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Barrios, Riley J

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Does Locus Coeruleus Structure Relate to Associative Memory Related-Activity in Older Adults?

Riley Barrios, Department of Neuroscience
Ilana Bennett, Ph.D.; Department of Psychology

ABSTRACT

Older adults show well-documented declines in memory for relationships among items, especially as the number of items being bound together increases. Less is known about the neural mechanisms that support this type of associative memory, particularly the role of the hippocampus and its neuromodulatory input from the locus coeruleus (LC). In the current study, cognitively healthy older adults completed the QuadMax associative memory task during fMRI scanning to assess hippocampal activity. They studied word pairs, triplets, and quadruplets and were subsequently tested on their memory for repeated, recombined, and novel word sets. Diffusion-weighted MRI was collected to assess LC microstructural integrity. Results revealed that associative memory, recognition, and hit rates declined significantly as associative load increased from pairs to triplets to quadruplets, but these effects were no longer significant when controlled for age and sex. Associative memory encoding led to greater hippocampal BOLD activity for pairs relative to quadruplets in the left hippocampus, with a similar trend in the right hippocampus, and this activity was significantly associated with worse associative memory and recognition performance for quadruplets. Finally, LC mean diffusivity was significantly associated with poorer recognition performance for pairs, but not with hippocampal associative memory-related activity. These findings suggest that age-related variability in hippocampal engagement, not LC integrity, contributes to individual differences in associative memory performance in older adults. Our study highlights the importance of examining both neural activity and neuromodulatory structure to better understand the neural mechanisms that support associative memory in aging.

KEYWORDS: Locus Coeruleus, Associative Memory, Cognitive Decline, Aging

FACULTY MENTOR - Dr. Ilana Bennett, Department of Psychology



Dr. Bennett earned her doctorate in lifespan cognitive neuroscience from Georgetown University. Her research seeks to advance our understanding of neurocognitive aging by examining age-related differences in the way we acquire, retain, and retrieve information and identifying the neural substrates that underlie these learning and memory processes. Her work has attracted funding from the National Institute on Aging.



Riley J. Barrios

Riley Barrios is a neuroscience major in the University Honors Program at the University of California, Riverside with a strong interest in Alzheimer's disease, cognition, and disparities in brain aging across different populations. As a researcher in the Lani Lab, Riley has studied glial cell activity in younger and older participants and has led the lab's Glia Project while presenting individual research related to neurodegeneration and aging in the Locus Coeruleus. Outside the lab, Riley is passionate about bridging medicine and advocacy through culturally informed research and healthcare.

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INTRODUCTION

A key component of our memory in daily life is inherently associative (Mayes, Montaldi, & Migo, 2007; Tulving, 1983). When we remember a past event (e.g., meeting a friend for coffee), we retrieve not only isolated items (e.g., a mug or café table), but we also retrieve the relationships among items (e.g., who sat where or who drank what), their features (e.g., the size or color of the mug), and the environment in which they occurred (e.g., the café's background noises). Relative to memory for isolated items, memory for associative relationships among items shows a pronounced age-related decline in accuracy (Franco et al., 2022). Functional magnetic resonance imaging (fMRI) has shown that the hippocampus is active during associative memory performance (Chen & Chang, 2016), indicating that it has a central role in constructing associative memory traces and that associative memory-related activity in the hippocampus varies with age. The hippocampal memory network is thought to be shaped by neuromodulatory input from the locus coeruleus (LC), which is the brain's primary source of noradrenaline, including projections to the hippocampus (Khakpour-Taleghani et al., 2021). However, no studies have examined if LC microstructure relates to hippocampal associative memory-related activity in older adults. The focus of the current study is to better understand how hippocampal and LC systems support associative memory.

