Functional Connectivity during Encoding Predicts Individual Differences in Long-Term Memory

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Abstract

What is the neural basis of individual differences in the ability to hold information in long-term memory (LTM)? Here, we first characterize two whole-brain functional connectivity networks based on fMRI data acquired during an n-back task that robustly predict individual differences in two important forms of LTM, recognition and recollection. We then focus on the recognition memory model and contrast it with a working memory model. Although functional connectivity during the n-back task also predicts working memory performance and the two networks have some shared components, they are also largely distinct from each other: The recognition memory model performance remains robust when we control for working memory, and vice versa. Functional connectivity only within regions traditionally associated with LTM formation, such as the medial temporal lobe and those that show univariate subsequent memory effect, have little predictive power for both forms of LTM. Interestingly, the interactions between these regions and other brain regions play a more substantial role in predicting recollection memory than recognition memory. These results demonstrate that individual differences in LTM are dependent on the configuration of a whole-brain functional network including but not limited to regions associated with LTM during encoding and that such a network is separable from what supports the retention of information in working memory.

INTRODUCTION

The ability to hold information in long-term memory (LTM) varies dramatically across individuals: Whereas some can instantaneously recognize a stranger whom they talked to at a party 20 years ago, some struggle to even remember a classmate they met earlier that week. Why is this the case? Previous work has investigated how specific neural measures, mostly involving the hippocampus or cortico-hippocampus networks, are correlated with trait-level variations in various forms of LTM (e.g., semantic and topographic memory: Trelle et al., 2020; Sormaz et al., 2017; associative memory: Touroutoglou, Andreano, Barrett, & Dickerson, 2015; free recall: Wang et al., 2010; autobiographical memory: Sheldon, Farb, Palumbo, & Levine, 2016; source memory: Sneve et al., 2017). Moving beyond correlation-based analysis, recent work has started to conduct out-of-sample prediction of individual differences in LTM (e.g., reading recall: Jangraw et al., 2018; item memory and spatial memory: Persson, Stening, Nordin, & Söderlund, 2018).

There has also been a burgeoning body of work characterizing the neural correlates of individual differences in working memory (WM), the ability to maintain and manipulate a limited amount of information actively over a short period (for a review, see Luck & Vogel, 2013). In fMRI studies of WM, the activity in posterior intraparietal sulcus (IPS) scales with WM load until the individual participant’s WM capacity is reached (Xu & Chun, 2006; Todd & Marois, 2004, 2005), and the difference in IPS activation between high and low set sizes is correlated with WM capacity (Todd & Marois, 2005). In addition to the activation difference in IPS, preparatory activities in the pFC and BG were also associated with individual differences in WM capacity (McNab & Klingberg, 2008). More recent work focuses on functional connectivity (FC), a measure of how synchronized different brain regions are, and characterizes whole-brain networks that are predictive of WM capacity within young adult populations and generalizable to older people or psychiatric populations (Avery et al., 2019; Bertolero, Yeo, Bassett, & D’Esposito, 2018; Yamashita et al., 2018).

The intense interest in individual differences in WM and its neural basis perhaps comes as no surprise given the foundational role of WM in supporting a suite of more complex cognitive abilities (such as reasoning, fluid intelligence, and planning; Conway et al., 2003; Süß, Oberauer, Wittmann, Wilhelm, & Schulze, 2002). Behaviorally, a moderate correlation is also often observed between WM and LTM performance across individuals, in terms of both recall and recognition (Unsworth, 2010). Moreover, a recent article combining the meta-analysis of 61 published experiments with 13 new experiments presented compelling evidence that actively maintaining an item in WM led to enhanced delayed recognition for that item (Hartshorne & Makowski, 2019). Considering the centrality of WM in such
a wide range of cognitive functions, could the individual variability in LTM be explained by the neural network underlying individual differences in WM?

The similarity and distinction between memory on different timescales is probably one of the oldest questions in memory research (Cowan, 2008; James, 1891). Despite the phenomenological differences of these two kinds of memory, there remain controversies about whether they are supported by distinct neural mechanisms, mostly centering around the medial temporal lobe (including the hippocampus), and whether these regions are necessary for both WM and LTM. Studies about patients such as H. M. show that damage to the medial temporal lobe leaves the patients’ WM intact but impairs their ability to form new LTM, suggesting the medial temporal lobe plays a critical role in LTM but not WM (e.g., Scoville & Milner, 2000). However, more recent work found activation in the medial temporal lobe during WM encoding (Ranganath & D’Esposito, 2001) as well as during WM retrieval (Öztekin, Davachi, & McElree, 2009). In addition, active maintenance of items during the early stage of WM delay contributes to later LTM formation, modulated by a network including dorsolateral pFC and the hippocampus (Blumenfeld & Ranganath, 2006; Ranganath, Cohen, & Brozinsky, 2005). In line with these results in healthy populations, patients with medial temporal damage showed impairments in WM for visual stimuli (Race, LaRocque, Keane, & Verfaellie, 2013; Olson et al., 2006), conjunctions (Olson et al., 2006), and relational bindings of object and spatial locations (Olsen, Rondina, Rigas, Meltzer, & Ryan, 2013). These results have led some researchers to cast doubt on the double dissociation between WM and LTM (for reviews, see Jenesson & Squire, 2012; Graham, Barense, & Lee, 2010; Ranganath & Blumenfeld, 2005; although also see Norris, 2017).

Although these previous works have made valuable contributions to understanding the neural mechanisms behind WM and LTM, they tend to focus on group level analysis and a circumscribed set of brain regions. To fully understand the functional architectures supporting these two memory functions, we need to consider the factors affecting the variation of WM and LTM across individuals (Dubois & Adolphs, 2016; Gabrieli, Ghosh, & Whitfield-Gabrieli, 2015). Theoretically, such findings will complement past studies on group level focusing on the mechanism consistent across individuals and may reveal novel neural factors critical for these functions. Clinically, focusing on individual differences can provide insights for characterizing different profiles of memory deficits observed in psychiatric or aging populations.

Recent developments in connectome-based predictive modeling (CPM; Shen et al., 2017) have validated the utility of building predictive models of different cognitive functions and traits such as fluid intelligence, sustained attention, extraversion, and WM from whole-brain FC (e.g., Avery et al., 2019; Hsu, Rosenberg, Scheinost, Constable, & Chun, 2018; Finn et al., 2015; Rosenberg et al., 2015). A distinct advantage of the CPM framework lies in its flexibility: On the basis of the same FC data, we can build different models that are predictive of a range of behaviors. By comparing these models, we can potentially identify the dissociable brain networks that support separable functions (e.g., IQ and sustained attention; Rosenberg et al., 2015) or overlapping brain networks underlying functions that may be related to each other (e.g., IQ and WM: Avery et al., 2019; sustained attention and reading: Jangraw et al., 2018). This flexibility of CPM has made it an ideal approach to probe the similarity and distinction between WM and LTM networks.

