first-step connections (i.e., indirect connections). Therefore, we sought to quantify the manner in which a given node's first-step connections reorganize via a novel metric, first-step reorganization (FSR_i^w). FSR_i^w is computed by comparing the strength of each individual connection from node v_i in the dim retrieval networks to the strength of the same "corresponding connection" in the vivid retrieval networks. As such, this measure is conceptually and mathematically distinct from computing a change in degree centrality, because changes in degree centrality are merely dependent upon the value of the summed strength of connections for node v_i for each network. Formally, for the entire distribution of scores, FSR^w is calculated as

$$FSR^w = \text{zscore}\left\{-\text{arctanh}\left(\frac{\text{Cov}(A_i, B_i)}{\sigma_{A_i}\sigma_{B_i}}\right)\right\}$$

where A_i is the connectivity profile of node i in network A, B_i is the connectivity profile of node i in network B, and the connectivity profile of node i is defined to be its distinct set of weighted connections (i.e., the column in the adjacency matrix corresponding to that particular node). A Fisher transformation (arctanh) was implemented to render the distribution Gaussian, followed by a z-scoring of that distribution. Due to the standardization of the measure by means of z-scoring, the FSR_i^w value of a given node is always relative to the rest of the nodes in the network. Once the FSR_i^w value is obtained for each node, paired-sample t-tests can be used to determine whether a node exhibits significant reorganization of connections at the group level. Higher values of FSR_i^w indicate that the set of direct connections from node i exhibit greater reorganization between networks; lower values of FSR_i^w indicate that the set of direct connections from node i exhibit less reorganization between networks. If, in fact, a network node exhibits a significant change in FSR_i^w between networks, we can reasonably conclude that changes in the set of direct connections are at least partly accounting for observed changes in path length, page rank centrality and leverage centrality. In contrast, if a network node changes minimally in FSR_i^w between networks, then any observed significant changes in path length, page rank centrality, and leverage centrality for that node are primarily due to changes in indirect connectivity elsewhere in the network.

Statistical Testing

Behavioral Data Analyses

Paired-samples t-tests were used to confirm the validity of the subjective in-scan memory ratings for the level of detail recollected at retrieval by comparing those scores to the responses for post-scan recognition and confidence ratings. Behavioral data were analyzed using SPSS and R statistical software.

Network Data Analyses

We used the permutation framework developed by Simpson et al. (2013) in conjunction with the Jaccardized Czekanowski index (Schubert 2013; Schubert and Telecs 2014) to assess significance for differences in each graph theory measure at the hippocampus between dim and vivid memory retrieval conditions. This same permutation framework was also used to assess differences in whole-brain network properties between dim and vivid memory retrieval. This permutation procedure allows for comparing groups of networks while accounting for the diverse topological features inherent in each individual network. All P-values presented are uncorrected for multiple comparisons across measures. In assessing nodal changes in graph theory measures, it is important to know not only which nodes showed significant changes in network properties (L_i^w, DC_i^w, PRC_i^w and LC_i^w) from dim to vivid memory retrieval, identified with the permutation test, but also which nodes showed the largest changes in relation to all other nodes in the network. To compare changes across nodes, we z-scored each network metric within subjects, and subsequently calculated the normalized difference between vivid and dim retrieval for each metric separately. All group-level statistics were formulated based upon this "nodal change score". All network data analyses were implemented using standard and custom scripts in MATLAB.

Results

Below we report behavioral results and the results of network analyses addressing our 4 questions concerning: (1) nodal changes in the hippocampus, (2) nodal changes in the hippocampus compared with other network nodes, (3) the extent to which the hippocampus reorganizes its set of first-step connections, and (4) global network changes.

Behavioral Results

During the image recall task in the scanner, participants distributed their responses across the 4 vividness ratings (mean proportion of responses for ratings 1–4 were 19.9%, 22.6%, 28.8%, and 28.7%, respectively). Confirming the validity of these ratings, the results of the postscan forced-choice scan scene recognition test showed that accuracy was significantly greater ($t_{20} = 4.20$, $P < 0.001$) for vivid (M = 82.3%; SD = 1.2%) vs. dim (M = 72.0%; SD = 1.4%) memory retrieval. Furthermore, when considering only successfully recognized old scenes (hits), recognition confidence was reliably higher ($t_{20} = 7.85$, $P < 0.001$) for vivid memories (ratings 3–4, M = 3.64, SD = 0.12) than for dim memories (ratings 1–2; M = 3.14, SD = 0.34).

