



# Age-Related differences in the relationship between sustained attention and associative memory and Memory-Guided inference

Tammy T. Tran<sup>1,2</sup> · Kevin P. Madore<sup>1</sup> · Kaitlyn E. Tobin<sup>3</sup> · Sophia H. Block<sup>3</sup> · Vyash Puliyadi<sup>2</sup> · Shaw C. Hsu<sup>4</sup> · Alison R. Preston<sup>5,6,7</sup> · Arnold Bakker<sup>2,3</sup> · Anthony D. Wagner<sup>1,8</sup>

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## Abstract

Episodic memory enables the encoding and retrieval of novel associations, as well as the bridging across learned associations to draw novel inferences. A fundamental goal of memory science is to understand the factors that give rise to individual and age-related differences in memory-dependent cognition. Variability in episodic memory could arise, in part, from both individual differences in sustained attention and diminished attention in aging. We first report that, relative to young adults ( $N = 23$ ;  $M = 20.0$  years), older adults ( $N = 26$ ,  $M = 68.7$  years) demonstrated lower associative memory and memory-guided associative inference performance and that this age-related reduction in associative inference occurs even when controlling for associative memory performance. Next, we confirm these age-related memory differences by using a high-powered, online replication study (young adults:  $N = 143$ ,  $M = 26.2$  years; older adults  $N = 133$ ,  $M = 67.7$  years), further demonstrating that age-related differences in memory do not reflect group differences in sustained attention (as assayed by the gradual-onset continuous performance task; gradCPT). Finally, we report that individual differences in sustained attention explain between-person variability in associative memory and inference performance in the present, online young adult sample, but not in the older adult sample. These findings extend understanding of the links between attention and memory in young adults, demonstrating that differences in sustained attention was related to differences in memory-guided inference. By contrast, our data suggest that the present age-related differences in memory-dependent behavior and the memory differences between older adults are due to attention-independent mechanisms.

**Keywords** Cognitive aging · Declarative memory · Integrative encoding · Generalization

## Introduction

The ability to sustain attention is a fundamental cognitive ability that is hypothesized to underlie a number of different cognitive functions (Sarter et al., 2001; Unsworth et al., 2010), including episodic memory (deBettencourt et al., 2018, 2021; Madore et al., 2020). Whereas multiple

attention processes are closely intertwined with episodic memory (Aly & Turk-Browne, 2016, 2017; Cabeza et al., 2008; Hannula, 2018; Hutchinson et al., 2009; Sherman et al., 2024; Uncapher et al., 2011), recent work has focused specifically on the impact of sustained attention on learning and memory. Emerging findings in young adults suggest that sustained attention has direct consequences

✉ Tammy T. Tran  
tammytt@stanford.edu

<sup>1</sup> Department of Psychology, Stanford University, Stanford, CA, USA

<sup>2</sup> Department of Psychological and Brain Sciences, School of Arts and Sciences, Johns Hopkins University, Baltimore, MD, USA

<sup>3</sup> Department of Psychiatry and Behavioral Sciences, Johns Hopkins University School of Medicine, Baltimore, MD, USA

<sup>4</sup> Biophysics Graduate Program, Stanford University, Stanford, CA, USA

<sup>5</sup> Center for Learning & Memory, University of Texas at Austin, Austin, TX, USA

<sup>6</sup> Department of Psychology, University of Texas at Austin, Austin, TX, USA

<sup>7</sup> Department of Neuroscience, University of Texas at Austin, Austin, TX, USA

<sup>8</sup> Wu Tsai Neurosciences Institute, Stanford University, Stanford, CA, USA

for performance; assays of sustained attention predict (a) variability in subsequent working memory (Hakim et al., 2020) and episodic memory (deBettencourt et al., 2018, 2021; Madore et al., 2020); (b) everyday cognitive errors (Cheyne et al., 2006; Manly et al., 1999); and (c) real-world academic and workplace performance (Gallen et al., 2023; Kalechstein et al., 2003). Whereas these and other observations demonstrate the importance of sustained attention for memory and knowledge-dependent behavior, including episodic encoding and retrieval, fundamental questions remain. Here we ask: Does variability in sustained attention explain variability in the ability to draw memory-guided inferences that bridge across related, but distinct events? And, what role does sustained attention play in age-related episodic memory differences and in memory variability between older adults?

It is well-established that aging is associated with an overall decline in episodic memory function ( Craik, 1994; Hedden & Gabrieli, 2004; Light, 2024; Nyberg et al., 2024). For example, previous studies have reliably reported diminished associative memory performance in older adults compared with young adults (Naveh-Benjamin & Mayr, 2018). Poor associative memory in older adults has been hypothesized to be due to binding deficits at encoding (Chalfonte & Johnson, 1996; Naveh-Benjamin, 2000; Naveh-Benjamin et al., 2003), diminished pattern separation (Bakker et al., 2012; Yassa et al., 2011), reduced executive function (Buckner, 2004; Raz, 2000), as well as impairments in memory retrieval processes (Cohn et al., 2008; Hertzog et al., 2013; Rugg & Srokova, 2024; Trelle et al., 2020). Moreover, there is considerable variability in associative memory performance across older adults, with multiple factors likely driving these between-person differences in how well older adults remember (Buckner, 2004; Hokett et al., 2021; Kidwai et al., 2024; Sadeh et al., 2020; Trelle et al., 2021).

Beyond associative memory, aging is linked to a decrease in memory-guided associative inference (Carpenter & Schacter, 2018) and inferential reasoning (Cohen, 1981; Moses et al., 2010; Ryan et al., 2009; Salthouse & Prill, 1987). Memory-guided associative inference entails the use of episodic memories to infer the relations between stimuli that were not directly experienced together but are related through common elements that span multiple events (Eichenbaum, 2000; Shohamy & Wagner, 2008; Zeithamova et al., 2012). Initial work suggests that older adults are less able to draw associative inferences compared with young adults (Carpenter & Schacter, 2018), and recent findings from a list-learning variant of the associative inference task suggest that this age-related decline may stem, in part, from increased proactive interference (Burton et al., 2019; Garlitch & Wahlheim, 2020). A central open question is what other processing differences might drive age-related decreases in memory-guided inferential behavior and

contribute to individual differences in associative memory and inference across older adults.

Building on the emerging literature on sustained attention and episodic memory, we posit that sustained attention may relate to between-person variability in the ability to (a) encode and retrieve direct associations between co-occurring stimuli and (b) flexibly use such associative memories to draw novel inferences about the relations between stimuli. There is a rich literature documenting the link between sustained attention and immediate task performance (Chun, 2011; Esterman et al., 2013; Ling & Carrasco, 2006; Rosenberg et al., 2013). Moreover, individual differences in sustained attention in young adults partially account for between-person variability in working memory (Adam & deBettencourt, 2019; Hakim et al., 2020; Keene et al., 2022) and episodic memory performance (deBettencourt et al., 2018, 2021; Madore et al., 2020). One proposed framework (i.e., “readiness-to-remember”) hypothesizes that variance in episodic memory performance emerges, in part, as a function of moment-to-moment and individual differences in sustained attention, alongside differences in other frontoparietal attentional and cognitive control processes (see Madore & Wagner, 2022, for review). From this and related perspectives, the encoding and retrieval of episodic memories depend, in part, on the ability to sustain attention to the task at hand, to attend to the elements of experience and to cues that can trigger retrieval, and to maintain attention on memory products. Although extant data document links between sustained attention and performance on episodic memory tasks (deBettencourt et al., 2018, 2021; Madore et al., 2020), it is unclear whether sustained attention also facilitates the ability to draw associative inferences and thus supports the ability to generate novel predictions. One possibility is that differences in sustained attention will relate to differences in associative inference performance, because the latter depends on the ability to encode and retrieve memories of specific experiences where stimuli co-occurred. Alternatively, it is possible that sustained attention will explain additional variance in associative inference performance, over and above memory for specific experienced associations, potentially impacting mnemonic integration (Ritvo et al., 2024; Shohamy & Wagner, 2008; Zeithamova & Preston, 2010) or recurrence mechanisms that have been posited to be critical for memory-guided inferences (Kumaran et al., 2016).

Considerably less is known about whether sustained attention processes, at least partially, underlie memory performance and explain memory decline in older adults. In older adults, divergent evidence alternatively suggests that sustained attention is diminished (Berardi et al., 2001; Fortenbaugh et al., 2015; McAvinue et al., 2012), remains relatively preserved (Jackson & Balota, 2012; Jackson et al., 2013; Staub et al., 2013), or, in some cases, is even superior

compared with young adults (Carriere et al., 2010; Robison et al., 2022; Staub et al., 2014; see Vallesi et al., 2021 for review). Concurrent with this mixed evidence on how aging impacts sustained attention, it is apparent from extant studies that sustained attention performance is highly variable across people, with marked individual differences in sustained attention in older adults (Carriere et al., 2010; Fortenbaugh et al., 2015). Yet, it is unknown whether between-person variability in sustained attention partially explains memory differences across cognitively unimpaired older adults. To address these knowledge gaps, we examined (a) whether individual differences in sustained attention relate to both associative memory and associative inference performance in young adults and older adults, and (b) whether age-related differences in sustained attention partially explain age-related memory decline.

To investigate attention-memory interactions at the individual level and as a function of age, we assessed how individual and age-related performance on a sustained attention task—the gradual-onset continuous performance task (gradCPT) (Esterman et al., 2013; Rosenberg et al., 2013)—relate to associative memory and associative inference performance on an AB-BC memory task. In this memory paradigm, participants encode and then are tested on object-scene stimulus pairs (referred to as AB pairs). Subsequently, they learn and then are tested on new object-scene pairs (referred to as BC pairs), where one item (B) belongs to a previously learned pair (AB). Nonoverlapping (DE and XY) control pairs are included in the initial and subsequent learning and test lists. Critically, in addition to being tested on memory for the directly experienced pairs (AB and BC), participants also receive a surprise test of their ability to bridge across events, inferring the associative relationship between items (A and C items) that were not directly experienced but that are related through a common associate (B items).