In the current study, we aim to investigate the individual differences in two widely studied forms of LTM, delayed recognition and recollection memory measured in a remember/know paradigm (Tulving, 1985). Using CPM to analyze data from the Human Connectome Project (HCP; Essen et al., 2013), we first characterized separate predictive models of individual differences in recognition and recollection based on whole-brain FC during a WM task (N-back) and rest. In addition, leveraging the predictive network models, we then investigate the similarity and distinction in the neural networks underlying LTM and WM by focusing on the contrast between recognition memory and WM. We then explored the utility of regions associated with LTM formation such as the medial temporal lobe (e.g., Scoville & Milner, 2000) and regions showing subsequent memory effects (Paller & Wagner, 2002) in predicting individual differences in recognition and recollection memory.

METHODS
Data Set
Data used in this study were released as part of the HCP S1200 release, described below.

Participants
We restricted our analyses to those participants who completed the two n-back fMRI runs and both runs of the recognition memory conducted outside the scanner. We also excluded participants whose e-Prime files during the N-back tasks and those during the recognition memory tasks did not match on at least one of the runs (i.e., the stimuli tested during the recognition memory task were never shown during the n-back task) and/or whose performance in the recognition memory tasks was below chance (overall d’ < 0). In addition, we excluded participants whose motion during the n-back runs did not meet any of following criteria: (1) grand mean root mean square relative motion across both runs < 0.1 mm, (2) maximum mean root mean square relative motion < 0.16, (3) maximum translation < 2 mm, and (4) maximum rotation < 3°. These motion thresholds were selected based on previous related work to mitigate the effect of excessive head...
motion on FC (e.g., Greene, Gao, Scheinost, & Constable, 2018; Rosenberg et al., 2015). Six hundred ninety-one participants were included in the final analysis (361 women, ages 22–36 years [$M = 28.52$ years, $SD = 3.70$, median = 29 years]).

$N$-back WM tasks

Details of the task can be found in Barch et al. (2013). Briefly, participants performed two runs of the $N$-back tasks while being scanned (about 5 min each). Each run consisted of eight task blocks of 10 trials. Within each run, half of the blocks are 0-back and the other half are 2-back. For 0-back blocks, participants were shown a target cue at the beginning of each block and had to respond “target” whenever they thought they saw this target during the block. For 2-back blocks, participants had to respond “target” whenever they thought the current stimulus was the same as the one presented two trials back. During each block, images can be from one of the four categories: faces, places, tools, and body parts. Each image was presented for 2 sec, followed by a 0.5-sec intertrial interval. Two-back accuracies (percent correct on both target and nontarget trials, i.e., both hit and correct rejection trials; collapsed across all four stimulus categories) were chosen as the target WM measure ($M = 85.40$, $SD = 9.49$, range = [48.61, 100]).

Delayed Memory Task

After the participants completed all fMRI runs during the session with the WM tasks, they were given an item recognition test for the faces and places images (48 in total) presented during the WM tasks, with an equal number of new faces and places. There were two runs of the recognition memory task, each consisting of 48 images (intermixed faces and scenes). Each image was presented with the three options (Remember, Know, or New) for 2 sec, followed by a 2-sec intertrial interval. No instructions about the recognition memory tests were given to the participants until after all the scans were finished. The delay between the end of $n$-back tasks and the recognition memory test is at least 13.5 min (assuming that there was no gap between tasks), which is considered to be well beyond the span of WM (Baddeley, 1992) and thus in the span of LTM. To measure recognition memory (Recognition) for each participant, $d'$ was calculated as $z(\text{hit rate}) - z(\text{false alarm rate})$ using the stats.norm.ppf function from the scipy package in Python ($M = 1.09$, $SD = 0.40$, range = [0.00, 2.38]). In addition, we measured recollection using the following formula: recollection = proportion of “Remember” responses to old items/(1 – proportion of “Know” responses to old items), which is the inverse of the formula for calculating familiarity-based recognition described in Yonelinas and Jacoby (1995). Recollection memory performance ranged from 0.00 to 0.95 ($M = 0.55$, $SD = 0.18$).

Imaging Parameters and Preprocessing

Details of imaging parameters (Essen et al., 2013) and preprocessing pipelines (Glasser et al., 2013) have been published elsewhere. Briefly, all fMRI data were acquired on a 3-T Siemens Skyra using a slice-accelerated, multiband, gradient-echo, EPI sequence (repetition time = 720 msec, echo time = 33.1 msec, flip angle = 52°, resolution = 2.0 mm$^3$, multiband factor = 8). Data from the two WM runs (one left/right phase encoding run and one right/left phase encoding run) as well as all four runs of resting state scan (split across two sessions; one left/right run and one right/left run per session) were used for this work. The scanning protocol (as well as procedures for obtaining informed consent from all participants) was approved by the institutional review board at Washington University in St. Louis. Use of HCP data for these analyses was deemed exempt from institutional review board review by the Yale Human Investigation Committee. The HCP minimal preprocessing pipeline was used on these data, which include artifact removal, motion correction, and registration to standard space (Glasser et al., 2013). All subsequent preprocessing steps were conducted with FMRIB Software Library (FSL; Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2011), FreeSurfer (Fischl, 2012), and the Python module Nilearn (Abraham et al., 2014), which includes the following steps conducted in the order described: detrending, bandpass filtering (range: 0.01–0.1 Hz), regressing out covariates of no interest (mean signals from gray matter, white matter, and cerebrospinal fluid and 24 motion regressors [six motion parameters, six temporal derivatives, and their squares]; all confounds were also detrended and bandpass filtered before being removed) and standardization. Mean frame-to-frame displacement ( FD) was calculated following Power et al. (2014) for each run and averaged to yield a motion value per each included participant and used for motion control analysis (e.g., partial-correlation-based feature selection; see below). All subsequent analyses and visualization were performed with MATLAB (Mathworks, Inc.) and Python.

