Prediction and encoding are coupled, not competitive

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Statement on Transparency and Openness:

All data, materials, and analysis scripts are publicly available at https://osf.io/m7und/.

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Abstract

Forming new memories requires a focus on the external world; retrieving existing memories requires attention to our internal world. Computational models propose that the hippocampus plays a central role in resolving the tension between encoding and retrieval by alternating between states that prioritize one over the other. We tested two opposing hypotheses about whether encoding and retrieval states in the hippocampus are associated with a behavioral *trade-off* or behavioral *coupling* between encoding and retrieval, with retrieval operationalized as the use of existing memories to make predictions about the future. Across 3 Experiments (N = 197), participants viewed a series of scene categories that contained structure (e.g., beaches are followed by castles); this structure enabled memory retrieval to guide prediction. After structure learning, participants completed a simultaneous prediction and encoding task. They were shown trial-unique category exemplars and asked to make predictions about upcoming scene categories. Finally, they were given a surprise memory test for the trial-unique images. This allowed us to test whether there was *competition* vs. *coupling* between encoding of trial-unique images and prediction of upcoming images. We consistently observed coupling between encoding and prediction: accurate predictions were associated with better encoding, and factors that hurt prediction also hurt encoding. This coupling could not be explained by generic on- vs. off-task states. Together, these findings suggest that distinct encoding and retrieval states in the brain need not be associated with a tension between encoding and prediction in behavior; instead, these cognitive states may be cooperative rather than competitive.

Public Significance Statement

At any given moment, we may focus externally on the world around us or internally on our thoughts and memories. Externally oriented states allow us to encode the present, whereas internally oriented states allow us to use our existing knowledge to make predictions about the future. Although it has traditionally been thought that these cognitive states may compete with each other, here we show that encoding the present and predicting the future can be coupled: being good at one is associated with being good at the other. This suggests that our ability to be in the present and project ourselves into the future need not be at odds with one another; instead, these abilities may synergize to allow adaptive behavior.

Keywords

Encoding; Prediction; Episodic Memory; Long-Term Memory; Hippocampus

Introduction

Learning requires *encoding* new information and the ability to *retrieve* that information later on. Encoding and retrieval are thought to depend on at least partly distinct mechanisms, with our memory system hypothesized to fluctuate between states optimized for encoding and states optimized for retrieval (Colgin et al., 2009; Hasselmo et al., 2002; Hasselmo & Stern, 2014, Honey, Newman, & Shapiro, 2017; Rizzuto et al., 2006; Tarder-Stoll*, Jayakumar* et al., 2020; Verschooren & Egner, 2023). In a retrieval state, attention is allocated internally toward stored representations, but potentially at the expense of encoding new memories (Duncan et al., 2012; Patil & Duncan, 2018; Sherman & Turk-Browne, 2020). Conversely, in an encoding state, attention is focused on the external world, but with potential costs to memory retrieval (Rademaker & Serences, 2024). These encoding and retrieval states might be associated with distinct computational modes, as implemented in foundational computational models of episodic memory (Hasselmo et al., 2002). According to these frameworks, encoding and retrieval have inherently opposing demands, which are balanced by our memory systems alternating between encoding and retrieval modes (Hasselmo, 2005). This in turn allows us to switch between encoding and retrieval without experiencing interference between them (O'Reilly & McClelland, 1994). Under these dominant frameworks, therefore, encoding and retrieval are competitive processes. However, a separate body of work investigating dual tasks suggests that there may be facilitation between two simultaneously engaged cognitive processes, especially when those processes share overlapping neural substrates (Navon & Gopher, 1979; Leone et al., 2017). From this perspective, memory encoding and retrieval may be *coupled* with one another, rather than *competitive*. Here, we test these opposing hypotheses about whether the behavioral dynamics of encoding and retrieval are competitive or coupled.

Support for the notion of competitive dynamics between encoding and retrieval comes from empirical studies and computational models of memory systems in the brain. These bodies of work implicate the hippocampus – a critical brain region for learning and memory (Scoville & Milner, 1957) – in switching between these processes (Poskanzer & Aly, 2023). Specifically, distinct neural pathways between subfields in the hippocampus support retrieval vs. encoding states (Kesner & Rolls, 2015; **Figure 1**). Recurrent connections in hippocampal subfield CA3 and connections between CA3 and CA1 are strengthened during internally oriented states that support memory retrieval. Conversely, afferent input from the entorhinal cortex to hippocampal subfields CA1 and CA3 is strengthened during externally oriented states that promote encoding. (**Figure 1**). Importantly, the strengthening of within-hippocampus recurrent connections can be accompanied by weakening of afferent input to the hippocampus, suggesting that prioritizing retrieval may come at the expense of encoding and vice versa (Hasselmo et al., 2002; Hasselmo, 2006). Therefore, the opposing demands of encoding and retrieval may be met by these distinct hippocampal states, giving rise to competition between encoding and retrieval states that may be observable both in the brain and in behavior (for reviews see Duncan & Schlichting, 2018; Kesner & Rolls, 2015;; Tarder-Stoll*, Jayakumar*, et al., 2020).

Much of the past work investigating these states has focused on rapid oscillations between encoding and retrieval states on the order of milliseconds (e.g., theta oscillations, Hasselmo et al., 2002; Hasselmo, 2005; Kerrén et al., 2018). However, recent work has suggested that these states also fluctuate over slower timescales on the order of seconds (Honey, Newman, & Shapiro, 2017). These sustained states are detectable with fMRI. For example, connectivity between human DG/CA2/3 and CA1 predicted retrieval success (Duncan et al., 2014), whereas EC-CA1 connectivity increased during an encoding state (Bein et al., 2020). Outside the hippocampus, encoding and retrieval states have been associated with distinct whole-brain activity and connectivity patterns (Huijbers et al., 2013; Long & Kuhl, 2019; Long & Kuhl, 2021; Poskanzer & Aly, 2023; Richter et al., 2016). These fluctuations between encoding and retrieval states over longer timescales in the brain suggest that they may exert powerful influences that can be detected at the level of slowly evolving behavior. Indeed, biases toward retrieval vs. encoding states that linger over several seconds have been detected in behavior (Douchamps et al., 2013; Duncan et al., 2012; Duncan & Shohamy, 2016; Patil & Duncan, 2018) and vary based on task demands, such as retrieval goals (Smith & Long, 2024; Tarder-Stoll*, Jaykumar*, et al., 2020).

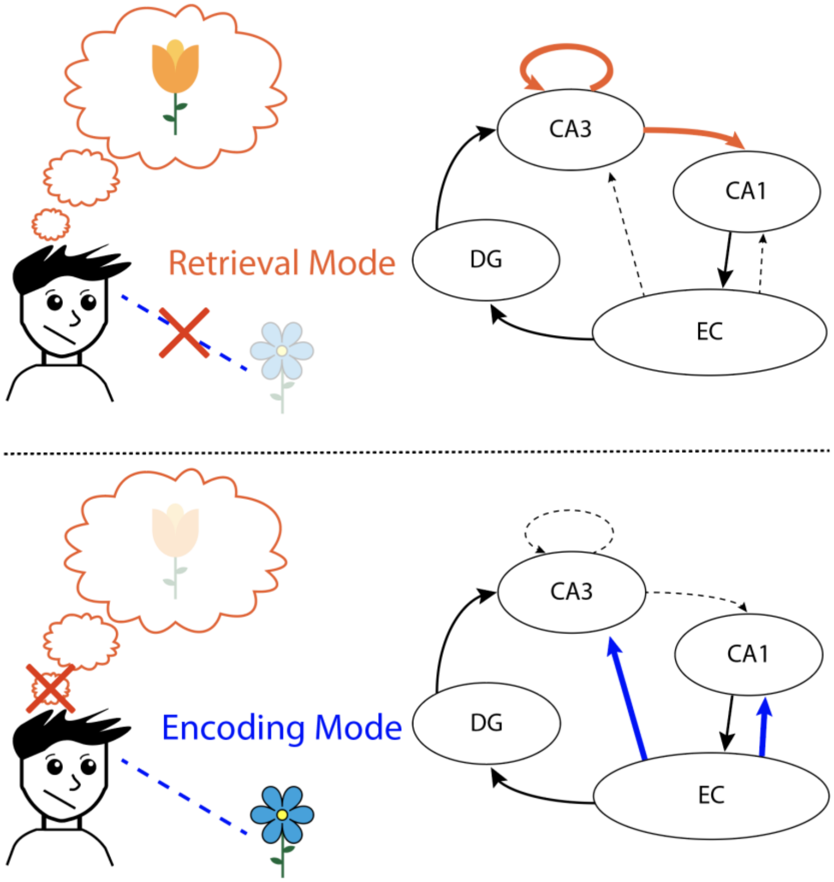

Figure 1. Model of hippocampal states during retrieval vs. encoding. (Top) A retrieval mode prioritizes internally oriented processing of experiences recalled from memory, at the expense of externally oriented processing of sensory information. In a retrieval mode, recurrent connections within hippocampal subfield CA3 are strengthened, as are connections between hippocampal subfields CA3 and CA1 (orange). Conversely, afferent connections between the Entorhinal Cortex (EC) and hippocampus are weakened (dotted line). This change in connectivity is hypothesized to bias the hippocampus towards processing previously stored representations (e.g., the orange flower) at the expense of encoding novel information (e.g., the blue flower). **(Bottom)** An encoding mode prioritizes externally oriented processing of sensory information at the expense of internally oriented processing of experiences recalled from memory. In an encoding mode, afferent connections between EC and CA1/CA3 are strengthened (blue), while the connections between CA3 and CA1, as well as recurrent connections within CA3, are weakened (dotted lines). This shift in the strength of connections is hypothesized to bias the hippocampus toward processing incoming, novel information (blue flower) at the expense of existing representations (orange flower).

Retrieval and encoding states therefore influence behavior, but do they trade off with one another? In support of competitive dynamics between memory encoding and retrieval, one prior study showed participants a series of trial-unique images while they underwent fMRI scanning (Sherman & Turk-Browne, 2020). Unbeknownst to participants, this stream of images contained underlying, category-level regularities (e.g., a picture of a forest was always followed by a picture of a castle). As participants viewed this structured stream of images, activity patterns in the hippocampus reflected representations of upcoming image categories, indicating memory retrieval. These hippocampal predictions, based on memory retrieval, impaired simultaneous encoding of the trial-unique images, consistent with a trade-off between a retrieval state in the brain and encoding in behavior (Sherman & Turk-Browne, 2020). This effect was replicated in an electroencephalography study in which brain activity was directly recorded from individuals with epilepsy: on trials in which predictions about upcoming categories could be decoded from neural firing in visual cortex, subsequent memory for the trial-unique images suffered (Sherman et al., 2022).

