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Mnemonic brain state engagement is diminished in healthy aging

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ABSTRACT

Healthy older adults typically show impaired episodic memory – memory for when and where an event occurred. This selective episodic memory deficit may arise from differential engagement in the retrieval state, a brain state in which attention is focused internally in an attempt to access prior knowledge, and the encoding state, a brain state which supports the formation of new memories and that trades off with the retrieval state. We hypothesize that older adults are biased toward a retrieval state. We recorded scalp electroencephalography while young, middle-aged and older adults performed a memory task in which they were explicitly directed to either encode or retrieve on a given trial. We used multivariate pattern analysis of spectral activity to decode retrieval vs. encoding state engagement. We find that whereas all age groups can follow task demands to selectively engage in encoding or retrieval, mnemonic brain state engagement is diminished for older adults relative to young and middle-aged adults. These findings suggest that differential mnemonic state engagement may underlie age-related memory changes.

1. Introduction

In healthy aging, many aspects of cognition decline (Craik and Bialystok, 2006; Lindenberger, 2014), including memory (Rabin et al., 2015). Healthy older adults exhibit selective deficits in episodic memory – the memory for events within a spatiotemporal context (Tulving, 1972) – but typically have intact semantic memory – memory for facts and concepts (Wingfield and Kahana, 2002). For example, an older adult may be easily able to remember that *Water Lilies* was painted by Claude Monet, but may fail to remember the specific details of their trip to the Art Institute of Chicago during which they viewed the painting. This selective episodic memory deficit may be due to a tendency to engage a retrieval state, given older adults' difficulty inhibiting the retrieval of prior knowledge from memory (Healey et al., 2014; Wynn et al., 2020). In young adults, engaging the retrieval state (Tulving, 1983) trades off with engaging the encoding state (Long and Kuhl, 2019; Smith et al., 2022) and can impair later memory (Long and Kuhl, 2019). Age-related episodic memory deficits may therefore arise from differential mnemonic state engagement. The aim of the present study is to investigate the extent to which older adults engage encoding and retrieval states.

Relative to young adults, older adults have impaired episodic memory and intact semantic memory. Older adults have difficulty forming and accessing episodic associations – connections between events that occur close in time or space (Wilkniss et al., 1997; Golomb et al., 2008), but typically have no such difficulty with semantic associations (Amer et al., 2019) – connections between events that share meaning. For instance, when studying realistic and unrealistic prices for grocery store items, older adults show memory comparable to young adults only for those items that are priced realistically, suggesting that older adults rely on prior knowledge to support memory judgments (Castel, 2005; Amer et al., 2018). Older adults also rely on semantic memory rather than episodic memory to guide decision-making, even when episodic memory is more task-relevant (Lalla et al., 2022). Together, these findings suggest that older adults may over rely on semantic information.

An overreliance on retrieving semantic information may prevent the encoding of episodic information. In young adults, attending to semantic associations can negatively impact the formation of episodic associations (Long and Kahana, 2017). Memory for semantic vs. episodic details – e.g. "Claude Monet was a French Impressionist" vs. "We visited the Art Institute of Chicago last Tuesday at noon" – are negatively associated, an effect which increases with age (Devitt et al., 2017). There is an overall shift toward semantic memory across the lifespan (Ofen and Shing, 2013) along with increases in default mode network (DMN) connectivity (Staffaroni et al., 2018), a brain network known to support semantic processing (Binder et al., 2009) among other internally-directed processes (Buckner and DiNicola, 2019). There is evidence to suggest that as older adults become more reliant on semantic memory and prior knowledge (Wynn et al., 2020) and less able to exert cognitive control (Park et al., 2001; Verhaeghen and Cerella, 2002), the DMN

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becomes increasingly engaged and coupled with prefrontal control regions (*default-executive coupling hypothesis of aging*; Turner and Spreng 2015, Spreng and Turner 2019). According to the default-executive coupling hypothesis of aging, if prior knowledge is relevant to the current task, older adults' increased default-executive coupling can be adaptive (Adnan et al., 2019; Spreng and Turner, 2019; Spreng et al., 2014), but if prior knowledge is irrelevant to the current task, older adults' increased default-executive coupling can be maladaptive (Rieck et al., 2017; Turner and Spreng, 2015). Given that in young adults DMN activation impairs episodic memory formation (Kim, 2011), older adults' tendency to engage in DMN-mediated semantic retrieval may prevent or diminish episodic encoding.

Older adults may engage in retrieval at the expense of encoding. Older adults are biased toward pattern completion – reactivation of a memory trace via the hippocampus from incomplete sensory input (McClelland et al., 1995) – whereby older adults are more likely than young adults to identify novel stimuli with low similarity to studied items as familiar (Vieweg et al., 2015). When older adults retrieve prior information to make predictions about future events, the retrieved information may be strengthened at the expense of encoding new events (Stawarczyk et al., 2023). Memory encoding and memory retrieval constitute neurally distinct brain states (Hasselmo et al., 2002; Hasselmo, 2005) – spatially distributed and temporally sustained neural activity patterns (Beaty et al., 2018; Kay and Frank, 2019; Tang et al., 2012) – which trade off such that they cannot be engaged in simultaneously. Encoding and retrieval states can be distinguished through neural activity patterns recorded via scalp electroencephalography (Long and Kuhl, 2019; Smith et al., 2022; Hong et al., 2023; Smith and Long, 2024) and functional magnetic resonance imaging (Long and Kuhl, 2021). An investigation of microstates, global patterns of voltage scalp topography that are stable over successive short time periods (Michel and Koenig, 2018), revealed that sustained engagement of microstate E – previously linked to the DMN (Custo et al., 2017; Bréchet et al., 2019) – characterizes the retrieval state (Hong et al., 2023). Young adults engage the retrieval state in response to top-down demands to retrieve (Smith and Long, 2024) as well as automatically when experiences overlap in time (Smith et al., 2022), suggesting that the retrieval state may be engaged even when counter to top-down goals. As older adults have a diminished ability to inhibit retrieval of semantic information (Wynn et al., 2020), they may be particularly susceptible to engaging the retrieval state. Older adults may additionally have difficulty switching out of the retrieval state, given evidence that older adults are less able to vary their processing in response to differing retrieval cues (Morcom and Rugg, 2002, 2004). An inability to switch out of an automatically induced, goal-irrelevant retrieval state will in turn impair encoding. Thus, an older adult may fail to remember their specific trip to the Art Institute because when they encountered *Water Lilies*, they automatically retrieved their prior knowledge about Claude Monet (e.g. Impressionism, France, gardening) which prevented them from encoding the current experience.

Our hypothesis is that older adults are biased toward the retrieval state. To test our hypothesis, we conducted a scalp electroencephalography study in which young (18–35), middle-aged (36–59) and older adult (60–85) participants studied two lists of object images. The second list was composed of images that were semantically associated with images from the first list (i.e., each image in a "pair" was drawn from the same object category). During List 2, participants were explicitly instructed to either encode the currently presented object image or retrieve the categorically related object image from List 1. Following study, participants completed a two-alternative forced-choice recognition test of all images from both lists. We used multivariate pattern analyses to assess engagement in memory encoding and memory retrieval brain states. To the extent that older adults are biased to retrieve, we should find differential mnemonic brain state engagement for older adults compared to young and/or middle-aged adults.

2. Materials and methods

2.1. Participants

Forty young adult (34 female, age range = 18–37, mean age = 20.3 years), forty middle-aged adult (34 female, age range = 39–59, mean age = 51.4 years) and forty older adult (26 female, age range = 60–85, mean age = 70.5 years) fluent English speakers from the University of Virginia (UVA) community participated. Young adult participants (YAs) were recruited from flyers posted around the UVA campus and surrounding areas. Middle-aged adults (MAs) and older adults (OAs) were recruited through the Virginia Cognitive Aging Project, a longitudinal study of cognitive aging in adults across a wide age range (Salthouse, 2011). The YA dataset has been previously reported (Smith et al., 2022); albeit with a slight modification as we have removed an additional participant (see below). Our enrollment targets for the MA and OA datasets were based on this YA dataset and are described in the pre-registration report of this study (https://osf.io/ytdcn). All participants had normal or corrected-to-normal vision. Informed consent was obtained in accordance with the UVA Institutional Review Boards for Social and Behavioral Research and Health Sciences Research, and participants were compensated for their participation. All MA and OA participants completed the Montreal Cognitive Assessment (MoCA); any participant who scored less than 26 was excluded, based on previous literature (Nasreddine et al., 2005).