In two experiments, we assessed whether (a) older adults exhibit reduced associative inference performance, when controlling for associative memory for the AB and BC pairs, and (b) whether age-related and individual differences in associative memory and associative inference performance relate to differences in sustained attention. In Experiment 1, we report that older adults demonstrate significantly lower memory for experienced associative pairs (AB/BC) as well as lower associative inference performance on AC pairs even when they can correctly remember the AB and BC pairs. These findings are replicated in Experiment 2 in a separate online experiment that also examined how sustained attention, assayed through the gradCPT, relates to individual and age-related differences in associative memory and associative inference. Experiment 2 demonstrates that, in our online cohort, (a) older adults do not demonstrate lower sustained attention performance relative to younger adults, and (b)

individual differences in sustained attention are associated with individual differences in associative memory and inference performance in young adults but not in older adults. Collectively, these results indicate that the observed age-related differences in associative memory and associative inference performance cannot be explained by differences in sustained attention, suggesting that these age-related differences in memory-dependent behavior relate to other variables.

## Methods

Participants were recruited from Johns Hopkins University and the greater Baltimore community (Experiment 1) or online through Prolific (Experiment 2); they received either course credit or financial compensation. All participants provided informed consent and were treated in accordance with guidelines approved by the Institutional Review Board at Johns Hopkins School of Medicine or Stanford University.

## Participants

In Experiment 1, eligibility for young adults (YA) and older adults (OA) included normal to corrected-to-normal vision and hearing. Young adults were enrolled if they were between the ages of 18 and 35 years. Older adults were enrolled if they were between the ages of 60 and 85 years. For OA, neuropsychological evaluations included the Mini Mental Status Exam (Folstein et al., 1975), the Buschke Selective Reminding Test (Buschke & Fuld, 1974), the Logical Memory subtest of the Wechsler Memory Scale (Wechsler, 2008), the Clock Drawing test (Sunderland et al., 1989), the Rey-Osterrieth test (Rey & Osterrieth, 1941), and the Benton Visual Retention Test (Benton, 1945) to ensure normal levels of cognitive performance. Participants were excluded if they had current neurological or psychiatric disorders, history of major head trauma, history of substance abuse or dependencies, or scored 2.5 standard deviations (SD) below the norms for their age and education level on multiple neuropsychological tests. All OA had a global CDR score of 0 (Table 1).

For OA, neuropsychological testing was conducted in the morning for all participants and prior to administration of the associative memory and inference task. Participants were given the opportunity for a break and lunch after neuropsychological testing and before proceeding to the memory test. A total of 26 YA and 30 OA enrolled in Experiment 1. Data from one YA and three OA were excluded from analysis, because the participants did not respond on greater than 20% of trials on one or more test blocks in the associative memory and inference task; two additional YA and one

**Table 1** Demographics of young and older adults and clinical characterization of older adults in Experiment 1

	Young adults		Older adults	
	Mean	SD	Mean	SD
<b>Demographics</b>				
Subjects	23		26	
Sex (M/F)	11   12		10   16	
Age (years)	20.04	1.71	68.73	6.86
Education (years)	13.78	1.24	17.00	2.04
<b>Ethnicity</b>				
Hispanic or Latino	2		0	
Not Hispanic or Latino	21		26	
<b>Race</b>				
Caucasian/White	5		21	
Asian	16		1	
Black/African American	1		3	
Other/unknown	1		1	
<b>General Cognition</b>				
Clinical Dementia Rating			0.00	0.00
Clinical Dementia—SB			0.00	0.00
Clock Drawing			23.42	1.63
MMSE			29.04	0.95
<b>Memory</b>				
Benton Visual Retention			6.96	1.31
BSRT Immediate Recall Total			50.84	8.01
BSRT Immediate Recall T-Score			0.31	0.83
BSRT Delayed Recall Total			8.58	2.55
BSRT Delayed T-Score			−0.41	1.12
LM Immediate Recall Raw			31.19	5.15
LM Immediate Recall Scaled			14.46	2.40
LM Delayed Recall Raw			32.50	5.99
LM Delayed Recall Scaled			15.12	2.25
R-O CFT Immediate Copy			32.33	2.57
R-O CFT Delayed Copy			17.39	5.15
R-O CFT Delayed T-Score			56.46	11.48
<b>Working Memory</b>				
Letter Number Sequencing Raw			12.15	2.39
Letter Number Sequencing Scaled			13.73	2.22
<b>Executive Function</b>				
SCWT – Word Raw			95.31	17.47
SCWT – Word Scaled			42.08	11.62
SCWT – Color Raw			64.92	14.16
SCWT – Color Scaled			40.69	11.53
SCWT – Color/Word Raw			38.12	9.61
SCWT – Color/Word Scaled			49.00	8.82
<b>Speed of Processing</b>				
Symbol-Digit Modalities Test Raw			44.22	2.85
Symbol-Digit Modalities Test Scaled			10.39	1.36
<b>Verbal Fluency</b>				
Verbal Fluency (FAS)			49.65	14.23

CDR Clinical Dementia Rating, MMSE Mini Mental Status Exam; Wechsler Logical Memory Delayed Recall, BSRT, Buschke Selective Reminding Test, Rey-Osterreith Rey-Osterreith Complex Figure Test

additional OA did not respond on any trials on one or more tests blocks, leaving 23 YA and 26 OA.

In Experiment 2, eligibility for YA and OA required that participants were based in the United States, had normal to corrected-to-normal vision, and a minimal approval rating of 80% on Prolific. Young adults were enrolled if they were between the ages of 18 and 35 years, while older adults were enrolled if they were between the ages of 60 and 85 years. Given the nature of online crowdsourcing platforms, while we did not conduct neuropsychological testing on enrolled OA and we were unable to determine the precise time of day at which the experimental task was performed, we applied rigorous inclusion criteria to ensure data quality (Thomas & Clifford, 2017): Participants were given a practice session consisting of encoding 10 unique scene-object associative pairs followed by a two-alternative forced choice test (2AFC). During the AB/XY and BC/DE encoding blocks, participants were instructed to press the spacebar on every trial; they also encountered one attention check per block wherein they had 10 s to respond to a prompt (“Are you paying attention? Press Y if you are.”). Participants were automatically terminated from enrollment if they failed the practice test (performance < 50%), failed any of the attention checks, or had a nonresponse rate > 20% during the AB/XY or BC/DE test blocks.

A total of 155 YA and 163 OA enrolled in Experiment 2. Of these, 7 YA and 14 OA failed to respond on any trials of the AC test and/or the AB/XY post-test and thus were removed from analysis as they were not engaged with the task. An additional 1 YA and 10 OA were excluded from analysis, because they did not respond to > 20% of trials on the AC test and/or AB/XY post-test. Finally, data from four YA and six OA were excluded owing to poor performance on the gradCPT (> 3 SD from the mean for omission or commission errors). This resulted in a total of 143 YA and 133 OA in the analyses (Table 2).

## Materials and design

In Experiment 1, participants completed an AB-BC associative memory and inference task (Fig. 1). Stimuli consisted of images of 180 common objects and scenes consisting of 120 familiar landmarks. For each participant, objects and scenes were randomly selected without replacement to generate 60 AB (object-scene) and 60 BC (scene-object) overlapping pairs and 60 nonoverlapping pairs (30 XY object-scene pairs and 30 DE scene-object pairs). The experiment consisted of six phases: AB/XY study followed by AB/XY test (2 cycles); BC/DE study followed by BC/DE test (2 cycles); the critical AC inference test; and a final AB/XY post-test. During all study and test phases, stimuli were presented for 3500 ms with a 500-ms interstimulus interval. At



**Table 2** Online demographics of young and older adults in Experiment 2

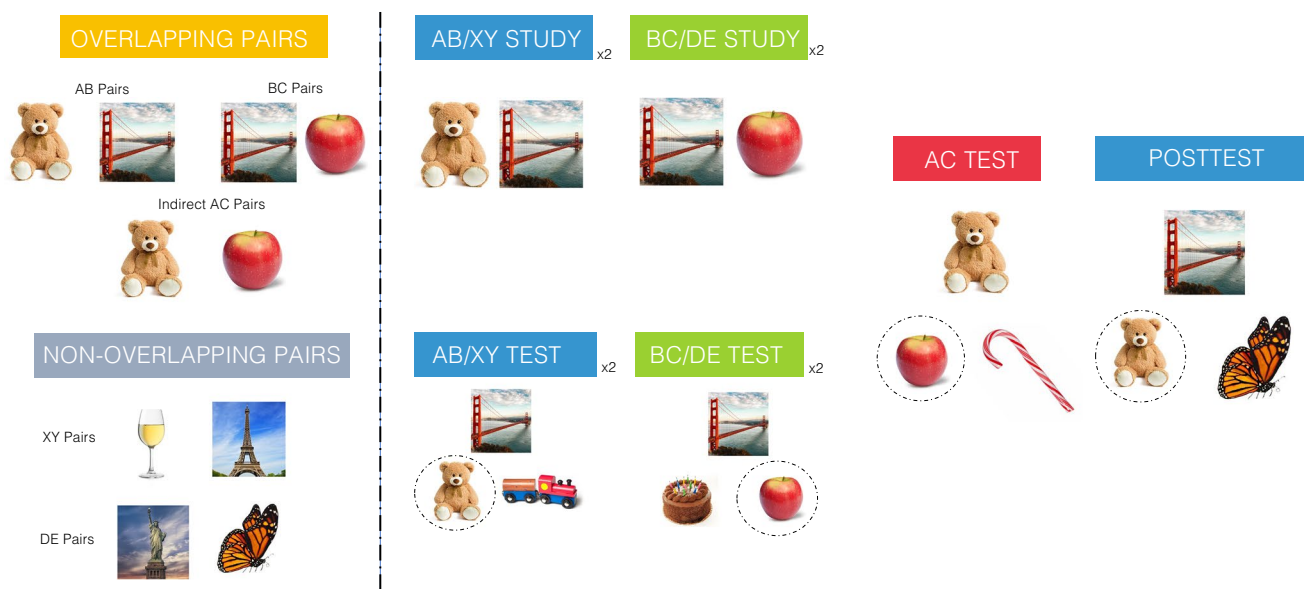
	Young adults		Older adults	
	Mean	SD	Mean	SD
<b>Demographics</b>				
Subjects	143		133	
Sex (M/F)	74   69		64   69	
Age (years)	26.24	4.13	67.65	3.9
<b>Ethnicity</b>				
Latino/Hispanic	20		3	
Not Hispanic or Latino	123		130	
<b>Race</b>				
Caucasian/White	97		127	
Asian	15		1	
Black/African American	14		1	
Other/unknown	17		4	

study, participants were instructed to remember each pair for a later memory test.

