Age-related differences in forming conjunctive memories of *what*, *when* and *where*

Xiangjuan Ren (xiangjuan.ren@uni-hamburg.de)
Institute of Psychology, Von-Melle-Park 5
20146, Hamburg, Germany

Marit Petzka (marit.petzka@uni-hamburg.de)
Institute of Psychology, Von-Melle-Park 5
20146, Hamburg, Germany

Nicolas W. Schuck (nicolas.schuck@uni-hamburg.de)
Institute of Psychology, Von-Melle-Park 5
20146, Hamburg, Germany

Abstract

Aging greatly affects memory, but not all aspects are impaired equally. Past research has demonstrated that older adults show greater deficits in remembering *where* an object was encountered compared to *what* was experienced. A third dimension, that has received less attention in this context is memory for *when* events occurred. In this study, we employed a Sequential Memory Task (SMT) in which participants memorized spatio-temporal visual object sequences over repeated exposures. In two experiments with 39 younger (YAs, 18–35 years) and 53 older adults (OAs, 65–75 years), we examined age-related differences in sequence memory (*when*) and the interplay between item (*what*), and location (*where*) knowledge. Our results revealed that memory was stronger for item sequences than for location sequences or item-location combinations in both younger and older adults. In addition, older adults exhibited greater age-related deficits in location–related memory. We also found that item and location memory were bi-directionally related and that even pure item sequence reports involved location memory and vice versa. Both age groups relied more on item-location binding associations than on transition learning, but computational modeling indicated a higher reliance on independent location transition learning in OAs than YAs. This suggests that the strong age-related impairment in spatial location memory was in part driven by age-differences in memory binding. These findings provide insights into age-related changes in spatio-temporal sequence memory, and highlight distinct learning strategies in younger and older adults.

Keywords: aging; sequence memory; transition; binding association; learning strategy.

Introduction

Aging is associated with a marked decline in episodic and working memory functions (Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012). But not all aspects of memory change uniformly with age. Previous studies reported that while older adults have relatively intact memory for *what* they have experienced (e.g., which object, or color), they are more impaired in recalling in which spatial location they have seen an object, i.e., *where*. Peterson and Naveh-Benjamin (2016), for instance, demonstrated in a working memory task that recognition of the item-location binding is impaired in older relative to younger adults, while their memory for intra-item binding (e.g., color + shape) remains intact. Similarly, age-related binding deficits have been observed in episodic memory tasks (Dai, Thomas, & Taylor, 2018; Muffato, Hilton, Meneghetti, Beni, & Wiener, 2019; Tran et al., 2021). Beyond the *what* (i.e., objects) and *where* (i.e., spatial location) dimensions, it is equally essential to remember *when* something was experienced, as it captures the sequential relationships between events.

A recent study using a Sequential Memory Task (SMT), which required participants to integrate *what*, *where* and *when* information, found that older adults exhibited deficits even in the individual dimension (*what* and *where*) when temporal information (*when*) was introduced (Ren, Petzka, & Schuck, 2024). Specifically, when older adults were presented with a sequence of images and spatial locations (e.g., a cat appearing at the 12 o'clock position, followed by a hat at 9 o'clock etc, see Fig.1), their memory performance declined significantly compared to younger adults—even when tested exclusively on either the item or location dimension.

In the SMT, participants could theoretically learn transition relationships within each dimension (items or locations) independently and use this knowledge to complete the task. If so, older adults' memory impairment could be solely attributed to errors in learning or retrieving these transitions. However, it is also possible that participants form integrated item-location representations, allowing information to be shared across dimensions. The two possibilities are supported by previous neurocognitive studies showing that the hippocampus is involved in both transition learning (Schapiro, Turk-Browne, Norman, & Botvinick, 2016; Schuck & Niv, 2019) and associative binding (Deuker et al., 2013; Kurth-Nelson et al., 2023; Yonelinas, Ranganath, Ekstrom, & Wiltgen, 2019). Nevertheless, the relative contributions of independent transition learning and binding association learning to memory performance remain unclear.