Decades of work have shown that older adults exhibit disproportionate impairments in associative memory relative to the memory of items alone (Naveh-Benjamin et al., 2004). For example, in typical paired-associative tasks, participants study pairs of items (e.g., word-word pairs) and are later tested on their ability to distinguish intact pairs from recombined pairs containing previously studied items presented in new combinations (Gold et al., 2006). In these tasks, associative memory is measured by how well participants can recognize intact pairs relative to recombined sets of previously studied items. Using these tasks, older adults reliably show lower associative memory (Naveh-Benjamin et al., 2004), despite preserved recognition of individual items. This pattern supports the idea that aging selectively disrupts associative binding, although these studies have been limited to associations between pairs of items.

Our group used the QuadMax task to extend this literature by parametrically increasing associative load. Participants studied sets of two, three, or four unrelated words and were later tested on their ability to distinguish intact (repeated) from recombined word sets. Prior work using this task showed that associative memory (hit rate minus recombined false alarms) and recognition (hit rate minus novel false alarms) declined significantly with increasing set size, with larger associative memory declines in older adults (Franco et al., 2022). These findings indicate that increasing associative load places greater demands on the memory processes that help link multiple elements into a single episodic representation and that these processes are impaired during aging.

Previous neuroimaging studies using paired-associative paradigms have consistently shown strong hippocampal engagement during associative encoding, with greater activity for conditions that require binding relations between items compared with conditions that emphasize single-item processing (Davachi, 2006). These findings support the idea that the hippocampus plays a central role in linking multiple elements of an experience into a unified memory representation, at least when examining associations between pairs of items.

The locus coeruleus (LC), the brain's primary source of noradrenergic input to the hippocampus, plays an important role in modulating hippocampal memory function. Noradrenergic input from the LC enhances synaptic plasticity and supports memory encoding, consolidation, and retrieval processes that are critical for episodic memory (Uematsu et al., 2015). The LC's microstructure has been shown to measurably decline with age (Bennett et al., 2024) and to be linked to episodic memory performance in older adults (Fukabori et al., 2020), albeit not to associative memory performance in humans. This suggests that LC structural variability may influence hippocampal recruitment and ultimately to associative memory success. Studies using associative memory tasks have found activity in the hippocampus, but none have examined if this activity is modulated by LC structure.

The current study aims to test if LC microstructural integrity is related to hippocampal activity during associative

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memory encoding in older adults. The older adults completed the QuadMax associative memory task during fMRI scanning along with diffusion-weighted imaging to assess LC microstructure. We predicted that older adults would show worse associative memory performance as associative load increased and would show measurable hippocampal engagement during study. We also predicted individual differences in LC integrity would relate to the level of hippocampal activity observed during associative memory processing, supporting the LC's role in moderating hippocampal function during demanding memory tasks.

METHODS

Participants

Forty-four older adults (>65 years old) were recruited from communities surrounding the University of California, Riverside. Prior to study enrollment, potential participants were screened over the phone for: (1) normal global cognition (>17 score on the Montreal Cognitive Assessment [MoCA] adapted for phone screening; [Pendlebury et al., 2013]); (2) hearing or vision loss, (3) history of neurological conditions or psychiatric disorders that could influence performance (e.g. depression, schizophrenia), (4) recent medications that could influence image quality (e.g. mood stabilizers, benzodiazepines, psychotropics), (5) major health conditions (e.g. diabetes), (6) MRI contraindications (e.g. pregnancy, claustrophobia), and (7) comfort using keyboard buttons. After enrollment, participants were excluded from final analyses due to issues with data collection ($n = 4$; e.g., not recording all responses, running the same condition twice, coughing fit during fMRI scans) or for failing to respond to more than 30% of the trials ($n = 1$). The final sample consisted of 39 older adults (mean age = 68.9 years; 71.8% female). All participants gave informed consent and received monetary compensation for participation.

General Procedure

After informed consent was provided, participants completed two MRI sessions as part of two separate studies using a 3.0 Tesla MRI system (Siemens Magnetom Trio) with a standard 32-channel head coil at the Center for Advanced Neuroimaging at the University of California, Riverside. Structural MRI sequences in Session 1 were used to assess

locus coeruleus structure and an associative memory task was completed during functional MRI acquisition in Session 2.