During the associative memory test phases (AB/XY and BC/DE tests), participants were presented with the scene stimulus as a retrieval cue and made a 2AFC associative memory decision, with choice stimuli consisting of the associated object for that scene (target) and an object that had been studied with a different scene (foil). Prior to the inference test phase, the associative structure of the design

was explained to participants—i.e., that there were overlapping AB and BC pairs, through which A and C are related. Participants then completed the critical AC inference test, during which they were cued with the A stimulus and made a 2AFC decision between the related C and an unrelated C (C foils were from other AB/BC sets). Finally, after the AC test, participants were tested on their retention of the original AB/XY pairs (i.e., AB/XY post-test) to rule out the possibility that AC inference failure was due to forgetting of AB pairs. The organization of stimuli into trial types and the trial order were randomized across participants. During the study and test cycles, both the orders of the pairs, the right-left presentation of the scene for the study cycles, and the right-left presentation of the target and the foil for the test cycles were pseudo-randomized across participants. Stimuli were presented and behavioral responses were collected by using an Apple Macintosh laptop computer running MATLAB 2019a software (The Mathworks, Natick, MA) with the PsychToolbox extension (Brainard, 1997).

In Experiment 2, participants completed a shorter version of the AB-BC associative memory and inference task (Fig. 1) as well as the gradCPT (Fig. 3A). The design of the memory task was identical to Experiment 1, with the following exceptions: there were 36 AB and 36 BC overlapping pairs, and a total of 36 unique nonoverlapping pairs (18 XY and 18 DE pairs). Stimuli were presented for 3000 ms with a 500-ms interstimulus interval through PsychoPy, hosted on Pavlovia (Peirce et al., 2019). The organization of stimuli



**Fig. 1** Associative memory and associative inference paradigm. Participants were shown a series of scene and object pairings (AB/XY & BC/DE) and later tested on the pairings. There were two study-test cycles for each, with nonoverlapping pairs (XY and DE) intermixed with overlapping pairs (AB and BC), wherein a scene (B) was shown

with two different objects (A and C), resulting in an indirect associative pairing. Participants were then tested on the indirect associative inference pairs (AC pairs). At the end of the experiment (i.e., post-test), participants were re-tested on the AB and XY pairs

into trial types, the trial order, the right-left presentation of the scene for the study cycle, and the right-left presentation of the target and foil at test were pseudo-randomized to create two presentation orders.

The gradCPT stimuli consisted of ten greyscale mountain scenes and ten greyscale city scenes (Esterman et al., 2013; Rosenberg et al., 2013). Images appeared in the center of the screen and gradually onset over 1200 ms, paused for 50 ms when fully cohered and then offset. Participants were instructed to respond to city scenes (90% of trials) and withhold responses to mountain scenes (10% of trials) across the 10-min task. The gradCPT was performed immediately after the AB/XY post-test.

## Results

Analyses were conducted by using RStudio (version 2022.07), employing the lme4 and lmerTest packages to fit linear mixed-effects models; standardized beta coefficients were estimated by using the lm.beta and effectsize packages. To provide evidence for interpreting nonsignificant findings, we used a Bayesian approach with statistics conducted using JASP software (version 0.19). All Bayesian models were specified with a uniform prior distribution, Markov Chain Monte Carlo (MCMC) methods with 10,000 iterations, and 10,000 iterations for the credible interval (CI) estimation. Bayesian Factors in favor of the null hypothesis and against the alternative hypothesis were considered if  $BF_{10} < 1$ . We report the Bayesian Factors alongside the 95% credible interval of the posterior.

## Experiment 1

**AB/XY Memory:** Memory performance in all phases of Experiment 1 is shown in Fig. 2A, and a summary of performance for each trial type is shown in Table 3. To examine associative memory performance between YA and OA (age group) and as a function of trial type (overlapping/AB vs. nonoverlapping/XY pairs) and test block (block 1 vs. block 2), linear mixed models were conducted, with subject treated as a random intercept; sex was included as a control covariate. All model results remain significant with sex removed as a covariate, unless otherwise noted. All betas reported are standardized; a summary of all model results for AB/XY trials in Experiment 1 is shown in the Supplement (Table S1).

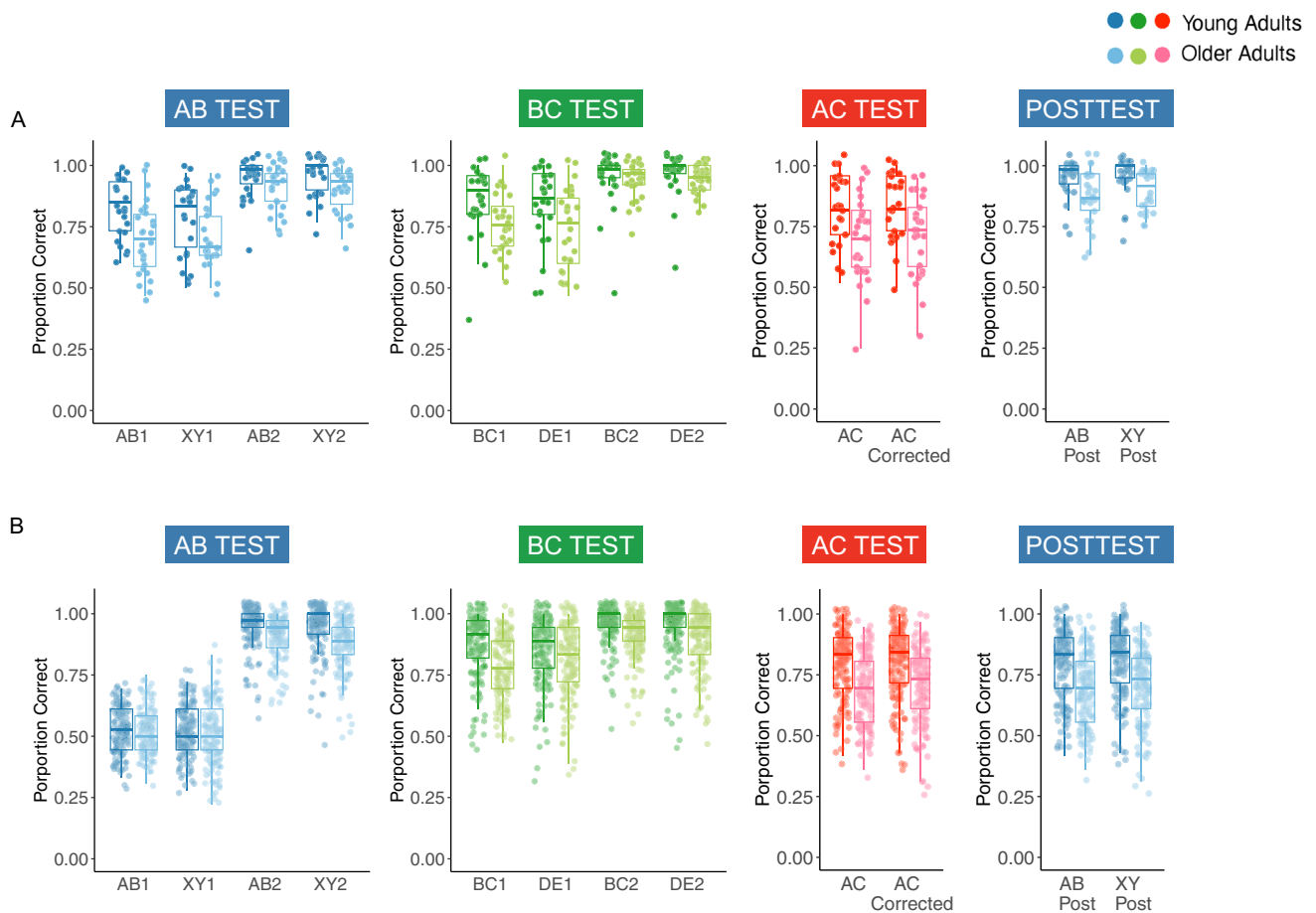
In a linear mixed model with trial type, test block, age group, and sex as covariates, there was a trend for YA to outperform OA on the AB and XY pairs ( $\beta = 0.39$ ,  $p = 0.07$ ). A second linear mixed model that included test block  $\times$  age and trial type  $\times$  age interaction terms revealed no significant effect of trial type ( $\beta = -0.02$ ,  $p = 0.85$ ) nor a

trial type  $\times$  age interaction ( $\beta = -0.15$ ,  $p = 0.26$ ), with both groups improving across the two blocks ( $\beta = 1.36$ ,  $p < 0.01$ ). Moreover, YA outperformed OA ( $\beta = 0.66$ ,  $p < 0.01$ ) on the AB/XY pairs, with a significant test block  $\times$  age interaction ( $\beta = -0.39$ ,  $p < 0.01$ ). To distinguish between the two linear mixed models, we used an AIC model selection and found the second model with the additional interaction terms was superior and carried 100% of the cumulative model weight. To further explore the interaction between age and test block, separate linear models examining performance for test block 1 and 2, with trial type, age, and sex as covariates variables, revealed that YA significantly outperformed OA on test block 1 ( $\beta = 0.59$ ,  $p = 0.04$ ) but not on test block 2 ( $\beta = 0.34$ ,  $p = 0.24$ ).

**BC/DE Memory:** Using the preferred linear mixed model parameters from the AIC model selection, which included age group, sex, test block, and trial type, as well as interaction terms for test block and trial type with age, YA showed superior BC/DE performance (age:  $\beta = 0.58$ ,  $p = 0.02$ ), with both groups improving across the two blocks ( $\beta = 1.30$ ,  $p < 0.01$ ). There was no effect of trial type ( $\beta = -0.04$ ,  $p = 0.65$ ) nor a trial type  $\times$  age interaction ( $\beta = 0.04$ ,  $p = 0.80$ ). Again, there was a significant block  $\times$  age interaction ( $\beta = -0.58$ ,  $p < 0.01$ ); separate linear models examining performance on test block 1 and 2, with trial type, age, and sex as covariates, revealed a trend for higher performance for YA compared with OA in test block 1 ( $\beta = 0.51$ ,  $p = 0.09$ ) but not in test block 2 ( $\beta = 0.13$ ,  $p = 0.69$ ). A summary of all model results for BC/DE trials in Experiment 1 is shown in Table S2. Additional exploratory analyses qualitatively characterized the relationship between age and performance on the AB/XY and BC/DE pairs in OA; these relationships are depicted in the supplementary materials (Fig. S1).