To address these question, we employed the same sequential memory task as Ren et al. (2024) to investigate how humans encode and retrieve sequences of images appearing in fixed spatial locations. Memory was tested after each sequence presentation, allowing us to quantify performance on a trial-by-trial basis and examine the interaction between *what* and *where* memory.

Our results replicated previous findings showing stronger memory for item sequences than spatial location sequences or item-location combinations in both younger and older adults. In addition, a detailed analysis of trial-

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wise error patterns demonstrated that participants' item memory was correlated with location memory and vice versa, suggesting a bi-directional binding association. Model-comparisons revealed that learning involved binding item-location information as well as forming item-item and location-location associations in both younger and older adults. Younger adults however relied more on the binding association for the location reports compared to older adults. These findings provide critical insights into how sequence memory change with aging, highlighting the interplay between independent transition learning and binding associations in shaping memory performance.

Methods

Participants

For Experiment 1, 24 younger adults (YAs, 18–35 years) and 25 older adults (OAs, 65–75 years) were recruited from the Prolific platform (https://www.prolific.com/; minimum Prolific approval rate: 95). For Experiment 2, 15 YAs (university students, 18–35 years) and 28 OAs (local residents, 65–75 years) participated in an MRI experiment. For the present analyses, we focus exclusively on their behavioral data. All participants were required to be physically and mentally healthy, and to have not had any history of head injury or mild cognitive impairment/dementia. The study was approved by institutional ethical review board and all participants provided informed consent prior to participation. The online participants were compensated with £10 per hour, plus a performance-based bonus of up to £3.6. For the in-lab experiment, YAs received course credits, while OAs were compensated at a rate of €15 per hour, plus a performance-based bonus of up to €10.

Stimuli and Design

The experimental program was coded using PsychoPy/JS and Python, with the online experiment being hosted on Pavlovia (https://pavlovia.org/).

Sequential Memory Task (SMT) The Sequential Memory Task (SMT) involved encoding spatio-temporal sequences of every day objects (e.g., hat, flower) displayed at different locations on a circle (0°, 45°, ...) (Fig.1A). Each trial consisted of an ***encoding*** stage during which one item+location sequence was shown to participants and a ***reporting*** stage in which memory was probed (Fig. 1A). To test different types of knowledge, participants were asked to complete three types of memory reports following sequence encoding (Fig. 1A):

Item Report: All five images from the current sequence, along with one distractor image from another sequence, were displayed in a row in a randomized order. Participants were asked to select the images to indicate the original item transitions.

Location Report: Same as the *Item Report*, but with five spatial locations from the current sequence and one distractor location displayed.

Reconstruction Report: Both the five images and five locations from the current sequence, along with one distractor image and one distractor location, were displayed. Participants were asked to drag and drop each image to its corresponding location and thus, reconstruct the original sequence.

The task comprised 8 blocks in Experiment 1 (8 trials/block, 64 trials total) and 6 blocks in Experiment 2 (48 trials total). In each block, participants completed all three reports ('three-reports trials') in 6 of 8 trials. In the remaining 2 trials, only the Reconstruction report was required (Fig. 1B). Each report had a maximum decision time of 30 seconds. Participants earned one coin for fully correct reports but received nothing for errors.

Each participant had to learn a total of four unique sequences, which were constructed by combining each of two unique item sequences (e.g., cat → hat → ... VS. sunflower → female → ...) with two unique spatial location sequences (90° → 180° → ...) (Fig.1C). Each of the four unique item+location sequences was presented twice per block. The eight trials in a block were structured so that across trials participants first experienced four repetitions of the same item sequence (labeled as a), followed by four repetitions of the other item sequence (b). Meanwhile, the corresponding location sequence (a' and b') alternated every two trials, resulting in a blocked curriculum (see Fig. 1C, (aa'), (aa'), (ab'), (ab'), (ba'), (ba'), (bb'), (bb')).

