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Cross-Modal Facilitation of Episodic Memory by Sequential Action Execution

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Abstract

Throughout our lives, the actions we produce are often highly familiar and repetitive (e.g., commuting to work). However, layered upon these routine actions are novel, episodic experiences. Substantial research has shown that prior knowledge can facilitate learning of conceptually related new information. But despite the central role our behavior plays in real-world experience, it remains unclear how engagement in a familiar sequence of actions influences memory for unrelated, nonmotor information coincident with those actions. To investigate this, we had healthy young adults encode novel items while simultaneously following a sequence of actions (key presses) that was either predictable and well-learned or random. Across three experiments ($N = 80$ each), we found that temporal order memory, but not item memory, was significantly enhanced for novel items encoded while participants executed predictable compared with random action sequences. These results suggest that engaging in familiar behaviors during novel learning scaffolds within-event temporal memory, an essential feature of episodic experiences.

Keywords

prior knowledge, motor actions, sequence learning, temporal memory, episodic memory, open data, open materials

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Our lives are imbued with structure and regularity. In particular, many of our behaviors can be organized into repetitive, well-defined sequences of actions. Consider your commute: You might walk to the subway station, then swipe your ticket at the turnstile, then step aboard the train. While engaging in this familiar sequence of actions, you are also likely to encounter an influx of novel sensory information, which may have little to do with your actual behavior (e.g., receiving a text while entering the subway). Despite the prevalence of familiar action sequences in everyday life, we know little about their impact on memory for novel experiences that unfold simultaneously. The current study was therefore designed to explore this cross-modal interplay between familiar action execution and novel episodic memories.

This investigation bridges two fields—motor learning and episodic memory—that have evolved in parallel with relatively little cross talk. Existing work at this intersection reveals that engaging in actions during learning boosts memory relative to passive encoding (Engelkamp & Cohen, 1991; Yebra et al., 2019) and that learning can transfer between motor sequences and other types of information (e.g., repeatedly encoded word lists; Mosha & Robertson, 2016; Mutanen et al., 2020; Thibault et al., 2021). Separately, a line of research on stimulus–response associations has characterized how motor actions can become rapidly integrated with the stimuli they are paired with, which serves to facilitate processing of those stimuli or actions during future encounters (Dobbins et al., 2004; Hommel, 2004; Schnyer et al., 2006). Through this binding mechanism, stimuli can be linked to individual actions even after a single stimulus–response encounter. However, these previous lines of work do not directly address how executing sequences of familiar actions impacts the simultaneous encoding of novel information. Furthermore, an understanding of how sequential actions affect multiple forms of one-shot episodic memory is lacking.

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In previous literature, it has been well-established that prior knowledge about the world can facilitate novel learning (e.g., Alba & Hasher, 1983; Anderson et al., 1978; Bransford & Johnson, 1972; Kole & Healy, 2007; Tse et al., 2007; van Kesteren et al., 2010, 2014). These findings even form the basis of strategic techniques such as the *method of loci*, in which people boost memory for new information by deliberately associating it with familiar spatial contexts (Bass & Oswald, 2014; McCabe, 2015; Reggente et al., 2020). However, the lion's share of this existing work focuses on how prior knowledge supports memory for information that belongs to the same domain or is meaningfully related to that knowledge. Here, we asked instead how familiar motor actions impact memory for novel, unrelated episodic experiences that belong to a different modality than those actions.

We propose that familiar action sequences enhance memory for concurrent experiences by providing a "temporal scaffold" for incoming information. When one executes a well-known motor sequence, the representation of that sequence may become activated in memory and remain on-line throughout the event. As new information is encountered, it can then become integrated within (or "slotted into") the existing event representation through their coactivation. This *scaffolding hypothesis* makes specific predictions for how action sequences should promote novel learning, based on multiple avenues of previous work. In particular, the hippocampus has been shown to support memory for both motor and episodic item sequences (Albouy et al., 2008, 2015; Curran, 1997; Schendan et al., 2003) and to form stable neural representations of sequential information that is studied repeatedly (Hsieh et al., 2014; Kalm et al., 2013; Paz et al., 2010). Greater stability in hippocampal activity patterns, in turn, can enhance temporal binding between items (DuBrow & Davachi, 2014; Ezzyat & Davachi, 2014). Integrating these results, we hypothesize that when participants encode new information during execution of a known action sequence, these items become linked to a highly stable event representation, which ultimately improves temporal memory.

This putative mechanism draws inspiration from research on event segmentation, which posits that stability and change in one's surrounding context help to organize continuous experience into discrete, unified memory episodes (Clewett & Davachi, 2017; Davachi & DuBrow, 2015). Although some work in this space has focused on how temporal memory is negatively impacted by boundaries *between* events (e.g., abrupt shifts in spatial context or task goals; Clewett et al., 2020; Horner et al., 2016; Kurby & Zacks, 2008), here we explored a mechanism by which memory for information from *within* the same event can be better integrated. Engaging in a familiar behavioral sequence may afford individuals with a level of mental context stability that benefits within-event temporal binding beyond what is granted by consistency in perceptual input or task demands alone. Our scaffolding hypothesis is also broadly consistent with extant models of prior knowledge-mediated learning, which posit that enhanced memory for new information occurs because these items are assimilated into existing memory representations through hippocampal-neocortical connectivity (Gilboa & Marlatte, 2017; McClelland, 2013).

Statement of Relevance

Our everyday behaviors—such as commuting to work or getting ready for bed—are a fundamental element of human experience. Moreover, these behaviors do not unfold in a vacuum. During your commute, for example, you may listen to a new podcast or receive a funny text from a friend. Despite the prevalence of familiar behavioral routines in daily life, their effects on how we remember simultaneous nonmotor information are poorly understood. Here, we asked how engaging in familiar motor actions during learning supports memory for novel, temporally coincident experiences. We found that executing a well-learned sequence of actions robustly enhances memory for the temporal order of novel information that is encoded in parallel. These results provide a novel demonstration of how our everyday motor actions impact concurrent cognitive processing while also shedding light on cross-modal interactions between motor and episodic memory systems.

We also tested the alternative hypothesis that familiar behaviors boost memory by freeing attentional resources. That is, when some part of our environment is familiar, we can direct more focus to information that is new (DeWitt et al., 2012; Reder et al., 2016). Under this *attentional-resource hypothesis*, memory for all novel elements of an experience—not just temporal order—should be enhanced by familiar action execution.

Critically, both our scaffolding and attentional-resource hypotheses raise the question of how motor actions per se drive any resulting memory improvements. It could be, for example, that engaging in familiar actions improves memory simply because individuals have predictions or expectations about the future. In this case, the capacity to make memory-based predictions about *any* element of upcoming events may be sufficient to scaffold concurrent learning. Extant work shows that the relationship between prediction and novel encoding is not clear-cut (Ritvo et al., 2019; Sherman & Turk-Browne, 2020). Nevertheless, we acknowledge this possibility and here have chosen to focus on motor actions as the modality through which such predictions are formed and expressed. This decision was motivated both by the prevalence of familiar behaviors in our day-to-day lives and by the previously discussed research on demonstrated interactions between motor and episodic memories (e.g., Engelkamp & Cohen, 1991; Mosha & Robertson, 2016). Further, this study helps to clarify and explore the range of circumstances in which prior knowledge and prediction aid novel learning.

Therefore, to investigate whether and how familiar action sequences impact new learning, we designed a novel paradigm (Fig. 1) in which participants encoded sequences of novel items while embarking on errands to two different stores. During each errand, they were also required to execute a sequence of simple motor actions. Critically, in one of the two stores—the *predictable store*—the sequence of actions executed during encoding always followed a familiar, well-learned pattern. We then examined whether temporal memory for the order of novel items encoded within the predictable store was enhanced relative to memory for novel items encountered in the *random store*, where actions were unpredictable. Further, we adjudicated between the scaffolding and attentional-resource hypotheses by asking whether familiar action sequences benefit memory only for the order of novel items or also for their perceptual details and spatial contexts. Across three experiments, we found that executing learned action sequences robustly and selectively bolsters memory for the temporal sequencing of novel information, consistent with our scaffolding hypothesis.

Open Practices Statement

All data, stimuli, and analysis scripts for this study are publicly available via OSF and can be accessed at https://osf.io/xgwzf/. The experiments reported in this article were not preregistered.

Experiment 1

Method

Participants. A total of 80 participants (29 female) were recruited online via Prolific (www.prolific.co). Previous studies in our lab have used samples of between 25 and 35 participants when exploring other effects of event structure on episodic memory (e.g., Clewett et al., 2020; DuBrow & Davachi, 2013). Given that here we explored a novel behavioral effect with an unknown size and that our data collection involved online participants (who likely exhibit greater heterogeneity than those recruited on university campuses), we chose to enroll a considerably larger sample to ensure sufficient statistical power. Specifically, a sample of 80 gave us 80% power to detect effect sizes (ds) of at least 0.31 (i.e., small to medium effects). All participants were healthy adults between 18 and 35 years old (M = 24.9, SD = 4.9), reported having normal or corrected-to-normal vision, and had a Prolific study approval rate of at least 60%. Participants received $14 on study completion (duration: M = 61.0 min, SD = 19.9). All participants provided informed consent, and all procedures were approved by the Columbia University Institutional Review Board.

Stimuli. Stimuli consisted of colorful, high-resolution images of objects from two semantic categories: animals (e.g., dog, elephant) and foods (e.g., banana, cupcake). There were 192 unique object images (96 per category) in total. All backgrounds from the images were removed via Adobe Photoshop. For the pretraining phase (see below), we also collected 24 abstract fractal images.

Task design.

Overview. Participants embarked on a series of errands to two different stores: the pet store and the grocery store. On each errand (i.e., event), their task was to collect a sequence of items by visiting a sequence of aisles (via key presses) in the current store. Importantly, events in one of these stores were defined as *predictable*, in that each time the participant ran an errand in this store, the sequence of aisles they visited followed a fixed, previously learned order. In the *random* store, however, participants visited a novel sequence of aisles during every event/errand they experienced. The identity of the predictable store (pet vs. grocery store) was counterbalanced across participants.