**AC Inference:** A multiple linear regression examined AC performance with age group and sex as covariates. On this critical associative inference test, OA demonstrated significantly lower AC performance relative to YA when considering all test pairs ( $\beta = 0.33$ ,  $p = 0.03$ ). Importantly, to determine whether this age-related difference in inference performance was simply due to poor memory for the AB and/or BC pairs, we restricted the analysis to AC inference pairs for which participants correctly recalled both the AB pair during the post-test and the BC pair during the second BC test and found lower associative inference performance in OA compared with YA on the AC-corrected trials ( $\beta = 0.32$ ,  $p = 0.04$ ). A summary of all model results for AC trials in Experiment 1 is shown in Table S3. See supplementary materials (Fig. S2) for exploratory analyses of the relationship between age and associative inference performance in OA.

**AB/XY Post-test:** In the post-test, a multiple linear regression revealed trends for decreased performance for trial type ( $\beta = 0.20$ ,  $p = 0.06$ ) and lower OA relative to YA



**Fig. 2** Associative memory and associative inference performance. **(A)** Experiment 1 performance for young and older adults is depicted for each phase of the experiment, including as a function of trial type (e.g., AB/XY), study-test block (e.g., AB1, AB2), and whether associative inference performance was calculated over all inference trials

(AC) or restricted to inference trials on which the AB and BC pairs were remembered (AC corrected). **(B)** Experiment 2 performance is depicted for each age group as a function of trial type, study-test block, and associative inference scoring approach

performance ( $\beta = 0.53$ ,  $p = 0.06$ ). With sex removed as a covariate, the age-difference between YA and OA is statistically significant. To compare differences in memory retention between YA and OA, a linear model examined performance between AB/XY in block 2 and post-test. There was no difference in performance between the two tests ( $\beta = -0.09$ ,  $p = 0.22$ ) nor a significant effect of age ( $\beta = 0.44$ ,  $p = 0.11$ ). A separate linear model found no time  $\times$  age interaction ( $\beta = 0.19$ ,  $p = 0.18$ ). A summary of all model results for the post-test trials is shown in Table S4.

## Experiment 2

### Memory performance

**AB/XY Memory:** Memory performance in all phases of Experiment 2 is shown in Fig. 2B, with a summary of performance

metrics shown in Table 4. Full correlation matrix of all variables in Experiment 2 is available in the Supplement (Table S5). As with Experiment 1, a linear mixed model was conducted by using the preferred parameters from the AIC model selection. A summary of model results for the AB/XY trials is shown in Table S6. While there was no significant effect of age ( $\beta = 0.03$ ,  $p = 0.58$ ), trial type ( $\beta = -0.07$ ,  $p = 0.06$ ), or trial type  $\times$  age interaction ( $\beta = 0.05$ ,  $p = 0.34$ ), there was a significant interaction between block  $\times$  age ( $\beta = 0.17$ ,  $p < 0.01$ ). Given the overall poor performance in the first block, separate linear models examining performance in test block 1 and 2 revealed no difference between YA and OA in test block 1 ( $\beta = 0.11$ ,  $p = 0.21$ ) but significantly higher YA compared with OA performance in test block 2 ( $\beta = 0.51$ ,  $p < 0.01$ ).

**BC/DE Memory:** OA demonstrated significantly lower performance than YA on the BC/DE pairs ( $\beta = 0.54$ ,  $p < 0.01$ ). There was no effect of trial type ( $\beta = 0.04$ ,  $p = 0.46$ ) or test block  $\times$  age ( $\beta = -0.10$ ,  $p = 0.13$ ).

**Table 3** Summary of performance for associative memory, associative inference, and post-test performance for Experiment 1

	Young adults			Older adults		
	Mean $\pm$ SD	Skew	Kurtosis	Mean $\pm$ SD	Skew	Kurtosis
<b>Associative memory</b>						
AB1 performance	0.83 $\pm$ 0.11	−0.38	1.92	0.70 $\pm$ 0.15	0.12	1.93
AB2 performance	0.94 $\pm$ 0.08	−2.76	11.24	0.91 $\pm$ 0.08	−0.75	2.30
XY1 performance	0.78 $\pm$ 0.15	−0.56	1.93	0.71 $\pm$ 0.12	0.50	2.29
XY2 performance	0.94 $\pm$ 0.07	−1.23	3.59	0.90 $\pm$ 0.09	−0.72	2.43
BC1 performance	0.85 $\pm$ 0.14	−1.55	5.35	0.76 $\pm$ 0.12	0.07	2.22
BC2 performance	0.94 $\pm$ 0.11	−3.09	12.29	0.94 $\pm$ 0.06	−1.39	3.83
DE1 performance	0.84 $\pm$ 0.15	−1.05	3.09	0.74 $\pm$ 0.17	−0.12	1.65
DE2 performance	0.96 $\pm$ 0.1	−3.15	12.68	0.94 $\pm$ 0.06	−0.71	2.52
<b>Associative inference</b>						
AC performance	0.83 $\pm$ 0.14	−0.46	2.14	0.70 $\pm$ 0.17	−0.53	3.16
AC corrected performance	0.83 $\pm$ 0.14	−0.57	2.51	0.71 $\pm$ 0.17	−0.54	2.68
<b>Post-test</b>						
AB post-test	0.94 $\pm$ 0.08	−1.82	5.71	0.87 $\pm$ 0.11	−0.65	2.50
XY post-test	0.95 $\pm$ 0.08	−2.04	6.67	0.90 $\pm$ 0.08	−0.36	1.78

**Table 4** Summary of associative memory, associative inference, and post-test performance, as well as gradCPT performance. Split-half reliability was calculated by using even and odds trials using the Spearman-Brown formula

	Young adults				Older adults			
	Mean $\pm$ SD	Skew	Kurtosis	Reliability	Mean $\pm$ SD	Skew	Kurtosis	Reliability
<b>Associative memory</b>								
AB1 performance	0.52 $\pm$ 0.09	−0.15	2.06	0.55	0.52 $\pm$ 0.09	0.22	2.53	0.34
AB2 performance	0.95 $\pm$ 0.08	−2.44	9.21	0.87	0.91 $\pm$ 0.09	−1.36	4.37	0.73
XY1 performance	0.52 $\pm$ 0.1	−0.2	2.48	0.37	0.51 $\pm$ 0.13	0.11	2.44	0.23
XY2 performance	0.94 $\pm$ 0.09	−2.11	7.83	0.68	0.88 $\pm$ 0.1	−1.18	4.56	0.52
BC1 performance	0.86 $\pm$ 0.13	−1.26	3.99	0.81	0.78 $\pm$ 0.13	−0.3	2.19	0.80
BC2 performance	0.96 $\pm$ 0.07	−2.73	11.76	0.86	0.91 $\pm$ 0.09	−1.68	5.56	0.84
DE1 performance	0.85 $\pm$ 0.14	−1.21	4.41	0.71	0.81 $\pm$ 0.14	−0.67	3.04	0.52
DE2 performance	0.94 $\pm$ 0.1	−2.62	10.46	0.77	0.90 $\pm$ 0.12	−1.25	3.90	0.67
<b>Associative inference</b>								
AC performance	0.80 $\pm$ 0.14	−0.69	2.55	0.78	0.68 $\pm$ 0.14	−0.07	1.97	0.77
AC corrected performance	0.80 $\pm$ 0.14	−0.90	3.11	0.77	0.70 $\pm$ 0.15	−0.60	2.81	0.70
<b>Post-test</b>								
AB post-test	0.92 $\pm$ 0.1	−1.79	6.06	0.80	0.83 $\pm$ 0.13	−0.74	2.62	0.85
XY post-test	0.93 $\pm$ 0.1	−1.95	7.11	0.83	0.88 $\pm$ 0.12	−1.53	5.77	0.61
<b>gradCPT</b>								
<i>d'</i>	3.15 $\pm$ 0.85	−0.45	2.73	0.92	3.47 $\pm$ 0.97	−0.46	2.83	0.94
commission error	0.2 $\pm$ 0.12	0.82	3.41	0.81	0.14 $\pm$ 0.11	1.2	4.33	0.89
omission error	0.03 $\pm$ 0.04	3.33	15.74	0.99	0.03 $\pm$ 0.04	2.58	9.68	0.98
RT variability	0.95 $\pm$ 0.36	2.64	13.82	0.99	0.84 $\pm$ 0.49	2.46	8.76	0.99
median reaction time	535.50 $\pm$ 87.33	0.24	3.56	0.99	629.62 $\pm$ 100.41	−0.62	3.87	0.99

However, there was an effect of test block ( $\beta = 0.81$ ,  $p < 0.01$ ) and a trial type  $\times$  age interaction ( $\beta = -0.16$ ,  $p = 0.02$ ). Separate linear models examining performance in test blocks 1 and 2 found that YA outperformed OA in

both block 1 ( $\beta = 0.43$ ,  $p < 0.01$ ) and block 2 ( $\beta = 0.46$ ,  $p < 0.01$ ). Within the OA group, age was not significantly related to associative memory performance (Fig. S3). A summary of model results is shown in Table S7.

**AC Inference:** Replicating Experiment 1, OA demonstrated significantly lower performance on AC pairs compared with YA when considering all test pairs ( $\beta=0.75$ ,  $p<0.01$ ). This effect remained significant when restricting the analysis to AC inference pairs for which the participant correctly recalled the AB pair on the post-test and the BC pair during the second BC test ( $\beta=0.67$ ,  $p<0.01$ ). A summary of model results is shown in Table S8. Within the OA group, age did not predict either uncorrected or corrected AC performance (Fig. S4).