Behavioral and statistical analysis

Memory performance. Participants' memory performance was assessed using accuracy, which was defined as the proportion of correct answers among the five responses in the items/locations/reconstruction report, ranging from 0 to 1.

Binding score. To evaluate whether participants' memory in one dimension was influenced by the correctness of the other dimension, we calculated a binding score. It was defined as the difference between two conditional probabilities of reporting an item or location correctly given that they had been correct or incorrect for the same and the other dimension. This analysis asked, for instance, whether the probability to report the third item correctly in the *Item report* was different when participants had reported the third location either correctly or incorrectly, while controlling for the correctness of the second item (details see below). A non-zero binding score indicates that participants' memory of an item was dependent on knowing the location of that item, and vice versa, when they reported these aspects separately.

Statistical analysis. Generalized linear mixed models (GLMM) assuming binomial distributed responses and LMM assuming normal distributed re-

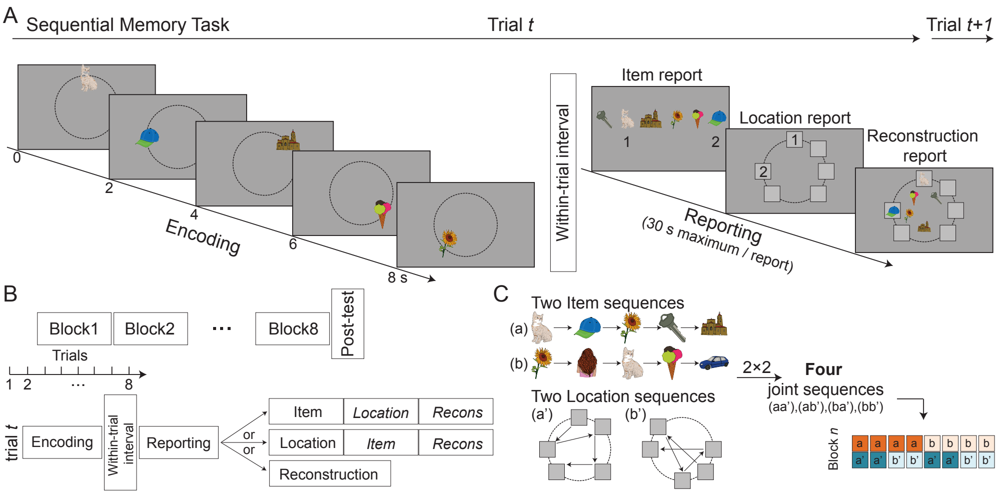

Figure 1: **Experimental Design. (A) Sequential Memory Task (SMT).** Each trial of the SMT consists of two stages: *encoding* and *reporting*. During the encoding stage, participants are presented with a 5-element sequence and had to memorize the what (which item), where (which location) and when (which order) aspects of the sequence. Following encoding, participants complete three types of reports. In the *item* and *location* reports (*marginal reports*), participants click on either the images or the locations in the correct order. In the *reconstruction report*, they had to report both, the item and location, by dragging and dropping images to the corresponding locations in the correct order. **(B) Task Structure.** In Experiment 1 and 2, participants completed 8 and 6 blocks of the SMT respectively, with each block consisting of 8 trials. In some trials, participants complete the reconstruction report immediately after encoding (*reconstruction-only trials*). In the remaining trials, they complete all 3 types of reports (*three-report trials*). **(C) Four Unique Joint Sequences.** Each participant learns four unique joint sequences, formed by combining two distinct item sequences with two distinct location sequences. These sequences are organized in a blocked way within a block.

sponses were used. Additionally, null hypothesis testings were conducted and reported.

Computational modeling

We developed five models to characterize participants' *marginal* reports in the Sequential Memory Task. Each model assumes two serial processing stages: (1) sequence learning; (2) retrieving relevant information and generating reports (see Fig. 4A).