Functional Parcellation

The Shen 368-node atlas (Shen, Tokoglu, Papademetris, & Constable, 2013) was applied to the preprocessed HCP data in standard space. After parcellating the data from each run into 368 nodes, the mean time courses of each node pair were correlated using Pearson’s $r$ and correlation coefficients were Fisher’s $z$ transformed, generating six $368 \times 368$ connectivity matrices per participant (two for $n$-back tasks; four for rest). These matrices for the same states were then averaged to produce two matrices (one for $n$-back, the other for rest) per participant.

Cognitive Prediction

A modified version of CPM (Shen et al., 2017; Finn et al., 2015; Rosenberg et al., 2015) was used to predict the
target behavior (2-back accuracy or $d'$) from the connectivity matrices using ridge regression (Greene, Gao, Noble, Scheinost, & Constable, 2020; Gao, Greene, Constable, & Scheinost, 2019). The models were trained and tested in a nested 10-fold cross-validated manner.

First, the participants were split into 10 groups, respecting family structure such that family members were always assigned to the same group. Nine of these groups served as training data; in the training set, features were selected on the basis of their Pearson correlation with the target score with a threshold of $p < .01$. Selected edges were then submitted as predictors (with the target score as response) to an L2-constrained linear least squares regression (lasso function in MATLAB with alpha set to 1e-6, which is equivalent to a ridge regression). The regression coefficients and intercept for each regression were estimated with an inner 10-fold cross-validation loop using only the training data. The set of parameters with the minimum cross-validated mean squared error was selected. These fitted coefficients and intercept were then applied to the corresponding edges in the left-out test participants to predict their target scores. For each fold, model performance was evaluated as the Pearson’s $r$ correlation between predicted and observed scores in the test participants. The above steps were performed iteratively with each group left out once. The resulting $r$ values between predicted and observed scores from the 10 folds were averaged to get a measurement of the model performance for the current iteration.

The entire pipeline described above was repeated 1000 times with different group partitions, resulting in 1000 mean $r$ values. Significance of the model performance was assessed with 1000 iterations of nonparametric permutation testing (Scheinost et al., 2019), and $p$ values were calculated as $(1 + \text{number of null models whose } r \text{ values } \geq \text{mean of all iterations of empirical models})/(1 + 1000)$ (Yoo et al., 2021; Avery et al., 2019). Resulting $p$ values were Bonferroni corrected for multiple comparisons (3, 2, 4, and 6 for the no-control, overlapping, partial regression, and orthogonalization models, respectively).

**Prediction with Only Overlapping Edges**

To investigate the commonalities in the functional networks supporting WM and Recognition, we also limited feature selection to only edges that were correlated with both WM and Recognition at a threshold of $p < .01$ and built ridge regression models to predict the given target measure. Statistical significance was assessed with the same permutation procedure as described above.

**Prediction while Controlling for Nontarget Behavior**

To investigate whether the functional networks supporting WM and Recognition are distinct from each other, we used the following three analyses to control for the nontarget behavior: partial correlation, orthogonalization of behavior measures, and edge exclusion. Statistical significance was assessed with permuted behavior labels (preserving behavior pairs, i.e., although assigned to the wrong participant, the WM and Recognition measures are still from the same participant) but the same analysis pipeline.

**Partial Correlation**

We controlled for the nontarget measure by running a partial correlation during the feature selection step described in the Cognitive Prediction section. Only edges that were correlated with the target behavior at $p < .01$ even after controlling for the nontarget behavior were included in the subsequent steps. In addition, we also tested if these control models trained on one target behavior generalized to predict the nontarget behavior (also in a fully cross-validated manner).

**Orthogonalization of Behavior Measures**

In addition to controlling for the nontarget behavior during edge selection, we also conducted a control analysis where we built models to predict the unique aspect of each memory measure by regressing out the shared components between the models. For each fold, before feature selection, using only the training data, we ran a linear regression where the target behavior was the response and the nontarget behavior was the predictor. Subsequently, the model was trained to predict the residuals of the target behavior after regressing out the nontarget behavior. The intercept and coefficient estimated from the training data were also applied to the two behavior scores in the test set to estimate the residuals in the target behavior after regressing out the nontarget behavior. The model performance was thus evaluated as the correlation between the predicted residuals and the actual residuals in the test set. To evaluate how much variance in the full memory scores was captured by the predicted residuals, we also tested the models trained using the residuals (after regressing out the nontarget behavior) on the full Recognition/WM scores. In addition, we tested if these control models trained on residuals in one target behavior generalized to predict the residuals in the nontarget behavior after regressing out the target behavior with the intercept and coefficients estimated from the training set.

**Evaluating and Visualizing Feature Contributions to a Predictive Model**

To evaluate the contributions of individual features and networks to the prediction of WM and Recognition, for each predictive model, we first identified the reliable edges that were selected on 100% of the feature selections (i.e., 10 folds × 1000 iterations = 10,000 feature selections). That is, these edges correlated with the target behavior.
significantly (at a threshold of \( p < .01 \)) on all the folds. The contribution of each selected feature was calculated as the mean of normalized beta weight assigned across all iterations of ridge regression. The normalized beta weight for a given edge during an iteration was calculated as the beta weight assigned to this edge divided by the sum of absolute values of ridge regression weights during the given iteration. The value assigned to each edge this way can be thought of a predictive utility where the absolute value indicates the fractional contribution of the feature to model performance, and the sign represents the relationship between the feature and the target behavior.

We first visualized the distribution of these reliable edges by grouping them into macroscale brain regions. We then explored the distributions of the models by grouping the nodes into 10 previously defined canonical networks (Greene et al., 2020; Noble et al., 2017) and summing the weights of features within each network and between each pair of networks. This sum is then normalized by the total number of edges between the given networks to account for differences in network size, resulting in a measure of the mean contribution of an edge in the given network pair.

To further characterize the contributions of different networks, we performed the following two complementary analyses. First, we only preserved connections within a given network during the feature selection step. The statistical significance of each network model was assessed via permutation tests. Second, we virtually “lesioned” each of the 10 networks by excluding all connections within and from the network during the feature selection step. The performance of each empirical model after excluding a given network was compared to the full model with all the networks using Wilcoxon signed-rank tests. The model building steps were the same as described in the Cognitive Prediction section. For each network that showed significant prediction for all three models, we additionally conducted pairwise comparisons between pairs of behaviors (i.e., recollection vs. recognition, recollection vs. WM, recognition vs. WM) with Wilcoxon signed-rank tests. All \( p \) values were corrected for multiple comparisons using Bonferroni correction (10 for true vs. null/full model comparison; 9 for between-behavior comparison).