Associative Memory Task

Participants completed two versions of the QuadMax task (Figure 1) in the MRI scanner. In the study phase, participants viewed 60 word sets of two (pairs), three (triplets), and four (quadruplets) semantically unrelated words (20 per set size) and indicated if they could “imagine the words doing something together” or not using button presses.

In the test phase, participants viewed 90 word sets: 30 identical to studied sets (repeated; 10 per set size), 30 recombinations of studied sets (recombined; 10 per set size), and 30 comprised of new words (novel; 10 per set size). Participants indicated if they had seen the exact word set in the study phase (“old”) or if they had not (“new”) using button presses.

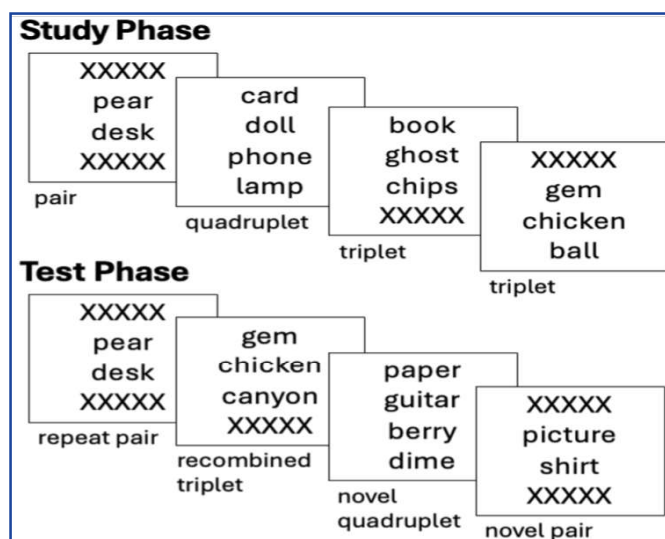


Figure 1: Example trials from the study phase (top) and test phase (bottom) of the QuadMax task show the set size (pairs, triplets, quadruplets) and trial type (repeated, recombined, novel) conditions.

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Metrics

For each participant and each set size, the proportion of correct “old” responses to repeated (hit rate), incorrect “old” responses to recombined (recombined false alarm [FA] rate), and incorrect “old” responses to novel (novel FA rate) sets were calculated. Associative memory was calculated as hit rate minus recombined FA rate. Recognition was calculated as hit rate minus novel FA rate. Average scores across set sizes and task versions were also calculated.

Structural Imaging Data

We acquired T1-weighted MP-RAGE (echo time (TE)/repetition time (TR)/inversion time = 3.02/2600/800 ms, GRAPPA acceleration = 2, flip angle = 8°, voxel size = 0.8 mm³), magnetization transfer-prepared gradient echo (MT-GRE; TE/TR = 3.21/385 ms, flip angle = 40°, field of view (FOV) = 220 × 186 mm², slice thickness = 3 mm), and diffusion-weighted single-shot spin-echo, echo planar (TE/TR = 75/4100 ms, voxel size = 1.15 × 1.15 × 2.5 mm³, 30 directions with gradient strengths of $b = 500$ s/mm² and 2000s/mm²) images.

Locus coeruleus region of interest. A standardized atlas of bilateral locus coeruleus (LC) (Langley et al., 2020) was aligned to each participant's MT-GRE and diffusion-weighted spaces using registration tools in the FMRIB Software Library (FSL) (Jenkinson et al., 2002).

MTC metrics. For each participant, raw MT-GRE acquisitions were corrected for motion and averaged. A maximum MT contrast (MTC) metric was calculated as the peak MTC value relative to the pontine reference region within the MT-GRE-aligned LC region of interest. Values exceeding four standard deviations from the sample mean were excluded ($n = 2$ older adults).