Four YA participants were excluded from the final dataset: three who had been excluded in our previous report (Smith et al., 2022) for poor task performance, prior knowledge of the task, or poor signal quality, and one additional participant who was older than our YA upper age cut off of 35 at the time of testing. Four MA participants were excluded from the final dataset: one who had poor task performance (recognition accuracy < 3 SDs of the mean of the full MA dataset), one because of permanent hair extensions that precluded scalp access, resulting in poor signal quality (impedances were above the threshold of 50 kΩ), and two who scored lower than 26 on the MoCA. Two OA participants were excluded from the final dataset: one who had poor task performance (recognition accuracy < 3 SDs of the mean of the full OA dataset) and one who scored lower than 26 on the MoCA. Thus, data are reported for the remaining 36 YA, 36 MA and 38 OA participants. The raw, de-identified data and the associated experimental and analysis codes used in this study are available for access via the Long Term Memory laboratory website (https://longtermmemorylab.com).

2.2. Materials

2.2.1. Mnemonic state task experimental design

Stimuli consisted of 576 object pictures, drawn from an image database with multiple exemplars per object category (Konkle et al. 2010, e.g. 'apple', 'suitcase', 'bench', 'blender'). From this database, we chose 144 unique object categories and 4 exemplars from each category. For each participant, one exemplar in a set of four served as a List 1 object, one as a List 2 object, and the two remaining exemplars served as lures for the recognition phase. Object condition assignment was randomly generated for each participant. After a given stimulus category was drawn from the pool of images, that category was removed from the pool such that the category was never repeated within or across runs for a given participant.

General Overview. In each of eight runs, participants viewed two lists containing 18 object images. For the first list, each object was new (List 1 objects). For the second list (List 2 objects), each object was again new, but was categorically related to an object from the first list. For example, if List 1 contained an image of an apple, List 2 would contain an image of a different apple (Fig. 1). Participants were explicitly directed to try to remember the images for a memory test prior to studying the List 1 and List 2 items. During List 1, participants were

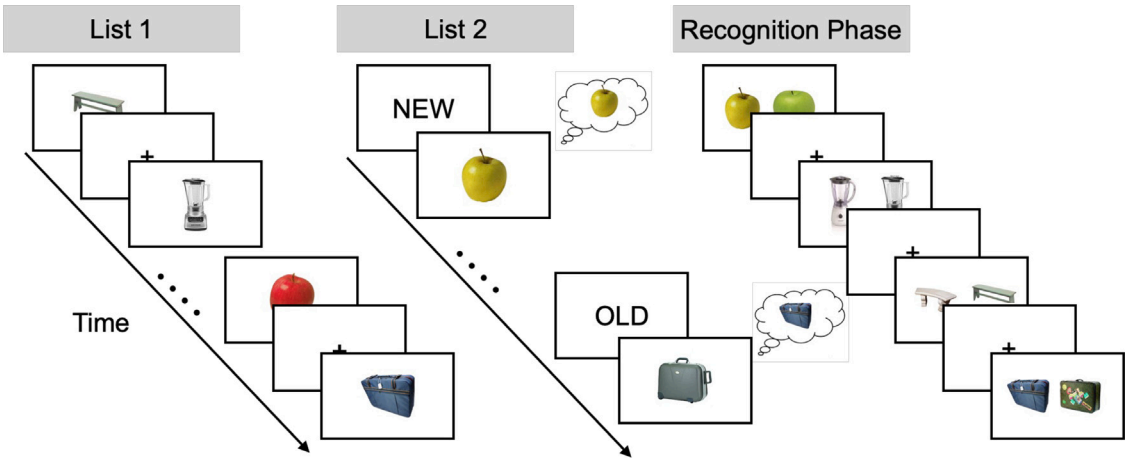

Fig. 1. Task design. During List 1, participants studied individual objects (e.g., apple, suitcase). During List 2, participants saw novel objects that were from the same categories as the objects shown in List 1 (e.g., a new apple, a new suitcase). Preceding each List 2 object was an OLD instruction cue or NEW instruction cue. The OLD cue signaled that participants were to retrieve the corresponding object from List 1 (e.g., the old suitcase). The NEW cue signaled that participants were to encode the current object (e.g., the new apple). Each run of the experiment contained a List 1 and List 2; object categories (e.g., apple) were not repeated across runs. After eight runs, participants completed a two-alternative forced-choice recognition test that tested memory for each List 1 and List 2 object. On each trial, a previously presented object, either from List 1 or List 2, was shown alongside a novel lure from the same category. The participant's task was to choose the previously presented object. List 1 and List 2 objects were never presented together.

instructed to encode each new object. During List 2, however, each trial contained an instruction to either encode the current object (e.g., the new apple) or to retrieve the corresponding object from List 1 (the old apple). Following eight runs, participants completed a two-alternative forced-choice recognition test that separately assessed memory for List 1 and List 2 objects.

List 1. On each trial, participants saw a single object presented for 2000 ms followed by a 1000 ms inter-stimulus interval (ISI). Participants were instructed to study the presented object in anticipation of a later memory test.

List 2. On each trial, participants saw a cue word, either "OLD" or "NEW" for 2000 ms. The cue was followed by presentation of an object for 2000 ms, which was followed by a 1000 ms ISI. All objects in List 2 were non-identical exemplars drawn from the same category as the objects presented in the immediately preceding List 1. That is, if a participant saw a suitcase and an apple during List 1, a different suitcase and a different apple would be presented during List 2. On trials with a "NEW" instruction (encode trials), participants were to encode the presented object. On trials with an "OLD" instruction (retrieve trials), participants tried to retrieve the categorically related object from the preceding List 1. Importantly, this design prevented participants from completely ignoring List 2 objects following "OLD" instructions in that they could only identify the to-be-retrieved object category by processing the List 2 object.

Participants completed eight runs with two lists in each run (List 1, List 2). Participants viewed 18 objects per list, yielding a total of 288 object stimuli from 144 unique object categories. Participants did not make a behavioral response during either List 1 or 2. Following the eight runs, participants completed a two-alternative forced choice recognition test.

Recognition Phase. Following the eight runs, participants completed the recognition phase. On each trial, participants saw two exemplars from the same object category (e.g. two apples; Fig. 1). One object had previously been encountered either during List 1 or 2. The other object was a lure and had not been presented during the experiment. Because both test probes were from the same object category, participants could not rely on familiarity or gist-level information to make their response (Brainerd and Reyna, 2002). Trials were self-paced and participants selected (via button press) the previously presented object. Trials were separated by a 1000 ms ISI. There were a total of 288 recognition trials (corresponding to the 288 total List 1 and 2 objects presented in the experiment). Note: List 1 and List 2 objects never appeared in the same trial together, thus participants never had to choose between two previously presented objects. List 1 and List 2 objects were presented randomly throughout the test phase.

2.2.2. EEG data acquisition and preprocessing

Electroencephalography (EEG) recordings were collected using a BrainVision system and an ActiCap equipped with 64 Ag/AgCl active electrodes positioned according to the extended 10–20 system. All electrodes were digitized at a sampling rate of 1000 Hz and were referenced to electrode FCz. Offline, electrodes were later converted to an average reference. Impedances of all electrodes were kept below 50 kΩ. Electrodes that demonstrated high impedance or poor contact with the scalp were excluded from the average reference calculations; however, all electrodes were included in all subsequent analysis steps following re-referencing. Bad electrodes were determined by voltage thresholding (see below).