Collectively, these studies suggest that there is competition between encoding and prediction. However, a separate body of work instead suggests that encoding and prediction may facilitate one another. Evidence for this perspective comes from studies of dual task facilitation. In these cases, performance on one task can facilitate performance on a concurrent task (Leone et al., 2017; for a review of dual task interference rather than facilitation, see Pashler, 1994). For example, performing a well-learned sequence of motor actions can facilitate simultaneous memory encoding, indicating cooperation between retrieving a learned sequence and encoding new information (Gasser & Davachi, 2023). Dual task facilitation has also been shown in studies in which a perception task is performed concurrently with a motor task (Deubel et al., 1998; Schütz-Bosbach & Prinz, 2007) or an imagery task (Ishai & Sagi, 1997). Further, externally and internally oriented states can cooperate to guide decisions: information from retrieved memories can be adaptively combined with external sensory evidence to inform perceptual decisions (Bornstein et al., 2023). Together, these results show that multiple cognitive functions can be carried out concurrently in such a way that they benefit, rather than compete, with one another (Leone et al., 2017; Navon & Gopher, 1979, Navon & Miller, 1987). These studies therefore raise the possibility that recruiting the hippocampus for one mnemonic operation (e.g., encoding) may boost its function for the other (e.g., prediction). In this case, successful encoding may be coupled with successful retrieval.

These two bodies of work therefore make diverging predictions about whether encoding and retrieval are competitive vs. coupled. Prior work, however, has not simultaneously measured encoding and retrieval in behavior to test their relationship on a trial-by-trial basis. Given evidence that encoding and retrieval states can linger over seconds and are observable in behavior (Duncan et al., 2012; Duncan & Shohamy, 2016; Meeter et al., 2004; Patil & Duncan, 2018; Sherman & Turk-Browne, 2020), we sought to address this gap in the literature.

To this end, we ran 3 behavioral experiments that examined the relationship between encoding and retrieval. As in prior work (Sherman & Turk-Browne, 2020), we measured memory retrieval as the successful use of learned information to generate predictions about the future. Our experiments shared a common structure (**Figure 2**), although the task details were specific to each experiment (see below). Each experiment began with an *Initial Structure Learning* phase, in which participants learned relationships between scene categories (e.g., category A predicts category B). Participants then performed a *Simultaneous Prediction and Encoding Task*. Here, they were presented with trial-unique category exemplars and asked to make predictions about upcoming scene categories, using the knowledge they acquired in Initial Structure Learning. Critically, each trial in the Simultaneous Prediction and Encoding Task taxed potentially opposing cognitive functions: to predict upcoming categories (indicating memory retrieval of upcoming scene categories) and/or successfully encode the trial-unique category exemplar. Finally, participants performed a *Surprise Memory Test*, in which their memory for the trial-unique scene images from the *Simultaneous Prediction and Encoding* Task was probed; this allowed us to assess encoding success for each image. In this way, we could obtain measures of prediction success (from *Simultaneous Prediction and Encoding*) and encoding success (based on recognition memory in the *Surprise Memory Test*) for each trial-unique image, and assess whether prediction and encoding were cooperative or competitive.

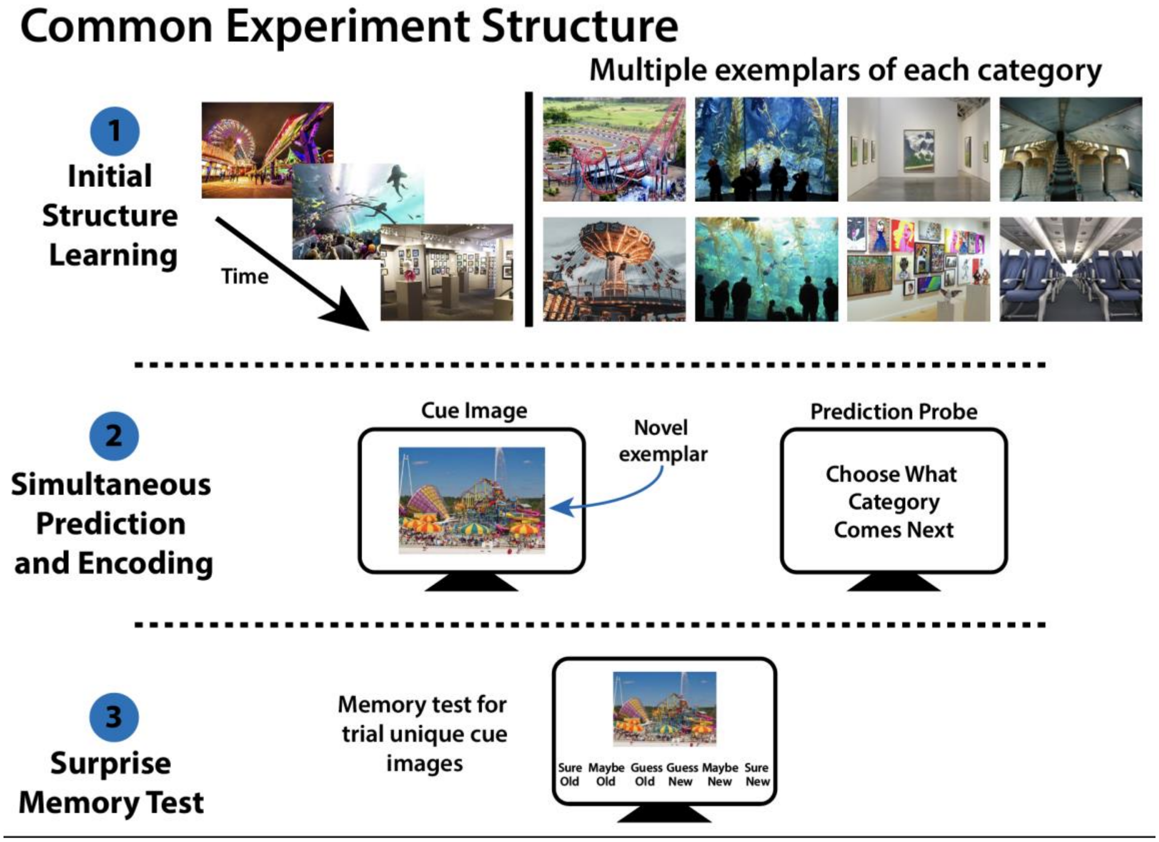

Figure 2. Common experiment structure. Each experiment had 3 phases. **(Top) Initial Structure Learning**: Participants viewed a series of scene images that had a defined statistical structure between the scene categories. The category-level structure remained constant throughout the experiment (e.g., amusement park followed by aquarium, followed by art gallery) but the specific scene exemplars could change from trial to trial (e.g., different amusement parks, different aquariums). **(Middle) Simultaneous Prediction and Encoding**: Participants viewed a *novel* exemplar of a previously seen category and were asked to use that image to predict upcoming scene categories. Crucially, viewing the cue image places potentially opposing demands

on the memory system: participants can encode the novel cue exemplar and/or retrieve upcoming scene categories. **(Bottom) Surprise Memory Test**: Participants were shown images from the "Simultaneous Prediction and Encoding" Task, as well as category exemplars that they had not seen before. Participants were asked to report if each image was "new" or "old" with a 6-point confidence scale. This "Surprise Memory Test" was the same for all 3 experiments, but "Initial Structure Learning" and "Simultaneous Prediction and Encoding" had experiment-specific features.

Experiment 1

Materials and Methods

Participants

57 participants were recruited using the Columbia University SONA system to take part in an online experiment. Participants provided informed consent and were compensated with course credit for their participation. We analyzed data from 47 participants after excluding 10 participants. Exclusion criteria were: responding to fewer than 80% of trials on either the Simultaneous Prediction and Encoding Task or the Surprise Memory Test and/or having below-chance performance on both the Simultaneous Prediction and Encoding Task (accuracy < 50%) and the Surprise Memory Test ($d' < 0$). We chose our target sample size with a goal of exceeding that of prior work from our lab that examined anticipation across image sequences within a similarly structured prediction task ($n = 32$; Tarder-Stoll et al., 2024a). We exceeded that prior sample size by 15 participants to overcome effect size overestimation (Bakker et al., 2012; Brand et al., 2008). All procedures were approved by the Columbia University Institutional Review Board. The demographics of the final sample were as follows: Age: mean = 19.7 years, range = 18 - 28

years; Education: mean = 13.4 years, range = 10 - 23 years; Race: 14 Asian, 3 Black or African American, 21 White, 1 American Indian or Alaskan Native, 1 Native Hawaiian or Pacific Islander, 6 Multiple Races [1 Asian and Black or African American; 1 Asian, Native Hawaiian or Pacific Islander, and White; 2 Asian and White; 2 Black or African American and White]; Ethnicity: 9 Hispanic/Latino, 37 not Hispanic/Latino; missing demographics for 1 participant.

Stimuli

Stimuli were 560 images of scenes collected from the SUN database (Xiao et al., 2010) and through Google image searches. Each image belonged to one of 40 categories: airplane cabins, amusement parks, aquariums, art galleries, basements, bathrooms, beaches, bedrooms, bridges, castles, caverns, churches, city skylines, deserts, factories, farms, football fields, forests, gyms, harbors, hospital rooms, junkyards, kitchens, labs, lecture halls, libraries, lighthouses, offices, outdoor concerts, outdoor skating rinks, roofs, playgrounds, restaurants, shopping malls, ski slopes, supermarkets, swimming pools, theaters, underwater, and zoos. The categories were selected such that 20 were outdoor scenes and 20 were indoor scenes. There were 14 exemplar images for each category. All images were resized to 740 pixels by 540 pixels with a resolution of 150 pixels/inch. An additional 3 images of green fields were inverted and reserved to use as attention checks throughout the experiment.

Procedure

The experiment was conducted on the Gorilla platform (www.gorilla.sc; Anwyl-Irvine et al., 2020). After providing informed consent, participants began the Initial Structure Learning phase. Each participant was randomly assigned 20 categories (10 indoor scenes and 10 outdoor scenes) that were arranged into 2 separate sequences of 10 scenes each. Each sequence was 100% deterministic, meaning the 10 categories were always presented in the same order (**Figure 3**). Additionally, both sequences formed a closed loop, meaning that the 10th category in a sequence would transition back to the 1st category in that sequence. Although the order of the categories within each sequence remained constant, the individual exemplar images could change with each presentation of the sequence. For example, an image of a beach would always follow an image of a castle, but the exact castle and beach would change from trial to trial. During this Initial Structure Learning phase, participants were shown 4 different exemplars of each category. The different exemplars were spaced such that participants were never shown the same exemplar for a category in adjacent presentations of a sequence. Participants were told that they would see a sequence of image categories in a fixed order and that they should try to create stories that would facilitate their ability to memorize the order of the scene categories. Participants then viewed the image categories in order. At the start of each sequence a blank screen with a fixation cross appeared for 5 seconds. Participants then viewed scene images one at a time for 3 seconds each, following the deterministic structure of each sequence. Between scene images, participants viewed a blank screen with a fixation cross for 500 ms. While an image was on the screen, participants were instructed to rehearse the story they generated for the order of the scene images, and to press "a" or "l" on their keyboard to indicate if the scene was "outdoor" or "indoor" respectively. Throughout this phase of the experiment, participants saw each sequence 10 times. First, the participants were shown 4 presentations of sequence 1. After each pair of presentations of sequence 1, they were asked to recall sequence 1 by writing down all the categories they could remember, in the order of sequence 1. Next, they were shown 4 presentations of sequence 2; again, after each pair of presentations, they were asked to recall sequence 2 by writing down as many categories as they could remember, following the order of sequence 2. After a 60-second break, participants were then shown alternating presentations of each sequence until they had seen each sequence 6 additional times. Finally, participants were asked to write down the order of the categories in each sequence and then the stories that they had generated to aid their memorization.