Diffusion metrics. For each participant, raw diffusion-weighted data were corrected for motion, susceptibility distortions, and eddy currents using FSL's TOPUP and EDDY (Andersson, Skare, & Ashburner, 2003; Andersson & Sotiropoulos, 2016). Mean diffusivity (MD) was estimated using the $b = 0$ and 500 data with FSL's DTIFIT. Mean MD in the LC was calculated by averaging values within the diffusion-aligned region of interest.

Functional Imaging Data

Acquisition. Separate echo-planar imaging (EPI) pulse sequences were acquired during performance of the study and test phases of each version (C, D) of the QuadMax task (TR/TE = 1750/32 ms, field of view = 221 × 190.4 mm, flip angle = 77 degrees, spatial resolution = 1.7 mm³, 72 slices with no gap, AP phase encoding direction, GRAPPA acceleration factor = 2, and multiband factor = 3). Additional spin echo EPI images with opposite phase-encoding directions were acquired to correct for susceptibility distortions (identical except TR/TE = 7700/58 ms). Only the study phase data are reported here.

Preprocessing. Raw fMRI data were corrected for susceptibility-induced distortions (TOPUP; Andersson et al., 2003) and then preprocessed using FEAT (fMRI Expert Analysis Tool), which included motion correction, brain extraction, spatial smoothing (5 mm FWHM Gaussian kernel), and high-pass filtering (100 s). Preprocessed data were registered to the participant's T1-weighted image using FLIRT (Jenkinson et al., 2002), and then to a standard Montreal Neurological Institute (MNI) 152 template that was resampled to 1.7 mm³ resolution using a combination of FLIRT with BBR and FNIRT (Andersson et al., 2007).

Lower-level analysis. Separate lower-level analyses were conducted for each participant and each task version (C, D) from the study phase, using FILM with local autocorrelation correction (Woolrich et al., 2001). Analyses modeled each set size (pairs, triplets, quadruplets) and these three explanatory variables were convolved with a gamma-variate hemodynamic response function (standard deviation = 3 s, mean lag = 6 s). Two contrasts captured associative memory-related activity by contrasting pairs and quadruplets (pairs > quadruplets, quadruplets > pairs).

Higher-level analyses. A mid-level analysis was conducted to capture variance across task versions within each participant using fixed effects. One explanatory variable modeled activity from the lower-level analyses for each participant and one contrast captured average activity for each participant across task versions.

Higher-level analyses were conducted across participants on outputs of the mid-level analyses using FSL's Local Analysis of Mixed Effects (FLAME) stage 1. One explanatory

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variable modeled activity from the mid-level analyses and one contrast captured within-group mean effects by average activity across participants. We applied the default nonparametric statistical threshold using clusters determined by $Z > 3.1$ and a (corrected) cluster significance threshold of $P = 0.05$ (Worsley 2001). FSL's Featquery was used to extract parameter estimates for each contrast for each participant from the left and right hippocampus.

RESULTS

Associative Memory Performance

Separate repeated-measures ANOVAs were conducted for each outcome metric (associative memory, recognition, hits, recombined FA, novel FA) using Set Size (pairs, triplets, quadruplets) as the within-subjects variable (Figure 2). For associative memory, there was a significant main effect of Set Size, $F(2, 78) = 25.2, p < 0.001$. Post hoc pairwise comparisons revealed that associative memory was worse (lower) for each increase in set size from pairs (0.51 ± 0.29) to triplets (0.33 ± 0.17) to quadruplets (0.23 ± 0.24), $p_s < 0.022$. For recognition, there was a significant main effect of Set Size, $F(2, 78) = 37.1, p < 0.001$, with worse recognition for each increase in set size from pairs (0.82 ± 0.17) to triplets (0.70 ± 0.17) to quadruplets (0.60 ± 0.19), $p_s < 0.001$. For hits, there was a significant main effect of Set Size, $F(2, 78) = 38.0, p < 0.001$, with lower hits for each increase in set size from pairs (0.90 ± 0.14) to triplets (0.76 ± 0.17) to quadruplets (0.66 ± 0.20), $p_s < 0.001$. There was no significant main effect of Set Size for recombined FA, $p = 0.108$, or novel FA, $p = 0.856$.