Pretraining. Before beginning their errands, participants completed a pretraining task, in which they learned the aisle/action sequence they would follow in the predictable store. The pretraining phase consisted of three cycles of alternating study and test periods, during which participants repeatedly executed the sequence of actions (i.e., keyboard presses) associated with the predictable store. Each study repetition began by displaying a banner for 3 s with the name of the store that was about to be visited, before moving on to a screen that displayed the four aisles within that store as four side-by-side circles (Fig. 1a). Participants were then cued to visit a sequence of six aisles one at a time. Specifically, prior to each response, the circle associated with the to-be-visited aisle turned red, cuing participants to enter that aisle by pressing the corresponding key (d, f, j, or k). Only correct responses were accepted, and participants

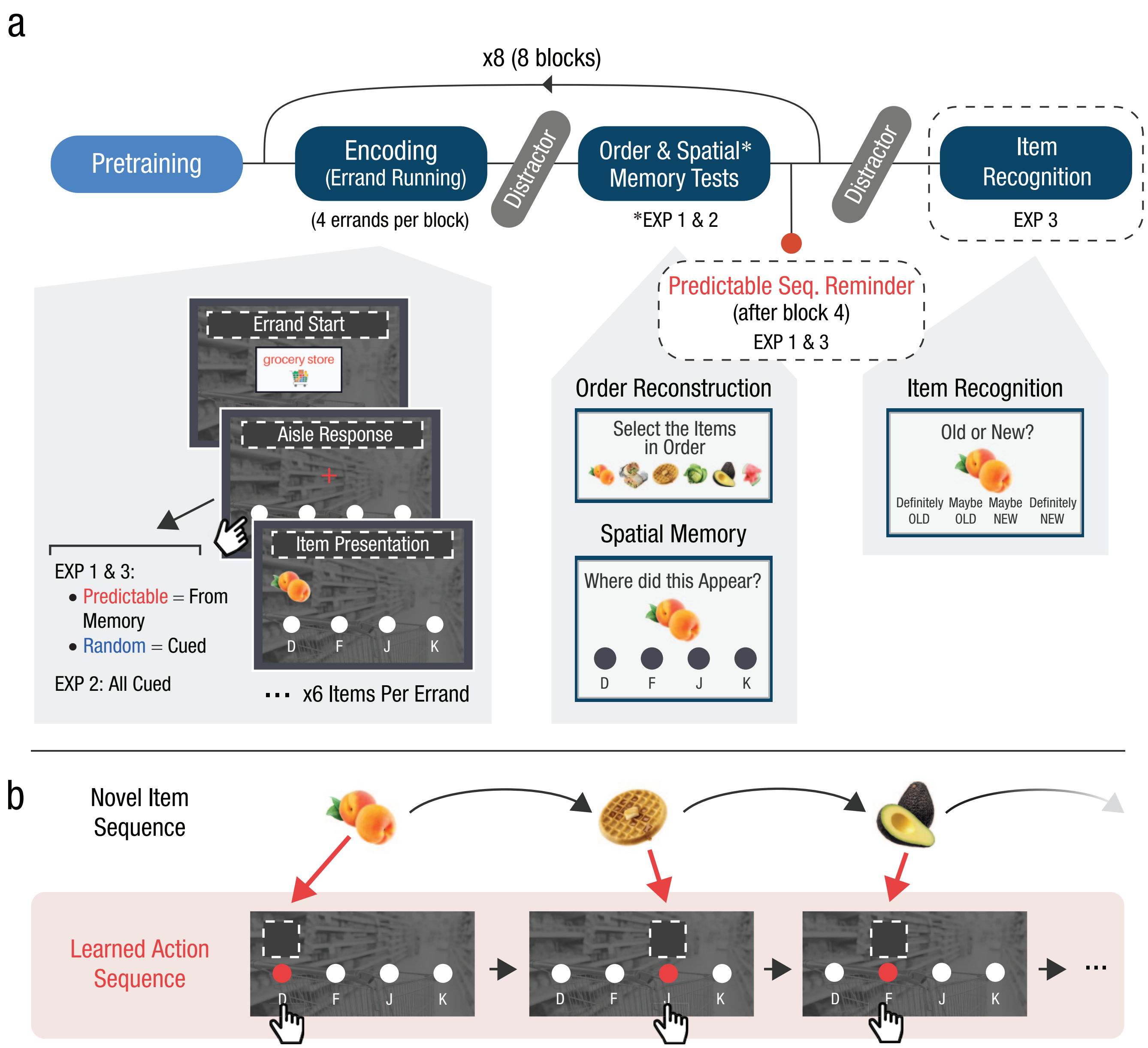

Fig. 1. Experiment design. The study procedure for all three experiments, including an example encoding sequence (left) and memory-test trials (middle and right), is shown in (a). During the encoding phase in Experiments 1 and 3, participants had to rely on memory when making responses during predictable events but were provided with cues during random events. In Experiment 2, all aisle responses were cued. The relationship between item and action sequences is illustrated in (b). The learned action sequence was hypothesized to provide a scaffold for novel items seen throughout a single errand/event.

were encouraged to respond as quickly as possible. Trials were self-paced (up to 6 s per aisle response), and 500 ms separated each response from the next aisle cue. Participants visited six aisles sequentially in this manner before moving on to the next study repetition. Throughout each repetition, a static gray-scale image of the store interior (pet or grocery store) remained on the screen in the background, providing a constant reminder of the current store's identity.

After finishing a set of study repetitions, participants completed a 20-s distractor task (see below). Next, during each pretraining test period, they had to recreate the aisle sequence (i.e., the sequence of key presses) that was associated with the predictable store from memory. As in the study period, each test trial began with a banner depicting the name of the to-be-tested store for 3 s. Then, participants had to press the sequence of keys associated with that store's aisle sequence. Visual feedback appeared on the screen for 500 ms after each response (green check marks for correct responses, red Xs for incorrect responses). Participants recreated the predictable store's aisle sequence twice in this manner before receiving feedback about their accuracy across both test repetitions (out of 100%).

The entire pretraining phase consisted of three study–test cycles/blocks (Fig. 2a). In the first two study periods (*predictable-only* blocks), participants visited the predictable store five times in a row and then were tested on the corresponding aisle sequence twice. However, during the third study period—the *intermixed* block—participants visited the predictable and random stores two times each (order randomized). This intermixed block also introduced a second new feature: After each aisle visit, participants viewed an abstract fractal image in that aisle (i.e., above the aisle circle) for 2.5 s before the next aisle cue appeared. Participants were explicitly told to observe these abstract images without trying to remember them. These novel additions to the intermixed block's study period—the inclusion of random store visits and of abstract stimuli—served two purposes: (a) to ensure that participants' memory for the predictable sequence was robust to interference (from executing random sequences) and (b) to introduce the structure of the subsequent encoding task (described below), in which participants would see (i.e., collect) a novel item after each aisle visit. Both predictable-only and intermixed study periods were followed by the same distractor task and test period, as described above. Across the entire pretraining period, therefore, participants completed 12 study repetitions and six test repetitions of the predictable aisle sequence.

Encoding. After the pretraining phase, the errand-running task began (Fig. 1). As during pretraining study periods, participants first saw a banner for 3 s depicting the upcoming store's identity. They then visited a sequence of six aisles by pressing keys on their keyboards. Critically, however, this procedure differed for predictable and random events. During random events, participants continued to see cues (i.e., red circles) specifying which aisle should be visited next. But in the predictable store, they instead had to execute the associated aisle sequence from memory. In this case, rather than a red circle cue, a red fixation cross appeared in the center of the screen to mark the onset of the aisle response period. Responses in both conditions were self-paced, with a maximum time limit of 6 s. All aisle responses were followed by trial-by-trial feedback similar to what was provided during the pretraining test periods (i.e., green check marks for correct responses, red Xs for incorrect responses). This feedback remained on the screen for 300 ms and was followed by a 200-ms intertrial interval (ITI).

After making each aisle response, participants went on to collect a novel item from the store by viewing it in the given aisle (i.e., above the aisle circle; Fig. 1a). Each item remained on the screen for 2.5 s, and a 500-ms ITI separated the end of the item presentation period and the start of the next trial. Items belonged to the semantic category consistent with the store's identity: foods in the grocery store and animals in the pet store. A static image of the store interior also remained in the background during each event. Crucially, all items presented during these events were novel, irrespective of condition (predictable vs. random). Again, each event involved six aisle visits and six novel items. Prior to encoding, participants were instructed to remember both the order of the stimuli they collected and the aisles that each item had been collected from. They were also told to imagine interacting with each item as it appeared on the screen in order to encourage deeper encoding.

Participants completed a total of eight errand blocks throughout the experiment. Each encoding block included four errands/events: two in the predictable store and two in the random store. The order of events was counterbalanced across blocks and participants, as was the order of object stimuli. After each encoding block, participants engaged in a short distractor task and then completed a set of memory tests for the items collected in that block (both tasks are described below).

Memory tests. After each encoding block, participants completed two memory tests about the items collected during their recent set of errands: an order reconstruction test and a spatial memory test (Fig. 1a). During the order reconstruction test, participants viewed all six of the collected items from a single event on the screen and were told to reconstruct the original order of the items by clicking on them in the order in which they had been presented during encoding. A text prompt appeared on the upper half of the screen to clarify which item in the sequence should be selected next (e.g., "click the *first* item you saw"). The order/position of items as they appeared on the screen was randomized, and participants had a maximum of 15 s to make each response. One predictable event and one random event (out of four events total per block) were included in each block of the reconstruction test. During the spatial memory test, we probed participants' memory for the aisles (i.e., spatial locations) that each item had been collected from. On each trial, a single item appeared in the center of the screen, and participants had a maximum of 8 s to indicate, via pressing a key, which of the four aisles it was associated with. In this spatial memory test, we presented only items from events that were not included in the order reconstruction test (one predictable and one