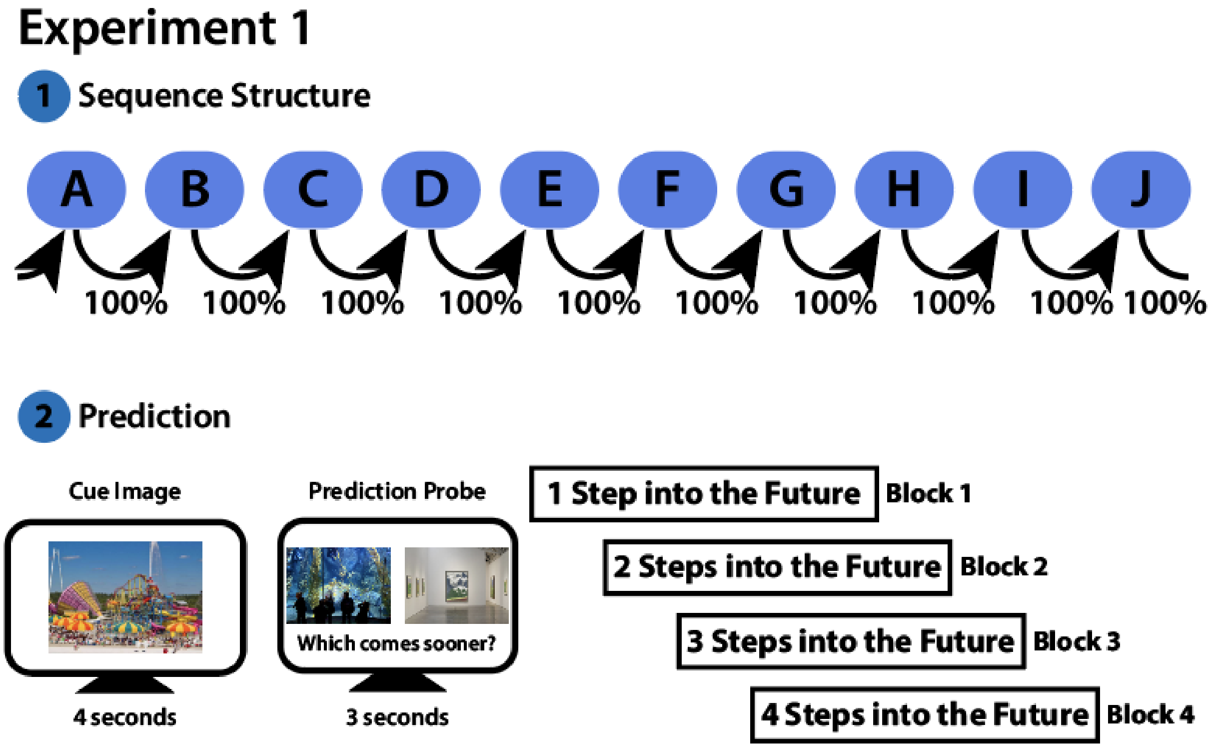

Figure 3. Design for Experiment 1. (Top) Participants viewed two sequences of 10 scene categories each. The sequences followed 100% deterministic transitions (e.g., category "A" always led to category "B") and formed a closed loop (category "J" transitioned back to category "A"). **(Bottom)** After learning the sequence, participants began the Simultaneous Prediction and Encoding phase in which they were shown an initial cue image for 4 seconds. They were then presented with 2 scene images of upcoming categories in the sequence. Participants were given 3 seconds to indicate which category comes sooner in the sequence after the cue image. In different blocks, correct answers were 1 to 4 steps into the future (order counterbalanced across participants). This was followed by the Surprise Memory Test (not shown; see Figure 2).

After completing Initial Structure Learning, participants began the second phase of the experiment: the Simultaneous Prediction and Encoding Task. During this section of the experiment, participants were shown an initial cue image for 4 seconds. All cue images were novel exemplars from the categories that they had learned during the Initial Structure Learning. After the cue disappeared from the screen, 2 probe images of upcoming categories in the sequence were shown side by side for 3 seconds. Probe images were category exemplars that had been previously seen during Initial Structure Learning. Participants were instructed to press "a" or "l" to indicate if the left or right image would appear sooner in the sequence, relative to the cue image. On each trial, the correct probe image was either 1, 2, 3, or 4 steps into the future from the cue image, and was randomly assigned to either the left or right position on the screen. The incorrect probe images were categories that were 1 to 4 steps *after* the correct probe in the sequence. Participants were presented with 4 blocks of 20 trials each. In each block, the correct answer was always the same number of steps into the future (e.g., all correct answers might be one step in the future). Each participant completed one block for each correct distance (1 to 4 steps). Participants were informed at the beginning of each block how many steps into the future the correct answers would be. The incorrect answer distance was randomized across trials and balanced within each block. For each block, participants were first shown 10 trials of categories from one sequence, before switching to 10 trials containing categories from the other sequence. Categories were presented in a random order, with the constraint that all 10 categories from one sequence would be presented before the other sequence was tested. The order of sequences, as well as the order of the prediction blocks, was counterbalanced across participants. To ensure participants were on task, 3 attention checks were randomly interspersed throughout this phase of the experiment. During each attention check, participants were shown an inverted image of a field and asked to press "x" on their keyboard. After each block, the participants received a 30 second break.

Finally, participants completed a Surprise Memory Test. The memory test consisted of 240 trials in which participants were shown either a novel exemplar from one of the categories in the sequence, or an exemplar that they had previously viewed in either the Simultaneous Prediction and Encoding Task or the Initial Structure Learning phase. During each trial, an image was presented for 5 seconds and participants were instructed to use their keyboard to indicate whether the image was old or new by using a 6-point confidence scale: "sure old", "maybe old", "guess old", "guess new", "maybe new", or "sure new". Of the 240 trials, 120 images were novel exemplars that had not been previously seen, 80 images had been shown as trial-unique cues during the Simultaneous Prediction and Encoding Task, and 40 images had been studied as part of the Initial Structure Learning. The 40 images from the Initial Structure Learning were included in the memory test to assess research questions not of primary interest in the current study and were not analyzed further. Halfway through this section, participants were given a 60-second break. Additionally, as in the Simultaneous Prediction and Encoding phase, 3 attention checks were randomly interspersed throughout this section of the task. As above, during each attention check, participants were shown an inverted image of a field and asked to press “x” on their keyboard. Across the 6 total attention checks in the experiment, average accuracy was 96% (5.74 out of 6), confirming that participants were generally attentive and engaged.

Statistical Analyses

We first examined prediction performance (accuracy and response times) during the Simultaneous Prediction and Encoding Task as a function of steps into the future.

To examine the relationship between prediction distance and accuracy, we used a mixed-effects logistic regression model, predicting binary prediction accuracy (0 = incorrect; 1 = correct) as a function of prediction distance (steps into the future; effect coded: 1 step = -1.5, 2 steps = -0.5, 3 steps = 0.5, 4 steps = 1.5), with random intercepts and slopes for each participant.

To examine the relationship between prediction distance and prediction response time (RT), we used a mixed-effects model predicting RT as a function of prediction distance (steps into the future; effect coded: 1 step = -1.5, 2 steps = -0.5, 3 steps = 0.5, 4 steps = 1.5), with random intercepts and slopes for each participant.

We examined RT on correct prediction trials only, because prediction accuracy was affected by prediction distance (as noted in Results). In this way, we could ensure that any effect of prediction distance on RT was not due to differences in accuracy with further steps in the future.

We next investigated how memory encoding of trial-unique cue images (as measured by performance in the Surprise Memory Test) was affected by concurrent prediction during the Simultaneous Prediction and Encoding Task. To that end, we conducted two analyses.

First, we used a mixed-effects logistic regression model to predict subsequent memory for the trial-unique cue images, assessed via the Surprise Memory Test (0 = miss, 1 = hit) as a function of prediction accuracy (effect coded; incorrect = -0.5, correct = 0.5), with random intercepts and slopes for each participant.

Finally, we used a mixed-effects logistic regression model to predict Surprise Memory Test accuracy (0 = miss, 1 = hit) for the trial-unique cue images from the Simultaneous Prediction and Encoding Task as a function of prediction distance at encoding (steps into the future; effect coded: 1 step = -1.5, 2 steps = -0.5, 3 steps = 0.5, 4 steps = 1.5), with random intercepts and slopes for each participant. We ran this model once on all trials regardless of prediction accuracy, and again when restricting the analysis only to correct prediction trials.

Statement on Transparency and Openness

All data, materials, and analysis scripts are publicly available at https://osf.io/m7und/.

Results

Overall Prediction and Encoding Performance

We first sought to verify that participants performed effectively on the Simultaneous Prediction and Encoding Task and the Surprise Memory Test. We measured accuracy on the Simultaneous Prediction and Encoding Task as the proportion of prediction trials answered correctly. We confirmed that participants' performance on the prediction task was higher than the chance level of 50% (mean = 0.73, $t(46) = 9.04$, $p < 0.001$). Next, we examined subsequent memory performance on the Surprise Memory Test using d' (normalized hit rate - false alarm rate). d' on the Surprise Memory Test was significantly above the chance level of 0 (mean = 0.72, $t(46) = 13.92$, $p < 0.001$). Thus, participants were able to both successfully generate predictions and encode images during the Simultaneous Prediction and Encoding Task.

Prediction Suffers with Increasing Prediction Distance

We next investigated whether our manipulation of steps into the future during the Simultaneous Prediction and Encoding Task had an impact on participants' ability to predict upcoming scene categories. We hypothesized that as prediction distance increased, participants would 1) be less accurate and 2) have slower response times (Tarder-Stoll et al., 2024a, 2024b). We first used a mixed-effects logistic regression to predict accuracy on a given trial from the prediction distance of that trial. Participants were, indeed, less accurate at prediction as steps into the future increased ($\beta = -0.28$, SE = 0.06, $p < 0.001$; **Figure 4A**). We then used a linear mixed-effects model to predict response times on correct trials as a function of prediction distance. As participants correctly predicted further steps into the future, they took longer to respond (β =

126.10, SE = 20.83, p < 0.001; Figure 4B). Together, these analyses replicate our prior work (Tarder-Stoll et al., 2024a, 2024b) demonstrating that predicting further into the future comes at a cost to both accuracy and response times.