Custom Python codes were used to process the EEG data. We applied a high pass filter at 0.1 Hz, followed by a notch filter at 60 Hz and harmonics of 60 Hz to each participant's raw EEG data. We then performed three preprocessing steps (Nolan et al., 2010) to identify electrodes with severe artifacts. First, we calculated the mean correlation between each electrode and all other electrodes as electrodes should be moderately correlated with other electrodes due to volume conduction. We z-scored these means across electrodes and rejected electrodes with z-scores less than -3. Second, we calculated the variance for each electrode as electrodes with very high or low variance across a session are likely dominated by noise or have poor contact with the scalp. We then z-scored variance across electrodes and rejected electrodes with a $|z| >= 3$. Finally, we expect many electrical signals to be autocorrelated, but signals generated by the brain versus noise are likely to have different forms of autocorrelation. Therefore, we calculated the Hurst exponent, a measure of long-range autocorrelation, for each electrode and rejected electrodes with a $|z| >= 3$. Electrodes marked as bad by this procedure were excluded from the average re-reference. We then calculated the average voltage across all remaining electrodes at each time sample and re-referenced the data by subtracting the average voltage from the filtered EEG data. The average number of bad electrodes identified for each participant ($M = 2.01$, $SD = 0.93$; YAs: $M = 2.22$, $SD = 0.92$; MAs: $M = 1.81$, $SD = 0.88$; OAs: $M = 2.00$, $SD = 0.95$) did not differ between the age groups (YAs vs. MAs: $t_{70} = 1.94$, $p = 0.056$, Cohen's $d = 0.46$; YAs vs. OAs:

t_{72} = 1.01, p = 0.315, Cohen's d = 0.24; MAs vs. OAs: t_{72} = 0.90, p = 0.369, Cohen's d = 0.21). Although bad electrodes were excluded from the average re-reference calculation, all electrodes were included for every participant for all subsequent analyses. We used wavelet-enhanced independent component analysis (Castellanos and Makarov, 2006) to remove artifacts from eyeblinks and saccades.

2.3. EEG data analysis

We applied the Morlet wavelet transform (wave number 6) to the entire EEG time series across electrodes, for each of 46 logarithmically spaced frequencies (2–100 Hz; Smith et al. 2022). After log-transforming the power, we downsampled the data by taking a moving average across 100 ms time intervals from 4000 ms preceding to 4000 ms following object presentation during List 1 and List 2. We slid the window every 25 ms, resulting in 317 time intervals (80 non-overlapping). Power values were then z-transformed by subtracting the mean and dividing by the standard deviation power. Mean and standard deviation power were calculated across all List 1 and List 2 objects across time points for each frequency.

2.3.1. Pattern classification analyses

Pattern classification analyses were performed using penalized (L2) logistic regression (penalty parameter = 1), implemented via the sklearn linear model module in Python. Classifier performance was assessed in two ways. "Classification accuracy" represented a binary coding of whether the classifier successfully guessed the instruction condition. We used classification accuracy for general assessment of classifier performance (i.e., whether encode/retrieve instructions could be decoded). "Classifier evidence" was a continuous value reflecting the logit-transformed probability that the classifier assigned the correct instruction for each trial. Classifier evidence was used as a trial-specific, continuous measure of mnemonic state information, which we used to assess the degree to which mnemonic state engagement varied across time as a function of the task instruction (encode, retrieve) and age group. Due to how we configured our classifier, positive classifier evidence values indicate more evidence for a retrieval state and negative classifier evidence values indicate more evidence for an encoding state, although we could have designed the classifier such that positive values reflect more evidence for an encoding state. This approach reflects our assumption – based on theoretical models of memory brain states (Hasselmo et al., 2002; Hasselmo, 2005) – that encoding and retrieval exist along a continuum. Relative to classifier accuracy, classifier evidence can provide greater insights into the strength or robustness of mnemonic state engagement. Although a classifier could assign the correct label (e.g. "retrieve") to a given trial, the evidence for that label may be strong (approaching 1, prior to logit-transforming) or weak (approaching 0.5, prior to logit-transforming). Thus, although classifier accuracy would be the same in both cases, classifier evidence varies considerably, suggesting differences in the strength of mnemonic state engagement.

We trained within-participant classifiers to discriminate List 2 encode vs. retrieve trials based on a feature space composed of all 63 electrodes × 46 logarithmically spaced frequencies ranging from 2 to 100 Hz. Before pattern classification analyses were performed, we performed an additional round of z-scoring across features (electrodes and frequencies) to eliminate trial-level differences in spectral power (Smith et al., 2022). For each participant, we used leave-one-run-out cross-validated classification in which the classifier was trained to discriminate encode from retrieve instructions for seven of the eight runs and tested on the held-out run. For classification analyses in which we assessed classifier accuracy, we averaged z-transformed power values over the 2000 ms stimulus interval. We conducted four separate classification analyses on z-transformed power averaged across four 500 ms intervals (0–500, 500–1000, 1000–1500, 1500–2000) spanning the stimulus interval. We evaluated classifier evidence as a function of instruction (encode, retrieve) across and within each of these intervals.

2.3.2. Cross study memory state decoding

We used an independently-validated mnemonic state classifier to test memory state engagement across YA, MA, and OA groups with a single training set, as within-participant classification can be driven by different features for different participants. We conducted three stages of classification using the same methods as in our prior work (Long, 2023; Smith and Long, 2024; Wheelock and Long, 2024; Han and Long, 2025). First, we conducted within participant leave-one-run-out cross-validated classification (penalty parameter = 1) on an independent set of young adult participants who completed the mnemonic state task and selectively excluded any of the YA participants reported here (N = 129, see Hong et al. 2023, Han and Long 2025 for details). The classifier was trained to distinguish encoding vs. retrieval states based on spectral power averaged across the 2000 ms stimulus interval during List 2 trials. For each participant, we generated true and null classification accuracy values. We permuted condition labels (encode, retrieve) for 1000 iterations to generate a null distribution for each participant. Any participant whose true classification accuracy fell above the 90th percentile of their respective null distribution was selected for further analysis (N = 44). Second, we conducted leave-one-participant-out cross-validated classification (penalty parameter = 0.0001) on the selected participants to validate the mnemonic state classifier and obtained classification accuracy of 59.69% which is significantly above chance (t_{43} = 6.029, p < 0.0001), indicating that the cross-participant mnemonic state classifier is able to distinguish encoding and retrieval states. Finally, we applied the cross-participant mnemonic state classifier to the List 2 data in the current study, specifically in 100 ms intervals across the 2000 ms stimulus interval. We selected 100 ms time intervals in order to detect potential underlying fluctuations in mnemonic state engagement that may be averaged over the pre-registered 500 ms time intervals selected for the within-participant analysis, and because the training and testing time intervals do not need to be matched in cross-participant classification, unlike the pre-registered within-participant classification. We extracted classifier evidence, the logit-transformed probability that the classifier assigned a given trial a label of encoding or retrieval. This approach provides a trial-level estimate of memory state evidence that is not constrained by participant-level differences in feature weights, enabling us to more directly compare mnemonic state engagement across the three age groups.

2.3.3. Statistical analyses

We used mixed effects ANOVAs and paired or independent samples t-tests to assess the effect of encode/retrieve instruction on behavioral memory performance. We used a 3 × 2 × 2 ANOVA with age (YA, MA, OA), instruction (encode, retrieve), and list (first, second) as factors.

To evaluate classification accuracy for MAs and OAs, we used paired-sample t-tests to compare classification accuracy across participants within each group to chance decoding accuracy, as determined by permutation procedures. Namely, for each participant, we shuffled the condition labels of interest (e.g., "encode" and "retrieve" for the instruction classifier) and then calculated classification accuracy. We repeated this procedure 1000 times for each participant and then averaged the 1000 shuffled accuracy values for each participant. These mean values were used as participant-specific empirically derived measures of chance accuracy. We used paired samples t-tests to compare the observed (unshuffled) accuracy values to the shuffled accuracy values.

To assess whether classification accuracy varies across age group, we used a one-way between-groups ANOVA with age (YA, MA, OA) as a factor. The dependent variable was classification accuracy from the classifier trained and tested on spectral data averaged over the 2000 ms stimulus interval.

To evaluate the extent to which within-participant classifier evidence predicts behavioral memory performance in OAs, we used logistic regression analyses. We performed separate logistic regression analyses for trials with encode and retrieve instructions. For each

analysis, regressors included: classifier evidence derived from within-participant classification, run number, and serial position. Classifier evidence was averaged across the 2000 ms stimulus interval.

To assess the time course and strength of classifier evidence as a function of age, we used mixed effects ANOVAs. We used a 3 × 2 × 4 ANOVA with age (YA, MA, OA), instruction (encode, retrieve), and time interval (four 500 ms intervals spanning the stimulus interval) as factors. To evaluate the degree to which older adults engage retrieval during encode trials, we performed post-hoc one-sample *t*-tests on each of twenty 100 ms time intervals spanning the entire 2000 ms stimulus interval with classifier evidence on encode trials as the dependent variable. We used false discovery rate (FDR) to correct for multiple comparisons (Benjamini and Hochberg, 1995).