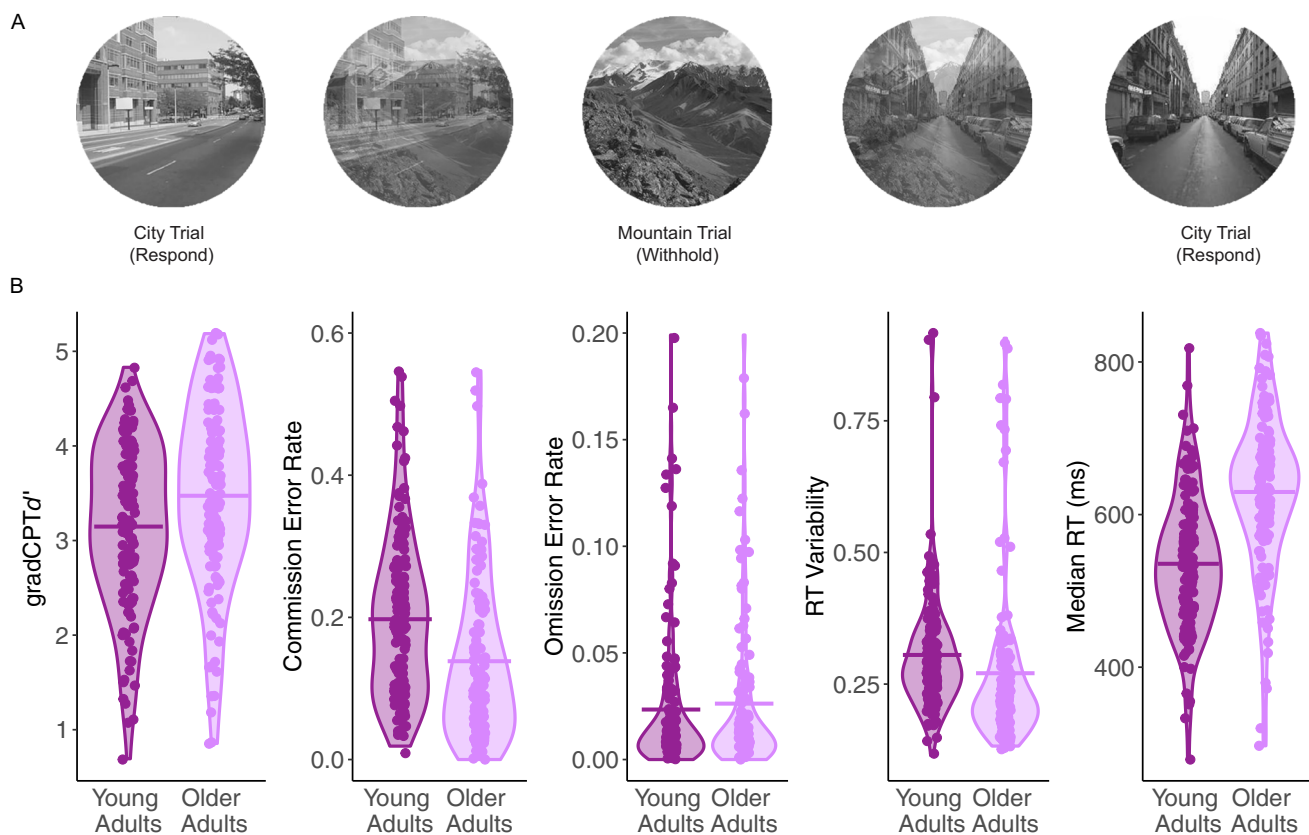
**AB/XY Post-test:** Consistent with the trend in Experiment 1, OA performed significantly worse than YA ( $\beta=0.56$ ,  $p<0.01$ ) during the post-test assessment with a significant effect of trial type ( $\beta=0.24$ ,  $p<0.01$ ). To investigate potential differences YA and OA memory retention, a linear model examined performance between AB/XY in block 2 and during the post-test. Overall, there was a decline in performance from block 2 to the post-test ( $\beta=-0.27$ ,  $p<0.01$ ) across all subjects, with OA demonstrating lower performance overall ( $\beta=0.53$ ,  $p<0.01$ ). A separate linear mixed model with an interaction term for time  $\times$  age revealed decreased memory

retention in OA relative to YA ( $\beta=0.17$ ,  $p<0.01$ ). A summary of all model results is shown in Table S9.

## Sustained attention

All gradCPT performance metrics in Experiment 2 are shown in Fig. 3B, with performance metrics shown in Table 4. The two primary sustained attention metrics were  $d'$  and reaction time (RT) variability (a coefficient of response-time variation on the correct responses to city trials (Esterman et al., 2013; Fortenbaugh et al., 2015). Prior work has demonstrated that intrasubject RT variability on cognitive tasks is predictive of performance on other cognitive tasks (Hultsch et al., 2002), metabolic risk (Wooten et al., 2019), and future cognitive outcomes in older adults (Bielak et al., 2010). We additionally report commission error rate (incorrect responses to mountain trials) and omission error rate (missed responses to city trials) for completeness.

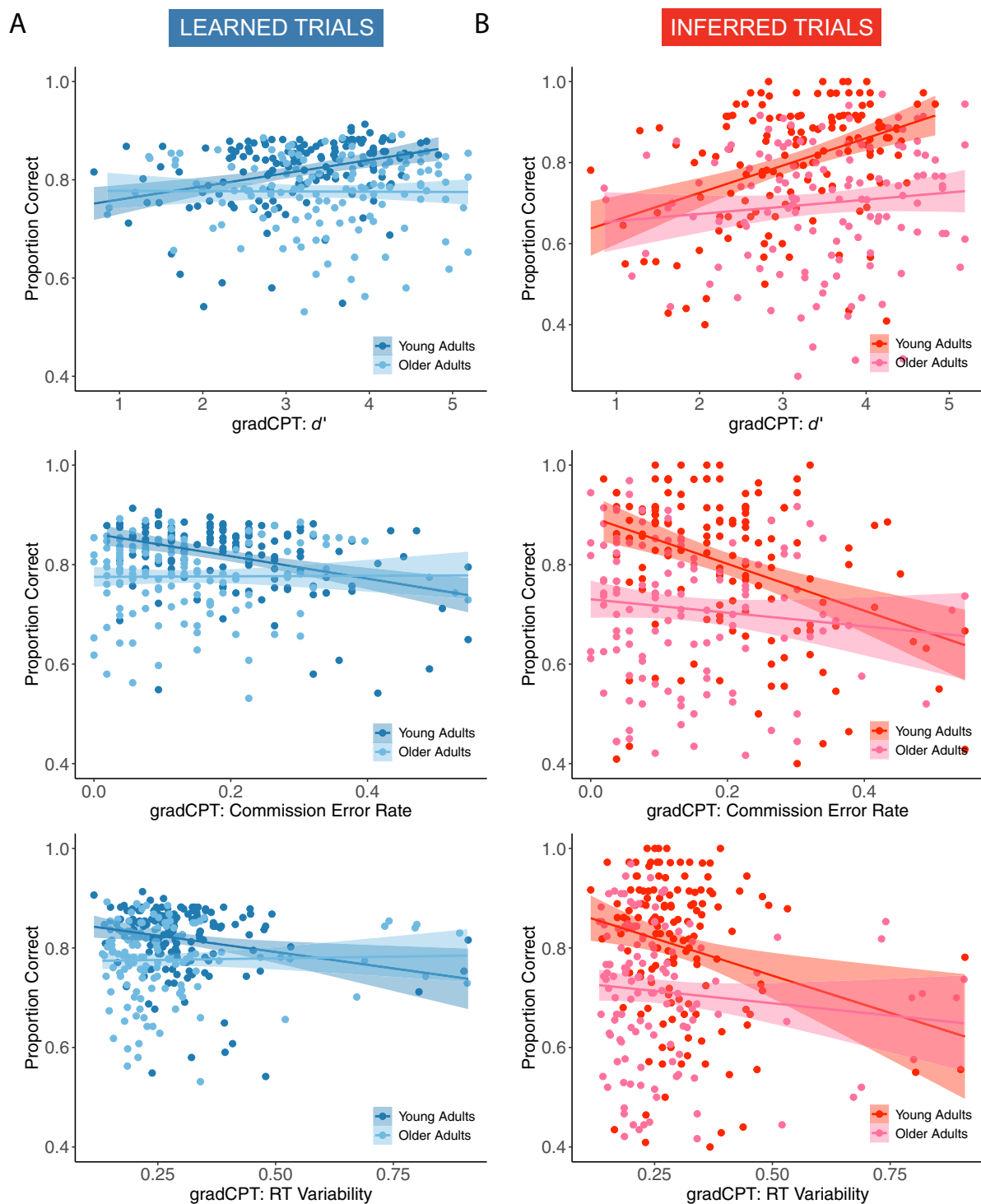
A multiple linear regression, with age group and sex as additional covariates, revealed that OA demonstrated significantly higher  $d'$  relative to YA ( $\beta=-0.18$ ,  $p<0.01$ ).



**Fig. 3** Gradual-onset continuous performance task (gradCPT) paradigm and observed performance. (A) The gradCPT measures sustained attention, with participants responding to city scenes (90% of trials) and withholding responses to mountain scenes (10% of trials). (B) Young and older adult performance metrics included  $d'$ , commis-

sion error rate (i.e., rate of responding to infrequent no-go mountain trials), omission error rate (i.e., failing to respond to frequent go city trials), and RT variability (i.e., differences in response time consistency across the 10-min task)





**Fig. 4** Relationship between sustained attention and associative memory and associative inference performance. **(A)** Relationships between gradCPT metrics of sustained attention and associative

memory performance in young and older adults. **(B)** Relationships between gradCPT metrics of sustained attention and corrected associative inference performance in young and older adults

This performance difference was due to OA making significantly fewer commission errors ( $\beta = 0.25$ ,  $p < 0.01$ ), with no significant age-related difference in omission error rate ( $\beta < 0.01$ ,  $p = 0.88$ ). Older adults had decreased RT

variability compared to young adults ( $\beta = 0.13$ ,  $p = 0.04$ ); analysis of median reaction time revealed that YA responded significantly faster than OA on correct city trials ( $\beta = -0.45$ ,  $p < 0.01$ ). As such and consistent with previous gradCPT

evidence of more conservative responding in OA (Carriere et al., 2010; Fortenbaugh et al., 2015), whereas OA performed more accurately than YA, this was within the context of YA responding more quickly compared with OA. Within each group, OA further demonstrated evidence for a speed-accuracy tradeoff ( $r=0.28$ ,  $p<0.01$ ), whereas YA did not ( $r=-0.12$ ,  $p=0.14$ ). A summary of all model results is shown in Table S10.