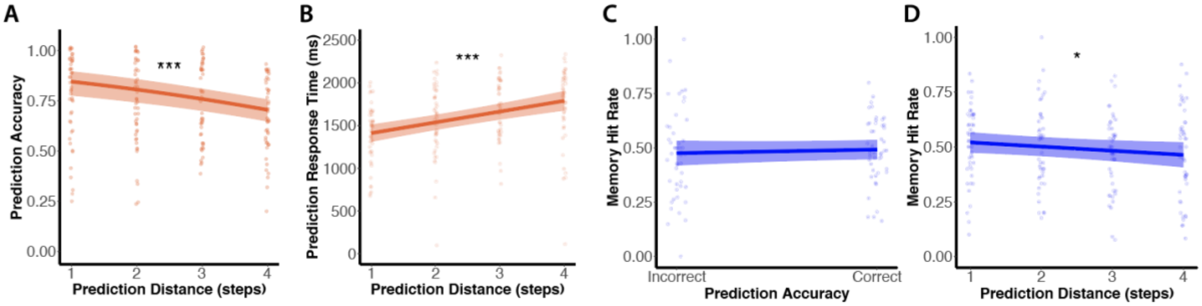

Figure 4. Experiment 1 results: Encoding and prediction are coupled, not competitive. With increasing prediction distance, both prediction and memory encoding suffer. As prediction distance increased, prediction accuracy significantly decreased **(A)** and prediction response time significantly increased **(B)**. There was no difference in subsequent recognition memory for cue images for which participants made a correct vs. incorrect prediction **(C)**. However, as prediction distance increased, subsequent recognition memory for the novel cue images significantly declined **(D)**. Points represent individual participants. Lines with shaded regions indicate model predictions for fixed effects along with 95% confidence intervals. (*p < 0.05, ***p < 0.001).

Competition or Coupling Between Prediction and Encoding?

Our primary analyses were focused on whether prediction and encoding trade off with each other or are coupled. To that end, we examined the relationship between prediction performance and subsequent memory for the trial-unique cues presented in the Simultaneous Prediction and Encoding Task. Prediction performance was measured during the Simultaneous Prediction and

Encoding Task, and memory encoding success for the trial-unique cues was based on performance in the Surprise Memory Test.

We first examined whether participants successfully encoded a trial-unique cue as a function of whether or not they generated correct vs. incorrect predictions from that cue. We found that there was no difference in participants' subsequent recognition hit rate on trials in which they made a correct vs. incorrect prediction ($\beta = 0.07$, SE = 0.08, $p = 0.43$; **Figure 4C**). Thus, this analysis did not show evidence for either a trade-off or coupling between prediction and encoding as a whole; however, this analysis ignores the effect of prediction *distance*, which had a strong effect on prediction behavior (**Figure 4A-B**).

We therefore examined memory encoding success as a function of prediction distance. We used a mixed-effects logistic regression model, in which we predicted subsequent memory for trial-unique cues (hit or miss) as a function of prediction distance during the Simultaneous Prediction and Encoding task. We first conducted this analysis on all trials regardless of prediction accuracy, and found no effect of prediction distance on subsequent recognition memory ($\beta = -0.06$, SE = 0.03, $p = 0.11$). We next restricted this analysis to only those trials in which predictions were correct; in this way, we could remove trials in which participants may have simply been off task or inattentive. We reasoned that if correct predictions with further reaching steps in the future are associated with slower response times (**Figure 4B**) but *better* memory, that would be suggestive of a trade-off between prediction and encoding. If, on the other hand, correct predictions with further reaching steps in the future are associated with slower response times and *worse* memory, it would suggest that both prediction and memory suffer together – i.e., that they are coupled.

We found that, when examining correct prediction trials only, subsequent recognition memory significantly declined as prediction distance increased (β = -0.08, SE = 0.04, p = 0.04; **Figure 4D**). These results therefore suggest that prediction and encoding are coupled: as prediction distance increases, prediction and encoding both suffer. Further-reaching predictions are less accurate and slower; and the response time cost associated with correct far-reaching predictions is associated with a *cost* to encoding, rather than a benefit.

Discussion

In Experiment 1, we found no evidence of a trade-off between encoding and prediction. Instead, we observed parallel behavioral costs to prediction and memory encoding with increasing prediction distance. Far-reaching (vs. nearer) predictions were associated with less accurate predictions, slower predictions, and worse memory encoding.

It is possible, however, that we failed to find a trade-off between encoding and prediction because participants knew in advance how far they had to predict. In each block, they were told that the correct answer would be a particular number of steps in the future. Thus, when participants know that the prediction distance is short (e.g., one step), they may predict only as far as they need to, leaving more time available for incidental encoding. Such balancing of encoding and prediction may be difficult when prediction distance is far, leading to the behavioral costs in prediction and encoding as prediction distance increases. To test whether the blocked structure of Experiment 1 allowed participants to avoid competition between encoding and prediction, we intermixed trials with different prediction distances in Experiment 2 – thus preventing participants from knowing in advance how far they have to predict.

Another potential limitation of Experiment 1 is that the transitions between scene categories were always 100% deterministic. It may be that encoding and prediction are easier to balance when it is clear what predictions should be made. If so, adding uncertainty to predictions may result in a trade-off between encoding and prediction. We addressed that possibility in Experiment 2 by adding probabilistic transitions between scene categories.

Together, these changes allowed us to test whether the coupling that we observed between encoding and prediction in Experiment 1 is due to idiosyncrasies of our paradigm, or if this coupling is a more general phenomenon.

Experiment 2

Materials and Methods

Participants

We first conducted a power analysis using the SIMR package in R (Green and MacLeod, 2016). We set the power level at 80% and based the simulations on the effect of prediction distance on subsequent recognition memory from Experiment 1. This analysis provided a target sample size of 91 participants, which we aimed to exceed to overcome effect size over-estimation (Bakker et al., 2012; Brand et al., 2008). We recruited 144 participants from the Columbia University SONA system and Prolific (https://app.prolific.com) to take part in our online experiment. Our final sample size was 104 participants, after the exclusion of 40 participants. Exclusion criteria were the same as Experiment 1: responding to fewer than 80% of trials on either the Simultaneous Prediction and Encoding Task or the Surprise Memory Test and/or having below-chance performance on both the Simultaneous Prediction and Encoding Task (accuracy < 50%) and the Surprise Memory Test (d′ < 0). As above, all procedures were approved by the Columbia University Institutional Review Board. All participants provided informed consent. Those who were recruited from the Columbia University SONA system were compensated with course credit; those who were recruited from Prolific were paid $12 for their participation. The demographics were as follows: Age: mean = 24.3 years, range = 18 - 39 years; Education: mean = 14.2 years, range = 11 - 20 years; Race: 18 Asian, 6 Black or African American, 63 White, 1 Native Hawaiian or Pacific Islander, 12 Multiple Races/Other [1 American Indian or Alaskan Native and White; 2 Asian and White, 2 Black or African American and White; 5 Other]; Ethnicity: 17 Hispanic/Latino, 83 not Hispanic/Latino; missing demographics for 4 participants.

Stimuli

Stimuli were 216 images of scenes, some reused from Experiment 1 and others newly collected through Google image searches. Images belonged to one of 8 categories (4 indoor, 4 outdoor): airplane cabins, beaches, bedrooms, city skylines, forests, kitchens, lecture halls, and ski slopes. There were 27 exemplar images for each category. Images were resized to 740 pixels by 540 pixels with a resolution of 150 pixels/inch. To account for differences in image memorability, we estimated the intrinsic memorability of each image using the ResMem model (Needell and Bainbridge, 2022). Images were selected such that there were no outlier memorability scores greater than 3 standard deviations from the mean across the complete set of 216 images. Finally, an additional 3 images of green fields were inverted and reserved to use as attention checks throughout the experiment.

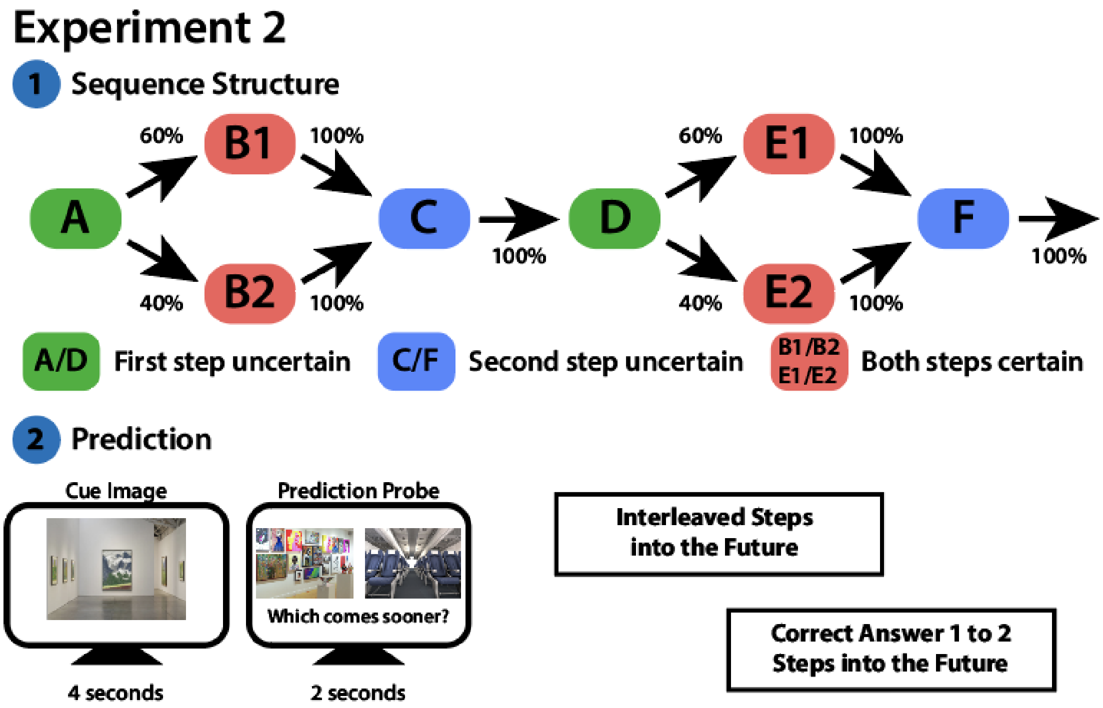

Figure 5. Design for Experiment 2. (Top) Participants viewed a sequence containing scene images from 8 categories. The structure of this sequence was partially nondeterministic: certain transitions were 100% deterministic, while other transitions were differentially likely. **(Bottom)** After learning the sequence, participants completed the Simultaneous Prediction and Encoding Task, in which they were shown an initial cue image for 4 seconds. They were then shown 2 scenes from upcoming categories. Participants had 2 seconds to select which category comes sooner in the sequence after the cue image. Correct answers could be 1 or 2 steps in the future. Trials were randomly interleaved by prediction distance. Finally, participants took the Surprise Memory Test (not shown; see Figure 2).