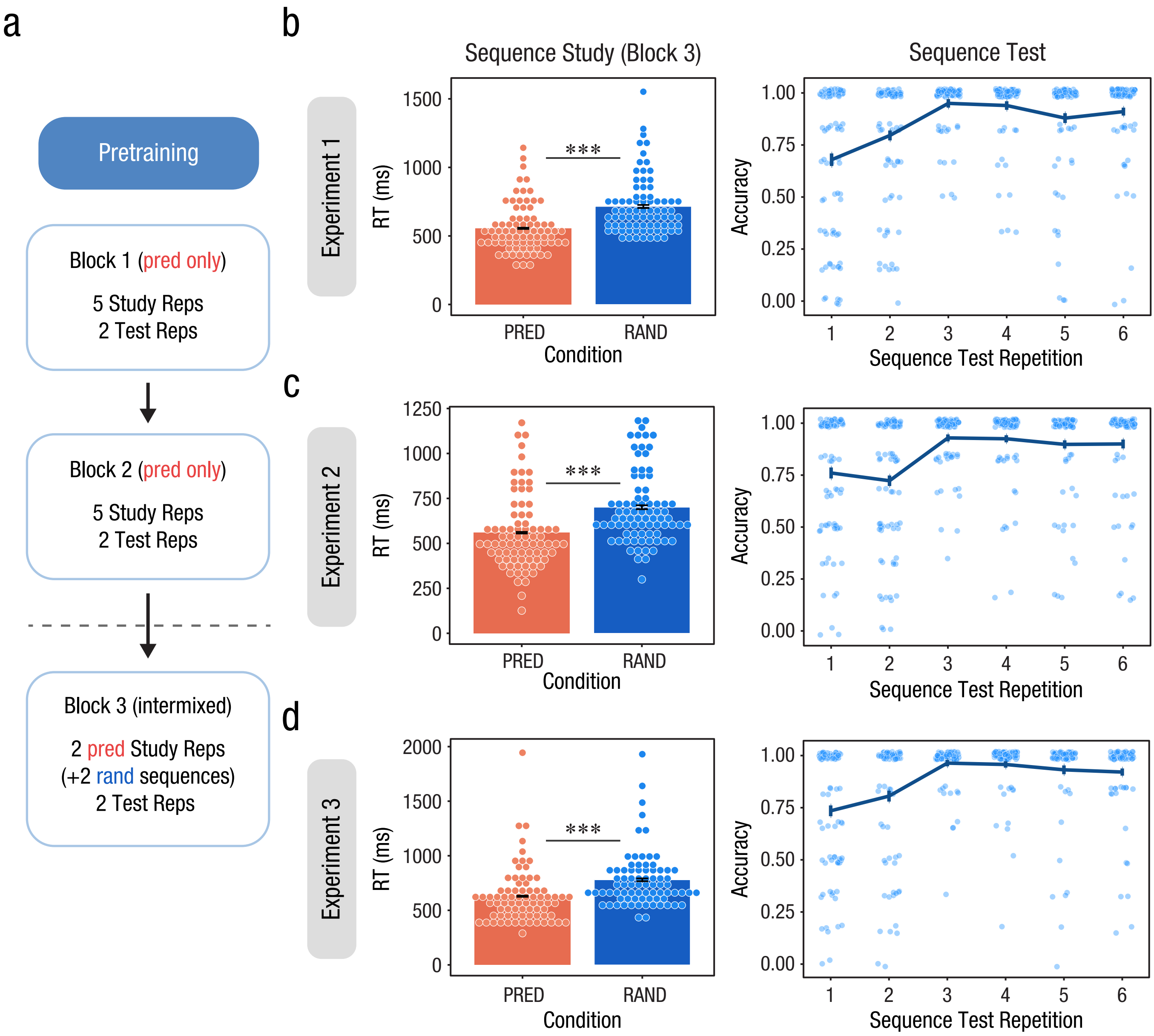

Fig. 2. Pretraining design and behavior. The pretraining procedure for all experiments is shown in (a). Participants completed three cycles of study and test periods to allow for robust learning of the predictable ("Pred") store's aisle sequence. Pretraining performance is plotted separately for Experiments 1 (b), 2 (c), and 3 (d). The plots on the left show mean reaction times (RT) for predictable and random ("Rand") aisle responses made during the study period of the third ("intermixed") block of pretraining. The plots on the right show accuracy across sequence test repetitions. Error bars indicate within-subjects standard errors, and dots represent individual participants. Asterisks indicate significant between-condition differences (***$p < .001$).

random event per block) to avoid overlap across the two memory judgments.

Distractor task. Participants completed a brief distractor task between study and test periods of the pretraining phase and between encoding and retrieval blocks of the main errand task. This task was intended to disrupt any influence of recency effects and/or rehearsal on performance during the pretraining test periods or the memory tests. On each trial, a random single-digit number was presented in the center of the screen for 1,250 ms (with 250-ms blank ITIs). Participants were told to press the space bar every time an even number appeared. Each repetition of the distractor task lasted approximately 20 s.

Reminder task. Although participants saw trial-by-trial feedback during encoding regarding the accuracy of their aisle responses, we also included a brief reminder task after the fourth retrieval block (halfway through the experiment) to refresh memory for the predictable aisle sequence (Fig. 1a). During this task, participants first passively observed the predictable sequence (as a series of red circle cues) twice in a row. Both of these sequence presentations were preceded by a banner for 3 s depicting the predictable store's identity. Each aisle cue appeared on the screen for 1 s, followed by a 500-ms ITI. No responses were collected during this period, nor were any stimuli presented after each aisle cue. Afterward, participants completed two test trials in which they had to recreate the aisle sequence twice from memory. These test trials followed the same structure and timing of the pretraining test periods, with the exception that no information about overall accuracy was provided at the end of the reminder task. Results from the reminder task are discussed in Supplemental Results in the Supplemental Material available online.

Aisle sequence generation. As described, each store contained four aisles, and each errand was composed of six sequential aisle visits (i.e., actions). Aisle/action sequences were generated with the following constraints: (a) Two out of four aisles were visited twice per sequence, (b) the same aisle could not be visited twice consecutively, (c) subsequences that traversed linearly through three or more adjacent aisles were forbidden (e.g., a subsequence that moved from the leftmost aisle immediately to the middle-left aisle and then to the middle-right aisle), and (d) the first aisle visited in each sequence was never revisited (during the same event). From within the pool of valid sequences, two were randomly selected to serve as predictable aisle sequences: one beginning with an aisle on the edge of the screen and one beginning with an aisle in the middle. Each participant was randomly assigned to one of these two predictable sequences.

A set of random aisle sequences were then selected for each participant from the same pool but with the following additional limitations: (a) Random sequences could not begin with the same first aisle as the given participant's predictable sequence, (b) random sequences could not contain more than three aisles with the same ordinal position as the predictable sequence, and (c) random sequences could not share more than four aisles in the same ordinal position with each other. These additional rules helped to ensure not only that the predictable sequence was as distinct as possible from all of the random sequences seen by a given participant but also that random sequences were dissimilar enough to each other to prevent the unintended learning of any pattern across them. A total of 18 random sequences were selected for each participant (two of which appeared during pretraining and 16 of which appeared during encoding).

Statistical analysis. For our main analyses, paired-samples *t* tests (two-tailed) were used to assess whether behavior differed as a function of event condition (i.e., predictable vs. random). Each of these *t* tests indicates the corresponding 95% confidence interval (CI). However, when such analyses involved reaction time (RT) data, we instead used nonparametric Wilcoxon signed-rank tests to account for the fact that RT distributions are typically skewed and thus often violate the assumptions of normality made by parametric tests. Repeated measures analyses of variance (ANOVAs) were also used to examine how accuracy differed by aisle location. For effect sizes, we report Cohen's *d* for *t* tests (Cohen, 1988), Cliff's delta for Wilcoxon signed-rank tests (Cliff, 1996), and η_p^2 for ANOVAs (Cohen, 1973), along with corresponding 95% CIs for each metric (95% CI_d for Cohen's *d* and Cliff's delta, 95% CI_η for η_p^2). In the case of negative Cohen's *d* or Cliff's delta values, the sign was flipped such that reported effect sizes are always positive.

Where applicable, we adjusted *p* values for multiple comparisons by controlling for the false discovery rate (FDR; Benjamini & Hochberg, 1995). Corrected CIs for these comparisons were computed by following the procedure of Benjamini et al. (2005) for calculating false-coverage-statement rate (FCR) adjusted CIs. Specifically, given the number of comparisons (m), the number of effects that reached significance after FDR correction (R), and a significance level (q), we report corrected CIs (CI_{FCR}) with width = $[100 \times (1 - R \times q/m)]\%$. All statistical analyses were conducted in the R programming environment (Version 4.1.1; R Core Team, 2021) using functions from R's built-in *stats* package (Version 4.1.1), *rstatix* (Version 0.7.0; Kassambara, 2021), *effsize* (Version 0.8.1; Torchiano, 2020), *Rmisc* (Version 1.5.1; Hope, 2022), *apaTables* (Version 2.0.8; Stanley, 2022), *lme4* (Version 1.1-27.1, Bates et al., 2015), and *brms* (Version 2.10.0; Bürkner, 2017).

We also ran a multilevel regression model to explore how order memory performance varied as a function of both condition (predictable vs. random) and sequence position (1–6). In this model, binary accuracy on each memory test trial was predicted by condition (effect coded), sequence position (mean centered), and their interaction, with a random intercept for each participant as well as both fixed and random slopes for each predictor. To allow for model convergence, we did not estimate correlations between random effects. This model was implemented using the glmer function from the *lme4* package. For each predictor, we report the associated unstandardized coefficient (*b*), standard error, 95% profile likelihood CI (as implemented by the confint function), and *p* value (estimated on the basis of asymptotic Wald tests, as implemented by the glmer function). Note that alternate methods of computing

p values for multilevel model terms (e.g., likelihood-ratio tests) produced nearly identical results. We also used Bayesian multilevel regression to examine the effect of predictable action sequences on order memory while controlling for a number of different confounds (for details, see Supplemental Methods in the Supplemental Material).

Data inclusion. All data inclusion criteria were determined a priori and were consistent across Experiments 1, 2, and 3. For all pretraining analyses, we included all participants who made at least 75% of aisle responses during the study portion of the pretraining task ($N = 80$). For all encoding analyses, we included all participants who (a) reached at least 80% accuracy on the final pretraining test repetition and (b) made at least 75% of aisle responses during encoding ($n = 69$). For analysis of each memory test, we included all participants who (a) reached at least 80% accuracy on the final pretraining test repetition, (b) made aisle responses in the predictable store with at least 80% accuracy, and (c) performed with above-chance accuracy on that test, according to a binomial test ($n = 63$ in both the order reconstruction and spatial memory tests). Finally, for reminder task analyses (see Supplemental Results), we included the same participants as those in the memory test analyses, prior to any test-specific exclusions ($n = 66$). Collectively, these criteria ensured not only that our sample of online participants followed task instructions (e.g., by making responses when required) but also that they acquired and retained memory for predictable aisle/action sequence throughout the experiment—a necessary prerequisite to test our hypotheses of interest.

We also implemented the following trial-level exclusions. For all analyses involving RTs, outlier data points (defined as >3 *SD*s above or below the mean) were removed. When examining data from the memory tests (e.g., order reconstruction), we also excluded all trials with RTs lower than 100 ms, as these responses were implausibly fast and thus likely to have been made in error. Such responses were exceedingly rare (< 0.9% of trials) and did not change our findings when included.

Results

Pretraining behavior. Prior to encoding, participants learned the action sequence associated with the predictable store during a pretraining phase, which consisted of three study–test blocks (Fig. 2a). We assessed learning in two ways. First, in the final study block, we examined RTs as a function of store condition (predictable vs. random). RTs were faster for predictable than for random trials on average (Wilcoxon signed-rank test: $V = 160$, $N = 80$, $p < .001$, Cliff's $d = 0.52$, 95% $\text{CI}_d = [0.35, 0.65]$; Fig. 2b) and within each sequence position (Fig. S1a in the Supplemental Material), providing evidence of learning. Second, during the final test block, we considered the accuracy with which participants reproduced the learned sequence from memory (unless otherwise noted, accuracy is reported as the proportion of correct responses). Participants were highly successful during this test, with mean accuracy reaching .91 ($SD = .21$) and 88% ($N = 70$) of our sample performing with at least 80% accuracy (Fig. 2b). Importantly, only participants who demonstrated strong memory for the predictable aisle sequence by the end of pretraining (and who continued to execute that sequence accurately during encoding) were considered in subsequent analyses (see Method for details).