Learning sequences Our models implemented two different approaches of learning the sequences. The first approach assumed that humans *learn sequential item-item and location-location transitions independently*. Specifically, the model assumes that item and location sequence learning consisted of acquiring directional transitions between items or locations in the form of *Successor Representation (SR)* (Dayan, 1993; Gershman, Moore, Todd, Norman, & Sederberg, 2012), which were updated via the temporal difference (TD) learning (Dayan, 1993; Gershman, 2018). Another mechanism that could also be at play is that humans form *bi-directional binding associations* between item and spatial location dimension, in addition to encoding sequential transitions. Specifically, we assumed that each item was associated with a particular location in the form of a Von–Mises distribution, which was updated following each observation in a trial. This process is simultaneously influenced by residual memory from previously learned item-location associations, which decays at a rate controlled by a free parameter.

Retrieval and Decisions The model further assumed a retrieval process that occurred immediately before choices and was based on the memory formed during encoding (without undergoing further consolidation or forgetting between encoding and reporting). The initial step was modeled as recognizing which sequence they are being queried about by using the set of six items or locations displayed on the screen to identify the most likely context (or sequence) through a maximum operation. This process hinges on their feature-to-context learning during the encoding stage, which serves as an additional and necessary component of the described learning hypotheses above. This feature-to-context associations was modeled as a negative exponential function of the distance between a feature (e.g., each item or location) to any contexts (e.g., the unique joint sequence) since their last occurrence, thus producing a primacy effect. A context retrieval then led to retrieving the starting element (either the first item or location in a sequence) through a softmax operation. For subsequent responses, the learned transition relationships and binding associations were applied to determine the next item or location in the report.

Results

Older adults show strong memory deficits in location-related reports compared to younger adults

As shown in Figure 2A, both young adults (YAs) and older adults (OAs) improved performance over time in all three report types, with the highest memory performance in item reports, followed by location reports, and the lowest performance in reconstruction reports in line with the previous findings (Ren et al., 2024, ANOVA from GLMM with likelihood ratio tests, main effect of report type: $\chi^2(2)=1930.73$, $p<0.001$; main effect of trials: $\chi^2(1)=697.98$, $p<0.001$; main effect of age group: $\chi^2(1)=597.21$, $p<0.001$; post-hoc comparisons on report types with Bonferroni correction from GLMM – for YAs, item vs. loc: $z=9.463$, $p<0.001$; item vs. recons: $z=25.722$, $p<0.001$; loc vs. recons: $z=17.695$, $p<0.001$; for OAs, item vs. loc: $z=22.686$, $p<0.001$; item vs. recons: $z=31.490$, $p<0.001$; loc vs. recons: $z=9.195$, $p<0.001$). A similar pattern was observed when aggregating all trials per participant (Fig. 2B, left panel). Age-group comparisons within each report type (item/location/reconstruction) exhibited a gradient pattern: item memory was least impaired in OAs compared to YAs, while location and reconstruction memory showed greater impairment (Fig. 2B, right panel; ANOVA from LMM with Satterthwaite approach for approximation of degrees of freedom, main effect of report types: $F(2,3973)=44.243$, $p<0.001$; post-hoc comparisons with Bonferroni correction from LMM, item vs. loc: $t=9.116$, $p<0.001$; item vs. recons: $t=6.835$, $p<0.001$; loc vs. recons: $t=-2.910$, $p=0.011$). This indicated a non-uniform decline across different types of knowledge.

Memory for item sequence and location sequence is interdependent

Testing memory separately for item and location sequences allowed us to study the dependence between these two memory types in detail. Specifically, if participants store independent transitions information for item and location sequences, then their response in a given report should mostly be influenced by whether the answer to the previous element within the same dimension was correct or not. If, however, participants have formed a binding of item-location memories, then we would expect that the probability to correctly report a specific location depends on correctly recalling the item that occurred at this location, and vice versa, even when reports require to report only locations or items, but not both.