Procedure

The experiment was conducted on the Gorilla platform (www.gorilla.sc; Anwyl-Irvine et al., 2020). Participants provided informed consent before beginning the Initial Structure Learning phase. For each participant, the 8 scene categories were randomly shuffled to form a single sequence following the structure: A → (B1 or B2) → C → D → (E1 or E2) → F (Figure 5). As in Experiment 1, the sequence formed a closed loop such that category F always transitioned back to category A. The transitions in this sequence could be 100% deterministic (transitions from B1 → C, B2 → C, C → D, E1 → F, E2 → F, and F → A) or probabilistic (A → B1 [60%] or A → B2 [40%]; D → E1 [60%] or D → E2 [40%]). Although the sequence position of the categories remained constant for each participant, the individual category exemplar images could change with each presentation of the sequence. For example, an image of a beach might always be followed by an image of a castle, but the exact castle and beach could change from trial to trial. To aid learning, participants were shown a diagram of the sequence structure (similar to Figure 5) prior to the start of the main task. This learning aid used scene categories rather than the letters shown in **Figure 5**; none of these categories appeared in the rest of the experiment. During the Initial Structure Learning phase, participants were shown 3 different exemplars of each category. As in Experiment 1, these exemplars were spaced such that participants were never shown the same exemplar for a category in adjacent presentations of a sequence. Throughout this phase, participants saw the sequence 20 times, with a 60-second break after the first 10 presentations. Participants viewed the image categories following the sequence order described above. Before each image, a blank screen with a fixation cross appeared for 0.5 seconds. Participants then viewed scene images one at a time for 5 seconds each, following the structure of the sequence. While an image was on the screen, participants were instructed to press "a" or "l" on their keyboard to indicate if the scene was "outdoor" or "indoor" respectively. For uncertain transitions (scene categories B1, B2, E1, and E2), participants saw all 4 possible categories across the first 2 and last 2 presentations of the sequence. This was done to expose participants to the possible transitions as early in sequence learning as possible, and to avoid recency biases at the end of sequence learning. After the 20 presentations of the sequence, participants were presented with 6 boxes (one for each position in the sequence) and asked to write down the order of the categories. They were told that if 2 categories could occupy the same position (e.g., B1 and B2 could both follow A; **Figure 5**), both categories could be written in the same box.

Next, participants began the Simultaneous Prediction and Encoding Task. At the start of each trial, the participants were shown a fixation cross and asked to press the spacebar to begin the trial. Once the participant responded (or if they failed to respond after 5 seconds) a separate fixation cross appeared for 0.5 seconds. The screen next advanced to a cue image for 4 seconds. As in Experiment 1, cue images were novel, trial-unique exemplars selected from the categories that participants had learned during Initial Structure Learning. After 4 seconds, the cue disappeared and 2 probe images of upcoming categories in the sequence were shown side by side for 2 seconds. As in Experiment 1, probe images were category exemplars that had been previously seen during Initial Structure Learning. Participants were instructed to press "a" or "l" to indicate if the left or right image would appear sooner in the sequence, relative to the cue image. The correct probe image was either 1 or 2 steps into the future from the cue image, and appeared an equal number of times on the left or right position on the screen. The incorrect probe image was usually 1 step after the correct probe image. The exception was trials in which B1 (or E1) was the correct answer and B2 (or E2) was the incorrect probe. In these cases, both probes were 1 step in the future but B1/E1 were more likely to occur than B2/E2 (60% transition probability vs. 40%). Inclusion of these trials allowed us to determine if participants were sensitive to the differential probabilities of B1/E1 and B2/E2 items. For analysis, we divided trials into 3 transition conditions depending on the sequence position of the cue image and the transitions for the upcoming 2 steps: i) first step uncertain, ii) second step uncertain, and iii) both steps certain (Figure 5). Participants were presented with 24 prediction trials for each transition condition, for a total of 72 prediction trials.

The choice to limit prediction distance to 1 and 2 steps (rather than 1-4 steps as in Experiment 1) was because of the increase in experimental conditions with the addition of probabilistic transitions between image categories. Testing up to 4 step predictions across the 3 transition conditions would have doubled the length of the experiment, potentially leading to participant fatigue and dropout.

Crucially, unlike Experiment 1, participants were not informed how many steps into the future the correct answer would be on a given trial. Trial order (steps into the future for the correct answer, and transition condition) was randomized for each participant. To ensure participants were on task, 3 attention checks were randomly interspersed throughout this phase of the experiment. During each attention check, participants were shown an inverted image of a field and asked to press “x” on their keyboard. Approximately halfway through the task, the participants received a 60-second break.

Finally, participants completed the Surprise Memory Test. The memory test consisted of 144 trials in which participants were shown either a novel exemplar from one of the categories in the sequence, or an exemplar that they had previously viewed in the Simultaneous Prediction and

Encoding Task. As in Experiment 1, during each trial, an image was presented for 5 seconds and participants were instructed to use their keyboard to indicate whether the image was old or new by using a 6-point confidence scale: "sure old", "maybe old", "guess old", "guess new", "maybe new", or "sure new". Of the 144 trials, 72 images were novel exemplars that had not been previously seen and 72 images had been shown as trial-unique cues during the Simultaneous Prediction and Encoding Task. At 3 evenly spaced time points in this phase, participants were given a 60-second break. Additionally, as in the Simultaneous Prediction and Encoding Task, 3 attention checks were randomly interspersed throughout this section of the task. Attention checks were identical to those in the Simultaneous Prediction and Encoding Task. Across the 6 total attention checks in the experiment, average accuracy was 97% (5.82 out of 6), confirming that participants were generally attentive and engaged.

Statistical Analyses

Analyses were identical to those used in Experiment 1 excepting the following changes:

1) The prediction distance regressor was effect coded such that 1 step = -0.5 and 2 steps = 0.5.
2) All models included a regressor for the transition condition (first step uncertain, second step uncertain, both steps certain). This regressor was dummy coded such that the "both steps certain" condition was the reference condition. Models were run both with transition condition as a main effect only and with transition condition as an interacting variable. The main-effects-only model allowed us to estimate the main effect of a variable of interest (e.g., prediction distance) across all transition conditions, whereas the model with interactions allowed us to explore differences in a variable of interest (e.g., prediction

distance) between the reference condition (both steps certain) and the other two transition conditions.

3) All models excluded trials in which the prediction probes were B1 vs. B2 and E1 vs. E2. Participants were at chance in choosing between these options, indicating that they either did not learn that transitions to B1/E1 were slightly more likely (60%) than transitions to B2/E2 (40%), or they did not understand that they should select the more likely transition when presented with these options. All other trials including B1/B2 and E1/E2 (e.g., B1 vs. C, E1 vs. F, etc) were included; for these trials, participants were consistently above chance.

Results

Overall Prediction and Encoding Performance

As in Experiment 1, we first verified that participants' performance on the Simultaneous Prediction and Encoding Task and the Surprise Memory Test were above chance. Performance on the Simultaneous Prediction and Encoding Task was measured as the proportion of prediction trials answered correctly. Accuracy on the prediction task was higher than chance (mean = 0.60, chance = 0.50, $t(103) = 7.06$, $p < 0.001$). Subsequent memory performance on the Surprise Memory Test was also significantly above chance (mean $d' = 0.76$, chance = 0; $t(103) = 19.00$, $p < 0.001$). Thus, participants were able to both successfully predict and encode images.

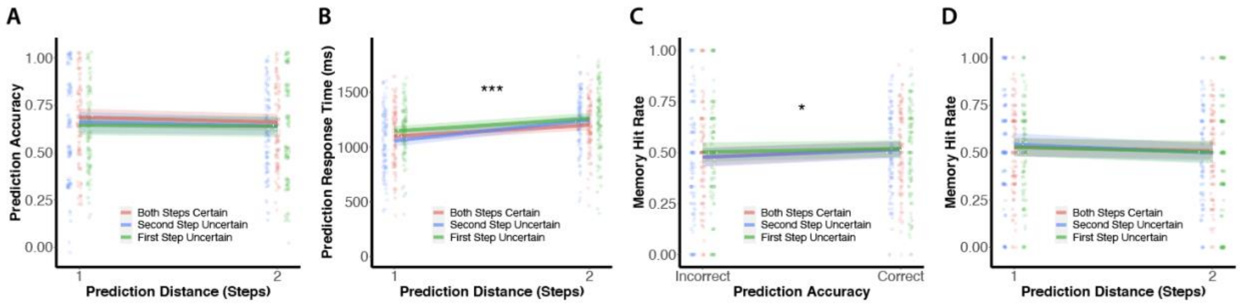

Figure 6. Experiment 2 results: Replication of findings that encoding and prediction are coupled, not competitive. As prediction distance increased, there was no significant change in prediction accuracy **(A)** but there was a significant increase in prediction response time **(B)**. **(C)** Participants were more likely to subsequently recognize cue images for which they made a correct (vs. incorrect) prediction. **(D)** Prediction distance did not affect subsequent recognition memory for cue images. Points represent individual participants. Lines with shaded regions indicate model predictions for fixed effects along with 95% confidence intervals. (*p < 0.05, ***p < 0.001).

Prediction Suffers with Increasing Prediction Distance

We next tested whether our manipulations of prediction difficulty during the Simultaneous Prediction and Encoding Task had an impact on participants' ability to predict upcoming scene categories. We hypothesized that we would replicate our results from Experiment 1 that further reaching predictions would 1) be less accurate and 2) have slower response times.

We first used a mixed-effects logistic regression to predict accuracy on a given trial from the prediction distance of that trial and the transition condition (first step uncertain, second step uncertain, both steps certain; **Figure 5**). Contrary to our hypothesis, there was no main effect of prediction distance on prediction accuracy ($\beta = -0.08$, SE = 0.06, $p = 0.18$). We next used a mixed-effects logistic regression with an interaction term between prediction distance and transition condition to explore any differences in the effect of prediction distance on prediction accuracy between the reference condition (both steps certain) and the other two transition conditions. There were no interactions between prediction distance and transition condition (all ps > 0.5, all betas < 0.09). There was, however, a significant reduction in prediction accuracy between the "first step uncertain" condition and the reference "both steps certain" condition ($\beta = -0.14$, SE = 0.07, $p = 0.04$; **Figure 6A**).

Next, we used a linear mixed-effects model to predict response times on correct prediction trials from prediction distance and transition condition. We found that, across transition conditions, correct two-step predictions took longer than correct one-step predictions ($\beta = 130.60$, SE = 13.36, $p < 0.001$; Figure 6B). We then examined differences in the effect of prediction distance on prediction response time between the reference condition (both steps certain) and the other two transition conditions using a mixed-effects model with an interaction term between prediction distance and transition condition. Participants were significantly slower on trials in the "first step uncertain" condition compared to the reference "both steps certain" condition ($\beta = 54.94$, SE = 12.84, $p < 0.001$). There was no significant difference in response times for the "second step uncertain" condition relative to the reference "both steps certain" condition ($\beta = 4.33$, SE = 12.76, $p = 0.73$). There was, however, an interaction, such that the response time cost for two-step vs. one-step predictions was larger for the "second step uncertain" condition compared to the reference "both steps certain" condition ($\beta = 88.96$, SE = 25.74, $p < 0.001$). No other interactions were significant (all ps > 0.6, all betas < 12.1). Together, these results and the analyses above confirm that our manipulation of prediction uncertainty affected behavior – both prediction accuracy and prediction response times.