Learning of action sequences persists throughout encoding. We also examined accuracy and RTs during the main errand-running task for both predictable and random aisle sequences. Accuracy was near ceiling in both conditions (predictable: $M = .96$, $SD = .08$; random: $M = .98$, $SD = .02$). Although participants were more accurate on average when making random than predictable responses, $t(68) = -2.59$, $p = .012$, 95% CI for the mean difference in accuracy = [−.04, −.01], $d = 0.36$, 95% $\text{CI}_d = [0.08, 0.64]$—a finding that is not unsurprising given that random responses were explicitly cued—this accuracy difference disappeared rapidly as participants gained experience with the task (Fig. S2a in the Supplemental Material). Namely, responses during random events were significantly more accurate than those during predictable events only in the first block, $t(68) = -4.13$, $p_{\text{FDR}} < .001$, CI_{FCR} for the mean difference = [−0.18, −0.03], $d = 0.72$, 95% $\text{CI}_d = [0.08, 0.64]$; all other blocks: $|t(68)| < 2$, $p_{\text{FDR}} > .2$.

Throughout the majority of the encoding task, therefore, participants were just as accurate when making aisle responses from memory as they were when responding to cues. Nevertheless, responses in the random/cued condition may still have been easier for participants to make. To address this possibility, we examined aisle response RTs for predictable and random trials. No difference in RTs was observed (Wilcoxon signed-rank test: $V = 1{,}112$, $N = 69$, $p = .57$, Cliff's $d = 0.04$, 95% $\text{CI}_d = [-0.15, 0.22]$), indicating that although predictable and random encoding trials differed in their task demands, participants' actions within each condition were comparable in both accuracy and speed.

Predictable action sequences scaffold temporal order memory. After each encoding block, participants completed an order reconstruction test (Fig. 3). Our critical question was whether engagement in a known (motor) action sequence during encoding would lead to a cross-modal enhancement in temporal memory for

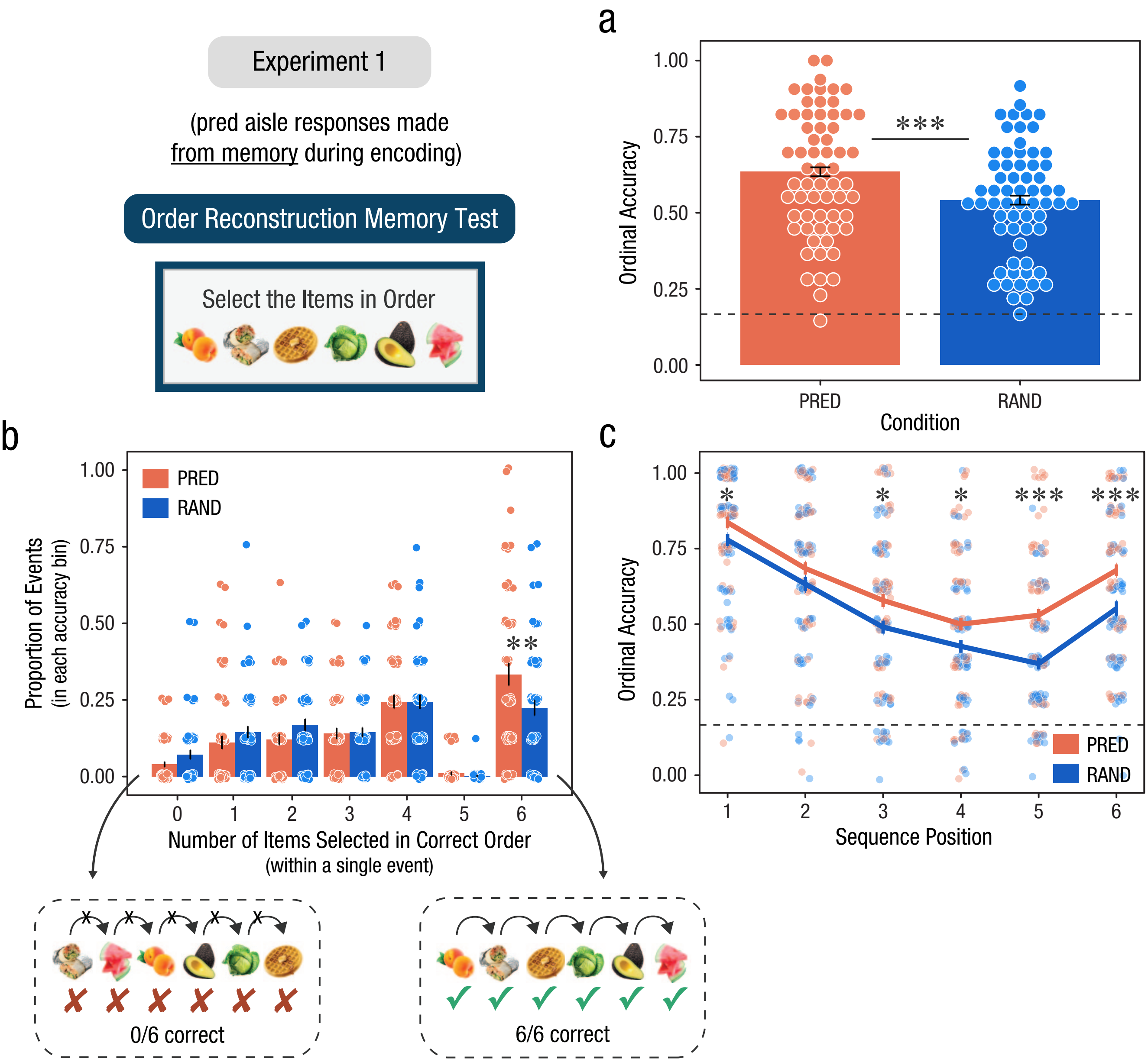

Fig. 3. Order reconstruction memory results for Experiment 1. The bar plot in (a) shows ordinal accuracy for novel items from predictable ("Pred") and random ("Rand") events. The bar plot in (b) shows the proportion of events in which zero to six items were selected in the correct ordinal position. (Note that the near-zero proportion of events in which five items were remembered stems from the fact that getting exactly five out of six responses correct required either missing one response or selecting the same item twice in different ordinal positions, both of which rarely occurred.) The plot in (c) shows ordinal accuracy as a function of sequence position within the event. Error bars indicate within-subjects standard errors, and dots represent individual participants. Dashed lines indicate chance performance (1/6 = .17). Asterisks indicate significant between-condition differences, corrected for multiple comparisons (*p < .05, **p < .01, ***p < .001).

novel and unrelated (visual) items. We first looked at ordinal accuracy, or the proportion of trials during which participants selected the correct item in the correct ordinal position (e.g., first, second). We found that ordinal accuracy was significantly higher for predictable than for random events, $t(62) = 4.45$, $p < .001$, 95% CI for the mean difference = [.05, .13], $d = 0.47$, 95% CI_d = [0.25, 0.69] (Fig. 3a). This enhancement in temporal memory for predictable events was also observed when using Levenshtein distance (Levenshtein, 1966) as our index of order accuracy, $t(62) = -4.07$, $p < .001$, 95% CI for the mean difference = [–.65, –.23], $d = 0.43$, 95% CI_d = [0.21, 0.65]. Levenshtein distance refers to the minimum number of "edits" (insertions, deletions, or subtractions) between the actual and reconstructed sequences, and it more readily accounts for situations in which participants correctly recalled subsequences of items but selected them in the wrong ordinal positions.

Importantly, the effect of condition on order memory held after we controlled for numerous confounds (sequence position, event position, block number, and item category) and when we considered memory only for items that were preceded by accurate aisle responses during encoding (see Supplemental Results and Table S1 in the Supplemental Material). We also sought to account for the fact that during encoding, each six-item aisle sequence included two aisles that were visited once and two that were visited twice. This aisle repetition structure was present in both predictable and random sequences, making it unlikely to explain our order memory effects. Nevertheless, it is possible that the association of two novel items with the same spatial location produced interference in memory, which could have different effects within each condition. To rule out this possibility, we examined ordinal accuracy as a function of whether items were associated with aisles that were visited once versus twice per event. Although ordinal accuracy was generally lower for items associated with repeated aisles, suggesting that aisle repetition did indeed generate interference, the predictable-versus-random-order memory benefit was robust to this confound (see Supplemental Results). Taken together, these results provide strong evidence that the execution of a familiar action sequence scaffolds temporal memory for simultaneously encoded novel items.

Predictable action sequences promote the formation of holistic event memories. According to our scaffolding hypothesis, engaging in a familiar sequence of actions during encoding facilitates temporal order memory for unrelated visual items by allowing them to be integrated within a preexisting event memory, in which each novel item gets slotted into a position of the action sequence representation (Fig. 1b). This framework predicts that sequences from predictable events are more likely to be remembered in their entirety, given that each novel visual item from the sequence can be integrated into the same, stable event representation. Indeed, the ability to recall the complete set of elements from an event is a hallmark of intact episodic memory (Horner et al., 2015). To test this prediction, we examined order accuracy at the level of entire events. For each participant, we determined the proportion of events in which n of six items (where n = zero to six) were selected in the correct ordinal position (Fig. 3b). We found that the proportion of events that were reconstructed in their entirety was greater in the predictable than in the random condition, $t(62) = 3.57$, $\mathrm{CI}_{\mathrm{FCR}}$ for the mean difference = [.02, .19], $p_{\mathrm{FDR}} = .005$, $d = 0.44$, 95% CI_d = [0.19, 0.70]. In contrast, there were no condition-related differences in the proportion of events from which participants accurately reported the order of zero to five items (all $|t(62)| < 2.3$, $p_{\mathrm{FDR}} > .05$).

To explore whether any position effects were evident, we also looked at order accuracy separately for each sequence position (1–6). Order memory for items in all positions, except the second, was higher for predictable than for random events—Position 1: $t(62) = 2.13$, $p_{\mathrm{FDR}} = .045$, $\mathrm{CI}_{\mathrm{FCR}}$ = [.001, .11], $d = 0.27$, 95% CI_d = [0.01, 0.53]; Position 2: $t(62) = 1.60$, $p_{\mathrm{FDR}} = .11$, $\mathrm{CI}_{\mathrm{FCR}}$ = [–.01, .12], $d =$ 0.20, 95% CI_d = [−0.05, 0.45]; Position 3: $t(62) = 2.68$, $p_{\mathrm{FDR}} = .019$, $\mathrm{CI}_{\mathrm{FCR}}$ = [.02, .16], $d = 0.35$, 95% CI_d = [0.08, 0.61]; Position 4: $t(62) = 2.24$, $p_{\mathrm{FDR}} = .043$, $\mathrm{CI}_{\mathrm{FCR}}$ = [.01, .14], $d = 0.30$, 95% CI_d = [0.03, 0.57]; Position 5: $t(62) =$ 5.33, $p_{\mathrm{FDR}} < .001$, $\mathrm{CI}_{\mathrm{FCR}}$ = [.10, .22], $d = 0.70$, 95% CI_d = [0.41, 0.98]; Position 6: $t(62) = 4.12$, $p_{\mathrm{FDR}} < .001$, $\mathrm{CI}_{\mathrm{FCR}}$ = [.06, .19], $d = 0.53$, 95% CI_d = [0.26, 0.80]. These results suggest that action sequences scaffold memory throughout the novel item sequence (Fig. 3c).