To test this, we analyzed the correctness of each response as a function of the correctness of preceding responses within the same dimension (*transitions*), and the correctness of response in the other dimension (*binding*; see left diagram in Fig. 2C). We can, for instance, differentiate the case of a correct response for the current item, given correct responses for its preceding item but an incorrect response for the location associated with it ($P(\text{item}_i = \text{correct} \mid \text{item}_{i-1} = \text{correct}, \text{loc}_i = \text{incorrect})$) from the conditional probability of correct response for the current item given a correct response for both its preceding item and associated location ($P(\text{item}_i = \text{correct} \mid \text{item}_{i-1} = \text{correct}, \text{loc}_i = \text{correct})$). The same calculation was applied to quantify the influence of correctness of items on locations.

The *binding score* is calculated as the relative difference between these two conditional probabilities. Depending on whether the preceding response in the current dimension is correct or incorrect, the *binding score* is categorized as a *cost* (negative influence) or a *benefit* (positive influence). If the two dimensions, *what* and *where*, are independent, the binding score should be close to zero.

As shown in Figure 2C, the non-zero cost and benefit quantifications revealed that participants drew on information from the other dimension, which provided direct evidence of bi-directional binding between item and location sequences. The pronounced binding scores in the reconstruction reports indicated a stronger interplay across dimensions (Fig. 2D; ANOVA from LMM with Satterthwaite, main effect of report types (marginal or reconstruction): $F(1,122.9)=83.854$, $p<0.001$). However, there was no significant difference in the reliance of binding between YAs and OAs from behaviour ($F(1,136.3)=1.750$, $p=0.188$). The findings obtained from online participants were further validated in an in-lab study (Fig. 3).

Two-system model supports the involvement of both directional transition learning and bi-directional binding association learning

We employed computational models with two primary objectives: (1) to demonstrate that participants' learning relies on two distinct systems – transition and binding association, and (2) to quantify the relative contributions of these systems to participants' performance. We hypothesized that humans learn ***directional transitions*** within each dimension independently, and additionally they learn ***bi-directional binding associations*** between the item and location sequence.