3. Results

3.1. Middle-aged and older adults selectively encode and retrieve in response to top-down instructions

We first sought to determine the extent to which middle-aged (MAs) and older adults (OAs) can follow task instructions to engage in encoding and retrieval in comparison to young adults (YAs; Long and Kuhl 2019, Smith et al. 2022). Specifically, we tested whether instructions influenced recognition task performance across age groups (Fig. 2). Following our pre-registration, we conducted a 3 × 2 × 2 mixed effects ANOVA to evaluate the effects of age group (YAs, MAs, OAs), instruction type (encode, retrieve) and list (first, second) on recognition accuracy. A two-way interaction between list and instruction type, with no three-way interaction between list, instruction type, and age group, would indicate that instruction type has a similar impact on memory behavior for all three age groups. We report the full ANOVA results in Table 1 and highlight key findings here. We find a significant two-way interaction between list and instruction type, driven by greater recognition accuracy for List 2 objects with an encode instruction (M = 0.84, SD = 0.09) compared to List 2 objects with a retrieve instruction (M = 0.80, SD = 0.08; $t_{109} = 4.91$, $p < 0.001$, Cohen's $d = 0.42$). Based on the assumption that encoding trades off with retrieval (Hasselmo et al., 2002; Hasselmo, 2005; Long and Kuhl, 2019; Smith et al., 2022), retrieving a List 1 object should prevent encoding the current, List 2 object. Therefore, the instruction-driven dissociation in List 2 recognition accuracy suggests that participants followed the trial-level task demands to selectively encode or retrieve. The three-way interaction of list, instruction type and age group was not significant and Bayes Factor analysis revealed that a model without the three-way interaction term (H_0) is preferred to a model with the three-way interaction term (H_1; $BF_{10} = 0.07$, strong evidence for H_0). These results suggest that like YAs, MAs and OAs can follow instruction cues to selectively encode or retrieve.

3.2. Middle-aged and older adults differentially engage mnemonic states

Having shown behavioral evidence that MAs and OAs can follow instructions to selectively engage in encoding and retrieval, we next sought to determine the extent to which they engage mnemonic brain states in response to the instruction cues. Following our pre-registration, we conducted a multivariate pattern classification analysis in which we trained within-participant, leave-one-run-out classifiers to discriminate encode vs. retrieve List 2 trials based on a feature space composed of 63 electrodes and 46 frequencies ranging from 2–100 Hz averaged over the 2000 ms stimulus interval (Fig. 3). For all age groups, mean classification accuracy (YAs: M = 54.09%; MAs: M = 58.24%; OAs: M = 54.81%) was significantly greater than chance (as determined through a permutation procedure; all $ps < 0.01$). At the individual participant level, we find that a substantial proportion of the participants within each age group have classification accuracy values significantly above chance (YAs: M = 44.44% or 16/36; MAs: M = 58.33% or 21/36; OAs: M = 52.63% or 20/38). These results suggest that like YAs, both MAs and OAs can shift between encoding and retrieval states in a goal-directed manner.

Our next goal was to determine if classification accuracy varies as a function of age. Following our pre-registration, we conducted a one-way between-groups ANOVA to evaluate the effect of age group (YAs, MAs, OAs) on classification accuracy. The main effect of age group did not reach significance ($F_{2,107} = 2.83$, $p = 0.064$, $\eta_p^2 = 0.05$) and Bayes factor analysis yielded a value of 0.84, indicating anecdotal evidence for the null hypothesis that there is no difference in classification accuracy on the basis of age group. These results indicate that we can successfully distinguish encode from retrieve trials in MAs and OAs and that decoding performance is comparable across age groups.

Although we hypothesized that OAs are biased toward a retrieval state, the similar decoding performance across YAs and OAs – as well as our behavioral findings – suggests that OAs do engage the encoding state when instructed to encode. However, classification accuracy may obscure both moment-to-moment differences in memory state engagement between age groups and overall differences in memory state engagement. Therefore, we next sought to assess classifier evidence across the 2000 ms stimulus interval. Classifier evidence provides a continuous measure of the degree to which brain patterns resemble either a retrieval state or an encoding state. We designed our classifier such that positive classifier evidence values indicate greater evidence for retrieval and negative values indicate greater evidence for encoding. Thus, we can use classifier evidence to measure the extent to which OAs compared to YAs and MAs engage in mnemonic states and whether this engagement fluctuates over time. We have previously found that YAs show robust dissociations in classifier evidence across encode and retrieve trials late in the stimulus interval (around 1000 ms following stimulus onset; Smith et al. 2022).

Based on our prior work and following our pre-registration, we assessed classifier evidence across four 500 ms time intervals spanning the stimulus interval (Fig. 4A). We conducted a 3 × 2 × 4 mixed effects ANOVA to evaluate the effects of age group (YA, MA, OA), instruction type (encode, retrieve) and time interval (0–500, 500–1000, 1000–1500, 1500–2000 ms) on classifier evidence. A three-way interaction between age group, instruction type, and time interval would indicate differential memory state engagement by age that fluctuates over time. Alternatively, a two-way interaction between age group and instruction type, with no three-way interaction, would indicate that age differences in memory state engagement are consistent throughout the stimulus interval. We report the results of this ANOVA in Table 2 and highlight the key findings here. We find a significant interaction between age group and instruction type. The three-way interaction between age, instruction, and time interval was not significant. Bayes Factor analysis revealed that a model without the three-way interaction term (H_0) is preferred to a model with the three-way interaction term (H_1; $BF_{10} = 0.08$, strong evidence for H_0).

Given the significant interaction between instruction type and age, we next directly compared average classifier evidence *differences* across age groups (Fig. 4B). We calculated evidence difference scores (retrieve instruction trials - encode instruction trials) for each age group and performed three two-sample *t*-tests comparing each set of age groups. Positive values indicate more classifier evidence for retrieve compared to encode trials. Difference scores were significantly lower for OAs (M = 0.45, SD = 0.82) compared to MAs (M = 0.96, SD = 1.10; $t_{72} = 2.27$, $p = 0.026$, Cohen's $d = 0.53$). YA difference scores (M = 0.55, SD = 0.60) did not significantly differ from either MAs ($t_{70} = 1.94$, $p = 0.057$, Cohen's $d = 0.46$) or OAs ($t_{72} = 0.63$, $p = 0.529$, Cohen's $d = 0.15$). Together, these results suggest that although OAs can selectively engage mnemonic states, the strength of this engagement – reflected by lower evidence values – is diminished relative to MAs.

To directly test the extent to which classifier evidence predicts memory performance, we performed exploratory logistic regression analyses. Specifically, we assessed whether within-participant classifier

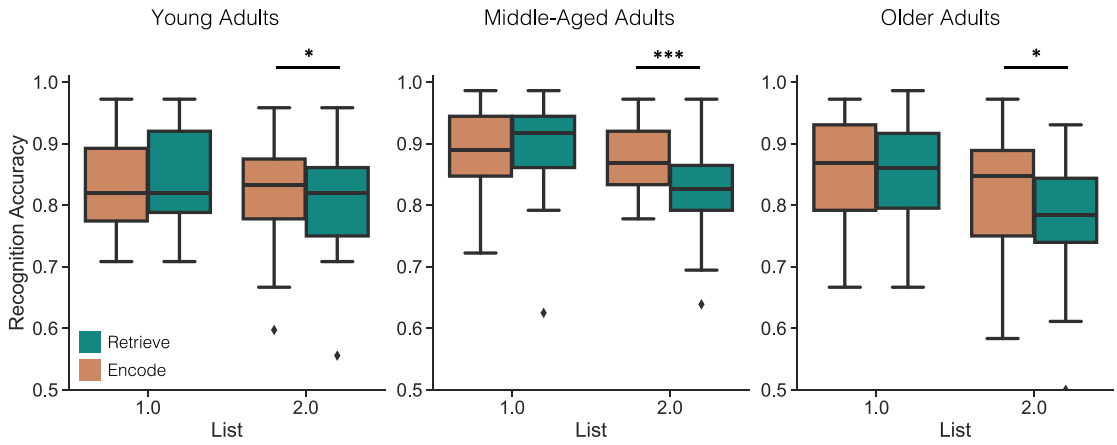

Fig. 2. Influence of age and mnemonic instructions on memory behavior. We assessed recognition accuracy as a function of list (1, 2) and instruction (orange represents encode; teal represents retrieve) for each age group. The boxes denote interquartile range, the horizontal bars denote median, and the whiskers denote minimum and maximum values. We find a significant interaction between list and instruction ($p < 0.001$) driven by greater accuracy for List 2 objects presented with an encode compared with a retrieve instruction. The three-way interaction of list, instruction type and age group was not significant ($p = 0.399$). *$p < 0.05$, ***$p < 0.001$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