The Roles of Medial Temporal Lobe and Other Regions Showing the Subsequent Memory Effect

To explore the roles of brain regions that were considered important for LTM formation based on previous literature, we identified these ROIs both anatomically and functionally and controlled for them during predictive modeling.

**Definition of an Anatomical Medial Temporal Lobe Mask**

We first defined an anatomical mask of the medial temporal lobe, known to be involved in LTM formation (e.g., Scoville & Milner, 2000), using the Harvard-Oxford Montreal Neurological Institute atlas (Center for Morphometric Analysis, Neuroscience Center, MGH-East) that encompassed hippocampus and parahippocampal gyrus (thresholded at probability = .25). Note that the anatomical mask is the same across all cross-validation iterations.

**Definition of a Subsequent Memory Mask**

We also defined a functional mask by running a univariate analysis using FSL in the training sample on each iteration to identify voxels that showed the subsequent memory effect (Paller & Wagner, 2002). First, we sorted the trials presented during the faces and places \( n \)-back blocks based on whether they were remembered or forgotten during the recognition memory tasks. This gave us a “remembered” predictor and a “forgotten” one for each run (with each trial covering 2.5 sec). We also included two predictors for the tools and body parts blocks (modeling each block as a 27.5-sec boxcar) to control for evoked activities from stimuli not tested in the recognition memory task. These four predictors were then convolved with a double-gamma “canonical” hemodynamic function to generate the main regressors. The temporal derivative terms of each predictor were added to the general linear model (GLM) as confounds of no interest to compensate for slice-timing differences and variability in the hemodynamic response function delay across regions. Subsequently, both the fMRI time series and the GLM design were temporally filtered with a Gaussian-weighted linear high-pass filter with a cutoff of 200 sec. The time series was prewhitened within FILM to correct for autocorrelations in the fMRI data before conducting the GLM. The contrast between the “remembered” and “forgotten” main regressors’ coefficients was used to estimate the subsequent memory effect. For each participant in the training sample, a 10,000 permutations using FSL’s randomise to identify voxels with a significant subsequent memory effect (i.e., higher activation during the encoding of remembered compared to forgotten trials) at a group level (in the training group). The resulting mask was thresholded at \( p < .01 \) (FWE-corrected) to generate a final subsequent memory mask for this iteration. Note that, unlike the anatomical mask, the exact voxels included in this functionally defined subsequent memory mask could differ across iterations because of the changing training samples.

After defining these two masks, we identified nodes in the Shen atlas that overlap with these two masks at least 5%, respectively, and explored their roles in the prediction of the full memory measures in four ways during feature selection: (1) only including edges connecting nodes within the mask of interest (i.e., medial temporal lobe or subsequent memory mask), (2) only including edges within nodes in the mask of interest and from nodes in the mask to other nodes, (3) including only edges connecting nodes in the mask of interest and nodes outside the mask, and (4) excluding any edges that involve the nodes in the mask of...
interest. Subsequent steps were the same as described in the Cognitive Prediction section. The statistical significance of each model was assessed via permutation tests. The performances of different models were compared using Wilcoxon signed-rank tests. All p values were corrected for multiple comparisons using Bonferroni correction.

The Effect of Head Motion
While we tried to mitigate the effects of head motion on FC by setting stringent inclusion criteria, in this section, we sought to more carefully control for motion in the analysis pipeline. Two-back accuracy was weakly negatively correlated with motion (measured with mean FD averaged across the two WM runs; \( r = -0.10 \), 95% CI from 1000 bootstrapping iterations: [−0.18, −0.02]), whereas neither dʹ nor recollection was correlated with motion (dʹ with motion: \( r = -0.02 \), 95% CI [−0.08, 0.05]; recollection with motion: \( r = -0.02 \), 95% CI [−0.02, 0.13]). Using the same partial correlation procedure as described above in the Prediction while Controlling for Nontarget Behavior section, we included mean FD as the covariate during edge selection and repeated the prediction analyses. As an additional way to further control for motion, we also controlled for motion by excluding any edges that correlated with mean FD. Namely, during edge selection, we ran two Pearson’s correlations with the edges during the feature selection stage: one with the target behavior and the other with mean FD. Thresholding at \( p < .01 \), we obtained two sets of edges that were correlated with the memory behavior and motion, respectively. Only edges that were included in the memory behavior set but not in the motion set were selected for the subsequent steps. In both cases, model performance remained robust (all \( p s < .001 \)).

RESULTS

FC during Task, But Not Rest, Predicts Individual Differences in LTM
We first demonstrated that FC during an n-back task successfully predicted out-of-scanner recognition (Figure 1; mean \( r = 0.32 \), \( p < .001 \)) as well as recollection memory performance (Figure 1; mean \( r = 0.23 \), \( p < .001 \)). Replicating Avery et al. (2019), a separate model built from the same n-back task FC also successfully predicted 2-back accuracy (Figure 1; mean \( r = 0.35 \), \( p < .001 \)). On the other hand, FC during rest carried limited predictive power in terms of all three memory measures (Figure 1; recognition: mean \( r = 0.10 \), \( p = 0.53 \); recollection: mean \( r = 0.11 \), \( p = 0.064 \); 2-back accuracy: mean \( r = 0.21 \), \( p < .001 \)).

Recognition Model Has Some Shared Components with But Is Also Distinct From WM Model
Behaviorally, the three memory measures were all moderately correlated with each other in our sample, suggesting shared behavioral variance (see Figure 2; all \( ps < .001 \) from 1000 bootstrapping iterations). To further investigate the similarities and distinctions in the networks supporting LTM and WM, we next focused on recognition memory and contrasted it with WM. The task models presented above for these two memory measures both generalized to predict the nontarget behavior (Figure 3; trained on Recognition, tested on WM: mean \( r = 0.21 \), \( p < .001 \); trained on WM, tested on Recognition: mean \( r = 0.11 \), \( p < .001 \)). To probe the overlap of the two networks, we only included edges that are correlated with both WM and Recognition (at \( p < .01 \)) during feature selection. The average number of edges included in the model was thus reduced to 326.18, an 89.60% reduction from the 3136.24 edges for the full WM model and an 84.19% reduction from the 2063.66 edges for the full Recognition model. Model performances remained robust for both memory constructs even when limiting features to only overlapping edges (Figure 3: Recognition: mean \( r = 0.26 \), \( p < .001 \); WM: mean \( r = 0.30 \), \( p < .001 \)), suggesting that WM and Recognition are supported by partially overlapping brain networks.