Given the potential age-related differences in accuracy owing to speed, we additionally combined speed and accuracy into a single measure, referred to as the balanced-integration score (BIS) (Liesefeld & Janczyk, 2019; Liesefeld et al., 2015). A linear regression with age group and sex as covariates, revealed that OA demonstrated a higher BIS relative to YA ( $\beta=0.21$ ,  $p<0.01$ ; Supplementary Fig. 5). We then conducted additional analyses to examine the relationship between gradCPT BIS with AB-BC associative memory and AC inference performance (see supplement for additional details). Briefly, gradCPT BIS significantly correlated with both associative memory performance ( $\beta=0.22$ ,  $p<0.01$ ) and associative inference performance ( $\beta=0.37$ ,  $p<0.01$ ) for YA, but not for OA (associative memory:  $\beta=0.05$ ,  $p=0.54$ , associative inference  $\beta=0.11$ ,  $p=0.37$ ).

### Sustained attention correlations with memory

To examine (a) the relationship between individual differences in sustained attention and memory and (b) possible interactions with age, several multiple linear regressions were conducted with specific sustained attention metrics and sex as predictors of associative memory and associative inference performance. Secondary models included age group as an additional predictor of associative memory and associative inference performance. For each participant, associative memory performance was averaged across the first and second test blocks for AB, XY, BC, and DE trials (Fig. 4A). Additional analyses assessed AB/XY and BC/DE performance in block 1 and 2 separately (Figs. S6 and S7). Associative inference performance was assessed through both uncorrected AC performance and corrected AC performance (Fig. 4B).

### Sustained attention and associative memory performance

#### gradCPT $d'$

Associative memory performance was not significantly predicted by gradCPT  $d'$  ( $\beta=0.10$ ,  $p=0.11$ ) in a model with gradCPT  $d'$  and sex. Adding age group as a predictor significantly improved the model fit ( $F(1, 272)=27.85$ ,  $p<0.01$ ). With age group included as a predictor, both gradCPT  $d'$  ( $\beta=0.15$ ,  $p<0.01$ ) and age group ( $\beta=0.31$ ,  $p<0.01$ ) were

significantly associated with performance. To explore this relationship between age group and gradCPT  $d'$ , a separate multiple linear model was conducted with a gradCPT  $d' \times$  age group interaction term, which was significant ( $\beta=0.61$ ,  $p<0.01$ ). To further unpack this interaction, separate linear models in young adults and older adults revealed that gradCPT  $d'$  significantly predicted memory performance in YA ( $\beta=0.33$ ,  $p<0.01$ ) but not in OA ( $\beta<0.01$ ,  $p=0.99$ ). A summary of the linear model results is shown in Table S11.

To further examine this null finding in older adults, an additional Bayesian linear regression was conducted to examine the link between gradCPT  $d'$  with associative memory performance, with sex as an additional covariate. The posterior distribution for the regression coefficient was estimated, yielding a mean of  $B=-3.23 \times 10^{-5}$  with a 95% CI of  $[-0.004, 0.007]$ , indicating that the relationship between gradCPT  $d'$  and associative memory performance was negligible in OA. Bayes factors were further calculated to assess the strength of evidence for the alternative hypothesis (i.e., a gradCPT relationship with associative memory) compared with the null hypothesis. Comparing alternative models (with or without sex as a covariate) against the null model revealed a  $BF_{10}=0.19$  in the model with gradCPT  $d'$  only and of  $BF_{10}=0.09$  in the model with both gradCPT  $d'$  and sex included; both models indicate strong evidence for the null hypothesis.

#### gradCPT commission error

A similar relationship emerged for gradCPT commission error and associative memory performance. In a model without age group as a predictor, gradCPT commission error did not significantly predict performance ( $\beta=-0.10$ ,  $p=0.11$ ); when adding age group as a predictor, both gradCPT commission error ( $\beta=-0.18$ ,  $p<0.01$ ) and age group ( $\beta=0.32$ ,  $p<0.01$ ) significantly predicted associative memory performance. Again, a model comparison indicated the second model was a better fit of the data ( $F(1, 272)=30.33$ ,  $p<0.01$ ). A separate model that included the interaction term commission error rate  $\times$  age revealed a significant interaction in predicting associative memory performance ( $\beta=-0.40$ ,  $p<0.01$ ). Separate linear models for young adults and older adults revealed that gradCPT commission error predicted performance in YA ( $\beta=-0.37$ ,  $p<0.01$ ) but not in OA ( $\beta=0.01$ ,  $p=0.90$ ). A summary of model results is shown in Table S12.

Again, to further examine this null finding in older adults, a Bayesian linear regression was conducted with commission error rate, associative memory performance, and sex as an additional covariate. The posterior distribution had mean of  $B=7.50 \times 10^{-4}$  with a 95% CI of  $[-0.03, 0.06]$ , indicating that the relationship of gradCPT commission error and associative

memory performance was negligible in OA. Model comparisons conducted against a null model revealed a  $BF_{10}=0.19$  for the model with commission error only and  $BF_{10}=0.09$  in the model with both commission error and sex as covariates. Both Bayes Factors strongly support the null hypothesis, indicating the relationship between commission error and associative memory performance is negligible in OA.

### gradCPT RT variability

When considering gradCPT RT variability, RT variability did not predict associative memory performance ( $\beta = -0.04$ ,  $p = 0.52$ ). When age group was added as a predictor, age significantly predicted associative memory performance ( $\beta = 0.29$ ,  $p < 0.01$ ) but RT variability remained nonsignificant ( $\beta = -0.08$ ,  $p = 0.19$ ). Model comparisons indicated the second model was a better fit of the data ( $F(1, 272) = 24.70$ ,  $p < 0.01$ ). A separate model that included an interaction term revealed an RT variability  $\times$  age interaction in predicting associative memory performance ( $\beta = 0.32$ ,  $p = 0.03$ ). When exploring RT variability and memory in young adults and older adults in separate models, gradCPT RT variability significantly predicted associative memory performance in YA ( $\beta = -0.21$ ,  $p = 0.01$ ) but not in OA ( $\beta = 0.02$ ,  $p = 0.83$ ). A summary of all linear model results is shown in Table S13.

To further examine this null finding in older adults, a Bayesian linear regression was conducted, with sex as an additional covariate. The posterior distribution had mean of  $B = 0.001$  with a 95% CI of  $[-0.02, 0.05]$ , further indicating that the relationship between RT variability and associative memory performance was negligible in older adults. Model comparison against the null model revealed  $BF_{10} = 0.20$  in the model with RT variability only and  $BF_{10} = 0.09$  in the model with both sex and RT variability. Again, both models indicate strong evidence for the null hypothesis of no relationship between RT variability and associative memory in OA.

Collectively, these findings indicate that, in our online cohort, sustained attention metrics significantly correlated with associative memory performance in young adults but not in older adults. Critically, significant interactions with sustained attention and age indicate that the relationship between sustained attention and associative memory performance significantly differed between young and older adults.

## Sustained attention and associative inference performance

### gradCPT $d'$

GradCPT  $d'$  was significantly correlated with uncorrected AC performance across all participants ( $\beta = 0.18$ ,  $p < 0.01$ ). When age group was added as a predictor, both gradCPT  $d'$  ( $\beta = 0.25$ ,  $p < 0.01$ ) and age ( $\beta = 0.42$ ,  $p < 0.01$ ) were

significantly associated with uncorrected AC performance. A comparison of these two models indicated that adding age group yielded a better fit ( $F(1, 272) = 58.61$ ,  $p < 0.01$ ). When examining whether there was a differential relationship between gradCPT  $d'$  and age with associative inference performance, a separate linear model with an interaction term revealed a gradCPT  $d' \times$  age group interaction predicting uncorrected AC performance ( $\beta = 0.54$ ,  $p < 0.01$ ). Separate linear models in young adults and older adults demonstrated that gradCPT  $d'$  was associated with AC performance in YA ( $\beta = 0.41$ ,  $p < 0.01$ ) but not in OA ( $\beta = 0.13$ ,  $p = 0.15$ ).

A Bayesian linear regression was conducted to examine the relationship between gradCPT  $d'$  with AC uncorrected inference performance in older adults, with sex as an additional covariate. The posterior distribution yielded a mean of  $B < 0.01$  with a 95% CI of  $[-1.67 \times 10^{-4}, 0.03]$ , indicating that the relationship between gradCPT  $d'$  and associative inference performance was negligible in older adults. With a model comparison against the null model, the model revealed  $BF_{10} = 0.45$  in the model with gradCPT  $d'$  only and  $BF_{10} = 0.17$  in the model incorporating both sex and gradCPT  $d'$ . Both models provide strong evidence for the null hypothesis of no association between gradCPT  $d'$  and associative inference in OA.

Similar relationships were observed when examining corrected AC performance. In a model without age group, gradCPT  $d'$  was significantly correlated with corrected AC performance across all participants ( $\beta = 0.18$ ,  $p < 0.01$ ); with age group added, both gradCPT  $d'$  ( $\beta = 0.25$ ,  $p < 0.01$ ) and age group ( $\beta = 0.38$ ,  $p < 0.01$ ) were both associated with corrected AC performance. A separate model with an interaction term revealed a gradCPT  $d' \times$  age group interaction ( $\beta = 0.53$ ,  $p < 0.01$ ) with corrected AC performance; separate linear models in young adults and older adults revealed that gradCPT  $d'$  was associated with corrected AC performance in YA ( $\beta = 0.40$ ,  $p < 0.01$ ) but not in OA ( $\beta = 0.12$ ,  $p = 0.18$ ). A summary of all linear model results for uncorrected and corrected AC performance is shown in Table S14.