Effects of age and sex. When controlling for age and sex, main effects of Set Size were no longer significant for any outcome metric, $p_s > 0.10$. However, age had a significant effect on associative memory, $F(1, 36) = 5.2, p = 0.029$, recognition, $F(1, 36) = 4.3, p = 0.044$, and novel FA, $F(1, 36) = 4.8, p = 0.035$, performance.

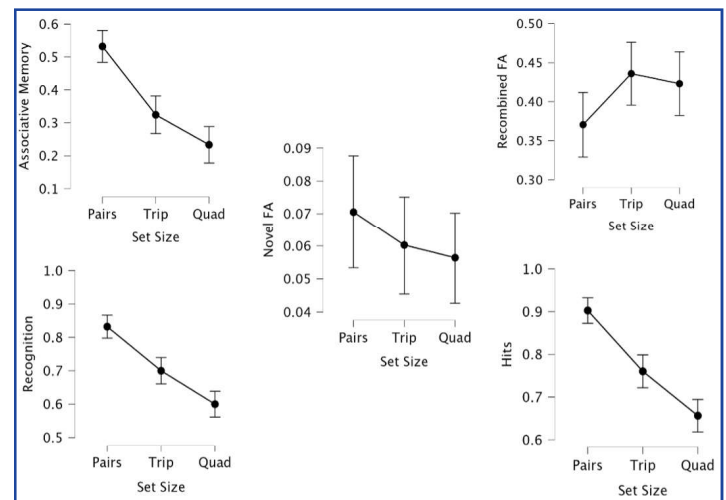
Associative Memory-Related Activity

Whole-brain maps showing regions with significant BOLD activation are shown in Figure 3. One sample t-tests determined if there was significant activity in the left and right hippocampus during the study phase of the associative

memory task. Results revealed significant activity for the pairs > quadruplets contrast in the left hippocampus (13.0 ± 3.6), $t(38) = 3.55, p = 0.001$. Results revealed no significant activity for the quadruplets > pairs contrast in the left hippocampus (2.2 ± 4.2), $p = 0.608$. Results revealed a non-significant trend for activity for the pairs > quadruplets (9.8 ± 5.1), $p = 0.059$, and quadruplets > pairs (6.8 ± 3.7), $p = 0.073$, contrasts in the right hippocampus. Although the right hippocampus only showed a trend-level effect, the results suggest associative memory related activity was higher for pairs compared to quadruplets in both hemispheres.

Effects of age and sex. Note that there were no significant correlations between age and task-related activity in either hippocampal hemisphere, $p_s > 0.36$. There were also no significant sex group differences in task-related activity in the hippocampus, $p_s > 0.17$.

Figure 2: Increasing set size from pairs to triplets to quadruplets led to lower associative memory, recognition, and hit rates, while recombined and novel false alarms showed no significant differences among set sizes.



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Associative Memory Performance Correlates with Associative Memory-Related Activity

Partial correlations examined relationships between associative memory performance (associative memory, recognition) for each set size (pairs, triplets, quadruplet) and associative memory-related activity in the left and right hippocampus, controlling for age and sex. For associative memory, results revealed that greater activity for the pairs > quadruplets contrast in the left, $r = -0.38$, $p = 0.021$, and right, $r = -0.34$, $p = 0.040$, hippocampus was significantly related to worse associative memory for quadruplets. For recognition, results revealed that greater activity for the pairs > quadruplets contrast in the left, $r = -0.43$, $p = 0.008$, and right, $r = -0.34$, $p = 0.037$, hippocampus was significantly related to worse recognition for quadruplets.