After demonstrating that there were shared components between Recognition and WM models, we sought to investigate the distinct functional architectures underlying Recognition and WM. First, both models remained robust after we controlled for the nontarget behavior with partial correlation during feature selection (Figure 3; Recognition: mean \( r = 0.30 \), \( p < .001 \); WM: mean \( r = 0.35 \), \( p < .001 \)). To further investigate whether partial correlation effectively isolated the two memory measures, we tested if the control models generalized to predict the nontarget behavior. Interestingly, both control models still generalized to predict the nontarget behavior, albeit to a lesser degree (Figure 3;
trained on Recognition, tested on WM: mean $r = .21, p < .001$; trained on WM, tested on Recognition: mean $r = .19, p < .001$). These generalization results suggest that the partial correlation procedure did not necessarily remove all edges that were correlated with the nontarget measure. That is, partial correlation only guaranteed that the selected edges were correlated with the residuals in the target behavior after the nontarget behavior was regressed out from both the edge strengths and target behaviors. However, this did not guarantee that the selected edges were not correlated with the nontarget behavior. Furthermore, the partial correlation models could still be capturing some of the shared components between WM and Recognition measures and thus generalize to predict the full nontarget scores.

To further establish that predictive models are able to capture the unique aspect of each memory measure, we regressed out the shared component between the two measures, built models, and tested them on the residuals. That is, we explicitly controlled for the nontarget behavior by orthogonalizing the two measures. Both models remained robust (Figure 3; Recognition: mean $r = .26, p < .001$; WM: mean $r = .31, p < .001$). The model trained on only Recognition residuals still predicted the full Recognition scores (mean $r = .20, p < .001$). The WM residuals model also significantly predicted the full WM scores (mean $r = .15, p < .001$). In contrast to the partial correlation models, the model trained on Recognition residuals did not generalize to predict the

Figure 2. The three memory measures are moderately correlated with each other. The histograms shown on the top and right sides of the graphs correspond to the distributions of the memory behaviors (orange: recollection, red: recognition, blue: WM).

Figure 3. Summary of model performance for predicting recognition (Recog.) and WM with different model training procedures. No control: full model without controlling for the nontarget behavior. Overlap: limiting edge selection to those correlated with both recognition and WM. Partial Correlation: controlling for the nontarget behavior during edge selection using partial correlation. Orthogonalizing behaviors: building models to predict the residuals in target behavior after regressing out the nontarget behavior. $y$ Axis represents Pearson’s $r$ between predicted and observed scores averaged across iterations. Error bars: standard deviation of the $r$ values across iterations. Legends were presented in terms of “training-testing” pairs: for example, Recog. full – WM full means that the model is trained on the original $d'$ but tested on the original 2-back accuracies. Recog. full: the original $d'$. WM full: the original 2-back accuracies. Recog. resid: the residuals in $d'$ after regressing out 2-back accuracies. WM resid: the residuals in 2-back accuracies after regressing out $d'$. ns = not significant; $^*p < .1$, $^*^*p < .05$, $^*^*^*p < .01$, $^*^*^*^*p < .001$. 
WM residuals (mean $r = .00$, $p = .420$). However, interestingly, the model trained on WM residuals was still able to capture some variance in the Recognition residuals, albeit to a much lesser degree (mean $r = .12$, $p = .003$). Collectively, these results suggest that the Recognition model is separable from the WM model.

**All Three Memory Models Are Spatially Distinct from Each Other**

We first compared the similarities between the different predictive models for the three target behaviors (Recollection/Recognition/WM) on the network level (Figure 4). For Recognition and WM, we additionally included the anatomical distributions of the predictive features from the models derived from the different procedures (partial correlation, regressing out control behavior, and overlapping edges). The features identified for the same target behavior are highly similar to each other except when features were forced to be the overlapping edge between the two memory measures. Because we only constrained the set of edges included

**Figure 4.** Multidimensional scaling plot illustrating the distance between the different models at the network level. Distance was calculated as the Euclidean distance between each pair of models after mean-centering and scaling along each dimension. No control: full model without controlling for the nontarget behavior. Overlap: limiting edge selection to those correlated with both recognition and WM. PartCorr: controlling for the nontarget behavior during edge selection using partial correlation. RegOut: building models to predict the residuals in target behavior after regressing out the nontarget behavior.

**Figure 5.** Anatomical distributions of predictive features for the three main models. For each panel, on the top are results from grouping nodes at the network level. Purple: features with positive weights; green: features with negative weights; shade: relative model contribution. Network labels: MF = medial frontal; FP = frontoparietal; DM = default mode; MT = motor; VI = Visual I; VII = Visual II; VA = visual association; SA = salience; Sub = subcortical; CBL = cerebellum. On the bottom are results from grouping nodes into macroscale brain regions. The entire circle represents all 368 nodes, divided into the macroscale brain regions. The different locations on each ribbon represent the different nodes that belong to this region. Each line represents a reliable predictive edge. Purple: features with positive weights; green: features with negative weights; shade: relative edge weight. Macroscale regions labels: Mot = motor cortex; Ins = insula; Par = parietal cortex; Tem = temporal cortex; Occ = occipital cortex; BSM = brainstem; LB = limbic regions (including the thalamus and striatum); Sub = subcortical regions (including the thalamus and hippocampus); CBL = cerebellum. (A) Predictive features of the recollection model. (B) Predictive features of the recognition model (without controlling for any nontarget behavior). (C) Predictive features of the model trained for WM (without controlling for any nontarget behavior).
in the ridge regression, the relative weights of the edges could still differ between the two target behaviors if they required distinct configuration of this set of edges. However, instead, we observed high rank similarity (Spearman rank correlation = 1.00) between the overlapping models for WM and Recognition, suggesting that the overlapping edges could be supporting cognitive processes that contribute to both the retention of WM and Recognition. Interestingly, the recollection memory model is highly dissimilar from all the other models (maximum Spearman rank correlation = .07).

As shown by the two clusters in Figure 4, the distributions of predictive networks for the same target behavior (Recognition/WM) from the no-control, partial correlation, and orthogonalizing behavior procedures are quite similar to each other on the canonical network level (Recognition: minimum $r = .70$; WM: minimum $r = .80$). For concision and clarity, only the predictive networks from the no-control procedure for all three memory measures are reported below (Figure 5) to demonstrate the patterns. In addition, we visualize the anatomical distribution of the overlapping models for both Recognition and WM (Figure 6).