Effects of Hippocampal Network Properties on Memory Vividness

The purpose of our first question was to investigate how complex patterns of hippocampal interactions with the rest of the network change from dim to vivid memory retrieval. To answer this question, we directly compared vivid versus dim memories using the permutation procedure developed by Simpson et al. (2013) in conjunction with the Jaccardized Czekanowski Index (Schubert 2013; Schubert and Telecs 2014) for the 4 nodal measures of interest at the hippocampus: path length, degree centrality, page rank centrality, and leverage centrality. Consistent with our prediction, all 4 measures showed significant differences between vivid and dim memories for the hippocampus. Possibly due to the visual nature of the stimuli, all of these effects were significant in the right but not in the left hippocampus (see Table 1 for a summary of results). (1) Path length was significantly shorter for vivid than dim memories ($P = 0.0002$), which we interpret as a greater capacity for more efficient communication between the right hippocampus and the rest of the network supporting vivid remembering. (2) Degree centrality was greater for vivid than dim memories ($P = 0.00009$), suggesting that stronger right hippocampal interactions with the rest of the network promote vivid remembering. (3) Page rank centrality was also

Table 1 Summary of medians and *P*-values obtained using the permutation framework for each network measure at the right hippocampus and for the entire brain network

Network measures		Dim memory	Vivid memory	*P*-value
Right hippocampus				
Path length	L_i^w	2.517	1.959	0.0002***
Degree centrality	DC_i^w	15.216	22.477	0.00009***
Page rank centrality	PRC_i^w	0.0094	0.0108	0.013*
Leverage centrality	LC_i^w	1.119	0.712	0.0029**
Global measures				
Path length	L_{net}^w	2.062	1.887	0.015*
Normalized path length	λ	1.045	1.022	0.0001***

*P < 0.05, **P < 0.01, ***P < 0.001.

higher for vivid than dim memories (P = 0.013), indicating that the right hippocampus is connected to more central, influential nodes for enhancing memory vividness. (4) Finally, leverage centrality was lower for vivid than dim memories (P = 0.0029), suggesting that the right hippocampus is connected with nodes of higher degree than itself promoting vividness in episodic memories. Given that the degree centrality of the right hippocampus significantly increased from dim to vivid memory retrieval and the right hippocampus still became more connected with nodes of a higher degree than itself for vivid memory retrieval, this indicates that the right hippocampus substantially strengthens its connections with the more central, influential nodes in the network to support memory vividness. In sum, all nodal measures investigated support the idea that nodal changes in the right, but not necessarily the left, hippocampus are especially important in supporting vivid remembering. However, the permutation did not reveal any significant dissociation for dim or vivid retrieval between the right and left hippocampus for any graph theory measure (all *P*'s > 0.11). Because degree centrality is the most fundamental graph theory measure, Figure 3 displays the change in the degree centrality for all nodes exhibiting higher degree centrality during vivid than dim memory retrieval in standard brain space.

We then sought to determine whether univariate measures of retrieval vividness in the right or left hippocampus correlated (across subjects) with our 4 graph theory measures of interest (path length, degree centrality, page rank centrality, and leverage centrality). Initial group-level effect paired-samples *t*-tests on parameter estimates of vivid versus dim memory retrieval yielded significant retrieval vividness effects (vivid > dim) for both the left and right hippocampal nodes (left: $t(20) = 4.82$, $P < 0.0001$; right: $t(20) = 5.04$, $P < 0.0001$). However, across subjects, univariate measures of activity within the vivid and dim conditions were not significantly correlated with graph theory metrics computed on the corresponding vivid and dim networks, nor was the vivid > dim univariate difference correlated with the corresponding difference between dim and vivid retrieval for any graph theory measures (all *P*'s > 0.25).

Effects of Hippocampal Network Properties on Memory Vividness Compared with Other Network Nodes

Our second question addressed how the magnitude and direction of hippocampal nodal changes supporting episodic memory vividness is related to observed changes in all other network nodes. Despite significant shifts in hippocampal network properties from dim to vivid memory retrieval, it is possible that properties of other network nodes are more closely tracking differences in memory vividness. To address this question, we (1) calculated the same 4 graph theory measures of interest (path length, degree centrality, page rank centrality, and leverage centrality) for each of the 90 nodes in the network and computed the nodal change score; (2) averaged these nodal change scores across participants and z-scored the result to determine which nodes exhibited the greatest changes in our 4 measures of interest in support of memory vividness.

Consistent with our predictions, the hippocampus (right) exhibited the greatest magnitude change of any network node for supporting vivid episodic remembering. From dim to vivid memory retrieval, the right hippocampus exhibited the largest decrease in path length and leverage centrality as well as the largest increase in degree and page rank centrality compared with all other network nodes (see Fig. 4). These results demonstrate for the first time that changes in the topological properties of the right hippocampus more closely track visual episodic retrieval performance than any other regions in the brain.