However, qualitative examination of the data in Figure 3c suggests that participants' temporal memory benefited from the predictable action sequence to a larger degree for items toward the end of the six-item event. To quantify this interactive effect, we ran a multilevel logistic regression model in which ordinal accuracy (on each trial) was predicted by condition, sequence position, and their interaction (with subject-specific random effects for each predictor and a random intercept for each subject). This model revealed strong main effects of both condition ($b = 0.49$, $SE = 0.11$, 95% CI = [0.28, 0.71], $p < .001$) and sequence position ($b =$ −0.24, $SE = 0.02$, 95% CI = [−0.28, −0.20], $p < .001$) on memory performance; specifically, participants were more accurate for items from predictable events and from earlier sequence positions. Critically, the interaction between these variables was also significant ($b =$ 0.07, $SE = 0.03$, 95% CI = [0.003, 0.14], $p = .038$), confirming that the memory benefit for predictable relative to random sequences was stronger at the end of the sequential event relative to the beginning. Such results can also be interpreted in light of the scaffolding hypothesis. As participants progress deeper into an event, the passage of time is likely to cause a gradual drift in their mental context; larger contextual drifts within an event, in turn, may disrupt temporal binding (Clewett & Davachi, 2017; DuBrow et al., 2017; Howard & Kahana, 2002). By anchoring participants to a familiar and well-defined event representation, it could be that the predictable action sequence mitigates the extent of this contextual drift, boosting the likelihood that items toward the end of a sequence can be effectively bound to the full event.

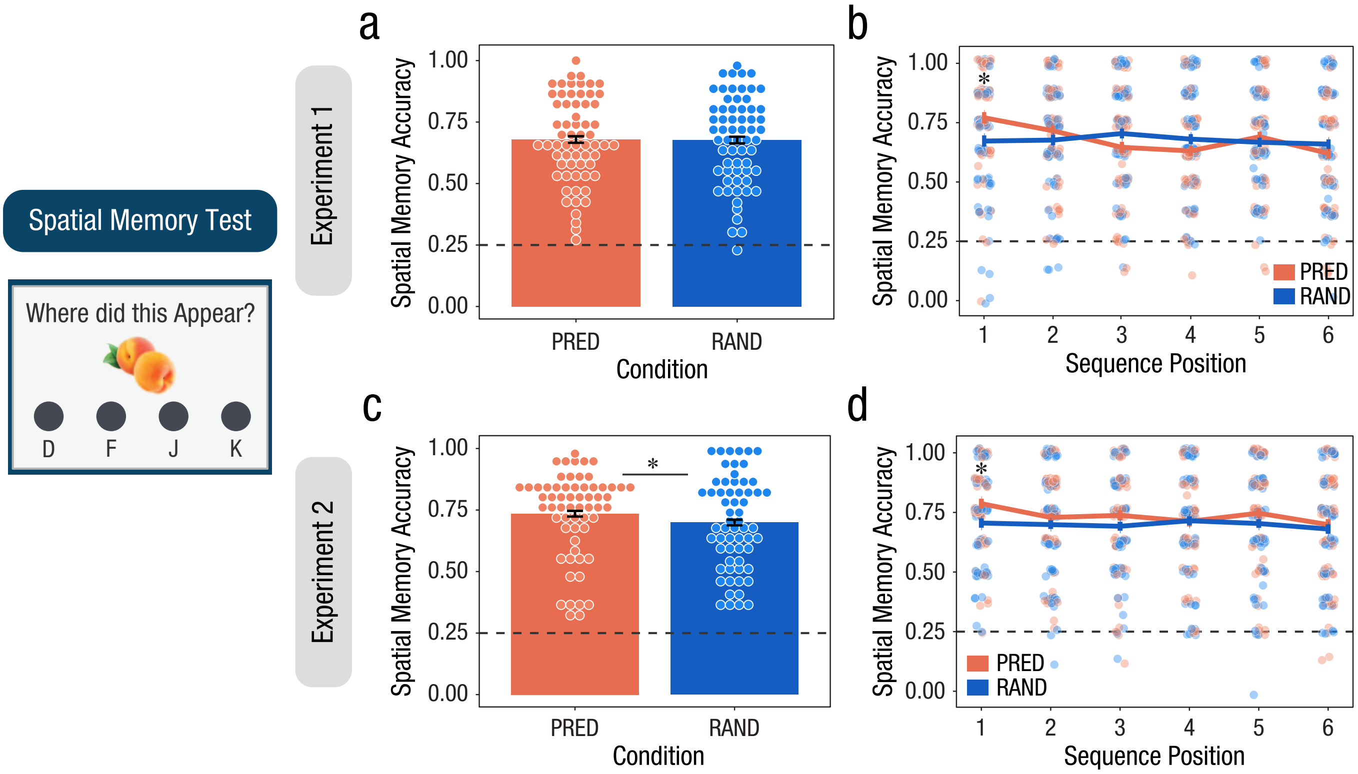

Fig. 4. Spatial memory test performance in Experiments 1 (top row) and 2 (bottom row). Panels (a) and (c) show mean accuracy as a function of store condition (predictable ["Pred"] and random ["Rand"]), whereas panels (b) and (d) show accuracy in each condition as a function of the sequence position in which an item was encountered during encoding (with significance values false-discovery-rate corrected for multiple comparisons). Error bars indicate within-subjects standard errors, and dots represent individual participants. Dotted lines indicate chance performance (1/4 = .25). Asterisks indicate significant between-condition differences (*p < .05).

Effects of action sequences on spatial memory. Thus far, we established that when participants encounter novel information in the context of a known action sequence, they are better able to remember the temporal links between those items. However, we saw no similar benefit in spatial context memory. Spatial memory performance was comparable for predictable and random events when we averaged across items from all sequence positions, $t(62) = 0.11$, $p = .91$, 95% CI for the mean difference = [–.04, .04], $d = 0.01$, 95% CI$_d$ = [–0.04, 0.04] (Fig. 4a). Breaking down memory performance by sequence position, we did find evidence that spatial memory for items at the start of each errand was better for predictable than for random events—Position 1: $t(62) = 2.95$, $p_{\text{FDR}} = .027$, CI$_{\text{FCR}}$ = [.01, .19], $d = 0.41$, 95% CI$_d$ = [0.12, 0.69]; all other positions: $|t(62)| < 2$, $p_{\text{FDR}} > .1$ (Fig. 4b). Although this effect is intriguing, we do not interpret it too strongly because it is partly confounded by the fact that participants' spatial memory performance also differed as a function of aisle location (with memory for items in the leftmost aisle being better than for other aisles on average) and that the location of the first aisle in each sequence was not matched across predictable and random events (see Supplemental Results). However, future work could explore how the onset of a familiar action sequence might trigger enhanced spatial context memory.

Discussion

Experiment 1 demonstrates that executing a well-learned action sequence significantly improves memory for the temporal order of novel, nonmotor items encountered simultaneously—but does not improve memory for items' spatial position. Next, we asked whether this order memory effect was dependent on the need to use one's memory for the familiar action sequence during encoding. In Experiment 1, participants made aisle responses in the predictable store from memory, whereas responses in the random store were cued. Although this difference in task demands did not induce condition-related differences in the speed or accuracy of participants' actions, it raises an intriguing question: Will the execution of a familiar action sequence scaffold temporal memory for novel items even when knowledge of that sequence is not necessary for behavior? To this end, in Experiment 2, we again trained participants on the predictable action sequence but then eliminated the need to retrieve aisle responses from memory by providing cues in both conditions.

Experiment 2

Method

Participants. Participants were recruited again through Prolific ($N = 80$, 32 female). All participants were healthy adults between 18 and 35 years old ($M = 26.4$, $SD = 5.0$), reported having normal or corrected-to-normal vision, and had a Prolific study approval rate of at least 60% prior to enrolling. Participants received $14 on study completion (completion time: $M = 61.6$ min, $SD = 23.6$). All participants provided informed consent, and all procedures were approved by the Columbia University Institutional Review Board.

Task design. Experiment 2 followed the same procedure as Experiment 1, with the following modifications. First, both predictable and random events included the presentation of aisle cues that instructed participants which aisle to visit on every trial, thus removing the need to use memory for the learned action sequences during the critical errand encoding phase. We also removed trial-by-trial feedback, given that such feedback should be unnecessary when explicit cues are available to inform participants of all correct responses (and given that accuracy in the cued/random condition in Experiment 1 was essentially at ceiling). To further ensure that participants executed the correct sequence of actions within each event even without feedback, we programmed the experiment such that only correct aisle responses were accepted and served to advance the trial to the item collection/presentation phase. In addition to these changes to the encoding phase, we also removed the reminder task after the end of the fourth block, given that all predictable events provided participants with repeated opportunities to observe and execute the predictable aisle sequence. We also added a final order reconstruction memory test at the very end of the experiment, in which we reassessed order memory for half of the events that participants had already been tested on. This final test is not detailed in the current article, but we note that order memory performance at this time point was enhanced for predictable compared with random events, consistent with results from the order reconstruction tests that followed each errand block (see Results).

Data inclusion. Data inclusion criteria in Experiment 2 were identical to those in Experiment 1. This resulted in 80 participants included in all pretraining analyses, 67 in all encoding analyses, and 61 in both order reconstruction test and spatial memory test analyses. Trials during pretraining or encoding with aisle response RTs greater than 3 standard deviations above the mean were removed as outliers from all RT analyses. For all memory test analyses, trials with implausibly fast responses were also removed (<0.4% of trials; again, keeping these trials in our analyses did not alter our results).

Results

Pretraining and encoding behavior. As in Experiment 1, participants in Experiment 2 effectively learned the predictable aisle sequence by the end of pretraining. During the final study period, in which participants were cued to visit aisles in both predictable and random stores (see Fig. 2a), RTs were consistently faster for predictable visits on average ($V = 207$, $N = 80$, $p < .001$, Cliff's $d = 0.46$, 95% $\text{CI}_d = [0.28, 0.60]$; Fig. 2c) and within each sequence position (Fig. S1b in the Supplemental Material). During the final pretraining test trial, performance was high ($M = .90$, $SD = .22$), with 84% ($n = 67$) of participants recalling the sequence with at least 80% accuracy. As in Experiment 1, only participants who successfully learned the predictable aisle sequence by the end of pretraining were considered in subsequent analyses (see Method for details).

We next turned to encoding periods to assess whether memory for this predictable action sequence persisted across errand blocks. In this experiment, participants' aisle responses were cued in both the predictable and random conditions, and only correct responses were accepted. Rather than examining response accuracy, therefore, we turned to the speed of aisle responses as a proxy for learning. Aisle response RTs were significantly faster during predictable than during random events (Wilcoxon signed-rank test: $V = 235$, $N = 67$, $p < .001$, Cliff's $d = 0.21$, 95% $\text{CI}_d = [0.02, 0.40]$). This effect reveals that memory for the predictable action sequence afforded predictive processes that allowed participants to deploy responses in this condition more rapidly—even though such predictions were not needed to guide behavior.