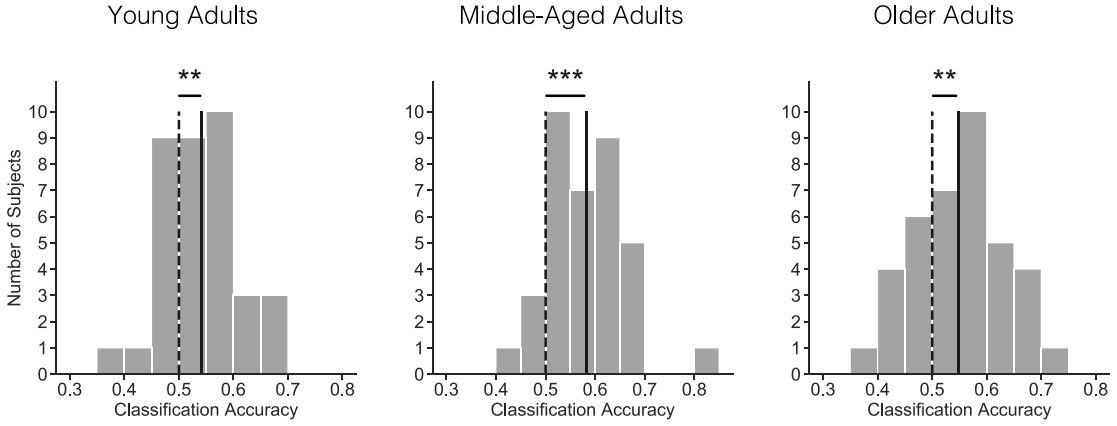

Fig. 3. Mnemonic state classification accuracy by age group. We conducted L2-logistic regression classification to discriminate encode versus retrieve trials during List 2 separately for each age group. Within-participant classifiers were trained and tested on a feature space of 63 electrodes and 46 frequencies averaged across the 2000 ms stimulus interval. Mean classification accuracy across all participants within each age group (solid vertical line) is shown along with a histogram of classification accuracies for individual participants (gray bars) and mean classification accuracy for permuted data across all participants (dashed vertical line). Mean classification accuracy was 54.09% for young adults, 58.24% for middle-aged adults, and 54.81% for older adults, each of which differed significantly from chance (all $ps < 0.01$). **$p < 0.01$, ***$p < 0.001$.

evidence predicted recognition accuracy in older adults for List 2 objects for the entire 2000 ms stimulus interval. We performed separate analyses for trials with an encode instruction and trials with a retrieve instruction. A positive beta value would indicate that more classifier evidence – greater evidence for retrieval – predicts better recognition accuracy, and a negative beta value would indicate that more classifier evidence predicts worse recognition accuracy. We find that the relationship between classifier evidence and recognition accuracy was not significant for encode trials (mean $\beta = -0.031$, $SD = 0.137$, one-sample t-test vs. 0, $t_{37} = -1.37$, $p = 0.180$) or retrieve trials (mean $\beta = -0.012$, $SD = 0.097$, one-sample t-test vs. 0, $t_{37} = -0.76$, $p = 0.454$). Although it is difficult to interpret a null result, the lack of a relationship between classifier evidence and behavioral performance may be due to diminished, and generally de-differentiated, brain state engagement in older adults.

3.3. Older adults show diminished mnemonic brain state engagement relative to both young and middle-aged adults

Our results suggest that although OAs can selectively engage memory encoding and memory retrieval states, the difference in engagement between the two mnemonic states is diminished relative to MAs. However, within-participant classification – although widely used – presents several challenges when attempting to interpret group-level differences. First, there is the possibility that the diminished dissociations in memory state evidence for OAs is due to issues with signal and/or data quality, rather than actual age-driven cognitive differences. Second, OAs may recruit different mechanisms when engaging in mnemonic states, as the exact features leveraged by each within-participant classifier can vary on a participant-by-participant basis. That is, although we find above chance classification for each age group, the features underlying classification success are not necessarily the same across age groups. Indeed, prior EEG work has shown that spectral signals change across the lifespan (Sander et al., 2012; Voytek et al., 2015; Tran et al., 2016; Healey and Kahana, 2020; Tran et al., 2020). In order to circumvent these limitations, we next utilized an independent dataset to assess mnemonic state engagement across the three age groups.

We developed a mnemonic state classifier based on an independent sample of young adult data that can reliably distinguish encoding from retrieval states. We then tested this mnemonic state classifier on the data reported here. This approach ensures that any differences that we observe in classifier evidence cannot be due to potential age-related differences in the classifier's ability to learn the mapping between

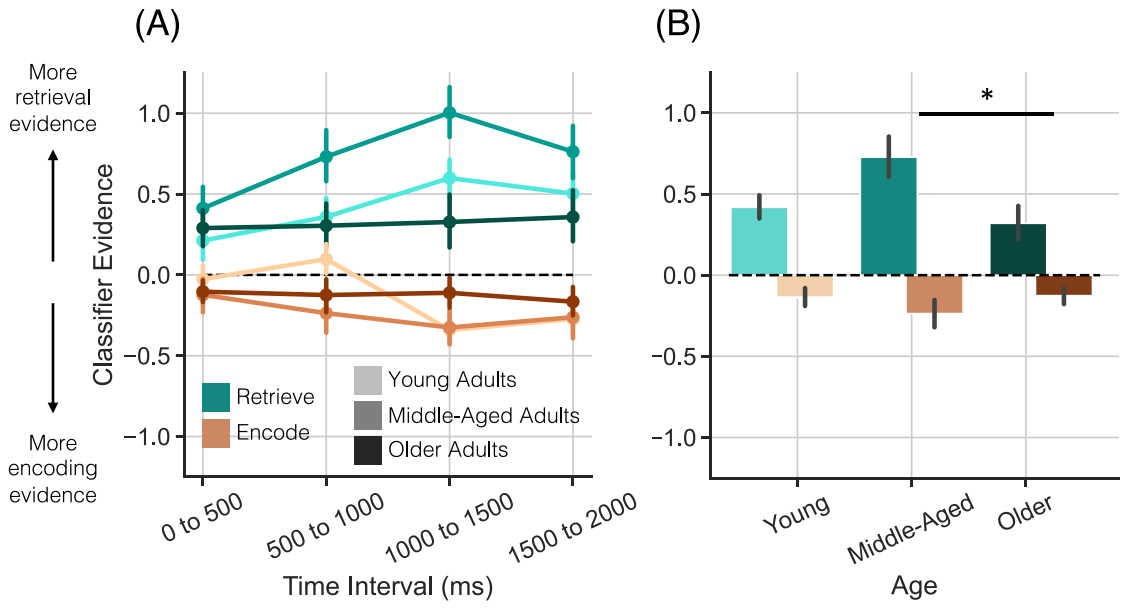

Fig. 4. Classifier evidence by age group. We trained and tested four sets of within-participant classifiers on four 500 ms time intervals within the 2000 ms stimulus interval separately for each age group. We assessed classifier evidence as a function of age group (young, lightest; middle-aged, intermediate; older, darkest), and instruction type (encode, orange; retrieve, teal). Positive values indicate greater evidence for retrieval; negative values indicate greater evidence for encoding. Error bars denote standard error of the mean. **(A)** Time interval (four 500 ms intervals) is included as a factor. We find a significant interaction between age group and instruction type ($p = 0.032$). **(B)** Classifier evidence averaged over time. The difference between retrieve and encode trials is significantly greater for middle-aged compared to older adults ($p = 0.026$). $^*p < 0.05$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

condition label (e.g. "retrieve") and spectral activity patterns. More critically, however, this approach allows us to gain insight into the extent to which young, middle-age, and older adults recruit shared vs. distinct mechanisms when engaging mnemonic states. In the extreme, if older adults recruit entirely different mechanisms from young adults, we would expect to find no 'transfer' – that is, we would not find any differences in classifier evidence at any time point or for any condition when the young-adult mnemonic state classifier is applied to the older adult data. However, based on the within-subject data above, we might anticipate that older adults recruit at least some of the same mechanisms as young adults, but to a lesser degree. That is, application of the mnemonic state classifier may reveal the same overall pattern in older adults – positive classifier evidence on retrieve trials – but with a smaller magnitude. Although older adults may engage additional compensatory mechanisms that we would miss with this approach, it would still elucidate the degree of overlap between young and older adult mnemonic state mechanisms. Importantly, cross-age classification can reveal the extent to which older adults may erroneously recruit mnemonic states. Our central hypothesis is that older adults are biased toward retrieval. We employed the cross-age mnemonic state classifier to detect the extent to which older adults potentially engage in a young adult-like retrieval state, both when instructed to encode and when instructed to retrieve.