Although we predicted that the hippocampus would display stark shifts in network properties as a function of memory vividness, we did not expect this region to necessarily be among the most central, influential nodes in the network independent from the shift in memory performance. In keeping with this idea, if instead of ranking the magnitude of the changes between vivid and dim conditions, we rank the absolute value of nodal measures within one of these conditions, such as the vivid condition, then the hippocampus is not among the subset of nodes with shortest path length, highest degree centrality, highest page rank centrality, or lowest leverage centrality. In the vivid condition, for example, the right hippocampus ranked 68th for path length, 67th for degree centrality, 67th for page rank centrality, and 61st for leverage centrality. That is, for vivid memories, the right hippocampus actually displayed a higher path length, lower degree centrality, lower page rank centrality, and higher leverage centrality than the average node in the network for each of these respective measures. Perhaps more surprisingly, for the dim memory condition, the right hippocampus had some of the lowest rankings in path length (85th), degree centrality (86th), page rank centrality (89th), and leverage centrality (88th). That is, the right hippocampus was among the select subset of nodes with the highest path length, lowest degree centrality, lowest page rank centrality, and highest leverage centrality for dim retrieval. Prior work has used degree centrality and page rank centrality to identify the most central nodes, or hubs, in brain networks. See Supplementary Materials for a ranking of the most central nodes in dim and vivid retrieval networks, respectively, as opposed to the shift in topological properties between conditions.

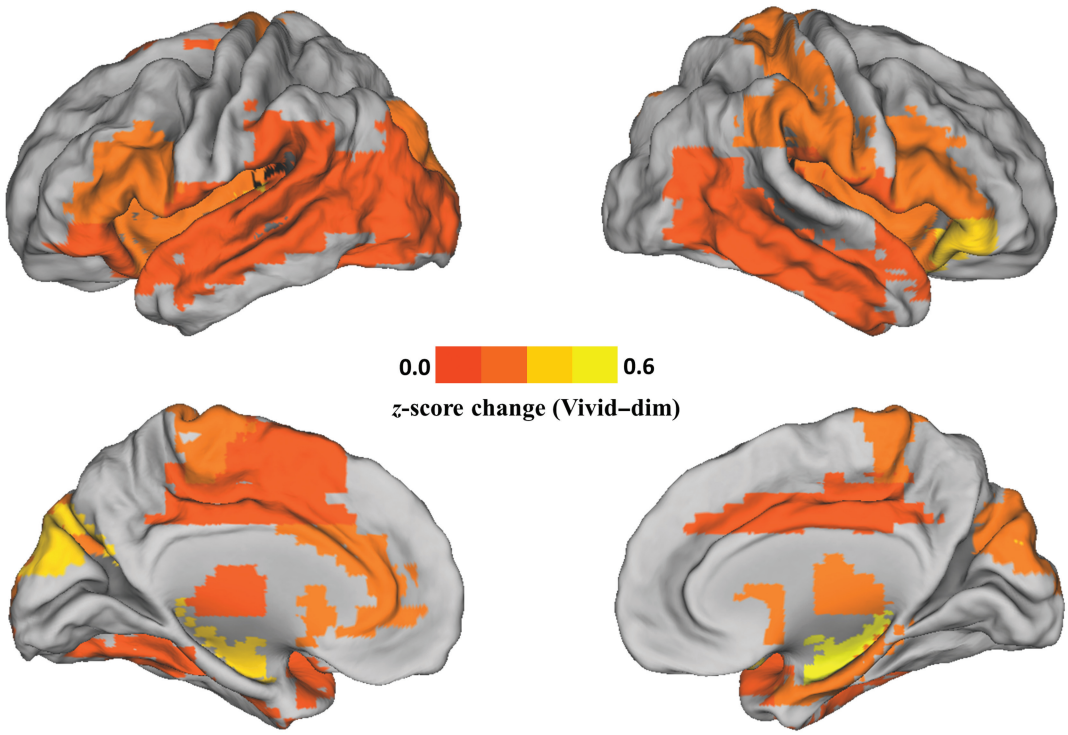

Figure 3. The change in (z-scored) degree centrality values are presented for all nodes that shift in a positive direction (i.e., nodes that exhibit higher degree centrality for vivid compared with dim retrieval) in standard brain space.