Accordingly, we constructed 5 model variants

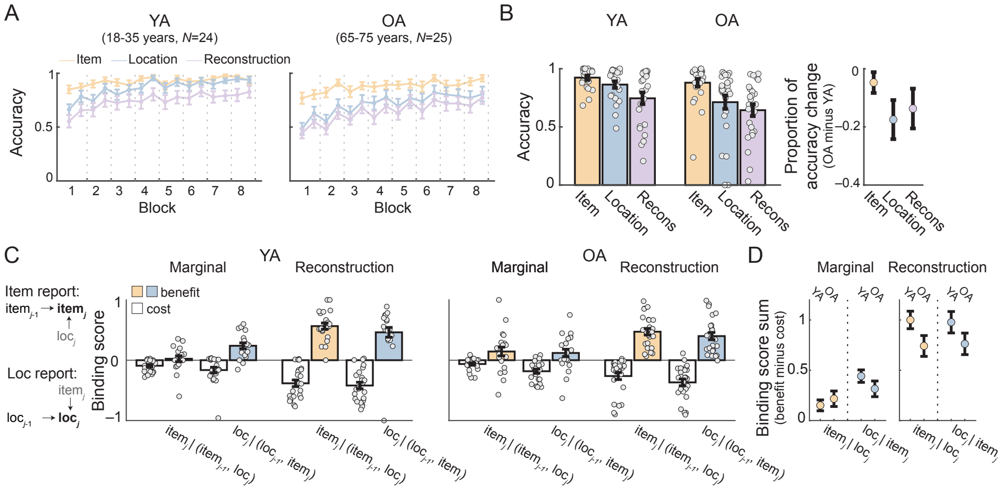

Figure 2: **Memory gradients and binding evidence in Experiment 1. (A) Memory performance increases across blocks.** Accuracy, defined as the proportion of correct responses in each report, increases across blocks for both younger (YA) and older adults (OA). Each data point (dot) represents the average accuracy across four trials within a block, and error bars indicate the standard error of the mean (S.E.M). **(B) Memory gradient across three report types in YA and OA.** Left Panel: Accuracy is calculated across all trials for each participant, revealing a similar memory gradient (item > location > reconstruction) for YAs and OAs. Right Panel: Age-related differences in accuracy are shown for each report type. **(C) Binding score suggests the interdependence between item and location knowledge.** The binding score is defined as the relative difference between two conditional probabilities that share the same preceding response (both correct or both incorrect) but differ in the other dimension. A non-zero binding score indicates interdependence between the two dimensions. **(D). Summed binding score.** Subtracting the *cost* from the *benefit* reflects a greater reliance on binding associations in the reconstruction report.

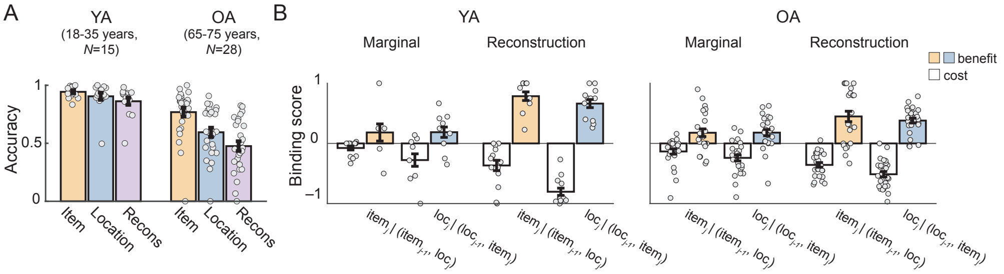

Figure 3: **Replication of memory gradients and binding evidence in Experiment 2.** An in-lab experiment was conducted with a setup similar to the online experiment in Experiment 1. Details of plots as in Fig 2.

(Fig. 4B) and fit each model to individual participant' responses (correct or incorrect) in each *marginal* report using maximum likelihood estimates (MLE). The models either included only independent sequence learning hypothesis ('Indep' and 'Indep+Unc', where 'Unc' accounts for spatial uncertainty arising from confusion between spatial locations during location sequence learning) or, building on this framework, incorporated the binding association hypothesis. Specifically, 'BindItem' and 'BindLoc' captured one-directional binding associations (item binding to location and vice versa), while the 'Two-system' model integrated bi-directional binding.

To evaluate the goodness of fit, we used the Akaike information criterion with a correction for sample sizes (AICc) (Akaike, 1974; Hurvich & Tsai, 1989), which punishes overfitting from additional free parameters. A lower AICc indicates a better fit. For each participant, the model with the lowest AICc served as a reference to compute ΔAICc for each model. Model comparison in each age group revealed that human behaviour in the sequential memory task was best explained by a two-system model that integrates both independent transition learning and binding association learning (Fig. 4B). We further assessed that the two-system model could predict participants' learning performance across trials closely (Fig. 4C).

For the two-system model, we assumed that human performance in the item reports was jointly influenced by independent item transition learning