We conducted an exploratory analysis in which we applied the independently-validated mnemonic state classifier to the current data. To capitalize on the high temporal resolution of scalp EEG, we tested this independent mnemonic classifier on twenty 100 ms intervals across the List 2 stimulus interval (Fig. 5). We utilized 100 ms time intervals because the 500 ms intervals used in the previous analysis, though selected *a priori* based on our prior work (Smith et al., 2022), may obscure underlying mnemonic state engagement fluctuations. Furthermore, whereas training and testing time intervals are matched for within-participant classification, the independent mnemonic classifier is trained on the entire 2000 ms stimulus duration comprising a single time interval (Long, 2023; Smith and Long, 2024; Wheelock and Long, 2024; Han and Long, 2025) as we do not expect the timing of mnemonic state engagement to be consistent across all participants. We tested for potential dissociations in mnemonic state engagement via a $3 \times 2 \times 20$ mixed effects ANOVA with factors of age (YA, MA, OA), instruction type (encode, retrieve) and time interval. We report the results of this ANOVA in Table 3; we find a significant three-way interaction between age, instruction type, and time interval, indicating that engagement of mnemonic brain states over time differs across age groups.

We conducted three follow-up ANOVAs (Table 4) in which we compared mnemonic state engagement for each pair of age groups across instruction type and time interval. We find significant age-related dissociations when we compare older adults to both young and middle-age adults. We find greater classifier evidence for YAs and MAs compared to OAs on retrieve trials. With the same training data, and hence, the same underlying spectral features, these data indicate that patterns of neural activity recruited in response to the instruction to retrieve are less consistent and/or robust in older adults. That is, when participants are instructed to retrieve a previously presented stimulus, older adults show less engagement in the retrieval state in comparison to young and middle-age adults. That we find greater classifier evidence for OAs relative to YAs and MAs on encode trials further suggests a tendency for older adults to engage in retrieval when task-irrelevant, which we explore further below. In contrast, we find no significant dissociations between young and middle-age adults. In combination with the within-participant classification evidence data, our interpretation is that older adults' mnemonic state engagement is diminished relative to young and middle-age adults.

Finally, we assessed the degree to which older adults have a bias toward the young adult-like retrieval state. We performed post-hoc one-sample *t*-tests in which we compared older adult classifier evidence (derived from the independent classifier) on trials with an encode instruction to 0. We find a significant increase in classifier evidence for the 1000 to 1100 ms time interval ($M = 0.03$, $SD = 0.06$; $t_{37} = 2.56$, $p = 0.015$, Cohen's $d = 0.42$; FDR corrected). Although classifier evidence was numerically greater than zero from 800 to 1300 ms, no other tests survived multiple comparisons correction (t's < 2.15, p's > 0.038). We additionally find a significant decrease in classifier evidence from 0 to 600 ms (0–100 ms, $t_{37} = -7.98$, $p < 0.001$, Cohen's $d = 1.31$; 100–200 ms, $t_{37} = -10.54$, $p < 0.001$, Cohen's $d = 1.73$; 200–300 ms,

Table 1
Analysis of variance for the effect of instruction type, age group (young, middle-aged, older), and list on recognition accuracy.

Effect	df	*F*	*p*	η_p^2
Main effect of age group	(2,107)	5.88	**0.004**	0.01
Main effect of list	(1,107)	34.09	<**0.001**	0.24
Main effect of instruction type	(1,107)	14.60	<**0.001**	0.12
Interaction of age group × list	(2,107)	2.27	0.108	0.04
Interaction of age group × instruction type	(2,107)	1.08	0.342	0.02
Interaction of instruction type × list	(1,107)	18.87	<**0.001**	0.15
Interaction of age group × instruction type × list	(2,107)	0.93	0.399	0.02

Bold values indicate $p < 0.05$.

Table 2
Analysis of variance for the effect of instruction type, age group (young, middle-aged, older), and time interval (500 ms) on classifier evidence.

Effect	df	*F*	*p*	η_p^2
Main effect of instruction type	(1,107)	61.3	<**0.001**	0.36
Main effect of age group	(2,107)	2.34	0.101	0.04
Main effect of time interval	(3,321)	0.90	0.440	0.01
Interaction of instruction type × age group	(2,107)	3.55	**0.032**	0.06
Interaction of age × time interval	(6,321)	0.58	0.748	0.01
Interaction of instruction type × time interval	(3,321)	7.16	**0.001**	0.06
Interaction of instruction type × age group × time interval	(6,321)	1.87	0.086	0.03

Bold values indicate $p < 0.05$.

Table 3
Analysis of variance results for instruction type, age group (young, middle-aged, older), and time interval (100 ms) on cross-study classifier evidence.

Effect	df	*F*	*p*	η_p^2
Main effect of instruction type	(1,107)	34.31	<**0.001**	0.24
Main effect of age group	(2,107)	2.30	0.105	0.04
Main effect of time interval	(19,2033)	164.1	<**0.001**	0.61
Interaction of instruction type × age group	(2,107)	5.87	**0.004**	0.10
Interaction of age × time interval	(38,2033)	2.36	<**0.001**	0.04
Interaction of instruction type × time interval	(19,2033)	13.18	<**0.001**	0.11
Interaction of instruction type × age group × time interval	(38,2033)	2.62	<**0.001**	0.05

Bold values indicate $p < 0.05$.

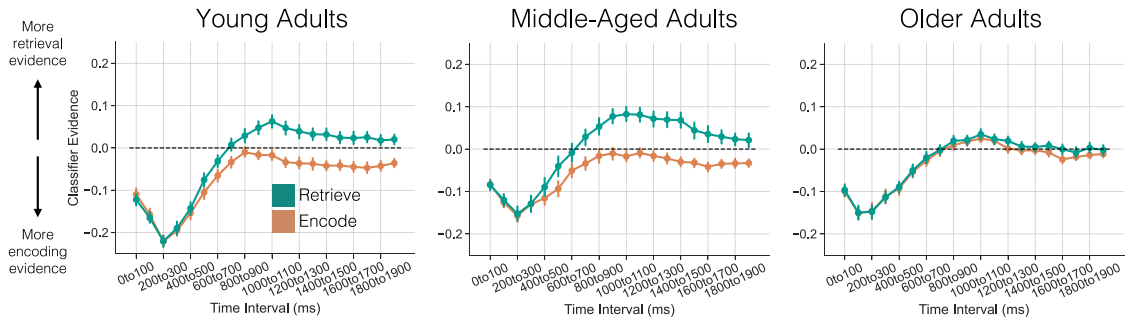

Fig. 5. Independent assessment of mnemonic state engagement by age group. We utilized an independently validated mnemonic state classifier to assess memory state evidence in twenty 100 ms intervals across the 2000 ms stimulus interval for young, middle-aged and older adults separately for encode (orange) and retrieve (teal) trials. We find a significant three-way interaction between age group, instruction type, and time interval ($p < 0.001$). Error bars denote standard error of the mean. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

$t_{37} = -7.79$, $p < 0.001$, Cohen's $d = 1.28$; 300–400 ms, $t_{37} = -6.99$, $p < 0.001$, Cohen's $d = 1.15$; 400–500 ms, $t_{37} = -5.91$, $p < 0.001$, Cohen's $d = 0.97$; 500–600 ms, $t_{37} = -3.67$, $p < 0.001$, Cohen's $d = 0.60$; all FDR corrected) and from 1600–1700 ms ($t_{37} = -2.61$, $p = 0.013$, Cohen's $d = 0.43$, FDR corrected). Given the nature of how we structured our classifier, negative classifier evidence reflects more evidence for an encoding state. Therefore, older adults show strong encoding state engagement during List 2 stimulus presentation, followed by modest engagement of the retrieval state. Together, these findings suggest that older adults recruit similar encoding mechanisms as young adults but additionally exhibit a subtle bias toward retrieval.