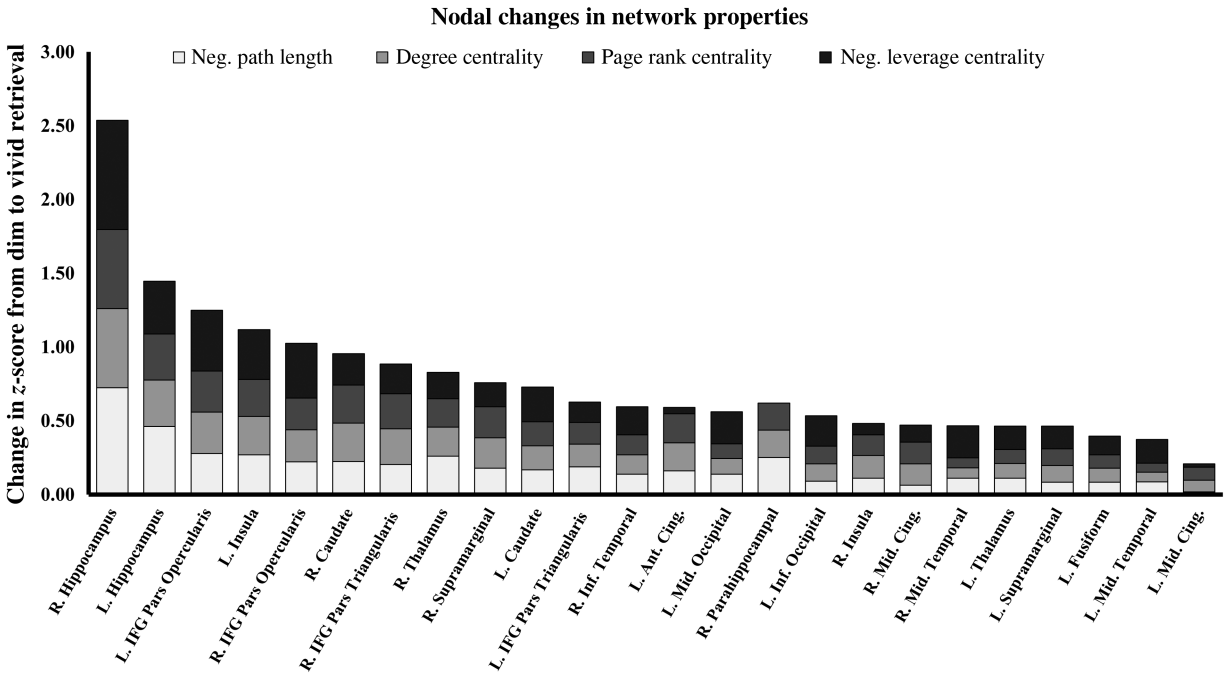

Figure 4. Figure 4 provides a summary of how potential memory-related network nodes change between dim and vivid retrieval with respect to the 4 nodal measures of interest: path length, degree centrality, page rank centrality, and leverage centrality. Only nodes for which each measure changes in the same direction as the hippocampus are included, because only changes in those directions result in a node more efficiently communicating with the rest of the network and becoming more central or influential in the network. The signs of the z-scored values for path length and leverage centrality were flipped on the figure, such that higher z-scores for path length and leverage centrality represent shorter path lengths and lower leverage centrality, respectively. The largest shifts in the entire network for each of these 4 nodal measures occur for the right hippocampus. Furthermore, while changes in page rank centrality and degree centrality appear to be inversely related to changes in path length and leverage centrality, respectively, this is not a mathematical certainty, as each measure characterizes unique features of the network in accordance with different criteria.

These results suggest that when participants were unable to vividly recollect the previously encoded scene, the right hippocampus did not participate in efficient information transfer with other nodes across the network, interacted with relatively few other nodes in the network, and did not connect with other central, influential nodes in the network. Collectively, these results suggest that the right hippocampus was not sufficiently involved in integrative processes in the case of dim memories but became sufficiently involved in integrative processes to support the recollection of vivid memories. The fact that the hippocampus displayed the greatest magnitude shift for each graph theory measure from dim to vivid retrieval but was not among the subset of nodes with lowest path length, highest degree centrality, highest page rank centrality, or lowest leverage centrality at either dim or vivid retrieval, separately, emphasizes the importance of examining shifts in nodal properties between dim and vivid memory retrieval as opposed to the absolute ranking of a node within each network separately.

Effects of Hippocampal First-Step Connection Reorganization on Memory Vividness

The purpose of our third question was to determine the extent to which the hippocampus reorganizes its set of first step (direct) connections from dim to vivid memory retrieval. To answer this question, we created a novel measure, called first-step reorganization (FSR_i^w). FSR_i^w is computed by comparing the strength of each individual connection from node v_i in the dim retrieval condition to the strength of the same corresponding connection in the vivid retrieval condition. In addition to significant changes in each graph theory measure, the right hippocampus also exhibited a significant reorganization of first-step connections between dim and vivid memory retrieval, $t(20) = 3.33$, $P = 0.003$. Because the right hippocampus exhibited such a change in FSR_i^w between dim and vivid retrieval conditions, we can reasonably conclude that this substantial reorganization of direct connections is at least partly responsible for observed changes in path length, page rank centrality and leverage centrality. Thus, the observed changes in path length, page rank centrality, and leverage centrality are not merely due to changes in connectivity elsewhere in the network that do not directly involve interactions with the right hippocampus. The extent to which a node reorganizes its set of connections was not trivially related to any of the 4 nodal measures of interest displayed for each node in Figure 4. Quantitatively, none of the 4 nodal measures of interest in dim or vivid retrieval conditions separately or the change in these measures from dim to vivid retrieval was significantly correlated with FSR_i^w (all P's > 0.15, uncorrected).