These results largely replicate our prior work (Tarder-Stoll et al., 2024a; Tarder-Stoll et al., 2024b) and our findings from Experiment 1 by showing that predicting further into the future comes at a cost to response times. We did not observe a difference in accuracy as a function of prediction distance; however, unlike our prior work and Experiment 1, we only included prediction distances of one and two steps, rather than one to four steps. Furthermore, our findings confirm that our experimental manipulation of prediction uncertainty was successful: predictions in the "first step uncertain" condition were slower and less accurate than predictions in the reference "both steps certain" condition.

Competition or Coupling Between Prediction and Encoding?

We next examined our primary question: the relationship between prediction performance and subsequent memory for the trial-unique cues presented in the Simultaneous Prediction and Encoding Task. As in Experiment 1, prediction performance was measured during the Simultaneous Prediction and Encoding Task, and memory encoding success was based on performance in the Surprise Memory Test.

We began by testing whether successful encoding of trial-unique cues was related to successful prediction for that given cue. Across the transition conditions, there was a significant relationship between participants' prediction accuracy and their subsequent recognition hit rate, such that participants were more likely to subsequently recognize the cue from trials in which they made a correct vs. incorrect prediction (β = 0.13, SE = 0.06, p = 0.03; **Figure 6C**). We next examined main effects and interactions involving transition condition. There were no main effects of transition condition (first step uncertain vs. both steps certain, β = 0.05, SE = 0.07, p = 0.41;

second step uncertain vs. both steps certain, β = -0.01, SE = 0.07, p = 0.92). There were also no interactions between prediction accuracy and transition condition (all ps > 0.5, all betas > -0.09). These results show that accurate predictions were associated with better memory encoding across all transition conditions, suggesting that prediction and encoding were coupled rather than competitive.

We next examined whether memory encoding declined as a function of prediction distance. Similarly to Experiment 1, we used a mixed-effects logistic regression model, in which we predicted subsequent memory for trial-unique cues (hit or miss) as a function of transition condition and prediction distance during the Simultaneous Prediction and Encoding task. We first conducted this analysis on all trials regardless of prediction accuracy, and found no effect of prediction distance on subsequent recognition memory (β = -0.04, SE = 0.06, p = 0.47). Additionally, there were no main effects of transition condition (first step uncertain vs. both steps certain, β = 0.03, SE = 0.07, p = 0.64; second step uncertain vs. both steps certain, β = -0.002, SE = 0.07, p = 0.98). There were also no interactions between transition condition and prediction distance (all ps > 0.8, all betas > -0.04). As in Experiment 1, we next restricted this analysis to only those trials in which predictions were correct. Subsequent recognition memory was not significantly related to prediction distance (β = -0.11, SE = 0.08, p = 0.14; **Figure 6D**). As above, there were no main effects of transition condition (first step uncertain vs. both steps certain, β = -0.01, SE = 0.08, p = 0.86; second step uncertain vs. both steps certain, β = 0.01, SE = 0.08, p = 0.93). There were also no interactions between transition condition and prediction distance (all ps > 0.5, all betas > -0.11). Therefore, though in the same direction as Experiment 1, we were unable to replicate our findings that prediction distance influenced memory encoding.

Discussion

In Experiment 2, we once again found no evidence that encoding and prediction compete. Instead, they were coupled, such that correct (vs. incorrect) predictions were associated with better encoding. Together with Experiment 1, our results suggest that when prediction is accurate, encoding benefits; and factors that cause prediction to suffer (e.g., far prediction distances) can sometimes cause encoding to suffer.

We did not replicate some findings from Experiment 1, specifically the finding that memory encoding suffers as predictions reach further in the future. One difference between Experiment 1 and Experiment 2, however, was that Experiment 1 had predictions up to four steps in the future while Experiment 2 only had predictions up to two steps in the future. To directly compare our Experiment 2 results to those of Experiment 1, we conducted an additional analysis of our Experiment 1 data, focusing on only those trials in which prediction distance was one or two steps in the future, to match Experiment 2. Replicating Experiment 2, we found that one- and two-step trials in Experiment 1 showed coupling between prediction and encoding: trials with correct (vs. incorrect) predictions were associated with superior subsequent recognition memory ($\beta = 0.34$, $SE = 0.13$, $p = 0.009$). Prediction distance, however, did not affect memory encoding success when only one- and two-step predictions were considered ($\beta = -0.06$, $SE = 0.11$, $p = 0.57$). Thus, Experiments 1 and 2 are consistent in showing that when predictions are relatively short (one to two steps), better predictions are associated with better encoding. When prediction has to reach further in the future (three or more steps), however, both prediction and encoding suffer.

One potential limitation of both Experiments 1 and 2 is that each scene category was at least somewhat predictive of upcoming categories. Even when predictions were uncertain, participants could try to predict on each trial. In Experiment 3, we therefore tested whether prediction and encoding continue to be coupled, or if they trade off, when there are situations in which accurate predictions are not possible. To that end, we conducted a replication study of Sherman & Turk-Browne (2020), and tested whether memory encoding shows a trade off with prediction when images that are predictive vs. non-predictive are compared.

Experiment 3

Materials and Methods

Participants

We first conducted a power analysis based on Sherman & Turk-Browne's findings of significantly worse subsequent memory for predictive items vs. control items (Sherman & Turk-Browne, 2020). When setting the power level to 80%, we determined that the target sample size was 46 participants. To reach this target, 61 participants were recruited using the Prolific platform (https://app.prolific.com) to take part in an online experiment. Participants provided informed consent and were paid $15 for their participation. We analyzed data from 46 participants after excluding 15 participants. Exclusion criteria were: 1) responding to fewer than 80% of trials on either question in the Simultaneous Prediction and Encoding Task (Predictability and Upcoming Category questions; Figure 7); 2) responding to fewer than 80% of trials during the Surprise Memory Test; 3) having below-chance performance on both questions in the Simultaneous Prediction and Encoding Task (Predictability <50% and Upcoming Category < 0.08%, **Figure 7**) *and* below-chance performance on the Surprise Memory Test (d' < 0); or 4) on trials in which the participant reported that they were "not able to predict", subsequently failing to correctly select "random image" on the Upcoming Category question (as they were explicitly instructed to do) more than 20% of the time (Figure 7). All procedures were approved by the Columbia University Institutional Review Board. The demographics of the final sample were as follows: Age: 28.3 years [19 - 35 years]; Education: 15.1 years [12 - 21 years]; Race: 3 Asian, 10 Black or African American, 32 White, 1 Multiple Races [1 Middle Eastern and White]; Ethnicity: 3 Hispanic/Latino, 43 not Hispanic/Latino.

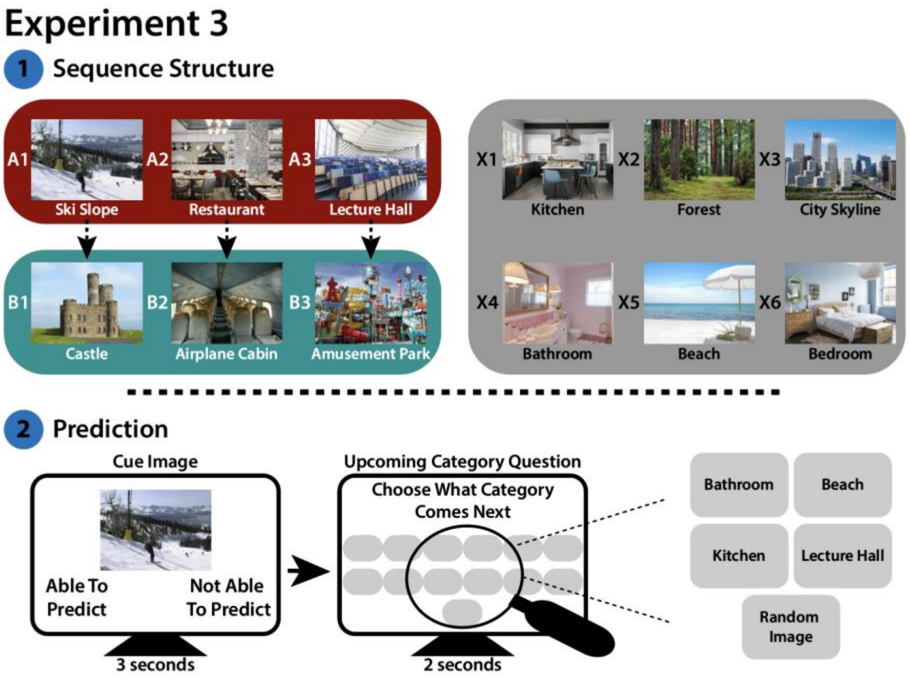

Figure 7. Design for Experiment 3. (Top) Participants were shown a series of images from 12 scene categories. 3 of these categories ("A" items) were designated as "predictive"; each predictive category preceded one of 3 corresponding "predictable" categories ("B" items) 100% of the time. The remaining 6 categories were not predictive or predictable: they were not reliably preceded or succeeded by any other category (control "X" items). During Initial Structure Learning (not shown), participants viewed a continuous series of images from these categories; the sequence of images contained the aforementioned structure. For each image, participants

answered whether they were “able to predict” or “not able to predict” the upcoming category. **(Bottom)** Participants then performed the Simultaneous Prediction and Encoding Task. They were first shown a cue image for 3 seconds. While the cue image was on the screen, participants were asked to respond whether they were “able to predict” or “not able to predict” the upcoming scene category. After the cue disappeared, participants were shown a screen with a single button for each of the 12 categories, and a “Random Image” button. Participants had 2 seconds to select the upcoming category, or “Random Image” if the preceding cue was not predictive. Trials contained the same predictive structure as Initial Structure Learning. Finally, participants took the Surprise Memory Test (not shown; see Figure 2).

Stimuli

Stimuli were 324 images of scenes; some were reused from Experiments 1 and 2, and others were newly collected from Google image searches. Images belonged to one of 12 categories (6 indoor, 6 outdoor): airplane cabins, amusement parks, bathrooms, beaches, bedrooms, castles, city skylines, forests, kitchens, lecture halls, restaurants, and ski slopes. There were 27 exemplar images for each category. Images were resized to 740 pixels by 540 pixels with a resolution of 150 pixels/inch. To account for differences in image memorability, we estimated the intrinsic memorability of each image using the ResMem model (Needell and Bainbridge, 2022). Images were selected such that none of the final set of 324 images had an outlier memorability score greater than 3 standard deviations from the mean.

Procedure

The experiment was conducted on the Gorilla platform (www.gorilla.sc; Anwyl-Irvine et al., 2020). Participants provided informed consent before beginning the Initial Structure Learning phase. For each participant, 3 of the 12 scene categories were randomly designated predictive A categories and 3 of the 12 scene categories were randomly designated predictable B categories. Each A category was 100% predictive of one of the 3 B categories, resulting in 3 A-B category pairs. The 6 categories that were not reliably preceded or succeeded by any other category were control X categories (Figure 7); these images were therefore neither predictive nor predictable. The assignment of categories to the A, B, and X conditions remained constant for each participant, but the individual category exemplar images could change with each presentation of the sequence. For example, an image of a beach might always be followed by an image of a castle, but the exact castle and beach could change from trial to trial.