Again, a Bayesian linear regression was conducted to examine gradCPT  $d'$  with AC corrected inference performance, with sex as an additional covariate in older adults. The posterior distribution had mean of  $B = 0.12$  with a 95% CI of  $[-0.15, 1.26]$ , indicating that the relationship between gradCPT  $d'$  and corrected associative inference performance was negligible. Model comparison against the null model yielded  $BF_{10} = 0.29$  in the model with gradCPT  $d'$  only and  $BF_{10} = 0.13$  in the model with both sex and gradCPT  $d'$  incorporated. Again, both models indicate strong evidence for the null hypothesis.

### gradCPT commission error

GradCPT commission error also was significantly related to uncorrected AC performance across all participants ( $\beta =$

–0.14,  $p=0.02$ ). When age group was added as a predictor, both gradCPT commission error ( $\beta = -0.25$ ,  $p < 0.01$ ) and age group ( $\beta = 0.44$ ,  $p < 0.01$ ) were significantly correlated with uncorrected AC performance. A model comparison of these two models suggested that adding age group resulted in a better fit ( $F(1, 272) = 61.37$ ,  $p < 0.01$ ). Again, a separate model with an interaction term revealed a gradCPT commission error  $\times$  age group interaction ( $\beta = -0.31$ ,  $p < 0.01$ ) when predicting uncorrected AC performance. Unpacking this interaction, multiple linear models revealed that gradCPT commission error was related to uncorrected AC performance in YA ( $\beta = -0.40$ ,  $p < 0.01$ ) but not in OA ( $\beta = -0.11$ ,  $p = 0.23$ ).

To investigate this null result in older adults, a Bayesian linear regression was conducted to examine commission error with uncorrected AC performance, with sex as an added covariate. The posterior distribution had mean of  $B = -0.03$  with a 95% CI of  $[-0.24, 0.002]$ , indicating that the relationship between gradCPT commission error and uncorrected associative inference performance was negligible. In a model comparison against the null model, the model with commission error rate included yielded  $BF_{10} = 0.37$ , while the model with both sex and commission error had a  $BF_{10} = 0.12$ ; both models indicate strong evidence for the null hypothesis of no association between gradCPT commission error and uncorrected AC performance in OA.

When looking at corrected AC performance in a model with all participants, without age group as a covariate, gradCPT commission error had a trending relationship with corrected AC performance across all participants ( $\beta = -0.11$ ,  $p = 0.06$ ); with age group added, gradCPT commission error ( $\beta = -0.21$ ,  $p < 0.01$ ) and age group ( $\beta = 0.39$ ,  $p < 0.01$ ) were both associated with corrected AC performance. Again, there was a significant gradCPT commission error  $\times$  age group interaction with corrected AC performance ( $\beta = -0.32$ ,  $p < 0.01$ ); separate linear models in young adults and older adults revealed that gradCPT commission error was associated with corrected AC performance in YA ( $\beta = -0.37$ ,  $p < 0.01$ ) but not in OA ( $\beta = -0.06$ ,  $p = 0.51$ ). A summary of all linear model results is shown in Table S15.

A Bayesian linear regression was conducted to examine this null relationship between commission error with AC corrected performance, with sex as an additional covariate. The posterior distribution had mean of  $B = -0.61$  with a 95% CI of  $[-8.11, 1.84]$ , indicating that the relationship between gradCPT commission error and corrected associative inference performance was limited in older adults. In a model comparison against the null model, the model with only commission error rate as a variable yielded  $BF_{10} = 0.24$ , while the model with both sex and commission error included had  $BF_{10} = 0.01$ . Both models indicate strong evidence for the null hypothesis of no relationship between commission error and AC corrected performance in OA.

### gradCPT RT variability

Finally, while gradCPT RT variability did not significantly relate to uncorrected AC performance across all participants ( $\beta = -0.09$ ,  $p = 0.15$ ), when age group was added as a covariate, both gradCPT RT variability ( $\beta = -0.14$ ,  $p = 0.01$ ) and age group ( $\beta = 0.39$ ,  $p < 0.01$ ) were significantly associated with uncorrected AC performance. Model comparisons revealed that adding age group resulted in a better fit ( $F(1, 272) = 49.43$ ,  $p < 0.01$ ). A separate model found no significant interaction between gradCPT RT variability and age group ( $\beta = -0.20$ ,  $p = 0.18$ ) with uncorrected AC performance. Nonetheless, separate multiple linear models revealed that gradCPT RT variability was significantly related to uncorrected AC performance in YA ( $\beta = -0.21$ ,  $p < 0.01$ ) but not in OA ( $\beta = -0.09$ ,  $p = 0.28$ ).

To further examine this null finding, a Bayesian linear regression was conducted to examine RT variability with AC uncorrected inference performance, with sex as an added covariate in the older adult sample. The posterior distribution had mean of  $B = -0.01$  with a 95% CI of  $[-0.16, 0.00]$ , indicating that the relationship between RT variability and associative inference performance was negligible in older adults. In a model comparison against the null model, the model with only RT variability as term yielded  $BF_{10} = 0.29$ , while the model with both sex and RT variability had a  $BF_{10} = 0.10$ ; both models indicate strong evidence for the null hypothesis.

RT variability also did not significantly relate to corrected AC performance in a model without age group as a covariate, ( $\beta = -0.10$ ,  $p = 0.11$ ); with age group added, gradCPT RT variability ( $\beta = 0.14$ ,  $p = 0.01$ ) and age group ( $\beta = 0.35$ ,  $p < 0.01$ ) were both associated with corrected AC performance. RT variability  $\times$  age group was not significantly related to corrected AC performance ( $\beta = -0.24$ ,  $p = 0.11$ ); nonetheless, separate linear models in young adults and older adults revealed that RT variability was related to corrected AC performance in YA ( $\beta = -0.23$ ,  $p < 0.01$ ) but not in OA ( $\beta = -0.08$ ,  $p = 0.38$ ). A summary of all linear model results for corrected and uncorrected AC performance is shown in Table S16.

To investigate this null finding in older adults, a Bayesian linear regression was conducted to examine the link RT variability and corrected AC performance, with sex as an additional covariate. The posterior distribution had mean of  $B = -0.46$  with a 95% CI of  $[-6.65, 1.01]$ , indicating that relationship RT variability and corrected AC performance was negligible in older adults. In a model comparison against the null model, the model with only omission error rate as a term yielded  $BF_{10} = 0.24$ , while the model with both sex and RT variability included had  $BF_{10} = 0.10$ . Both models providing strong evidence for the null hypothesis of no association between gradCPT RT variability and corrected AC performance in OA.

## Discussion

Sustained attention is a fundamental cognitive function and is hypothesized to underlie more complex cognitive expressions (Barkley, 1997; Sarter et al., 2001). While prior studies revealed divergent findings on the relationship between age and sustained attention (Carriere et al., 2010; Fortenbaugh et al., 2015; Robison et al., 2022; Staub et al., 2013), there is little work exploring whether differences in sustained attention contribute to age-related differences in episodic memory performance despite the wealth of evidence, in young adults, that the ability to sustain attention is integral for memory encoding and retrieval (deBettencourt et al., 2018, 2021; Madore et al., 2020). We examined whether age-related differences in memory expressions co-occur with differences in attention, as well as how sustained attention relates to individual differences in associative memory and memory-guided associative inference in young and older adults.

In two experiments, we demonstrate that older adults show both decreased associative memory and associative inference performance compared to young adults, even when restricting the memory-based inference analyses to pairs in which participants correctly recalled both constituents of the learned pairs. These findings are consistent with prior reports of a general decline in inferential reasoning and transitive inference in aging (Burton et al., 2019; Ryan et al., 2009; Salthouse & Prill, 1987), which has been hypothesized to arise from decreased working memory capacity and/or diminished overall episodic memory function (Carpenter & Schacter, 2018; Light et al., 1982). Older adults demonstrate decreased inferential memory performance, despite having knowledge of the individual memory subcomponents, suggesting that their decline in memory-guided inferential performance is not solely driven by diminished episodic memory for the constituent associative elements/overlapping events.

We further address whether this age-related decline in memory-guided inference, as well as the decline in associative memory, relates, in part, to age-related changes in sustained attention. To the contrary, when probing the ability to sustain attention, we find that, in our online sample, older adults show higher  $d'$ , longer reaction times, and fewer commission errors compared to young adults, which builds on previous findings (Carriere et al., 2008; Jackson & Balota, 2012; Staub et al., 2014). Furthermore, we report that in older adults, response slowing correlates with better performance, consistent with an age-related speed-accuracy tradeoff (Salthouse, 1996). Collectively, our data provide no evidence for an age-related decline in sustained attention, despite clear evidence for age-related differences in associative memory and associative inference. As such, age-related differences in sustained attention cannot account for

the decline in associative memory and associative inference performance in the present online sample of older adults.

The absence of an age-related sustained attention deficit in our older adult sample could stem from a variety of factors. First, higher sustained attention performance accuracy combined with response slowing could be driven by older adults adopting a more conservative strategy compared to young adults (Staub et al., 2013), potentially due to differences in motivation (Carr et al., 2022; Mather & Carstensen, 2005). Motivation differences in aging have been observed in lab-based research (Ryan & Campbell, 2021; Seli et al., 2017). Such differences may extend to, and are possibly amplified in, online samples (Greene & Naveh-Benjamin, 2022). Second, previous work suggests that older adults must exert greater cognitive engagement to perform at the same level as young adults across cognitive tasks in general (Smith & Hess, 2015) and on sustained attention tasks specifically (Jackson & Balota, 2012; Staub et al., 2014). Another possibility is that sustained attention tasks may measure only partially overlapping or even different cognitive constructs in young adults compared to older adults (Jackson & Balota, 2012; Seli et al., 2017).

In addition to examining age-related cross-sectional differences in attention and memory, we report that between-person variability in sustained attention explains between-person variability in memory and inference performance in our young adult cohort, but not in our older adult cohort. While previous evidence indicates that event-level and between-person fluctuations in associative memory performance relate to moment-to-moment and between-person differences in sustained attention in young adults (deBettencourt et al., 2018, 2021; Madore et al., 2020), we extend these observations to between-person variability in associative inference performance in our young sample. Moment-to-moment fluctuations in attention represent temporary disengagement with the task, as well as reduced preparatory attention and goal-state coding (see Madore & Wagner, 2022, for review). From the readiness-to-remember framework, decreased sustained attention prior to a task trial is indicative of overall lower preparatory attention, potentially reflecting lower levels of arousal, vigilance, selective attention, and/or motivation towards the task at hand. This reduced readiness may subsequently result in lower cognitive performance, including in the ability to retrieve and draw on the products of memory. Moreover, previous research has linked sustained attention performance to a number of real-world activities, including decreased academic performance (Gallen et al., 2023; Shannon et al., 2021), driving (Walker & Trick, 2018), and workplace success (Kalechstein et al., 2003). Future work should explore the extent to such real-world links are partially mediated through sustained attention's impacts on memory.