Predictable action sequences scaffold order memory even when not critical for behavior. In this experiment, participants were not explicitly required to use their memory for the predictable action sequence during encoding. Nevertheless, here we replicated all of the main effects observed in Experiment 1 (Figs. 5a–5c). Performance on the order reconstruction test was enhanced for predictable compared with random events, as revealed by both ordinal accuracy, $t(60) = 2.74$, $p = .008$, 95% CI for the mean

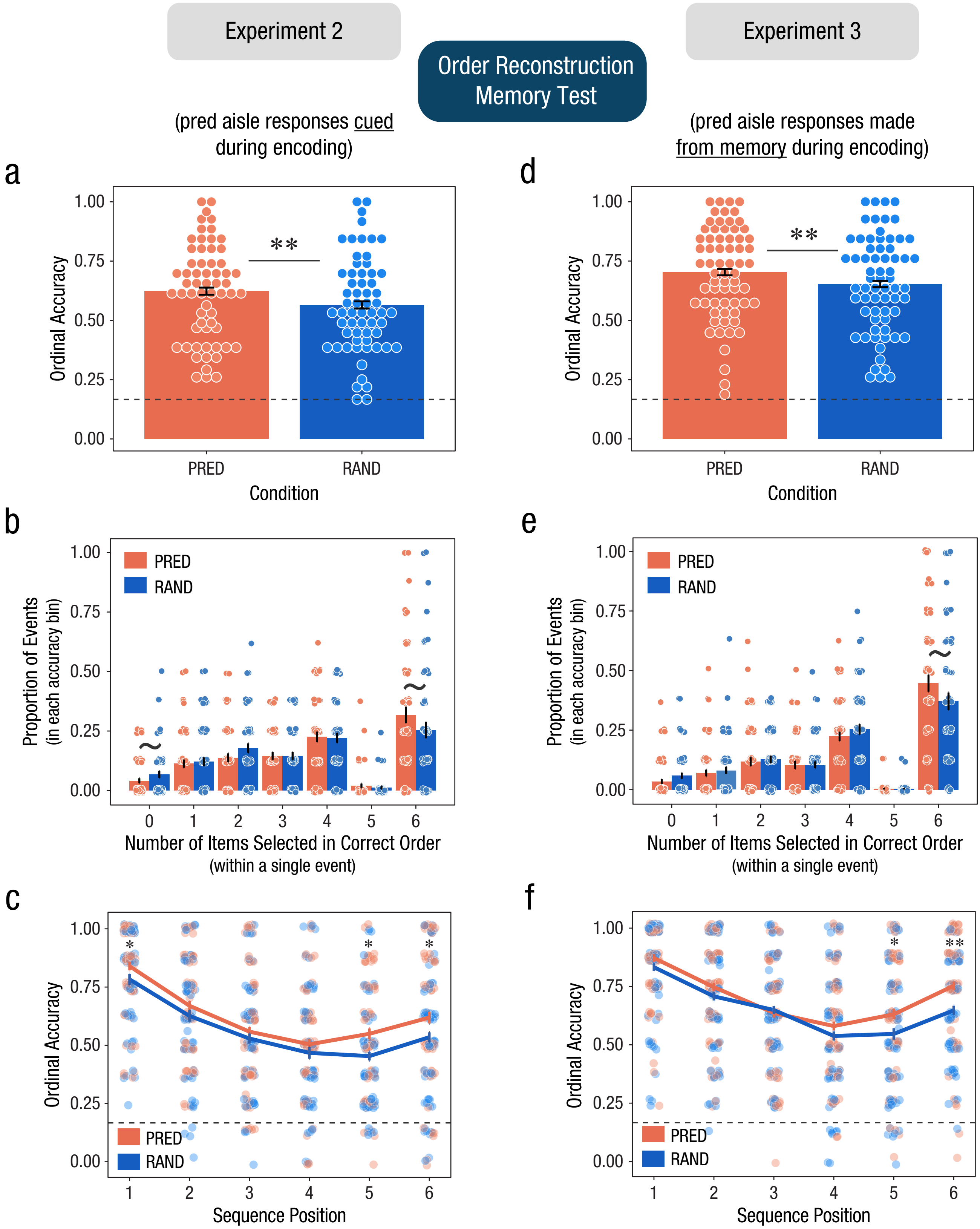

Fig. 5. Order reconstruction memory results for Experiments 2 (left column) and 3 (right column). Plots in (a) and (d) show order memory performance as mean ordinal accuracy for predictable ("Pred") and random ("Rand") events. Plots in (b) and (e) show the proportion of tested events in which zero to six items were selected in the correct ordinal position. Plots in (c) and (f) show memory performance within each condition as a function of sequence position (1–6). Error bars indicate within-subjects standard errors, and dots represent individual participants. Dashed lines indicate chance performance (1/6 = .17). Symbols indicate significant between-condition differences (~$p < .05$, uncorrected; *$p < .05$, **$p < .01$, corrected for multiple comparisons).

difference = [.02, .10], d = 0.29, 95% CI$_d$ = [0.08, 0.50], and Levenshtein distance, $t(60) = -2.80$, p = .007, 95% CI for the mean difference = [–.54, –.09], d = 0.29, 95% CI$_d$ = [0.08, 0.50]. This effect was also robust to the influence of confound variables—including whether items were associated with repeated or nonrepeated aisles (see Supplemental Results and Table S2 in the Supplemental Material). These findings demonstrate that the mere presence of familiar sequential actions during novel encoding scaffolds memory for how events unfold across time even if this prior knowledge is not necessary for an individual's moment-to-moment behavior.

As with Experiment 1, we also saw evidence that participants were more likely to accurately reconstruct the complete sequence of novel items for predictable compared with random events (Fig. 5b), pointing to the capacity of a known action sequence to facilitate the formation of holistic event representations. Participants were again more likely to select all six items in the correct order for predictable than for random events, $t(60) = 2.15$, p = .035, 95% CI for the mean difference = [.01, .12], d = 0.24, 95% CI$_d$ = [0.01, 0.47]; however, this comparison did not survive FDR correction for multiple comparisons (p_{FDR} = .15). There were also no significant condition-related differences in the proportion of events in which zero through five (out of six) items were selected in the correct ordinal position (all $|t(60)| < 2.1$, all $p_{\text{FDR}} > .15$).

Finally, we replicated the qualitative pattern that predictable action sequences might have a stronger temporal memory-enhancing effect for items toward the end of an event (Fig. 5c). When examining accuracy separately for each sequence position, we found that only items in the first, $t(60) = 2.41$, p_{FDR} = .038, CI$_{\text{FCR}}$ = [.003, .11], d = 0.26, 95% CI$_d$ = [0.04, 0.47]; fifth, $t(60) = 3.27$, p_{FDR} = .011, CI$_{\text{FCR}}$ = [.03, .16], d = 0.40, 95% CI$_d$ = [0.15, 0.65]; and sixth, $t(60) = 2.62$, p_{FDR} = .033, CI$_{\text{FCR}}$ = [.01, .16], d = 0.30, 95% CI$_d$ = [0.07, 0.54]), sequence position were significantly better remembered during predictable than during random events (all other positions: $|t(60)| < 1.5$, $p_{\text{FDR}} > .2$). To better quantify the interactive effects of condition and sequence position, we again ran a trial-level logistic regression model with the same design as that used in Experiment 1. This model revealed significant effects of both condition (b = 0.29, SE = 0.11, 95% CI = [0.08, 0.50], p = .007) and sequence position (b = –0.24, SE = 0.02, 95% CI = [–0.29, –0.19], p < .001); specifically, participants showed a greater enhancement in order memory for predictable than for random items and for items at the end of an event. The interaction term in this model was again positive (b = 0.04, SE = 0.04, 95% CI = [–0.03, 0.11], p = .29)—indicating that predictable action sequences enhanced temporal memory more strongly for items toward the end of an event—but this effect did not reach significance.

Taken together, these results show that demand to use one's memory for a familiar action sequence is not a necessary prerequisite for its faciliatory effects on order memory. That is, even though participants received cues to guide their actions during predictable events, their preexisting familiarity with this sequence nevertheless functioned as a scaffold for novel temporal event memories.

Effects of action sequences on spatial memory. Next, we turned to the spatial memory test. In Experiment 1, we saw no difference in average spatial context memory for predictable compared with random events. However, in Experiment 2, spatial memory was slightly but significantly higher in the predictable condition, $t(60) = 2.20$, p = .032, 95% CI for the mean difference = [.003, .06], d = 0.20, 95% CI$_d$ = [0.02, 0.38] (Fig. 4c). This effect was driven by enhanced spatial memory for the location of the first item within predictable events (as we also observed in the previous experiment despite the lack of a significant difference when averaging across sequence positions), $t(60) = 2.73$, p_{FDR} = .050, CI$_{\text{FCR}}$ = [.0001, .16], d = 0.41, 95% CI$_d$ = [0.10, 0.71] (Fig. 4d). Performance did not differ across conditions in any other sequence position (all $|t(60)| < 2$, $p_{\text{FDR}} > .2$). As discussed, this result is difficult to interpret in light of the fact that spatial memory also differed as a function of aisle location (see Supplemental Results) and that aisle locations were not balanced equally across sequence positions and conditions. The effect of condition on spatial memory in this experiment was also not significantly greater than the null effect in Experiment 1, further limiting our interpretation (Table S4 in the Supplemental Material).

Discussion

Experiment 2 replicated Experiment 1, showing that familiar motor action sequences benefit memory for the order of novel, unrelated visual items. Further, we found that the demand to retrieve this action sequence from memory during encoding is not required to benefit temporal memory. These results suggest that familiar action sequence memories may be automatically or implicitly engaged during encoding, which in turn is sufficient to bolster temporal integration of novel items.

Thus far, our conclusions that familiar motor sequence execution selectively or disproportionately supports temporal order memory are consistent with the scaffolding hypothesis, which posits that predictable action sequences specifically aid in the construction of temporally coherent event memories—as opposed to the attentional-resource hypothesis, which predicts widespread memory benefits. However, spatial context memory performance does not directly reflect attention to individual items. Thus, to better adjudicate between our hypotheses, we tested detailed item memory in addition to order memory in Experiment 3.

Experiment 3

Method

Participants. We again used Prolific to recruit 80 participants (47 female). All participants were healthy adults between 18 and 35 years old (M = 24.7, SD = 4.8), reported having normal or corrected-to-normal vision, and had a Prolific study approval rate of at least 60% prior to enrolling. Participants received $14 on study completion (completion time: M = 57.5 min, SD = 14.4). All participants provided informed consent, and all procedures were approved by the Columbia University Institutional Review Board.