During Initial Structure Learning, participants were shown up to 7 different exemplars of each category. Participants were instructed that they would see a series of scene categories and that some categories would always be followed by the same category, while others might be followed by a randomly selected category. In the instructions, participants were shown an exemplar image and the name for each category to facilitate familiarity with the category labels (which were needed in the subsequent experiment phase). Following the instructions, participants viewed the image categories following the predictive/non-predictive structure described above. When an A category was presented, it was always followed by its corresponding B category; similarly, when a B category was presented, it was always preceded by its corresponding A category. Images in the X categories were randomly interspersed between the A/B presentations. A given A-B pair could not appear on back-to-back trials. Each category was presented once before the image categories were shuffled (with the constraint that A-B pairs were presented sequentially) and shown again. Before each image, participants were presented with a fixation cross for 0.5 seconds. Participants viewed scene images one at a time for 3 seconds each. While an image was on the screen, participants were instructed to press “a” or “l” on their keyboard to indicate if they were “able to predict” or “not able to predict” the upcoming scene category. Throughout this phase of the experiment, participants saw the entire set of categories 15 times, with a 60-second break after the first 5 presentations. After each category was presented 15 times, participants were presented with 6 boxes and were asked to write down the predictive/predictable scene category pairs. They were told that if 2 categories formed a predictive/predictable pair, both categories could be written in the same box.

Next, participants began the Simultaneous Prediction and Encoding Task (**Figure 7**). They saw a series of novel exemplars of the same categories from Initial Structure Learning, presented in the same structure described above. On each trial, participants were presented with a cue image from one of the previously learned categories and asked to respond whether they were “able to predict” or “not able to predict” the upcoming scene category by clicking on one of the two response options. Critically, although the cue image was always from one of the learned categories, each cue was a trial-unique novel exemplar of that category – allowing us to subsequently test episodic memory for that trial-unique image. Participants had 3 seconds to respond before the image disappeared and the screen advanced. On the next screen, participants saw 13 buttons; 12 buttons each had the name of one of the scene categories, and one button read “random image.” Participants had 2 seconds to select which category was coming up next, or if the category would be a “random image.” Participants were told that if they had selected “not able to predict,” on the previous screen, they should select “random image” on this subsequent screen (Figure 7). In the instructions to this phase, participants were reminded of the category names and shown the layout of the 13 category buttons in order to facilitate speedy responses. Throughout this section of the experiment, participants saw 10 novel exemplars for each category, resulting in 120 trials total. Participants were given a 60-second break halfway through the task.

Finally, participants completed the Surprise Memory Test. The memory test consisted of 240 trials in which participants were shown either a novel exemplar from one of the categories in the experiment (new images, 120 trials), or an exemplar that they had previously viewed in the Simultaneous Prediction and Encoding Task (old images, 120 trials). As in Experiments 1 and 2, during each trial, an image was presented for 5 seconds and participants were instructed to use their keyboard to indicate whether the image was old or new by using a 6-point confidence scale: "sure old", "maybe old", "guess old", "guess new", "maybe new", or "sure new". At 3 approximately evenly spaced time points in this phase, participants were given a 60-second break.

Statistical Analyses

To examine performance across the three conditions of interest (A, B, and X images), we followed the approach taken in Sherman & Turk-Browne (2020). We used repeated-measures ANOVAs to analyze participants' prediction performance and subsequent recognition memory performance across image types (predictive "A" images, predictable "B" images, and control "X" images). Post-hoc paired-samples t-tests were used to perform follow-up comparisons.

To explore the trial-wise relationship between prediction and subsequent recognition memory, we used a mixed-effects logistic regression model to predict binarized Surprise Memory Test accuracy (0 = miss, 1 = hit) for the trial-unique cue images from the Simultaneous Prediction and Encoding Task as a function of prediction accuracy on the Upcoming Category question (effect coded: -0.5 = incorrect, 0.5 = correct), image type (dummy coded with control X categories as the reference condition), and their interaction. We included image type as an interacting variable to study the difference between the effect of prediction accuracy on subsequent recognition memory in the reference/control condition and the predictive/predictable conditions.

Results

Overall Prediction and Encoding Performance

We first verified that participants' performance on the Simultaneous Prediction and Encoding Task and the Surprise Memory Test were above chance. Here, there were two prediction measures during the Simultaneous Prediction and Encoding Task: the Predictability question (in which participants responded whether they were "able to predict" vs. "not able to predict") and the Upcoming Category question (in which participants reported the category of the following image). Performance on both questions was measured as the proportion of trials answered correctly. Accuracy on the Predictability question was higher than chance (mean = 0.68, chance = 0.50, $t(45) = 5.45$, $p < 0.001$), as was accuracy on the Upcoming Category question (mean = 0.63, chance = 0.08, $t(45) = 14.68$, $p < 0.001$). Accuracy on the Upcoming Category question remained above chance when we considered only those trials in which predictions could be made (i.e., excluding trials in which the correct answer was "random image", mean = 0.47; chance = 0.08; $t(45) = 8.56$, $p < 0.001$). Subsequent memory performance on the Surprise Memory Test was also significantly above chance (mean $d' = 0.48$, chance = 0; $t(45) = 11.60$, $p < 0.001$).

We further tested whether performance on the Simultaneous Prediction and Encoding Task was influenced by image type (A = predictive, B = predictable, X = control, see Figure 7). We measured the likelihood that a participant would choose "able to predict" on the Predictability question across the image types (A, B, or X). If participants learned the task structure, they should correctly identify that they were "able to predict" more often for the predictive A images vs. the B and X images, which were not predictive of the upcoming category. We found a significant difference in the probability of choosing "able to predict" across image types (F(2,90) = 32.89, $p < 0.001$, Figure 8A). Follow-up t-tests confirmed that participants were significantly more likely to choose "able to predict" for A categories vs. X categories (t(45) = 7.11, $p < 0.001$) and for A categories vs. B categories (t(45) = 5.33, $p < 0.001$). There was no significant difference in the likelihood of selecting "able to predict" between B and X categories (t(45) = 1.13, p = 0.26). Together, this shows that participants were able to both successfully predict and encode images, and detected predictive structure in the stimuli.

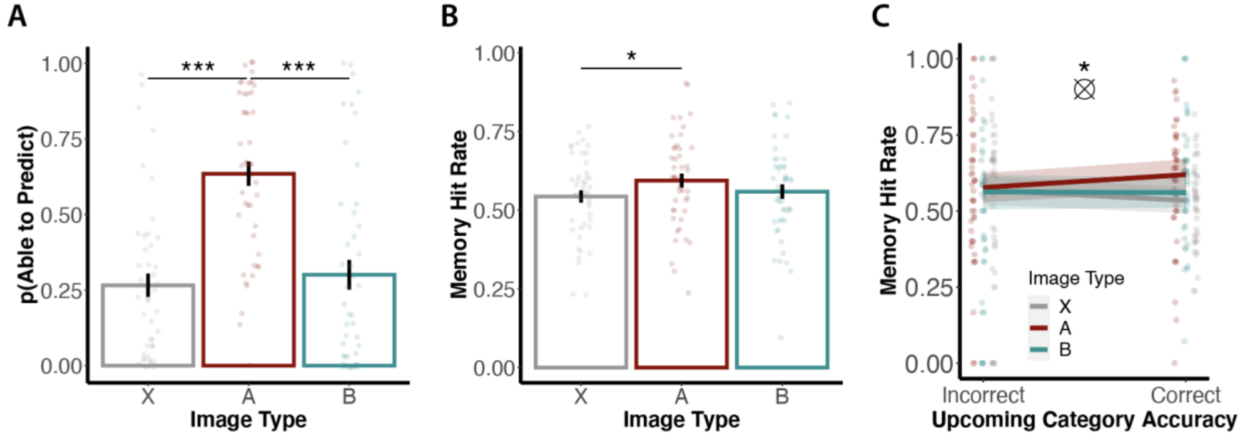

Figure 8. Experiment 3 results: Memory encoding is superior when prediction is possible. (A) Participants were significantly more likely to respond "Able to Predict" for predictive "A" images compared to either predictable "B" images or control "X" images. Points represent individual participants. Error bars indicate standard error of the mean. **(B)** Participants remembered predictive "A" images significantly better than control "X" images. Points represent individual participants. Error bars indicate standard error of the mean. **(C)** An examination of category selection accuracy as a function of image type (X: control; A: predictive; B: predictable) yielded a significant difference between the X and A conditions but not between the X and B conditions. The interaction arose because memory tended to be superior when category selection was correct (vs. incorrect) for (predictive) A items but this relationship was reversed for the (control) X items. Points represent individual participants. Lines with shaded regions indicate model predictions for fixed effects along with 95% confidence intervals. (*$p < 0.05$).

Ability to Predict Enhances Subsequent Memory

We next shifted to our primary focus: to determine whether predictive images are subsequently remembered better or worse than non-predictive images. Results from Experiments 1 and 2 suggested that there is coupling between prediction and encoding; this would lead to the hypothesis that predictive ("A") images might be *better* encoded than non-predictive images. On the other hand, Sherman & Turk-Browne (2020) proposed that there is competition between prediction and encoding: they found that predictive images ("A" images) were encoded *worse* than non-predictive images (specifically, "X" images).

To test these alternative possibilities, we first determined if subsequent memory differed by image type. Indeed, we found a significant difference in participants' memory across image types ($F(2,90) = 3.14$, $p = 0.04$, see Figure 8B). Follow-up t-tests revealed that subsequent recognition memory for predictive A images was significantly better than memory for control X images (t(45) = 2.63, p = 0.01) but not significantly different from B images (t(45) = 1.53, p = 0.13). There was no difference in subsequent recognition memory between B and X images (t(45) = 0.86, p = 0.39). Thus, in our task, encoding was better when prediction was possible: unlike Sherman & Turk-Browne (2020), we found *superior* rather than inferior memory for A vs. X images. We discuss potential reasons for the differences between our findings and those of Sherman & Turk-Browne further below.

We next examined the trial-wise relationship between prediction and encoding by testing whether participants were more or less likely to remember an image if they correctly answered the Upcoming Category question. A trial-wise mixed-effects logistic regression model predicting subsequent recognition memory (0 = miss, 1 = hit) from accuracy on the Upcoming Category question and image type (A, B, X) confirmed our finding (above) that memory is superior for predictive A images vs. control X images (β = 0.19, SE = 0.07, p = 0.01). Importantly, this effect was modulated by accuracy on the Upcoming Category question: there was a significant interaction between condition (predictive A image vs. control X image) and accuracy on the upcoming category question (β = 0.31, SE = 0.15, p = 0.03, see Figure 8C). This interaction arose because of opposite trends in the relationship between Upcoming Category accuracy and memory encoding for A vs. X images. When participants correctly reported the upcoming category for predictive A images, their memory encoding tended to be superior; conversely, when participants correctly identified that a random image was the upcoming category for control X images, their memory encoding tended to be worse. There was no significant difference between the B vs. X images, either in terms of a main effect (β = 0.04, SE = 0.07, p = 0.58) or interaction with Upcoming Category accuracy (β = 0.12, SE = 0.15, p = 0.40).