For the Recollection model (Figure 5A), edges within the Visual I network and between Visual I and frontoparietal networks emerged as the most important positive features, whereas edges in the Visual I–cerebellum, frontoparietal–subcortical, and visual association–subcortical networks are the most important negative features. For the Recognition model (Figure 5B), edges in the Visual I, Visual I–visual association, and Visual I–subcortical networks emerged as the most important positive features, whereas edges in the default mode, Visual I, and default mode–subcortical networks emerged as the most important negative features. The importance of edges in the visual networks was further demonstrated by the distribution of predictive edges across the macro-scale brain regions as the occipital and temporal lobes were involved in most of the positive features. In contrast to the Recognition model, the WM model contained edges that were more widespread (Figure 5B bottom vs. Figure 5C bottom) and engaged more networks (Figure 5C). Edges in the motor, default mode, and salience networks emerged as the most important negative features in predicting WM, whereas edges in the default mode–frontoparietal, default mode–salience, and default mode–subcortical networks emerged as the most important negative features. When we limited the features to only edges correlated with both WM and Recognition (Figure 6A and 6B), the predictive models for the two measures were highly similar in terms of both distribution across macroscale brain regions and the canonical network level.
networks. Edges within the prefrontal and parietal regions of the salience network were the most important positive features, whereas edges between the default mode and Salience networks were the most important negative features.

The different patterns of critical features for the three memory networks are further supported by the following two complementary analyses. First, we only preserved connections within a given network during the feature selection step. For the recollection memory model, preserving the frontoparietal, Visual I, and default mode networks led to the highest prediction (Figure 7A). For the full Recognition scores, preserving the default mode, Visual I, and salience networks led to the highest prediction performance (Figure 7B). For the full WM scores, preserving the salience, frontoparietal, motor, default mode, and Visual I networks led to the highest prediction performance (Figure 7C). Among the three networks that showed significant prediction for all three behaviors (frontoparietal, Visual I, and default mode networks), the frontoparietal network was most important for the prediction of WM (both ps < .001), whereas both the Visual I and default mode networks were most important for the prediction of Recognition (all ps < .001).

Figure 7. Boxplots of model performance when controlling for each of the 10 different networks. Network labels: MF = medial frontal; FP = frontoparietal; DM = default mode; MT = motor; VI = Visual I; VII = Visual II; VA = visual association; SA = salience; SubC = subcortical; CBL = cerebellum. For some networks, no edges passed the thresholding step (p < .01), and thus no prediction was generated. This is reflected by missing boxes. (A) Predicting recollection when edge selection was restricted to within-network edges. (B) Predicting recognition when edge selection was restricted to within-network edges. (C) Predicting WM when edge selection was restricted to within-network edges. (D) Predicting recollection when edge selection was performed after excluding edges from a given network. (E) Predicting recognition when edge selection was performed after excluding edges from a given network. (F) Predicting WM when edge selection was performed after excluding edges from a given network. Dashed lines represent the mean performance of the models without any control. For the within-network results (top row), statistical annotations indicate whether the given network significantly predicted the target behavior compared to a null model. For the exclude-network results (bottom row), statistical annotations indicate whether excluding the given network led to a significant change in prediction performance compared to the full model where all networks were included. All p values were corrected for multiple comparisons using Bonferroni correction (ns = not significant; ∼p < .1, *p < .05, **p < .01, ***p < .001).
Second, we virtually “lesioned” each of the 10 networks by excluding all connections within and from the network during the feature selection step. Mirroring the results above, the lesioning analyses again highlighted the importance of Visual I network to the prediction of recollection memory (Figure 7D), that of Visual I and default mode networks to Recognition (Figure 7E), and that of the motor, frontoparietal, and salience networks to WM (Figure 7F).

**Brain Regions Associated with LTM Formation Are Useful But Not Sufficient to Predict LTM**

In the following section, we explicitly related our findings to the brain regions identified in the previous literature to be important for LTM formation. To this end, we first defined an anatomical medial temporal lobe mask based on the Harvard-Oxford Atlas and then defined a functional mask containing voxels that showed the subsequent memory effect in a univariate analysis.

We identified 11 nodes in the Shen atlas that overlap with the anatomical medial temporal lobe mask over 5% (see Figure 8A for a visualization of these nodes) and investigated the role of the medial temporal lobe during model training (see Cognitive Prediction under the Methods section) in four ways: (1) including only edges within these 11 nodes, (2) including only edges connecting within these nodes and from these nodes to other nodes, (3) including only edges connecting the medial temporal lobe nodes and nodes outside the medial temporal lobe (but not within the medial temporal lobe), and (4) excluding any edges that involve medial temporal lobe nodes.

The results from the medial temporal lobe analysis were shown in Figure 8B. None of three models built from edges within the medial temporal lobe provided significant prediction of the target behavior, suggesting that the successful prediction observed above in the full models is not driven by localized regions within the medial temporal lobe. All other models performed above chance (all ps < .001). These results exhibited a clear gradient of importance of the interaction between the medial temporal lobe and other brain regions across the three different memory behaviors (recollection, recollection, and WM). The interaction between the medial temporal lobe and other regions is critical for the prediction of recollection memory such that using limiting feature selection to only medial temporal lobe and medial-temporal-lobe-related edges or only medial-temporal-lobe-related edges led to a prediction performance for recollection that is almost the same as or even slightly better than the whole-brain model (only medial temporal and medial-temporal-lobe-related edges vs. whole-brain model: $\Delta r = .00, z = .61, p = .542$; only medial-temporal-lobe-related edges vs. whole-brain model: mean $\Delta r = .004, z = 5.03, p < .001$). On the contrary, for recognition memory, limiting feature selection to only medial temporal lobe and/or medial-temporal-lobe-related edges led to a substantial drop in the model performance (minimum mean $\Delta r = .08, z = 38.72, p < .001$). Interestingly, medial temporal lobe is still more useful for predicting individual differences in recognition memory than WM (both ps < .001), consistent with the previous finding that medial temporal lobe is more important for retaining information over longer timescale (Eichenbaum, Yonelinas, & Ranganath, 2007). This gradient of importance of the medial temporal lobe to the three memory measures is mirrored in the excluding edges analysis. Excluding all medial temporal lobe related edges leads to the largest drop in performance for recollection memory ($\Delta r = 0.05, z = 28.87, p < .001$), followed by a smaller drop in performance for recognition memory ($\Delta r = 0.02, z = 26.21, p < .001$) and then by a very small drop for WM ($\Delta r = 0.002, z = 4.25, p < .001$).