4. Discussion

The goal of the current study was to measure the extent to which older adults engage in memory encoding and memory retrieval states. We directly tested the hypothesis that older adults are biased toward a retrieval state. We recorded scalp electroencephalography while young, middle-aged and older adult participants performed a memory task in which they were explicitly directed to either encode the currently presented object stimulus or retrieve a previously presented, categorically-related object stimulus. We report three key findings. First, we find that like young adults, middle-aged and older adults can follow top-down instructions to selectively engage in encoding or retrieval. Second, we find that we can successfully decode mnemonic brain states in all three age groups. Finally, we show that mnemonic

Table 4
Analysis of variance results for instruction type, age group (pairwise comparisons) and time interval (100 ms) on cross-study classifier evidence.

Young vs. Older adults				
Effect	df	*F*	*p*	η_p^2
Main effect of instruction type	(1,72)	20.90	<**0.001**	0.22
Main effect of age group	(1,72)	3.15	0.080	0.04
Main effect of time interval	(19,1368)	115.6	<**0.001**	0.62
Interaction of instruction type × age group	(1,72)	10.79	**0.002**	0.13
Interaction of age × time interval	(19,1368)	3.95	<**0.001**	0.05
Interaction of instruction type × time interval	(19,1368)	5.61	<**0.001**	0.07
Interaction of instruction type × age group × time interval	(19,1368)	3.34	<**0.001**	0.04
Middle-aged vs. Older adults				
Effect	df	*F*	*p*	η_p^2
Main effect of instruction type	(1,72)	15.78	<**0.001**	0.18
Main effect of age group	(1,72)	0.19	0.661	< 0.01
Main effect of time interval	(19,1368)	92.93	<**0.001**	0.56
Interaction of instruction type × age group	(1,72)	9.48	**0.003**	0.12
Interaction of age × time interval	(19,1368)	1.04	0.408	0.01
Interaction of instruction type × time interval	(19,1368)	6.42	<**0.001**	0.08
Interaction of instruction type × age group × time interval	(19,1368)	4.27	<**0.001**	0.06
Young vs. Middle-aged adults				
Effect	df	*F*	*p*	η_p^2
Main effect of instruction type	(1,70)	34.31	<**0.001**	0.33
Main effect of age group	(1,70)	3.66	0.060	0.05
Main effect of time interval	(19,1330)	121.9	<**0.001**	0.64
Interaction of instruction type × age group	(1,70)	0.47	0.495	0.01
Interaction of age × time interval	(19,1330)	2.08	**0.004**	0.03
Interaction of instruction type × time interval	(19,1330)	16.18	<**0.001**	0.19
Interaction of instruction type × age group × time interval	(19,1330)	0.46	0.977	0.01

Bold values indicate $p < 0.05$.

brain state engagement is diminished in older adults as compared to both young and middle-aged adults. Taken together, these results suggest that differential mnemonic brain state engagement for older adults compared to young and middle-aged adults may underlie age-related changes to memory.

Middle-aged and older adults selectively encode and retrieve in response to task demands. We find that across all age groups, memory is low for currently presented objects paired with a top-down demand to retrieve a previously presented object. As older adults have deficits in executive function (Foster et al., 2007; Plancher et al., 2009; Salthouse, 2010, 2012), including difficulty inhibiting retrieval of semantic information (Wynn et al., 2020) and increased susceptibility to interference (Hasher and Zacks, 1988), we might have expected older adults to have worse memory performance for objects paired with the encode instruction relative to young and middle-aged adults. However, we did not find strong evidence for behavioral differences across age groups. Yet, it is possible that older adults do still engage some degree of retrieval on encode trials, but the nature of what is being retrieved differs by age. As we did not directly assess retrieval success of the previously presented objects – by design, to minimize differences in behavioral demands between encode and retrieve trials – we cannot know what, if anything, participants retrieve during either encode or retrieve trials. Given older adults' tendency to rely on gist-level information (conceptual essence of an event without specific details) rather than verbatim information (episodic, defining details of an event; Koutstaal and Schacter 1997, Tun et al. 1998, Koutstaal et al. 1999, Brainerd and Reyna 2002, Koutstaal 2003), older adults may have retrieved gist-level information, such as the object category, on encode trials. Verbatim retrieval may result in attention to details specific to the previous object that do not apply to the currently presented object, which may interfere with the participant's ability to encode the current object. In contrast, gist-level retrieval may not produce interference insofar as the retrieved information will apply to both the previous and current object as the two belong to the same category. Future work is needed to disambiguate these alternatives. Furthermore, as memory can be facilitated when older adults are aware of changes during new learning (Garlitch and Wahlheim, 2020), the impacts of interference might have been reduced in the current study given that we explicitly instructed participants as to the change in stimuli between the two object sets. Although there may yet be mechanistic differences as a function of age, our findings suggest that all three age groups can follow task instructions to selectively encode or retrieve.

Based on the well-established testing-effect (e.g. Roediger and Karpicke 2006), we might have expected to find that memory is higher for previously presented, to-be-retrieved objects. The logic is that the retrieve instruction affords the opportunity to practice retrieving the previously presented object. However, across all three age groups we failed to find a significant difference in memory for previous items on the basis of the instruction. Although we cannot draw strong conclusions from a null result, our speculation is that this lack of dissociation – consistent with our prior work (Long and Kuhl, 2019) – is due in part to the lack of interference that participants experience upon first encountering these objects. Performance is overall high for these objects such that the retrieval practice opportunity may not provide a substantial boost to memory for those objects. Relatedly, as mentioned in the paragraph above, we cannot know if the participants successfully retrieved the previously presented objects, thus there may exist dissociations that are masked by our inability in the present study to separate retrieval success from retrieval failure.

We find that mnemonic brain states are decodable within each age group, demonstrating that middle-aged and older adults, like young adults, can shift between encoding and retrieval states in response to task goals. Although the mnemonic state classification accuracy values are lower than those reported in studies that decode visually presented object stimuli (e.g. faces and scenes, Kuhl et al. 2012), the classification accuracies reported here (YAs: M = 54.09%; MAs: M = 58.24%; OAs: M = 54.81%) are both significantly above chance and highly similar to those we have reported in previous mnemonic state decoding experiments (Long and Kuhl, 2019). In our view, mnemonic states represent a culmination of multiple processes, including but not limited to: internal and external attention, search processes, perception, and binding, which contribute considerable variability to the patterns that underlie encoding and retrieval states. That we can distinguish between encoding and retrieval states consistently across studies suggests

that the mnemonic state decoding approach is a reliable method. On the basis of evidence that older adults exhibit a bias toward semantic memory (Ofen and Shing, 2013) and difficulty inhibiting semantic retrieval (Wynn et al., 2020), we formed our hypothesis that older adults are biased toward a retrieval state. Strong support for this hypothesis would be provided by a *failure* to decode mnemonic states specifically for older adults. That is, if older adults engaged in retrieval on both encode and retrieve trials, the classifier would be unable to distinguish between those trials and mean classification accuracy would be at chance. That we find reliably above chance decoding in older adults provides evidence against our hypothesis and instead suggests that older adults can selectively engage in encoding despite potential interference from previously presented, categorically-related objects.

Despite finding above chance mnemonic state decoding across all age groups, the precise engagement of mnemonic states varies across age groups. In contrast to classifier accuracy, classifier evidence can provide more nuanced insights into the strength of mnemonic state engagement. We find that within-participant classifier evidence is less positive on retrieve trials for older, compared to middle-aged adults. We also find that classifier evidence does not predict memory performance in older adults. The decrease in classifier evidence suggests that the patterns of neural activity associated with the retrieval state – though not entirely inconsistent with the learned 'retrieve' pattern – are less consistent and/or robust in older relative to middle-aged adults, suggesting diminished engagement of retrieval or retrieval-like mechanisms. Although caution is warranted regarding null findings, the lack of a significant relationship between classifier evidence and recognition accuracy may similarly reflect a reduction in differentiation between mnemonic brain states in older adults. A growing body of literature suggests that older adults exhibit de-differentiation – a reduction in the distinctiveness of their neural representations of stimuli themselves (Koen and Rugg, 2019; Folville et al., 2020; Hill et al., 2021; Pauley et al., 2024; Srokova et al., 2024). The present work offers complementary insights into the *processes* that may act on those representations. Mnemonic brain states themselves may become de-differentiated in aging, and impact downstream processing.