To further investigate how the right hippocampus reorganizes its set of first-step connections, we computed the average change in connectivity strength between the right hippocampus and every other network node from dim to vivid memory retrieval. As illustrated by Figure 5, the right hippocampus exhibited substantial increases in average connectivity strength with nodes commonly assumed to be functionally connected with the hippocampus during successful and/or vivid episodic retrieval, such as occipital regions supposed to store visual memory traces and frontal regions supposed to mediate retrieval control operations (Rugg and Vilberg 2013; Schedlbauer et al. 2014; King et al. 2015).

Extra-Hippocampal Global Network Effects on Memory Vividness

Whereas our first 3 questions were about the topological properties of the hippocampus, our last question concerned the

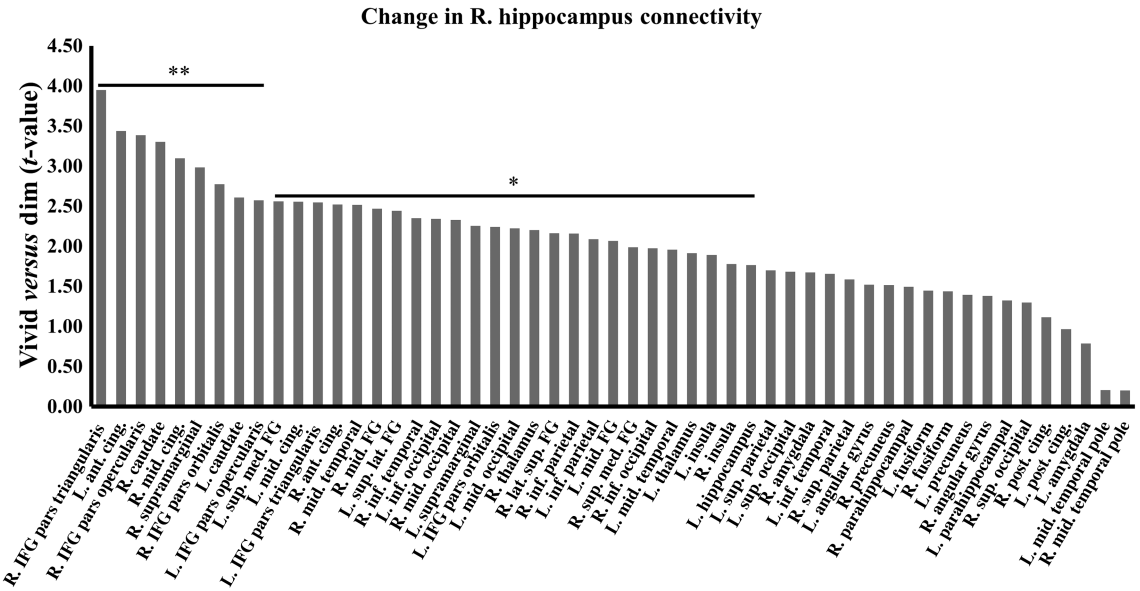

Figure 5. Figure 5 provides a summary of the t-values associated with the average change in connectivity strength between the right hippocampus and the set of potential memory-related nodes from dim to vivid memory retrieval (*$P < 0.05$, **$P < 0.01$). Only nodes for which the right hippocampus exhibited increased connectivity from dim to vivid retrieval are presented in the figure. The right hippocampus exhibited the largest magnitude increases in its connectivity strength with inferior frontal regions thought to mediate retrieval control, caudate, inferior lateral temporal regions thought to be critical for visual memory, and occipital regions thought to store visual memory information. This demonstrates that the right hippocampus was, in fact, communicating more strongly with the select subset of regions thought to be highly involved in episodic memory for visual stimuli. It is important to note that this figure is meant only to show which nodes the right hippocampus tends to become more connected with for vivid memory retrieval (i.e., which nodes contributed more than others to the increase in hippocampal degree centrality); as such, we did not correct for multiple comparisons.