Higher sustained attention may improve associative memory performance and guide associative inference through several different mechanisms. As successful associative inference requires bridging across multiple overlapping yet distinct events and attending to specific features during encoding and/or retrieval to infer the relations between stimuli, increased sustained attention performance could reduce interference during memory reactivation and/or when working with the products of retrieval, subsequently improving associative inference performance. On the flip-side, decreased sustained attention may reduce engagement with and monitoring of key event features (Adam & Vogel, 2017; Unsworth & Robison, 2016), including of retrieval cues and products, potentially resulting in reduced reactivation of related events. Prior work indicates that such reactivation tempers forgetting (Kuhl et al., 2010) and assists in inferential reasoning and generalization (Carpenter et al., 2021; Shohamy & Wagner, 2008; Zeithamova et al., 2012). Futures studies should explore how moment-to-moment and individual differences in fluctuations in attention relate to the probability of memory reactivation and to the fidelity of reactivated neural representations, particularly in older adults. Studies that experimentally manipulate sustained attention, including through closed-loop intervention designs, are also needed to support stronger causal conclusions about the putative impacts of sustained attention on associative memory and inference (Schwartz et al., 2024).

Individual differences in memory performance in cognitively unimpaired OA could arise from a number of other variables, including the presence of Alzheimer's disease pathology within the medial temporal lobe and variability in the structural integrity and function of medial temporal lobe cortical and hippocampal subfields (Carr et al., 2017; de Flores et al., 2015). Similarly, age-related differences in associative inference could be driven, in part, by functional and structural changes within the medial temporal lobe and hippocampus that impact mnemonic integration (Shohamy & Wagner, 2008; Zeithamova & Preston, 2010), statistical learning (Schapiro et al., 2017), and/or retrieval-based recursive processes that are thought to be necessary for drawing inferences that bridge across events (Kumaran et al., 2016).

From one perspective, hippocampal subfield CA1 may be particularly relevant for associative inference (Molitor et al., 2021; Schapiro et al., 2017; Schlichting et al., 2014); recent work in young adults demonstrates that CA1 both reactivates during the encoding of new overlapping representations (Molitor et al., 2021) and reinstates prior neural patterns during correct inference trials (Schlichting et al., 2014). Notably, in both healthy aging and Alzheimer's disease, CA1 appears to be differentially vulnerable. For example, structural imaging indicates that CA1 volume declines across the lifetime (Daugherty et al., 2016); decreased thickness of the CA1 apical neuropil layer is related to poorer associative

memory performance in older adults (Carr et al., 2017). However, extant evidence indicates that approximately 25% to 30% of cognitively unimpaired older adults may be in the preclinical stage of Alzheimer's disease, as demonstrated by elevated cerebrospinal fluid or plasma markers of amyloid beta and tau (Cullen et al., 2021; Milà-Alomà et al., 2021; Trelle et al., 2021; Wilson et al., 2022). In the present older adult online sample, constraints precluded conduct of neuropsychological testing nor the collection of biofluids. As such, we cannot definitively state that all older adults in our sample are cognitively unimpaired and free of biomarker evidence of preclinical Alzheimer's disease. Greater integration of easy-to-acquire and sensitive plasma assays into studies of older adults holds promise for determining disease-related and disease-independent drivers of age-related and individual differences in CA1 structure and function, and ultimately differences in cognition.

Additional age-related changes, such as structural and functional effects within prefrontal cortex, likely also contribute to individual and group differences in associative memory and associative inference, perhaps by altering critical executive control processes that are necessary for memory and that decline later in the lifespan (Kupis et al., 2021). While multiple prefrontal subregions subserve processes important for episodic memory (Badre & Wagner, 2007; Dobbins & Wagner, 2005; Preston & Eichenbaum, 2013), of particular relevance to associative inference performance is ventromedial prefrontal cortex (vmPFC), which is hypothesized to extract statistical regularities across multiple experiences, supporting novel inference judgments and abstract knowledge formation (Kroes & Fernández, 2012; van Kesteren et al., 2010). Converging evidence from animal models and postmortem studies document early synaptic loss in medial prefrontal cortex in aging (Morrison & Baxter, 2012), while structural imaging studies observe decreased cortical thickness in this region in older humans (Salat et al., 2001). In older adults, activation in the medial prefrontal cortex has been demonstrated to assist in schematic retrieval of related information (Webb & Dennis, 2019) with overreliance on a schematic-gist retrieval strategy subsequently assisting transitive inference performance in older adults (Golkashani et al., 2021; Ostreicher et al., 2010; Ryan et al., 2009, 2020).

While we observed group differences in associative inference performance even on inference probes for which the underlying direct memory associations were remembered, it nonetheless remains possible that reduced associative inference performance in older adults could be driven, in part, by age-related differences in the strength or precision of reinstated associative memories (e.g., of the AB and BC events). As noted above, to mitigate effects due to memory for the experienced associative events, the experimental design included a longer presentation duration during encoding and

retrieval, as well as two encoding-retrieval cycles for AB and BC events; both design features sought to foster memory for the direct associations. Indeed, performance during the second memory test for AB and for BC associations was high for both young and older adults. Nonetheless, we observed an age-related difference on the AB post-test, which points to lower associative memory in older relative young adults, perhaps due to weaker memory encoding and/or increased sensitivity to interference during retrieval in older adults. Our restriction of associative inference analyses to include only trials where both the AB and BC pairs were remembered (corrected AC performance) tempers the possibility that age-related differences in associative inference were due to frank differences in remembering, but nonetheless leave open the possibility that reduced memory strength or precision in aging impacted associative inference performance.

The current study utilized an online sample of older and younger adults recruited through Prolific (Palan & Schitter, 2018), which replicated age-related differences in associative memory and associative inference observed with an in-person, lab-based sample. Age was not sampled across the entire lifespan, as we specifically targeted younger and older adults to examine age-related changes in sustained attention and associative inference. Compared to the in-person, lab-based sample, it is unclear what the cognitive status was for older adults recruited through Prolific. Previous work examining lifespan changes in sustained attention also utilized online samples (Fortenbaugh et al., 2015; Riley et al., 2017; Rothlein et al., 2018). Other online studies have examined sustained attention metrics in young adults (Jayakumar et al., 2023; Ralph et al., 2015; Rioja et al., 2023; Steinkrauss et al., 2023). A comparison of different online research platforms (e.g., Mechanical Turk, Prolific) revealed high similarity in gradCPT performance between young adults recruited online compared to an in-person sample (Rioja et al., 2023), although it is unclear whether this would extend to older adult populations. The benefits of using online platforms are clear, because they allow for rapid collection of larger datasets (including during the COVID pandemic), even in more challenging populations such as older adults. Conversely, a limitation is that the older adults who enroll in research studies online are generally well-educated, non-Hispanic white individuals who are technologically more advanced, which may limit the ability to generalize findings to the broader population (Turner et al., 2021). Beyond demographic differences, additional sources of variance between online and in-person samples could arise from differential distractions during testing and differences in motivation, both of which might impact attentional engagement and might differ between young and older adults. Most relevant here, if younger adults in our online study experienced greater distraction and/or lower motivation relative to older adults, this

might account for why sustained attention performance was similar across younger and older adults in our study (i.e., greater distraction/lower motivation in young adults offset an age-related difference in sustained attention). Future studies that sample across the lifespan are needed, as are studies that systematically explore sample characteristics and the potential effects of online vs. in-person contexts when examining cross-sectional differences in cognition.

In the current study, we observed minor differences between in-person and online associative memory and associative inference task. These differences occur predominately within the first AB/XY memory test, where both older and young adults demonstrate lower performance in the online experiment compared to the in-person experiment. For all other associative memory and associative inference tests, online performance for both groups were similar to in-person performance. The online and in-person samples were given the same set of instructions as well as several practice trials before the experiment began. One important note to consider is that most psychological experiments conducted online are relatively short (e.g., 5 min or less), with some researchers recommending that online experiments be less than 30 to 40 min for tasks requiring higher engagement (Greene & Naveh-Benjamin, 2022). The current experimental design mimics an in-person laboratory visit, which may be relatively unfamiliar to online users. The present initially low AB performance for both groups in the online study could have arisen from a number of different variables, including a lack of familiarity with the experimental format and testing and initial confusion about the instructions. Despite this reduced initial performance, young and older adults significantly improve their performance on the second AB/XY test and retained AB/XY memory to the post-test, suggesting that age-related memory effects can be reliably measured even when transitioning from traditional in-person laboratory assessments to online formats.

The presently observed age-related difference in associative memory and memory-guided inference performance, which does not stem from group differences in sustained attention, motivates future structural and functional studies of the hippocampus, prefrontal cortex, and locus coeruleus alongside their interactions, to further understand age-related and between-person variability in memory performance and sustained attention. Such investigations promise to further elucidate how multiple cognitive and neural systems enable people to encode information and draw novel inferences that bridge experience, and how these systems change with age and disease, impacting one's ability to leverage memory to understand structure in the world.

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**Data availability** The data for the current experiment are publicly accessible at <https://osf.io/9thg8/>.

**Code availability** The code for the current experiment are publicly accessible at <https://osf.io/9thg8/>.

## Declarations

**Ethics approval** For Experiment 1, the study protocol was approved by the Johns Hopkins School of Medicine Institutional Review Board. For Experiment 2, the study protocol was approved by Stanford University's Institutional Review Board.

**Consent to participate** All participants gave informed, written consent and received compensation for their participant through either monetary payment or class credit.

**Consent for publication** All co-authors have agreed to the publication of the manuscript.

**Conflict of interest** A.B. is an inventor on Johns Hopkins University intellectual property with patents pending and licensed to AgeneBio. A.B.'s role in the current study is in compliance with the conflict of interest policies of the Johns Hopkins School of Medicine.

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