Within-participant classification is a powerful tool; however, estimates of group-level differences in classifier evidence derived from this approach may be the result of disparities in the training set, rather than reflecting true cognitive differences. To overcome this limitation, we used a single independently-validated mnemonic state classifier trained on a separate dataset of young adults performing the mnemonic state task. This approach provides insights into the extent to which mnemonic state mechanisms are shared across age groups. In contrast to the robust instruction-driven dissociations that we find in classifier evidence for both young and middle-aged adults (and no differences between these two groups), older adults show diminished engagement of mnemonic states overall with a tendency to over-engage the retrieval state. Whereas extensive prior work has demonstrated age-related neural dissociations in memory encoding and retrieval, the majority of investigations have centered around univariate activity differences underlying successful memory and multivariate analysis of representations, rather than processes. For instance, older adults show both diminished subsequent memory effects in anterior temporal regions as well as enhanced subsequent memory effects in posterior regions (e.g. Morcom et al. 2003). As discussed above, the current study does not assess successful encoding or retrieval and instead is focused on the mnemonic states thought to be deployed prior to memory success (Tulving, 1983; Rugg and Wilding, 2000). Identifying age-related changes in brain states – spatially distributed patterns of activity or connectivity that are sustained over time (Beaty et al., 2018; Kay and Frank, 2019; Tang et al., 2012) – is critical given that brain states broadly influence cognition, including subsequent memory (Long and Kuhl, 2019; Smith et al., 2022) and decision making (Duncan et al., 2012; Duncan and Shohamy, 2016). Diminished mnemonic state engagement in older adults will have downstream effects, including both the immediate potential for retrieval success and how older adults represent stimuli more generally (Long and Kuhl, 2021). To the extent that older adults over-recruit the retrieval state – and thus under-recruit the encoding state – they may fail to encode the event-specific details that enable subsequent memory of the currently presented object.

Older adults may engage a young adult-like retrieval state due to both a diminished ability to use top-down control to engage task-relevant mnemonic states and because automatic processes take over when control fails. Executive function deficits in healthy aging (Foster et al., 2007; Plancher et al., 2009; Salthouse, 2010, 2012) may result in a tendency toward the retrieval state. Specifically, researchers have posited that age-related memory declines may be the result of diminished executive functions with age (*executive decline hypothesis*; Dempster 1992, Moscovitch and Winocur 1992, Parkin and Walter 1992, Troyer et al. 1994). The executive decline hypothesis is supported by evidence that older adults generally have worse performance on executive function tasks compared to young adults (Daigneault and Braun, 1993; Brennan et al., 1997; Bryan et al., 1999) and is consistent with findings that older adults have difficulty with strategic encoding (Greene et al., 2020) and inhibition (Hasher and Zacks, 1988; Connelly et al., 1991; Hartman and Hasher, 1991; Hamm and Hasher, 1992; Hasher et al., 1997; Lustig et al., 2007; Lalla et al., 2022). Despite evidence that older adults are able to engage mnemonic brain states to some extent, we find that their engagement in these states appears diminished relative to young and middle-aged adults, which may be the result of age-related executive control deficits. These potential executive function deficits may be exacerbated by a baseline "shift" in the tendency to engage in semantic retrieval. Young adults automatically engage in retrieval when experiences overlap in time (Smith et al., 2022) and older adults have difficulty inhibiting retrieval from semantic memory (Wynn et al., 2020). In the event that older adults cannot sufficiently engage in either brain state, they might fall back on automatically engaged brain states. Specifically, when older adults are unable to sufficiently engage encoding, they may rely on retrieval. Evidence of age-related increases in coupling between the DMN and control regions is consistent with this interpretation (*default-executive coupling hypothesis of aging*; Turner and Spreng 2015, Spreng and Turner 2019). Namely, this age-related coupling enables information consistent with prior knowledge to be readily integrated with existing representations (Amer et al., 2019), a process which has been linked to de-differentiation (Spreng and Schacter, 2012; Geerlings et al., 2014; Amer et al., 2016; Rieck et al., 2017). Given that older adults have greater DMN activity (Lustig et al., 2003; Grady et al., 2006) and substantial prior knowledge (Park et al., 2001), they may be automatically drawn into retrieval when they are unable to encode. Thus, although all age groups appear to recruit similar mechanisms to engage the encoding state in response to the presentation of the object stimulus, our results suggest that older adults have a greater tendency to engage in young adult-like retrieval when experiences overlap.

The age-related differences in mnemonic state engagement that we find may also be indicative of compensatory mechanisms recruited by older adults. According to the Scaffolding Theory of Aging and Cognition, additional brain regions are recruited as 'scaffolding' to maintain cognitive performance amidst the neural degradation associated with aging (Park and Reuter-Lorenz, 2009; Reuter-Lorenz and Park, 2014). Specifically, neural changes in older adulthood degrade inputs for cognitive processing such that additional cognitive control is needed to extract task-relevant signals amongst the increased noise (Spreng and Turner, 2019). In line with this prior work, we speculate that older adults performing the mnemonic state task may recruit additional neural resources to exert the cognitive control necessary to engage task-relevant mnemonic states. One potential compensatory mechanism invoked by older adults is increased connectivity between the DMN and the frontoparietal control network (FPCN), which may compensate for reduced within-DMN connectivity (Spreng and Schacter, 2012; Turner and Spreng, 2015; Grady et al., 2016). Older adults therefore may

have elevated DMN-FPCN connectivity for both encode and retrieve trials in the present experimental paradigm, in order to exert cognitive control in response to task demands. However, elevated DMN-FPCN connectivity across both task instruction conditions would also come at the cost of reducing distinctiveness between the two brain states. Such an effect would make it more difficult to distinguish between encode vs. retrieve trials, which is consistent with our finding of lower classifier evidence in older adults. Thus, the diminished mnemonic state engagement that we observe in older adults may be indicative of compensatory mechanisms.

Older adults' diminished mnemonic state engagement may be further exacerbated by difficulties in switching between tasks in response to task instructions. In the present experimental paradigm, participants were explicitly directed to encode or retrieve on each trial such that they frequently had to toggle between different top-down task demands. Given that older adults may have difficulty maintaining distinct task sets (Verhaeghen, 2011) and specific evidence for age-related difficulties in appropriate processing of retrieval cues (Morcom and Rugg, 2004), older adults may have more difficulty switching between task instructions compared to young and middle-aged adults, contributing to diminished mnemonic state engagement. Thus, older adults need to exercise a high degree of control — to instantiate the task-relevant state, inhibit the task-irrelevant state, and switch between states in response to task demands.

Our interpretation that older adults' executive control deficits may manifest as diminished mnemonic state engagement is consistent with a growing body of work suggesting that the mnemonic states measured here may reflect how attention is oriented rather than memory per se. That is, the current results may reflect attentional rather than – or in addition to – memory deficits. Attention can be divided into internal vs. external (Chun et al., 2011), whereby internal attention constitutes focusing on thoughts and representations in the mind whereas external attention constitutes focusing on sensory stimuli outside of the mind. Prior work has shown that the retrieval state as measured here is engaged in response to the top-down demand to retrieve (Smith and Long, 2024) in addition to spatial attention demands (Long, 2023) and changes in task demands (Wheelock and Long, 2024). Thus, older adults' diminished engagement in memory encoding and retrieval states may reflect a decreased ability to deploy sustained attention to specifically focus their attention internally or externally.

In conclusion, we show that older adults' mnemonic state engagement is diminished relative to young and middle-aged adults. Diminished mnemonic brain state engagement may arise from executive control deficits in older adults and may in turn account for episodic memory deficits in healthy aging. To the extent that the mnemonic states measured here reflect how attention is oriented and/or sustained, (Long, 2023; Smith and Long, 2024; Wheelock and Long, 2024), the age-related differences in mnemonic state engagement that we observe in the present study have a strong potential to influence cognition more broadly. These results advance our understanding of how mnemonic brain states change over the lifespan.

Submission declaration and verification

This work has not been published previously and it is not under consideration for publication elsewhere. This publication is approved by all authors and will not be published elsewhere.

Consent statement

All participants provided informed consent.

CRediT authorship contribution statement

Isabelle L. Moore: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Devyn E. Smith:** Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation. **Nicole M. Long:** Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

The raw, deidentified data and the associated experimental and analysis codes used in this study are available via the Long Term Memory lab website (https://longtermmemorylab.com)

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