Procedure. Experiment 3 largely followed the same procedure as Experiment 1, in that participants made aisle responses from memory when running errands in the predictable store (instead of seeing cues in both conditions, as in Experiment 2). Although both Experiments 1 and 2 revealed comparable order memory results (Table S4), effect sizes were numerically larger in the first—perhaps because the explicit demand to use action sequence knowledge during encoding increased its effectiveness as a memory scaffold. Given that in Experiment 3 we aimed to test whether familiar action sequences generally increase attention to/encoding of novel items, we chose the design in which we saw the most robust (temporal) memory effects. We also made two additional modifications to our procedure. First, the spatial memory test was removed, so after each errand block, participants completed only the order reconstruction test. Second, we administered an item recognition test at the very end of the experiment.

Item recognition test. After completing all encoding and reconstruction test blocks, participants first engaged in a brief distractor task (lasting ~5 min). This task comprised a set of 20 simple addition and subtraction problems (e.g., "28 + 76"). Participants saw one math problem at a time and were given 15 s to type their response. Next, the item recognition test began. In this test, participants discriminated between previously encoded items and similar lures. For this experiment, we thus created two sets of stimuli: set A and set B. These sets contained the same specific categories of stimuli (e.g., cat, burrito) but different exemplar images. Approximately half of participants saw stimulus set A during their errands, with matching lure stimuli drawn from set B. The other half saw set B during their errands and saw lures drawn from set A. During the test, participants viewed a series of individual items on the screen and indicated whether each one was "old" (i.e., had been seen or collected during one of their errands) or "new" (i.e., had never appeared throughout the experiment). Four response options allowed for varying levels of confidence: "definitely OLD," "maybe OLD," "maybe NEW," and "definitely NEW" (Fig. 6). Importantly, all new images belonged to the same type (e.g., cat, pizza) as one of the old images and thus functioned as similar lures. See Figure 6c for examples. Thus, successful performance on this task required memory for the specific details of individual items, above and beyond memory for their verbal category labels or general semantics. Participants were explicitly told that new images might be very similar to items they had collected during their errands but that they should use only the old response when an image was exactly the same as something they had already seen.

The item recognition test included 96 trials: Half contained items from the predictable store (or were the same item type as something seen in the predictable store), and the other half contained items associated with the random store. Within each condition, there were 24 *old* trials and 24 *new* trials (i.e., trials presenting similar lures). Both condition (predictable vs. random) and recognition trial type (*old* vs. *new*) were sampled evenly across encoding blocks and sequence positions (within each event/errand). Trials were separated by an ITI of 1 s, and participants were given up to 8 s to make each response. Importantly, there was no overlap between the item recognition and order reconstruction tests. That is, items from half of all events (one predictable and one random event per block) were included in the order reconstruction test, and the remaining half were reserved for the item recognition test.

Data inclusion. Data inclusion criteria for Experiment 3 were identical to those in Experiments 1 and 2. This left 78 participants in pretraining analyses, 70 in encoding analyses, 67 in reminder task analyses, 66 in order reconstruction test analyses, and 53 in recognition test analyses. As described in the Method of Experiment 1, participants who did not perform with above-chance accuracy on a particular memory test, according to a binomial test, were removed from analyses of that test. The number who failed to meet this criterion for the recognition test (n = 13) was notably larger than that observed for other memory tests (mean n = 3.8 across tests and experiments), suggesting that item recognition was generally more difficult. However, the effects described in the Results did not change when we included all low-performing participants in our recognition test analyses. Finally, trials during pretraining or encoding with aisle response RTs greater than 3 standard deviations above the mean were removed as outliers from all RT analyses, and trials with implausibly fast responses were removed from all memory test analyses (< 0.3% of trials; as with other experiments, keeping these trials in our analyses did not change our results).

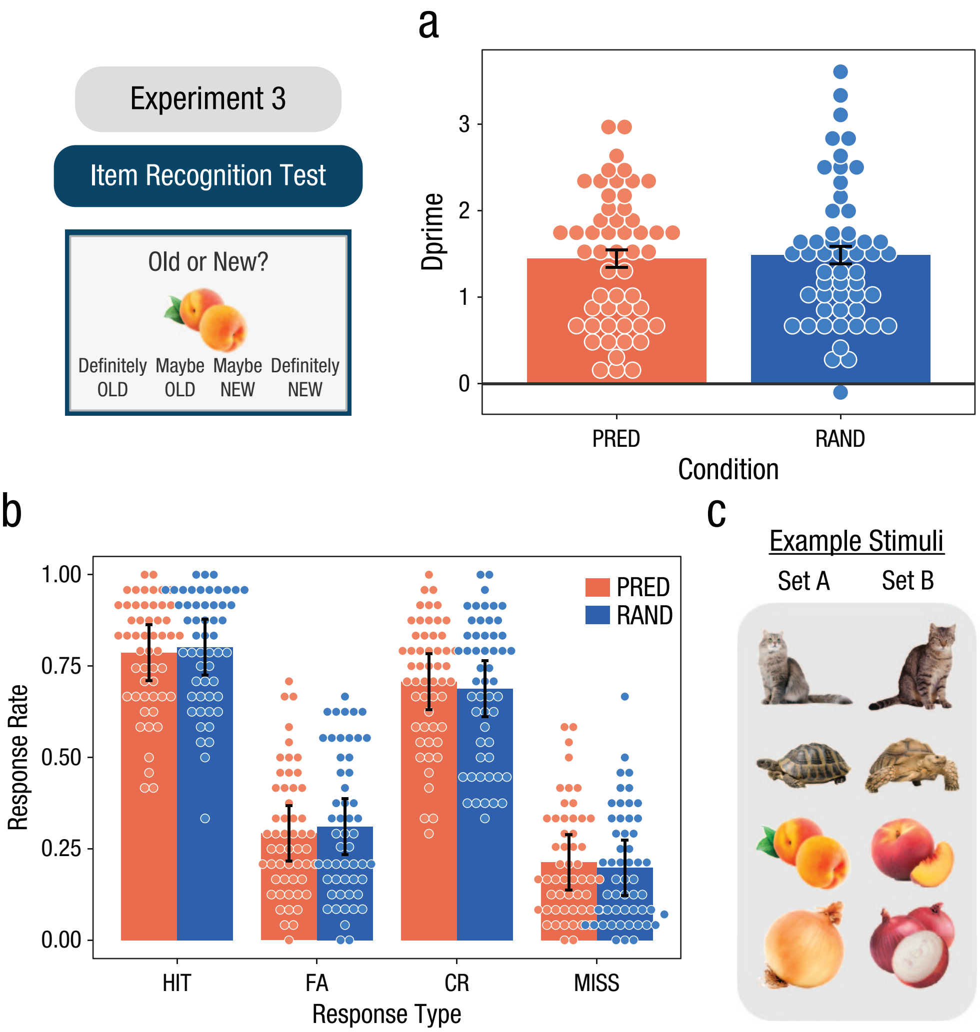

Fig. 6. Item recognition memory test results for Experiment 3. The bar plot (a) shows the difference in d' (a measure of recognition accuracy) for items from the predictable ("Pred") and random ("Rand") store. Panel (b) shows the rate of each response type during the recognition test, split by condition (FA = false alarm, CR = correct rejection). Error bars indicate within-subjects standard errors, and dots represent individual participants. Examples of "old" images and corresponding "new" lures are shown in (c).

Results

Pretraining and encoding behavior. Participants' behavior during pretraining replicated the results of Experiments 1 and 2 and indicated effective learning of the predictable aisle sequence. Specifically, during the final pretraining study block, aisle response RTs were consistently faster for predictable than for random store visits, both on average ($V = 226$, $N = 78$, $p < .001$, Cliff's $d = 0.44$, 95% CI_d = [0.27, 0.59]; Fig. 2d) and across all sequence positions (Fig. S1c in the Supplemental Material). Accuracy during the final pretraining test was also very high (M = .92, SD = .19), with 91% (n = 71) of participants reproducing the aisle sequence with at least 80% accuracy.

Experiment 3 largely followed the same procedure as Experiment 1, in that participants made aisle responses from memory when running errands in the predictable store (instead of seeing cues in both conditions, as in Experiment 2). Aisle response behavior during this experiment replicated the effects in Experiment 1. That is, aisle response accuracy in the cued, random condition was slightly greater than in the predictable condition, $t(69) = -2.57$, p = .012, 95% CI for the mean difference = [−.04, −.004], d = 0.39, 95% CI_d = [0.08, 0.70], but this difference disappeared after the first block of the experiment—Block 1: $t(69) = -3.41$, p_{FDR} = .009, CI_{FCR} = [−.18, −.02], d = 0.54, 95% CI_d = [0.20, 0.87]; all other blocks: $|t(69)| < 2.4$; $p_{\text{FDR}} > .07$

(Fig. S2b in the Supplemental Material). We also found that participants did not significantly differ in their RTs to predictable and random aisle responses (Wilcoxon signed-rank test: $V = 1{,}143$, $N = 70$, $p = .56$, Cliff's $d = 0.02$, 95% $\mathrm{CI}_d = [-0.17, 0.21]$)—even though these conditions differed in their task demands. These two results demonstrate that participants were able to effectively execute the predictable action sequence from memory during encoding and did so with similar accuracy and speed as they showed in the random, cued condition. As with previous experiments, only participants who demonstrated effective learning of the predictable aisle sequence during pretraining and maintained their memory throughout encoding were included in subsequent analyses (see Method).

Replication of temporal memory enhancement for predictable events. The results from Experiment 3 replicated those observed in Experiments 1 and 2 (Figs. 5d–5f). Participants were again significantly more accurate in their reconstruction of the order of items from the predictable than from the random store, both according to ordinal accuracy, $t(65) = -2.68$, $p = .009$, 95% CI for the mean difference = [.01, .09], $d = 0.25$, 95% $\mathrm{CI}_d = [0.06, 0.44]$, and Levenshtein distance, $t(65) = -2.58$, $p = .012$, 95% CI for the mean difference = [–.43, –.06], $d = 0.24$, 95% $\mathrm{CI}_d = [0.05, 0.43]$. This effect held after we controlled for confound variables, considered only trials in which participants visited the correct aisle during encoding, and looked separately at items associated with aisles visited once or twice per sequence (see Supplemental Results and Table S3 in the Supplemental Material).

We also again replicated the finding that participants were more likely to remember the order of predictable events holistically (i.e., in their entirety) relative to random events (Fig. 5e). That is, participants selected all six items in the correct order more often when they had been encoded in the predictable than in the random store, $t(65) = 2.36$, $p = .021$, 95% CI for the mean difference = [.01, .14], $d = 0.27$, 95% $\mathrm{CI}_d = [0.04, 0.50]$; although as with Experiment 2, this difference was significant only at an uncorrected threshold ($p_{\mathrm{FDR}} = .15$). There were no significant condition-related differences in the proportion of events in which zero through five (out of six) items were selected in the correct ordinal position (all $|t(65)| < 2.4$, all $p_{\mathrm{FDR}} > .14$). We interpreted this pattern of results, taken together with those of the previous experiments, to reflect that participants' engagement in a familiar action sequence during a visual encoding event increased the likelihood that all elements of that event can be embedded within the same sequential memory representation.