capacity for effective information integration in the entire brain network. More specifically, are there global changes in path length from dim to vivid memory retrieval, and do those global changes persist even after removing the right hippocampus from the networks? To answer these questions, we computed the vivid–dim difference in path length across the entire brain network (L^{w}_{net}). Using the permutation framework developed by Simpson et al. (2013) in conjunction with the Jaccardized Czekanowski index (Schubert 2013; Schubert and Telecs 2014), we found a significant difference in L^{w}_{net} between vivid and dim memory retrieval conditions, such that the path length in the entire brain network was shorter for vivid than dim memory retrieval (see Table 1). We then normalized L^{w}_{net} by dividing by L^{w}_{rand} to obtain values of lambda (λ) for vivid and dim retrieval conditions, respectively. Even after normalizing the path length across networks, the permutation revealed that the vivid retrieval networks demonstrated a greater capacity for efficient communication across the entirety of the network (see Table 1). Even after removing both hippocampi from the network and recalculating the global path length, the permutation revealed that the global path length was shorter for vivid than dim retrieval ($P < 0.05$). Furthermore, after removing both hippocampi from the network, recalculating the global path length, and normalizing the global path length, the permutation revealed that the normalized global path length was still shorter for the vivid retrieval condition than dim retrieval condition ($P < 0.001$). This demonstrates that significant changes in path length for the hippocampi are not exclusively responsible for driving the average global change in path length from dim to vivid retrieval.

While the hippocampus (right) maintained the largest magnitude change in path length of any network node, the fact that the network as a whole exhibited a shorter average path length during vivid retrieval (even after removing the hippocampi from the network) suggests that many other nodes exhibited a lower path length at vivid retrieval as opposed to dim retrieval. In fact, Figure 4 shows which other nodes, previously identified as involved in memory-related processes in activation (Spaniol et al. 2009; Kim 2015) and connectivity analyses (Schedlbauer et al. 2014; King et al. 2015), tended to exhibit shorter path lengths at vivid retrieval as opposed to dim retrieval relative to each other. Interestingly, these tend to be the same nodes identified in Figure 5 that significantly increase in connectivity strength with the hippocampus to support vivid memory retrieval.

General Discussion

The purpose of this study was to investigate properties of the large-scale network underlying episodic memory by using graph theory measures, focusing in particular on the contribution of the hippocampus in supporting patterns of connectivity underlying vivid memories for visual scenes. The study yielded 4 main findings. First, when recollecting vivid compared with dim memories, the hippocampus displayed greater efficiency in communication with the rest of the network (shorter path length), connected more strongly with the rest of the network (greater degree centrality), preferentially connected with the most central nodes in the network (higher page rank centrality), and still connected with nodes of a higher degree than itself (lower leverage centrality). Second, among all 90 nodes in the network, nodal changes in the right hippocampus made the largest contributions to visual memory vividness. Third, the stark shifts in hippocampal network properties were at least partly due to the fact that the hippocampus massively reorganizes its set of direct connections to support vivid memory retrieval. Finally, beyond the hippocampus, the brain network as a whole displayed a greater capacity for efficient communication throughout the network (shorter global path length) to facilitate vivid memory retrieval. This shift in the functional profile of the hippocampus to support vivid memory retrieval provides novel insight into why the hippocampus is a critical brain area for episodic memory processes. These 4 main findings are discussed in separate sections below.

Right Hippocampal Network Interactions Significantly Impact Memory Vividness

While episodic memory is subserved by complex neural interactions and the continuous exchange of information between circuits distributed across several brain regions, the hippocampus in particular stands out as the critical structure for the encoding, storage, and retrieval of such memories (Battaglia et al. 2011; Watrous and Ekstrom, 2015). Determining how the hippocampus supports the unique demands of retrieving experienced events from memory is fundamental to understanding the biological basis of episodic memory. Although lesion studies have provided clear evidence for the destructive effects of hippocampal damage on episodic memory and prior functional neuroimaging studies of healthy adults have demonstrated greater hippocampal activations for successful than unsuccessful episodic memories (Eichenbaum et al. 2007; Skinner and Fernandes 2007; Spaniol et al. 2009; Rugg et al. 2012), these methods have not characterized how the hippocampus dynamically interacts (directly or indirectly) with other relevant brain regions during intact episodic memory retrieval. Given that the human hippocampus is thought to provide the vital integrative link that receives relevant sensory information during encoding and ultimately facilitates memory retrieval via reactivation of memory traces with input from frontal regions mediating retrieval control operations (Alvarez and Squire 1994; McClelland et al. 1995; Teyler and Rudy 2007; Danker and Anderson 2010; Ritchey et al. 2013), understanding the role of the hippocampus in the large-scale episodic memory network is critical for understanding the neural basis of memory. While this prior work has provided evidence for the importance of the hippocampus to episodic memory, our results provide a unifying framework showing that the direct and indirect connections between the hippocampus and all other network nodes contribute to stark changes in the complexity of the system to support vivid episodic memory retrieval.