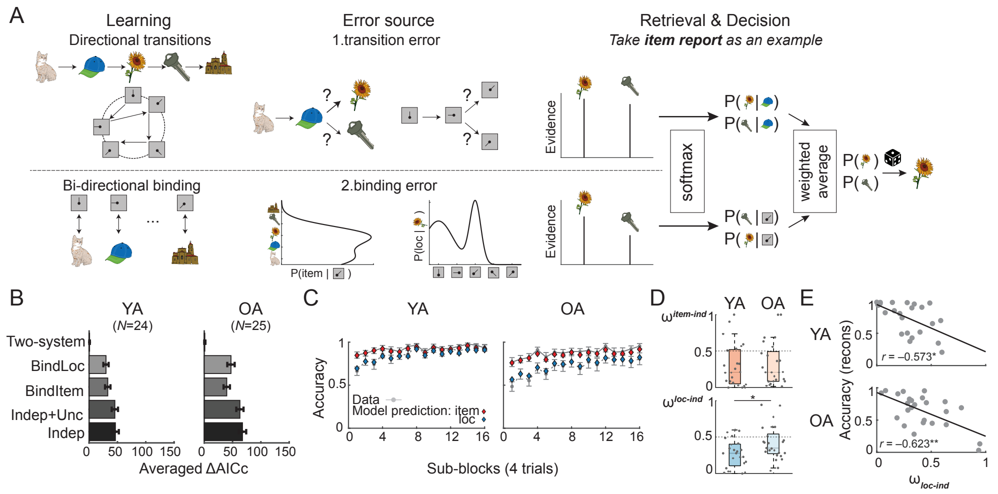

Figure 4: **Model specification and comparison. (A) Two-system model specification.** The two-system model assumes that participants learn directional transitions for each dimension (item or spatial location) independently, while also forming bi-directional binding associations between the two dimensions. The final responses in each report are determined by a weighted average of predictions from both learning systems. **(B) Model comparison.** Model comparison based on *AICc* indicate that the two-system model outperforms the alternatives. Error bars represent the S.E.M. ΔAICc is computed for each participant by using the best-fitting model as the reference, where lower values indicate better model fit. **(C) Two-system model prediction.** The two-system model captures trial-by-trial accuracy. Gray lines represent the observed data, while diamonds indicate the model predictions. **(D) Independent transition learning weights.** The weights for independent item sequence learning ($\omega^{item-Ind}$) do not differ between age groups. However, older adults (OAs) show significantly higher weights for independent location sequence learning ($\omega^{loc-Ind}$) compared to younger adults (YAs). Gray dots represent individual participants. **(E) Smaller $\omega^{loc-Ind}$ correlates with higher accuracy in the reconstruction report.** The negative correlation suggests that greater reliance on binding association learning leads to improved performance in the reconstruction report.

and binding associations from the location dimension to the item dimension. Their relative contributions were controlled by the parameter $\omega^{item-Ind}$ and its counterpart, 1-$\omega^{item-Ind}$ respectively. Similarly, location reports were explained by independent location transition learning and binding associations from the item dimension to the location dimension, with their relative contributions controlled by the free parameter $\omega^{loc-Ind}$. A value of $\omega^{item-Ind}$ or $\omega^{loc-Ind}$ smaller than 0.5 indicates a stronger reliance on bi-directional binding associations. As shown in Figure 4D, we found that both YAs and OAs primarily relied on binding associations in their reports. Second, OAs demonstrated a higher reliance on independent location transition learning than YAs (independent sample t-test: $t(47)=-2.353$, $p=0.023$). Further, $\omega^{loc-Ind}$ correlated with the *reconstruction report* accuracy for both YAs and OAs, suggesting more binding information from the item dimension contributed to better performance in the reconstruction report (Fig. 4E; YAs: $r=-0.573$, $p=0.038$; OAs: $r=-0.623$, $p=0.009$, with *FDR* correction).

Discussion

In the current study, we used a sequential memory task to investigate how memory for two-dimensional sequences—integrating *what*, *where*, and *when*—differs between younger adults (YAs) and older adults (OAs). Our findings were threefold. First, memory performance was stronger for item (*what*) sequences than for location (*what*) or item-location conjunctions (*what+what*) in both age groups, with OAs exhibiting disproportionately greater impairments in location-related memory. Second, item and location memory were bidirectionally related: even item-only sequence reports were influenced by location memory, and vice versa. Finally, two-system computational modeling confirmed the contributions of directional transition learning within each dimension and bidirectional association learning between item and location dimensions. OAs relied more on independent learning for the location sequence, which may underlie their worse performance on location-related reports.

The superior memory for the item sequence cannot be attributed to the blocked design, in which the item sequence changed more slowly across trials than the location sequence. A previous study (Ren et al., 2024) demonstrated that the superiority of the item sequence memory persists in both YAs and OAs even when the location sequence is more strongly blocked than the item sequence.

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