When breaking ordinal accuracy down by sequence position, we also replicated the pattern that the order memory benefit for predictable compared with random events was strongest for items toward the end of an event (Fig. 5f). Specifically, the difference in ordinal accuracy across conditions was significant only for items in the fifth, $t(65) = 2.36$, $p_{\mathrm{FDR}} = .021$, $\mathrm{CI}_{\mathrm{FCR}} = [.01, .18]$, $d = 0.32$, 95% $\mathrm{CI}_d = [0.04, 0.59]$, and sixth, $t(65) = 3.71$, $p_{\mathrm{FDR}} = .004$, $\mathrm{CI}_{\mathrm{FCR}} = [.03, .18]$, $d = 0.45$, 95% $\mathrm{CI}_d = [0.20, 0.71]$, sequence positions (all other positions: $|t(65)| < 2.0$, $p_{\mathrm{FDR}} > .1$). When quantifying this pattern using a logistic regression model, we found significant effects of both condition ($b = 0.28$, $SE = 0.11$, 95% CI = [0.06, 0.49], $p = .012$) and sequence position ($b = -0.20$, $SE = 0.02$, 95% CI = [−0.25, −0.16], $p < .001$), as well as a marginal interaction ($b = 0.07$, $SE = 0.04$, 95% CI = [0.003, 0.14], $p = .059$). Although this interaction did not quite reach significance, it suggests that predictable action sequences afforded a marginally greater enhancement in order memory for items seen at the end versus the beginning of an event.

Item memory is not impacted by engagement in predictable action sequences. Finally, we turned to the critical question of how engaging in a familiar action sequence during encoding impacts detailed memory for the novel visual items from each event. During this item recognition test, participants had to discriminate between items that had been presented during one of their errands ("old" items) and similar lures ("new" items; Fig. 6). We computed d' (Dprime) as a measure of recognition accuracy, adjusted for extreme values following Hautus (1995). Using this metric, we found no difference in item memory as a function of whether an item (or its matched pair) had been encountered in the predictable or random store, $t(51) = -0.29$, $p = .78$, 95% CI for the mean difference = [–.33, .26], $d = 0.05$, 95% $\mathrm{CI}_d = [-0.31, 0.41]$ (Fig. 6a). We also computed a corresponding Bayes factor (BF) for this analysis, which allowed us to more directly assess evidence for the null hypothesis (i.e., that predictable action sequences had no effect on item recognition). To this end, we calculated a close approximation of $\mathrm{BF}_{\mathrm{null}}$ based on the Bayesian information criterion (Brydges & Bielak, 2020; Rouder et al., 2009). We obtained a $\mathrm{BF}_{\mathrm{null}}$ of 6.44, which indicates moderate evidence in favor of the hypothesis that there was no difference in item recognition performance as a function of encoding condition.

To examine item recognition at a more granular level, we next split trials into four different response bins: hits (responding "old" to an old item), misses (responding "new" to an old item), false alarms (responding "old" to a new item), and correct rejections (responding "new" to a new item). Participants were just as likely to make each type of response for items associated with the predictable store versus those associated with the random store—confirming that the predictable structure of one's motor behavior during encoding had no significant impact on the visual encoding of individual items—hits: $t(52) = -0.69$, $p = .50$, 95% CI for the mean difference = [−.06, .03], $d = 0.10$, 95% $\text{CI}_d = [-0.18, 0.38]$; false alarms: $t(52) = -0.51$, $p = .61$, 95% CI for the mean difference = [−.09, .06], $d = 0.10$, 95% $\text{CI}_d = [-0.30, 0.51]$ (Fig. 6b). We also confirmed that no differences emerged when looking only at high- or low-confidence responses or when examining memory as a function of sequence position (Fig. S3 in the Supplemental Material). Ultimately, these null effects suggest that the impact of familiar action sequences on visual order memory is unlikely to stem from increased attention to and/or encoding of those novel items but rather through a mechanism that selectively supports linking information together across time.

Discussion

In Experiment 3, we again showed that engaging in a familiar action sequence enhances memory for the order of novel, temporally coincident events. Conversely, familiar actions did not affect memory for the details of individual items. Although null effects must be interpreted cautiously, these findings suggest that participants did not simply allocate more attention to novel stimuli in the presence of prior knowledge. Instead, we argue that their traversal through a known behavioral routine allowed novel items to be embedded within a stable, preexisting memory representation, which specifically supports memory for temporal relationships.

General Discussion

Across three experiments, we found that novel visual item sequences were better remembered when they were encountered during the execution of a familiar motor sequence. This work significantly extends previous studies showing enhanced learning of new information from the same modality and/or conceptual space as existing knowledge (e.g., Anderson et al., 1978; Bein et al., 2019; King et al., 2019; Reder et al., 2016; van Kesteren et al., 2013). Specifically, here we showed that engaging in highly familiar action sequences—which are ubiquitous in everyday life and yet underappreciated in existing literature—is sufficient to boost one-shot learning of unrelated visual items seen simultaneously.

This work also deepens our understanding of how motor and episodic memory systems interact. Existing research has shown that motor sequence learning can benefit performance on an asynchronous and unrelated memory task (Mosha & Robertson, 2016; Mutanen et al., 2020). In this previous work, the learning of a finger-tapping sequence enhanced participants' ability to recall a repeatedly studied word list and vice versa. Here, we demonstrated that engagement in familiar behaviors can also enhance memory for episodic sequences encoded at the same time. This distinction is significant, given that our everyday actions are frequently coincident with exposure to other stimuli. Interestingly, in this prior work, cross-task learning transfer occurred only when finger-tapping sequences and word lists shared a high-level structure; specifically, the order of fingers in the motor task mirrored the order of semantic categories in the word list. The authors subsequently argued that this learning transfer occurred via "memory leaks," whereby abstract sequential information learned in one context can be shared across multiple memories (Robertson, 2022). In our task, item and action sequences did not share this kind of abstract high-level structure—which, according to their framework, is a necessary prerequisite for memory leaks. Our findings instead demonstrate that an abstract correspondence need not be present for cooperation between memories to occur and that the simultaneous coactivation of motor and episodic sequence representations improves temporal memory—whereas in paradigms involving separate tasks, a more abstract shared structure may be necessary for integration across asynchronous sequence memories.

We further suggest that familiar action sequences benefit order memory by activating a holistic representation of the learned event structure during encoding (Fig. 1b), within which novel item representations can become embedded (Gilboa & Marlatte, 2017; McClelland, 2013). Because this "temporal scaffold" specifically represents how events unfold across time, we predicted that order memory, and not item memory, would benefit from this structure, and our results confirmed this prediction. This putative explanation is rooted in work on the neurocognitive bases of sequence memory, which has found that memory for temporal links between items is enhanced when they belong to similar mental contexts (Clewett et al., 2020; DuBrow & Davachi, 2013; Heusser et al., 2018). Because repeated exposure to sequential information can increase the stability of sequence representations in the brain (Hsieh et al., 2014; Kalm et al., 2013), we hypothesize that well-learned action sequences bolster the stability of participants' mental context while encoding novel items, which then enhances temporal binding.

Similarly, the stable representation afforded by the familiar action sequence may also benefit order memory retrieval. Successful episodic recall is thought to be accompanied by reactivation of a memory's broader context, which in turn promotes access to other memories nearby in time (Howard & Kahana, 2002; Manning et al., 2011; Polyn et al., 2009). In our task, during retrieval of predictable events, participants may reactivate their memory for the known action sequence to guide recovery of the corresponding item sequence. In future work, we aim to clarify the precise neural mechanisms by which action sequences support temporal memory.

We also considered an alternative hypothesis, the attentional-resource hypothesis—or the idea that prior knowledge about one's behavior diverts more attention to new information (Diana & Reder, 2006; Reder et al., 2016)—as the potential mechanism driving our temporal memory effects. However, if enhanced memory in our experiments stemmed from a broad increase in goal-directed attention during predictable events, we would expect benefits for item memory in addition to order memory. Given that item memory was unaffected by familiar actions, differences in attention are unlikely to explain our results.

It is perhaps surprising that familiar action sequences did not robustly facilitate spatial context memory. If participants remember the order of novel items and of predictable aisle responses, they could theoretically infer item–aisle pairings. However, the lack of clear spatial memory effects in our experiments suggests that participants did not adopt that strategy here. Further, although spatial context memory was enhanced for items in the first position of predictable versus random effects across Experiments 1 and 2, this benefit alone could not explain our finding of enhanced temporal memory for the complete order of items within predictable events. It could be that the format of the spatial memory test—in which participants made spatial context judgments for one item at a time—hindered access to other items in the event and their temporal position. It is also possible that in our paradigm, spatial information was simply not salient enough to be integrated within item sequences.

It is important to acknowledge that in our task, we cannot be certain that the execution of motor behaviors during encoding is necessary for temporal sequence memory enhancements to occur. Instead, it is also possible that predictability within an event in general—for example, expectations about where to-be-encoded items will appear in space—is itself enough to enhance temporal memory, even when no responses are made. In the current experiments, we chose to have participants execute the learned sequence to ensure that this predictable event structure was made sufficiently salient during simultaneous encoding. Without this demand, there is the concern that making the action sequence irrelevant to ongoing episodic encoding may reduce its ability to impact memory processing, given prior work showing that contextual features of an event must be task relevant in order to influence memory (e.g., Ecker et al., 2007). However, future work examining the effects of predictable sequential structure without any motor execution will be necessary to establish to what degree sequential action-execution behavior is an essential prerequisite to our observed effects.

Ultimately, these experiments demonstrate how simple behavioral routines can support the formation of temporally intact episodic memories. A substantial portion of our experiences are action centered. Investigating how these actions impact concurrent memory processes, then, is critical to our comprehension of how learning occurs in real-world, naturalistic environments. Additional work will be necessary to establish the limitations of our effects. It could be, for example, that when behavioral routines become too automatic, they instead lead to disengagement from external stimuli (e.g., "zoning out" during a familiar drive). Nevertheless, the demonstration that cross-modal facilitation of episodic memory can occur is an important and novel contribution to our understanding of how prior knowledge facilitates new learning, as well as how different memory systems cooperate to support learning behavior.

Transparency

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Author Contributions

Camille Gasser: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing – original draft, writing – review & editing.

Lila Davachi: conceptualization, funding acquisition, methodology, supervision, writing – original draft, writing – review & editing.

Declaration of Conflicting Interests

The author(s) declared that there were no conflicts of interest with respect to the authorship or the publication of this article.

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Supplemental Material

Additional supporting information can be found at http://journals.sagepub.com/doi/suppl/10.1177/09567976231158292

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