**Figure 8.** Results from controlling for nodes in the medial temporal lobe (MTL). (A) Nodes in the Shen atlas that overlap with the MTL mask over 5%. Individual nodes are represented by distinct colors. (B) Boxplot of model performance when controlling for nodes in MTL using different methods. Within: limiting edges to only those within the control mask; Within&Related: limiting edges to those within and from the control mask; Related: limiting edges to only those between nodes in the control mask and nodes outside the control mask; Exclude: excluding any edges involving nodes in the control mask. Red: Dashed lines represent the mean performance of the different memory models without any control. *$p < .1$, **$p < .05$, ***$p < .01$, ****$p < .001$. ns = not significant; L = left; R = right.
Next, we explored the role of regions showing subsequent memory effect. Figure 9A shows a Remembered versus Forgotten contrast map defined on the entire sample. Across all the folds, there were 10-44 nodes (median = 24) in the Shen atlas that overlap with the MTL mask over 5% across all validation folds. Note that the subsequent memory mask includes regions beyond the medial temporal lobe, in the frontal and occipital lobes.

The results from subsequent memory mask analysis were shown in Figure 9C. All the models performed above chance (all ps < .01) except for the recollection memory model built with only edges within the subsequent memory mask. Unlike the medial temporal lobe mask, edges within the subsequent memory mask actually carry some predictive power for recognition and WM. Interestingly, in this case, the WM model performed better than the recognition model (Δr = .02, z = 21.82, p < .001). On the contrary, when feature selection was expanded to include edges connecting the subsequent memory mask or only edges between the mask and other regions, the recognition models performed better than the WM models (both ps < .001). As for recollection, the models with only edges within and/or related to subsequent memory mask capture substantially less variance as the full model (only edges within and related to subsequent memory mask vs. whole-brain model: Δr = −.017, z = 20.00, p < .001; only subsequent-memory-mask-related edges vs. whole-brain model: mean Δr = −.014, z = 16.98, p < .001). As for recognition, both the recognition model with just edges within and connecting the subsequent memory mask and one with just edges connecting the subsequent memory mask and other nodes performed worse than the full recognition model (within and related edges: mean Δr = .06, z = 38.35, p < .001; only related edges: mean Δr = .05, z = 38.33, p < .001). This is further supported by the observation that including edges both within and from subsequent memory mask did not lead to better performance in predicting recognition than including only those connecting these mask and other regions (mean Δr = .0006, z = 0.93, p = .350) and that excluding any
edges involving the subsequent memory ROIs still yielded a robust prediction compared to the full model (mean $\Delta r = .01, z = 19.11, p < .001$), again demonstrating the importance of large-scale brain networks to the prediction of LTM, rather than localized regions.

**DISCUSSION**

In this study, we are primarily interested in exploring the basis of individual differences in LTM, focusing on delayed recognition and recollection memory. We successfully built predictive models of individual differences in recognition and recollection memory performance based on whole-brain FC during an N-back task. On the contrary, we found that FC during rest had limited predictive power compared to task, consistent with other recent works on increased prediction performance from task data compared to resting data (e.g., Yoo et al., 2018, 2020, 2021; Jiang et al., 2020; Tomasi & Volkow, 2020; Greene et al., 2018; Rosenberg et al., 2016). By comparing the recognition memory model and a model built to predict WM performance based on the same FC data, we found that there are some shared components between WM and recognition memory supported by evidence from overlapping predictive networks and cross-measure prediction. By orthogonalizing the two memory measures, we were also able to build networks that are predictive of the unique components in each memory measure. Our results shed new light on the similarity and distinction between the neural networks supporting WM and delayed recognition. In addition, we also showed that models built on only ROIs previously shown to be associated with within-participant fluctuations in LTM performance are useful but not sufficient to capture across-participant differences in recognition and recollection memory, demonstrating the importance of considering large-scale networks in understanding the functional architecture supporting LTM.

Our approach complements previous research on the relationship between WM and delayed recognition in two important ways. First, we were able to build recognition memory and WM models with only features that were predictive of both kinds of memory, suggesting that they are supported by overlapping edges mainly in the salience network. Furthermore, the relative importance of these selected edges was highly similar for predicting WM and recognition memory, further demonstrating that there are shared cognitive processes supported by the salience network (e.g., attention allocation to salient stimuli; Uddin, 2015; Menon & Uddin, 2010). However, one limitation of interpreting the nature of the shared variance between the WM and Recognition models in the current study is that the models were built on the same fMRI data and therefore could reflect a more general brain state that may affect any concurrent cognitive processes, rather than the specific cognitive process involved in the retention of information in both short and long timescales. Future work should explore whether the overlapping component identified in the current study is specifically related to memory processes or is predictive of other cognitive functioning as well.

Second, we showed that the recognition memory model remained robust when we controlled for WM and vice versa. Given that the recognition memory and WM models were identified from the same brain activities during the n-back tasks and thus effects from stimuli and neural states were held the same for the two models, our finding of dissociable WM and Recognition networks revealed a true distinction between the neural architectures supporting the retention of the same information in WM versus Recognition. Functional connections in the visual, default mode, and subcortical networks contributed more to the prediction of recognition memory performance, whereas those in the motor, frontoparietal, default mode, and salience networks were more important for the prediction of WM.

The partitioning of shared and unique components between Recognition and WM networks in our study could be especially useful in identifying which of these components are selectively associated with normal and pathological aging, thus providing implications for developing more targeted treatment. Both WM and LTM showed substantial decline with advanced aging (Park et al., 2002, 1996). However, memory systems are differentially affected by normal aging and age-related disease such as Alzheimer’s disease (Gabrieli, 1996). Moreover, previous work has suggested that there are multiple factors linked to memory decline in aging and distinguished between changes in the frontal–striatal system, which primarily affects executive functioning, and changes in the medial temporal lobe memory system (Buckner, 2004). Separate studies have found that FC measured during resting state is predictive of WM (Avery et al., 2019), LTM (Meskaldji et al., 2016), and general cognitive impairment (Lin et al., 2018) in an aging population. These studies suggest that there were functional connections shared by models of these memory-related constructs, such as those in the frontoparietal control and default mode networks. However, there were also differences: The motor network has been implicated in the WM and general cognitive impairment networks, whereas the thalamus plays an important role in modulating LTM. Extending on these previous results, our study investigated the overlapping and unique features supporting WM and an important type of LTM, delayed recognition memory in the same sample, and thus better controlled for the effect of samples and analysis pipeline on the identified features. Future work can validate the overlapping and unique features from our models in aging populations, which could potentially complement behavioral testing and serve as a tool for characterizing distinct neural profiles of cognitive impairment because of normal aging or pathological conditions.