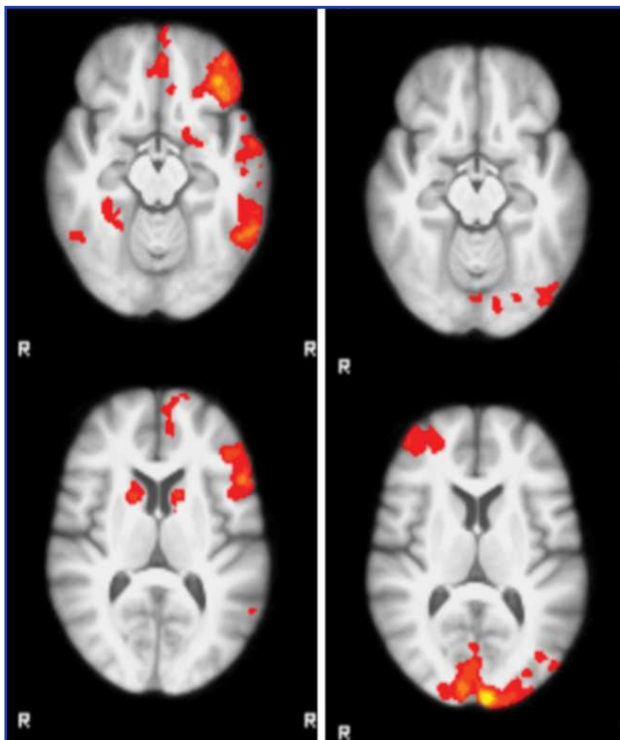


Figure 3: Whole-brain maps showing regions with greater BOLD activation for pairs compared to quadruplets (left) and quadruplets compared to pairs (right) during the study phase.

Locus Coeruleus Structure Correlates with Memory Performance

Partial correlations then examined relationships between memory performance (associative memory, recognition) for each set size (pairs, triplets, quadruplet) and locus coeruleus metrics (MD and Maximum CNR), controlling for age and sex. Results revealed that higher LC MD was significantly associated with worse recognition for pairs, $r = -0.48$, $p = 0.029$. No other relationships achieved significance, p 's > 0.16.

Locus Coeruleus Structure Does Not Correlate with Associative Memory-Related Activity

Partial correlations examined relationships between locus coeruleus structural metrics (MD, Maximum CNR) and task-related hippocampal activity (pairs > quadruplets, quadruplets > pairs) in the left and right hippocampus, controlling for age and sex. Results revealed no significant relationships, p 's > 0.14.

DISCUSSION

The current study examined if locus coeruleus (LC) microstructural integrity relates to associative memory performance and hippocampal associative memory-related activity in older adults. Thirty-nine cognitively healthy older adults completed the QuadMax associative memory task during fMRI scanning, along with diffusion-weighted and magnetization transfer imaging to assess LC microstructure. At the behavioral level, associative memory, recognition, and hit rates declined significantly as associative load increased from pairs to triplets to quadruplets, but only before controlling for age or sex. At the level of hippocampal BOLD activity, associative memory encoding elicited significantly greater activity for pairs relative to quadruplets in the left hippocampus, with a similar trend observed in the right hippocampus. Greater hippocampal activity for the pairs > quadruplets contrast was significantly associated with worse associative memory and recognition performance for quadruplets. Finally, LC structure was selectively related to behavior such that higher LC mean diffusivity was associated with worse recognition performance for pairs, but not with hippocampal associative memory-related activity.

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When not controlling for age or sex, associative memory, recognition, and hit rates were significantly worse for quadruplets than for triplets and for triplets than for pairs. This replicates our prior work in which we found declines in associative memory and related measures as set size increased in older adults (Franco et al. 2022). Interestingly, when controlling for age and sex, these effects were no longer significant, suggesting that age- and sex-related differences were the primary drivers of performance rather than associative load. Recombined and novel false alarm rates did not differ with set size, regardless of if age and sex were controlled. This finding was unexpected given our prior work and may reflect methodological differences among the studies that reduced sensitivity to associative load effects on FA rates, including the use of two task versions with a larger total number of study sets as well as a substantially smaller sample size. This may have increased variability and limited the power to detect load-related differences in false alarms. Nonetheless, these behavioral findings suggest that age and sex are key factors that play a significant role in associative memory performance in older adults.