The information processing properties of the hippocampus have traditionally been studied at the more microscopic, local level with a focus on information flow and plasticity exclusively within the hippocampal formation (Battaglia et al. 2011). Watrous and Ekstrom (2015) recently proposed that both cell assembly firing patterns and global patterns of brain oscillatory activity within hippocampal–neocortical networks form the basis of a memory. Our results also suggest the hippocampus is critical for information processing at the more macroscopic level of the entire functional brain network to facilitate vivid visual memory retrieval, building on and extending considerable work regarding the role of hippocampal–cortical projections related to memory processes (McIntosh et al. 1997; Rolls 2000; Ranganath et al. 2005; Takahashi et al. 2008; Bai et al. 2009; McCormick et al. 2010; Sadeh et al. 2011; Ritchey et al. 2013; Schott et al. 2013; Robin et al. 2015). The integration of information from diverse functional domains at a more macroscopic level may serve as a key feature enabling the hippocampus to support not only the vivid retrieval of episodic memories, but also their translation into more complex, adaptive behaviors.

Several recent studies have extended existing task-based functional connectivity analyses of memory retrieval by identifying changes in bivariate connections (King et al. 2015) or basic graph theory measures (Schedlbauer et al. 2014) between small subsets of a priori selected, memory-related brain regions. Of particular relevance to the current study, Schedlbauer et al. (2014) demonstrated that several areas within the medial temporal (including the hippocampus), frontal and parietal lobes exhibited significantly greater connectivity with several other brain regions and were more often along shortest paths in the network during successful retrieval, underscoring the importance of integrative processes in supporting memory. However, there may be differences in multivariate graph theory measures between small networks comprised of a small proportion of brain space and larger-scale networks that include all cortical and subcortical regions (Stanley et al. 2013). To the best of our knowledge, no existing whole-brain network analyses during active memory retrieval have been reported in the literature. Our study also extends this prior work by using more data-driven analysis methods, utilizing multiple multivariate graph theory measures to better assess integrative properties in the networks, and creating an innovative new measure to aid in understanding why these shifts in multivariate graph theory measures were observed.

Network Measures for the Right Hippocampus Tracked Memory Vividness More Than any Other Brain Region

When separate brain networks were constructed in accordance with measured performance during the retrieval of visual scenes, the topological properties of the right hippocampus shifted more than any other node in the network between vivid and dim memory retrieval. The right hippocampus exhibited a greater capacity for efficient communication with the rest of the network (shorter path length), communicated more strongly with directly connected nodes (higher degree centrality), interacted with more central nodes (higher page rank centrality), and preferentially strengthened connections with more connected nodes than itself (lower leverage centrality). In other words, compared with all other brain areas, the hippocampus was the brain region where improvements in the capacity for efficient communication and integration of disparate information most closely tracked reports of memory vividness.

These findings provide novel insight into existing memory theories that identify the hippocampus as a "bottleneck" or "convergence zone" at which information from distributed brain regions is processed and integrated to facilitate memory retrieval (Damasio 1989; Moll and Miikkulainen 1997; Mišić et al. 2014). Though it is widely assumed that the hippocampus operates as a convergence zone during the encoding and retrieval of episodic memories, the lack of an adequate, multivariate analytic methodology has stymied progress on properly investigating this idea in healthy, living humans. With the explosion of interest in large-scale complex network analyses coupled with recent advances in statistical physics that have produced relevant graph theory measures, we now have the requisite measures for identifying brain regions that facilitate the convergence and joint processing of specialized information from distributed brain regions while participants actively engage in memory-related tasks. The ability to identify the hippocampus as the network node that adjusts its integrative properties the most in accordance with the vividness of retrieved memories provides novel evidence for the hippocampus as a convergence zone in the brain. Future studies using high-resolution fMRI and manual ROI tracing might be able to investigate whether episodic memory for object features involves other convergence zones besides the hippocampus, such as perirhinal cortex (Bussey et al. 2005; Mclelland et al. 2014; Ryan et al. 2012).