In addition to providing insights into the functional architectures supporting WM and recognition memory, our
study also posts interesting questions about the neural sources of between- and within-individual differences in recognition memory performance. We found that, although functional connections of ROIs associated with subsequent recognition captured some variance in the recognition memory performance across individuals, the predictive power of a model built on only these connections was substantially weaker than the whole-brain model. Furthermore, excluding these ROIs from our analysis led to only a negligible drop in predictive power. There are at least two possible explanations for this pattern of results. First, these ROIs were originally derived based on group-based studies (for reviews, see Squire, Stark, & Clark, 2004; Paller & Wagner, 2002) where data from individual participants were aggregated to find common neural processes underlying subsequent memory. Therefore, these ROIs should show stability across individuals and may not be informative for revealing between-participant variance. Second, these ROIs were identified using task activation, whereas the neural measure in our study is FC. These two measures are not redundant (Greene et al., 2020): In fact, a certain brain region can show a decrease in activity but an increase in connectivity with other brain regions and vice versa (Bassett, Yang, Wymbs, & Grafton, 2015). Our results show that the ability to successfully encode information into LTM so that these items can be later recognized is an emergent property of large-scale functional brain networks, rather than localized brain regions, which is consistent with previous works on the role of large-scale networks in memory and other cognitive domains (Bassett & Sporns, 2017; Petersen & Sporns, 2015; Shieh et al., 2019; Turk-Browne, 2013; Bullmore & Sporns, 2009). One prominent example is the posterior-medial and anterior–temporal framework, which posits that there are two dissociable cortico-hippocampal networks with distinct anatomical and FC profiles and important for different aspects of memory. The AT network is primarily involved in the processing of items, whereas the PM network is more involved in the processing of contextual information that support the construction of rich episodic representations (for reviews, see Ritchey & Cooper, 2020; Ranganath & Ritchey, 2012). More recently, researchers have found that stimulating the left lateral parietal cortex using TMS leads to better episodic memory and FC changes in the PM network (e.g., paired-associated memory: Wang et al., 2014; objection-location recall: Tambini, Nee, & D’Esposito, 2018; for a review, see Hebscher & Voss, 2020). In addition to cortical–hippocampal networks, Westphal, Wang, and Rissman (2017) have found that memory retrieval is marked by a less segregated whole-brain network and higher internetwork connectivity between the frontoparietal and default mode networks.

Our finding that the recognition memory model extends beyond ROIs identified in previous studies is also consistent with the recent findings by Keerativittayut, Aoki, Sarabi, Jimura, and Nakahara (2018), who studied how dynamic FC during encoding captured within-individual fluctuations in memory performance using a classic incidental encoding task and a surprise recognition memory test. They found that, within the subsequent memory ROIs, only FC between the hippocampus and occipital cortex differed between good and bad encoding states. Furthermore, they also observed that edges in areas beyond the subsequent memory ROIs, mostly in the salience, subcortical, default mode, and visual networks, played an important role in distinguishing encoding states. Corroborating these within-individual findings, our results also highlighted the importance of these same networks in predicting between-individual differences. Recent work showed that a sustained attention model built to predict attention performance across individuals generalized to predict the temporal fluctuations of attention within the same individual, that the FC-based sustained attention model captures a combination of trait-like and state-like sustained attention (Rosenberg et al., 2020). The similarities in the features identified by Keerativittayut et al. (2018) and our study suggest that the recognition memory network in our study may contain both features that underlie trait-level differences in recognition memory and those that underlie state-level fluctuations. Future work can directly compare the within- and between-participant memory networks to delineate the neural sources of between- and within-individual differences in recognition memory performance.

As a first step in delineating the neural basis of individual differences in LTM, we focused on item recognition memory and recollection memory. Using HCP data, Przezdzik, Faber, Fernández, Beckmann, and Haak (2019) found that how neocortical–hippocampal connectivity differs along the hippocampal long axis is specifically associated with individual differences in recollection (the “Remember” responses). Consistent with their finding, our analysis also revealed that the medial temporal lobe plays a critical role in predicting recollection, but not so much for recognition. However, there are other important forms of LTM such as free recall and associative memory (Unsworth, 2019). These forms of LTM are dependent on different neural mechanisms (e.g., Du et al., 2019; Staresina & Davachi, 2006). Moreover, the LTM predictive network in the current study was identified during encoding. Yet, successful memory performance also depends on many other memory processes such as consolidation and retrieval. Previous work found that FC between the hippocampus and sensory cortex during the rest period after encoding was correlated with later associative memory performance above and beyond FC during encoding (Tambini & Davachi, 2019; Tambini, Ketz, & Davachi, 2010). A similar set of brain regions that are related to better encoding is also implicated in successful retrieval (Rugg & Vilberg, 2013). Furthermore, recent work has shown that FC between memory-related regions (the hippocampus and parahippocampus) and reward-related
regions (ACC, OFC, and ventral striatum) even during the pretask rest are predictive of individual differences in the extent to which reward modules memory performance (Frank, Preston, & Zeithamova, 2019). Our individual differences approach can be flexibly applied to study the networks supporting other kinds of LTM as well as those related to individual differences in LTM during memory stages other than encoding. Furthermore, comparing the similarity and difference of these networks can help us gain a more comprehensive understanding of LTM functioning.

In summary, our study demonstrates the utility of adopting an individual differences approach in revealing the neural architecture supporting the formation of LTM and how it is related to and separable from other memory measures or processes, using the comparison of recognition memory with WM as a case study. Identifying predictive models of different cognitive components involved in LTM not only provides new insights into the interaction and distinction of these components but also can facilitate the identification of separable neural networks underlying these components in memory-related disorders.

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Funding Information

This work was supported by National Institutes of Health, Grant Number MH108591 to M. M. C.

Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the Journal of Cognitive Neuroscience (JoCN) during this period were M/man/M = .508, W/woman/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., JoCN, 53:1, pp. 3–7). Consequently, JoCN encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article’s gender citation balance. The authors of this article report its proportions of citations by gender category to be as follows: M/M = .521, W/M = .254, M/W = .099, and W/W = .127.

Note

1. There were five participants who had 100% hit rates in the recognition memory task for stimuli from one of the runs. If any of these participants were included in the training sample in a given iteration, they were left out from the univariate analysis because no contrast between remembered and forgotten trials could be run on these participants. However, they were still included during the CPM building procedure.

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