fMRI data revealed significantly greater hippocampal BOLD activity for pairs relative to quadruplets during the study phase of the associative memory task in the left hippocampus, with a non-significant trend in the right hippocampus. This finding is consistent with prior literature showing that the hippocampus is critical for binding multiple items into a cohesive memory representation (Davachi, 2006). However, our finding that hippocampal activity during encoding was higher for pairs than for triplets or quadruplets (i.e., higher associative loads) is not consistent with prior work, which has instead found that hippocampal activity during encoding was higher for conditions in which two items needed to be associated relative to conditions with one or zero items to be associated (Addis et al., 2006). One interpretation is that the hippocampus may be recruited when binding two items, whereas binding four may exceed the capacity of its binding mechanisms in older adults, resulting in lower activity (Reuter-Lorenz and Cappell, 2008).

Individual differences in hippocampal activity were related to memory performance at higher loads. Greater hippocampal activity for the pairs > quadruplets contrast was associated with worse associative memory and recognition performance

for quadruplets. This negative correlation suggests that heightened hippocampal engagement under lower associative loads may reflect inefficient processing rather than more effective memory formation. As associative load increases, the hippocampus may reach a functional limit in its ability to bind multiple elements into a cohesive representation, similar to what has been previously reported in frontal cortex during high working memory load (Reuter-Lorenz and Cappell, 2008). This limit may result in reduced engagement during quadruplet trials in the study phase, impairing encoding of the word sets and ultimately leading to worse memory performance, especially for quadruplets. Together, these findings may suggest that reduced hippocampal engagement at higher associative loads may contribute to poorer associative memory performance in aging adults.

Finally, LC microstructure was selectively related to memory performance, but not to associative memory-related hippocampal activation. Specifically, higher LC mean diffusivity was significantly associated with worse recognition performance for pairs. This finding extends prior work that has similarly shown that LC microstructure relates to episodic memory performance in older adults (Fukabori et al., 2020) and is consistent with the notion that noradrenergic input from the LC enhances synaptic plasticity and processes that are critical for episodic memory (e.g., encoding, consolidation, and retrieval) (Uematsu et al., 2015). However, because LC microstructural measures were not significantly related to hippocampal associative memory-related activity during the study phase, the contribution of LC microstructure to individual differences in recognition accuracy may be independent of mechanisms captured by task-related hippocampal BOLD activation. Thus, our findings did not support the notion that activity in the hippocampal memory network is shaped by neuromodulatory input from the LC.

Several limitations should be considered. Although the QuadMax task isolates associative memory demands by holding item familiarity constant and increasing the number of inter-item relationships, larger set sizes may place greater demands on working memory and strategic organization during study, particularly in older adults. Thus, some of the associative load effects in performance and the BOLD response may reflect both associative binding demands and

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age-related differences in maintaining multiple elements in working memory during study. Although hippocampal activity was measured during task performance, fMRI cannot determine if LC-related influences on memory occur through modulation of hippocampal associative binding or broader network-level effects. Future studies using higher-resolution LC imaging, functional connectivity approaches, and larger samples could clarify these mechanisms. Despite these limitations, the present study extends prior work using the QuadMax task by demonstrating that associative load impairs associative memory and recognition memory performance in older adults including at higher set sizes, that greater activity in the hippocampus during study of pairs relative to quadruplets was associated with worse performance (associative memory and recognition for quadruplets), whereas LC microstructural variability was selectively related to recognition performance. Together, these findings suggest that age-related associative memory decline may separately reflect hippocampal engagement and integrity of the neuromodulatory LC system that supports memory. These results return to the broader idea that successful memory for daily events relies on both hippocampal and LC systems that become increasingly vulnerable with aging. Importantly, these findings strengthen models of cognitive aging by identifying hippocampal inefficiency under increasing load as a key mechanism of associative memory decline and suggest that hippocampal function may be a more sensitive target for intervention than LC integrity.

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