Together, these results confirm and extend Experiments 1 and 2 by showing that when prediction is possible and accurate, memory encoding is superior.

Discussion

As in Experiments 1 and 2, Experiment 3 found coupling rather than competition between encoding and prediction. Compared to control images that are not predictive, images that are predictive of upcoming categories are associated with superior memory encoding. Further, accurate (vs. inaccurate) predictions are associated with enhanced episodic memory encoding, whereas accurate identification that predictions are not possible is associated with worse memory encoding. Our results deviate from those of Sherman & Turk-Browne (2020): they found worse memory for predictive A images vs. control X images, whereas we found the opposite. We discuss potential reasons for the discrepancy in results in the General Discussion.

General Discussion

Across three experiments, we consistently found that encoding and prediction are coupled, rather than competitive. In Experiment 1, we showed that making predictions further into the future (vs. closer) was associated with longer response times and worse memory encoding, indicating parallel costs to prediction and encoding. In Experiment 2, we observed that accurate (vs. inaccurate) predictions were associated with better simultaneous encoding, indicating trial-by-trial coupling between prediction and encoding. In Experiment 3, encoding was improved when predictions were possible (vs. impossible), particularly when those predictions were accurate.

Collectively, these findings suggest that encoding and prediction can cooperate rather than compete with one another, enabling successful retrieval and encoding over behaviorally relevant timescales.

Our findings of behavioral coupling between prediction and encoding are in stark contrast to work suggesting a trade-off between these two processes. Foundational theories and empirical work have long proposed that encoding and retrieval operate in opposing states (Colgin et al., 2009; Hasselmo et al., 2002; Hasselmo & Stern, 2014, Honey, Newman, & Shapiro, 2017; Rizzuto et al., 2006; Tarder-Stoll*, Jayakumar* et al., 2020). These states have lingering influences on behavior lasting several seconds (Duncan et al., 2012; Duncan & Shohamy, 2016; Patil & Duncan, 2018; Sherman & Turk-Browne, 2020). Contrary to this prevailing view, our studies revealed that successful retrieval did not conflict with, but rather facilitated, successful encoding. This discrepancy is even more striking given that Experiment 3 employed an adapted version of the experimental paradigm used in Sherman & Turk-Browne (2020). Why did we observe coupling, while other work has found evidence for competition between encoding and prediction?

We note at least three differences between the current study and Sherman & Turk-Browne (2020) that could drive inconsistencies in the dynamics between encoding and prediction, leading to coupling or competition across different studies. One possibility is that competition or coupling depends on whether predictions are explicitly generated. In the current study, we observed coupling when participants made explicit predictions about upcoming categories during simultaneous memory encoding, whereas Sherman & Turk-Browne (2020) observed competition during neural predictions that were unaccompanied by an explicit, behaviorally measured, predictive judgment. Another possibility for the discrepancy between our experiment and prior work is that competition vs coupling may depend on the amount of exposure to predictive structure. In our experiments, participants first learned the predictive structure of the scene categories in a separate phase of the experiment before completing a behavioral prediction and encoding task. On the other hand, Sherman & Turk-Browne (2020) measured neural prediction without prior exposure to the structure: they had participants implicitly learn the structure over the course of the simultaneous prediction and encoding task. This raises the possibility that, while encoding and retrieval might trade off during initial exposure to, and learning of, temporally structured stimuli, they need not be competitive after more extensive exposure to the predictive structure, as shown in the current study. Lending support to this hypothesis, prior work has shown that performance of a well-learned motor sequence facilitates simultaneous memory encoding (Gasser & Davachi, 2020). A third difference is that the current study observed trial-wise coupling between encoding and prediction – on trials in which a given participant accurately predicted upcoming categories, their memory encoding was also enhanced. In contrast, Sherman & Turk-Browne's finding linking hippocampal prediction to worse encoding was across participants: participants who showed more evidence of hippocampal prediction were worse at encoding. We note, however, that even when conducting the same behavioral analyses as Sherman & Turk-Browne (**Figure 8B**), we found opposing results, with better (rather than worse) encoding for predictive vs. control images – perhaps for the two reasons mentioned above. Future research should investigate how each of these factors contribute to competition or coupling between encoding and prediction.

Another possibility for the observed behavioral coupling between encoding and prediction is differences in task engagement. Might this coupling arise because participants are generally good at cognitive tasks when they are attentive, and bad when they are inattentive? This explanation cannot account for our findings for two reasons. First, in Experiment 1, there were costs to both prediction and encoding when considering *only* correct prediction trials. Specifically, when predictions were correct, prediction response times were slower and memory encoding was worse with increasing prediction distance. Thus, participants were sufficiently on-task to make the correct prediction, but they experienced costs to both prediction response times and memory encoding with increasing prediction distance, despite being on task and accurate. Second, across conditions in Experiment 3, we found opposite effects on memory encoding as a function of accuracy in the prediction judgment (selection of the upcoming category; **Figure 7**). For the control X images, correctly indicating that prediction is not possible was associated with slightly *worse*, not better, encoding. This is the opposite of what we found for the predictive A images, for which correctly identifying the upcoming category was associated with *better* encoding. Thus, being on-task for the prediction judgment was not generally associated with better encoding: instead, the relationship between accuracy for the upcoming category judgment and memory encoding reversed for the predictive A vs. control X images. Together, these lines of evidence argue against the supposition that coupling between prediction and encoding can be explained as behavioral differences in on vs. off-task performance.

Importantly, despite observing *behavioral* coupling between encoding and prediction, we do not believe that the current findings argue against the existence of separate states. Theoretical and empirical work highlights two factors that play important roles in modulating encoding and retrieval states in the brain: theta oscillations and acetylcholine (Douchamps et al., 2013; Hasselmo, 2006). First, prior work has suggested that separate phases of the theta oscillation may optimize encoding vs. retrieval: encoding states may be enhanced at the peak of theta, whereas retrieval states may be enhanced at the trough (Hasselmo et al., 2002; Hasselmo, 2005;

Kerrén et al., 2018; Kerrén et al., 2022; Norman et al., 2006). Because theta oscillates relatively rapidly, at approximately 4-8Hz in humans, encoding and retrieval states can also fluctuate on a similarly fast timescale (Hasselmo, 2005). Consequently, in our study, it is possible that encoding and prediction states were fluctuating on fast timescales that were not captured by slower behavioral measures. This raises the intriguing possibility that fast fluctuations between encoding and retrieval states, such as those linked to theta oscillations, might support coupling between these memory processes on behaviorally relevant timescales.

Second, the neuromodulatory state of the brain, and particularly the cholinergic system, may play an important role in shaping dynamics between encoding and retrieval (Decker & Duncan, 2020; Hasselmo, 2006; Tarder-Stoll*, Jayakumar*, et al., 2020;). High acetylcholine levels may bias the hippocampus toward an encoding state whereas low acetylcholine levels may bias the hippocampus toward a retrieval state to make predictions about upcoming events (Hasselmo, 2006; Poskanzer & Aly, 2023). Importantly, cholinergic modulation of the hippocampus can linger over several seconds (Meeter et al., 2004), suggesting that acetylcholine-induced biases toward encoding vs retrieval may oscillate more slowly, on timescales relevant for behavior. Indeed, cholinergic agonists enhance performance on a hippocampally-dependent external attention task (Ruiz et al., 2021), which may lead to enhanced encoding. Further, behavioral manipulations linked to acetylcholine release can prioritize encoding vs. retrieval states in behavior that persist for several seconds (Duncan et al., 2012, Duncan & Shohamy, 2016; Patil & Duncan, 2018). Together, this body of work raises the possibility that high or low cholinergic states – by virtue of pushing the hippocampus toward either an encoding mode or a retrieval mode – may reveal sustained competition between encoding and prediction, leading to a behavioral trade-off. Conversely, intermediate cholinergic states may allow encoding and retrieval modes to be on more even footing, and thus reveal behavioral coupling between them. These hypotheses can be tested in future work that examines hippocampally relevant behaviors in tandem with either behavioral (e.g., Duncan et al., 2012, Duncan & Shohamy, 2016; Patil & Duncan, 2018) or pharmacological (e.g., Ruiz et al., 2021) manipulations of the cholinergic system.

One potential limitation of the current study is that our experimental paradigm differed across the three experiments. Although all three studies contained the same three phases, differences in the three experiments may have led to the appearance of inconsistent effects, specifically across Experiments 1 and 2. In Experiment 1, far (vs. near) prediction distances were associated with costs to memory encoding, but we did not observe this in Experiment 2. Conversely, in Experiment 2, correct (vs. incorrect) predictions were associated with superior encoding, but we did not observe this effect across all trials in Experiment 1. This apparent inconsistency, however, was due to experimental design decisions that were made to accommodate a larger number of conditions in Experiment 2 (due to the addition of probabilistic transitions). When we analyzed only 1-2 step trials in Experiment 1, to match Experiment 2, the results were consistent: both studies showed that correct (vs. incorrect) predictions were associated with superior encoding; and that encoding success was comparable across prediction distances of 1-2 steps. Thus, the effects of prediction distance on encoding success may be most pronounced when far-reaching predictions (more than 2 steps) are included in the experiment. Regardless of this caveat, however, both Experiments 1 and 2 converged in showing no evidence for competition between encoding and prediction; instead, any evidence of an association between encoding and prediction was in the direction of coupling rather than a trade-off.

Together, across three experiments, we showed that encoding and prediction are coupled with one another in behavior. Accurate prediction enhanced simultaneous memory encoding, and factors that hurt prediction also hurt encoding. This suggests that encoding and prediction need not trade off, and can instead facilitate one another, enabling cooperation between opposing memory processes and ultimately contributing to successful behavior.

Constraints on Generality

This research was conducted using an online sample of healthy adults ages 18 to 39 who were English speakers and resided in the United States. Furthermore, a subsample of the reported participants were all students at Columbia University. The results reported here may therefore be limited to the characteristics of the current sample. Future studies should examine encoding and prediction dynamics in a variety of populations to determine the generalizability of the current results. For example, competitive dynamics between encoding and retrieval may be modulated by the neurotransmitter acetylcholine, which varies across the lifespan and in clinical populations, such as Alzheimer's disease (Muir, 1997). Future work can determine how the brain balances encoding and retrieval over the course of healthy aging, as well as in clinical populations in order to understand how cognitive impairments might impact our ability to simultaneously encode new information while making predictions about the future.

CRediT Statement

Craig Poskanzer: Formal analysis, Investigation, Data Curation, Methodology, Project Administration, Software, Validation, Visualization, Writing—original draft, Writing—review and editing; **Hannah Tarder-Stoll**: Conceptualization, Data Curation, Investigation, Methodology, Project Administration, Software, Writing—original draft, Writing—review and editing; **Raheema Javid**: Investigation, Methodology, Writing—original draft, Writing—review and editing; **Edoardo Spolaore**: Investigation, Writing—review and editing; **Mariam Aly**: Conceptualization, Methodology, Funding Acquisition, Project Administration, Resources, Supervision, Writing—original draft, Writing—review and editing.

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