Despite the assumption that the hippocampus occupies a convergence zone in the brain, graph theory analyses of structural (Hagmann et al. 2008; van den Heuvel et al. 2012; Gong et al. 2009) and functional (Buckner et al. 2009; Tomasi and Volkow 2010) whole-brain networks "at rest" in humans have consistently demonstrated that the hippocampus is not topologically central in brain network. The hippocampus has not been identified as among the most highly connected network nodes, nor has it been shown to occupy a critical position along shortest paths in the network. Similarly, we found that the hippocampus was not among the most highly connected, influential network nodes in vivid or dim retrieval networks taken separately. This does not imply, however, that the hippocampus should not be considered a convergence zone in these episodic networks; it is the "relative change" in network properties at the hippocampus in accordance with memory performance that provide insight into the integrative functions of the hippocampus for memory retrieval. Interestingly, the most central nodes in the network identified for dim and vivid retrieval separately were not among the nodes that exhibited the largest shifts in degree and page rank centrality between dim and vivid retrieval conditions (Fig. 4 and see Supplementary Materials). A more general implication of this finding is that to investigate the properties of brain regions within large-scale memory networks, it is necessary to focus on functional connectivity patterns associated with memory performance. This typically requires the use of event-related fMRI and the construction of separate connectivity matrices for trials that differ in behavioral performance.

Hippocampal First-Step Connections Substantially Reorganize to Support Vivid Memory Retrieval

Even though observed shifts in network properties of the right hippocampus can only be explained in full by appealing to the entire network architecture, those shifts are at least partly due to a substantial reorganization of connectivity strengths for the set of first-step (direct) connections. Because the right hippocampus exhibited a substantial reorganization of its direct connections between dim and vivid retrieval, we can reasonably conclude that this substantial reorganization is at least partly responsible for observed changes in path length, page rank centrality and leverage centrality. Thus, the changes in these measures are not merely due to changes in connectivity elsewhere in the network that do not directly involve interactions with the right hippocampus. The finding that the hippocampus drastically reorganized its set of direct connections from dim to vivid retrieval provides complementary support for the idea that this region can alter its connectivity profile to operate as a convergence zone during successful episodic memory.

To acquire more specific information about how the right hippocampus reorganizes its set of first-step connections, we identified the magnitude and direction of changes in connectivity strength between the right hippocampus and every other network node from dim to vivid memory retrieval. The right hippocampus exhibited significant increases in connectivity strength with nodes commonly assumed to directly interact with the hippocampus during vivid episodic retrieval, such as occipito-temporal regions supposed to store visual memory traces and frontal regions supposed to mediate retrieval control operations (see Fig. 5). This finding is consistent with recent work from King et al. (2015), who have demonstrated that the hippocampus

shows increased direct connectivity with many diffuse, functionally distinct brain regions for recollecting picture–word pairs. Relatedly, the stark reorganization in first-step connections to the right hippocampus suggests that the significant overall increase in connectivity strength (degree centrality) of the right hippocampus from dim to vivid memory retrieval is not due to a relatively even strengthening of all hippocampal connections. Instead, there is substantial variability in the magnitude of connectivity strength shifts between corresponding connections during vivid vs. dim memories.

Extra-Hippocampal Global Network Changes Support Vivid Memory Retrieval

Beyond the hippocampal structures, studies with brain-damaged patients and more traditional functional activation analyses in healthy adults have demonstrated that numerous other brain regions are critically important for episodic memory retrieval, including: posterior parietal regions, precuneus, prefrontal cortex, thalamus, retrosplenial and posterior cingulate regions, occipito-temporal regions, and other medial temporal lobe structures (Cabeza and Nyberg 2000; Wagner et al. 2005; Cabeza et al. 2008; Spaniol et al. 2009; Huijbers et al. 2011; Rugg and Vilberg 2013). Importantly, the prefrontal cortex, precuneus, visual cortex, thalamus, posterior parietal regions, and other medial temporal lobe structures (in addition to the hippocampus) have been identified as densely interconnected during successful episodic memory retrieval (Preston and Eichenbaum 2013; Staresina et al. 2013; Schedlbauer et al. 2014). These results collectively emphasize the idea that a dense, interconnected, interdependent network of disparate brain regions, each with a particular function, facilitates episodic memory retrieval. Although the hippocampus may be necessary for vivid, rich episodic memory retrieval, its proper functioning in the network is likely not sufficient. Thus, it is reasonable to hypothesize that more global integrative properties of the network are predictive of vivid memories of recently encoded events. Supporting this hypothesis, our results demonstrated that the network as a whole exhibited a greater capacity for effective information integration supporting vivid memory retrieval. Even after removing the right hippocampus from the networks, vivid retrieval networks still exhibited a greater capacity for efficient information integration.

Conclusions

In sum, the results obtained in this study demonstrate that the manner in which the network as a whole efficiently integrates information and the specific role of the right hippocampus in integrating information changes significantly between vivid and dim retrieval of recently encoded scenes. Our results, therefore, provide a new perspective on the neural basis of episodic memory, capturing the importance of optimal integration in the large-scale network as a whole and among critically important network nodes embedded within the network in generating vivid, detailed episodic memories.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/online.

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Notes

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