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Episodic memory processes modulate how schema knowledge is used in spatial memory decisions

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ABSTRACT

Schema knowledge can dramatically affect how we encode and retrieve memories. Current models propose that schema information is combined with episodic memory at retrieval to influence memory decisions, but it is not known how the strength or type of episodic memory (i.e., unconscious memory versus familiarity versus recollection) influences the extent to which schema information is incorporated into memory decisions. To address this question, we had participants search for target objects in semantically expected (i.e., congruent) locations or in unusual (i.e., incongruent) locations within scenes. In a subsequent test, participants indicated where in each scene the target had been located previously, then provided confidence-based recognition memory judgments that indexed recollection, familiarity strength, and unconscious memory for the scenes. In both an initial online study ($n = 133$) and replication ($n = 59$), target location recall was more accurate for targets that had been located in schema-congruent rather than incongruent locations; importantly, this effect was strongest for new scenes, decreased with unconscious memory, decreased further with familiarity strength, and was eliminated entirely for recollected scenes. Moreover, when participants recollected an incongruent scene but did not correctly remember the target location, they were still biased away from congruent regions—suggesting that detrimental schema bias was suppressed in the presence of recollection even when precise target location information was not remembered. The results indicate that episodic memory modulates how schemas are used: Schema knowledge contributes to spatial memory judgments primarily when episodic memory fails to provide precise information, and recollection can override schema bias completely.

1. Introduction

Each day we make predictions about where objects will be in the world around us. These predictions are often based on memory for past experiences: We can find an object, such as our keys, by remembering where the object was the last time we saw it. Alternatively, we can draw on our knowledge about where objects are *typically* located, using semantic knowledge in the form of schemas (Bartlett & Burt, 1932; Ghosh & Gilboa, 2014; Henderson, 2003; Rumelhart, 2017). Although schemas can often facilitate performance (Alba & Hasher, 1983; Anderson, 1981; Bartlett & Burt, 1932; Greve, Cooper, Tibon, & Henson, 2019; Rumelhart, 2017), they can also lead to memory impairments and distortions (Johnson, 1997; Lew & Howe, 2017; Ortiz-Tudela, Milliken, Botta, LaPointe, & Lupiañez, 2017; Roediger & McDermott, 1995; Sweegers, Coleman, van Poppel, Cox, & Talamini, 2015; Tompary & Thompson-Schill, 2021), and their inappropriate application has been linked to catastrophic aviation and driving errors (Dismukes, 2008; Hole, 2014; Plant & Stanton, 2012) as well as prejudice and depression (Cox, Abramson, Devine, & Hollon, 2012; Hawke & Provencher, 2011). While it is clear that both schemas and memory can separately guide our behavior, it is not yet well understood how schemas and memory interact to influence behavior (Gilboa & Marlatte, 2017; van Buuren et al., 2014; van Kesteren, Ruiter, Fernández, & Henson, 2012).

Prior work on schemas and memory has indicated that the hippocampus is critical in supporting memory for individual episodes, whereas the neocortex and the medial prefrontal cortex are involved in supporting schema knowledge (Gilboa & Marlatte, 2017; McClelland, McNaughton, & O'Reilly, 1995; Robin & Moscovitch, 2017; van Kesteren, Rijpkema, Ruiter, & Fernández, 2010). It has been proposed that these systems function in a complementary manner (McClelland, 2013;

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McKenzie et al., 2014; McKenzie, Robinson, Herrera, Churchill, & Eichenbaum, 2013; Preston & Eichenbaum, 2013) with schema knowledge and episodic memory synergistically contributing to a desired behavioral outcome. Based on this proposal, behavioral performance is expected to be better when both forms of information are available than either one alone.

In contrast, however, recent work has suggested that schemas and episodic memory may instead operate in a competitive or inhibitory manner (Gilboa & Marlatte, 2017; Sommer, 2017; van Kesteren et al., 2012; Wagner et al., 2015). For example, whereas novel learning is generally related to hippocampal activity, schema-related learning has been associated with a shift to medial prefrontal involvement (Sommer, 2017; Wagner et al., 2015). When schema knowledge becomes more relevant, cortical representations are engaged, and the hippocampus appears to be suppressed (Bein, Reggev, & Maril, 2014; Gilboa & Marlatte, 2017; van Kesteren et al., 2012, 2013). If these neural findings are reflected in behavior, schema knowledge and episodic memory may compete to influence performance. Based on this competition hypothesis, therefore, one might expect that when memory is stronger, schema knowledge may contribute less to behavioral performance, and vice versa.

Additionally, work with Bayesian models of memory has suggested that rather than cooperating or competing per se, episodic memory and schema knowledge are rationally combined to support behavior (Duffy, Huttenlocher, & Elizabeth Crawford, 2006; Hemmer & Persaud, 2014; Hemmer & Steyvers, 2009; Hemmer, Tauber, & Steyvers, 2015; Huttenlocher, Hedges, & Duncan, 1991; Huttenlocher, Hedges, & Vevea, 2000; Persaud & Hemmer, 2016; Persaud, Macias, Hemmer, & Bonawitz, 2021). For example, work using these models has found that memory responses are consistently biased by category-related schema information, such that people draw upon schemas in order to maximize the accuracy of memory decisions (e.g., Huttenlocher et al., 1991). Some of these models suggest that the relative weighting of schemas versus memory may depend on the strength of the memory (e.g., Hemmer et al., 2015; Hemmer & Steyvers, 2009), but to our knowledge, this has not yet been tested directly. Therefore, similar to the neural competition models outlined above, based on results from work with Bayesian models, one might expect that as memory strength increases, schema knowledge will exert less of an influence on behavior.

Preliminary evidence supports the possibility that memory strength

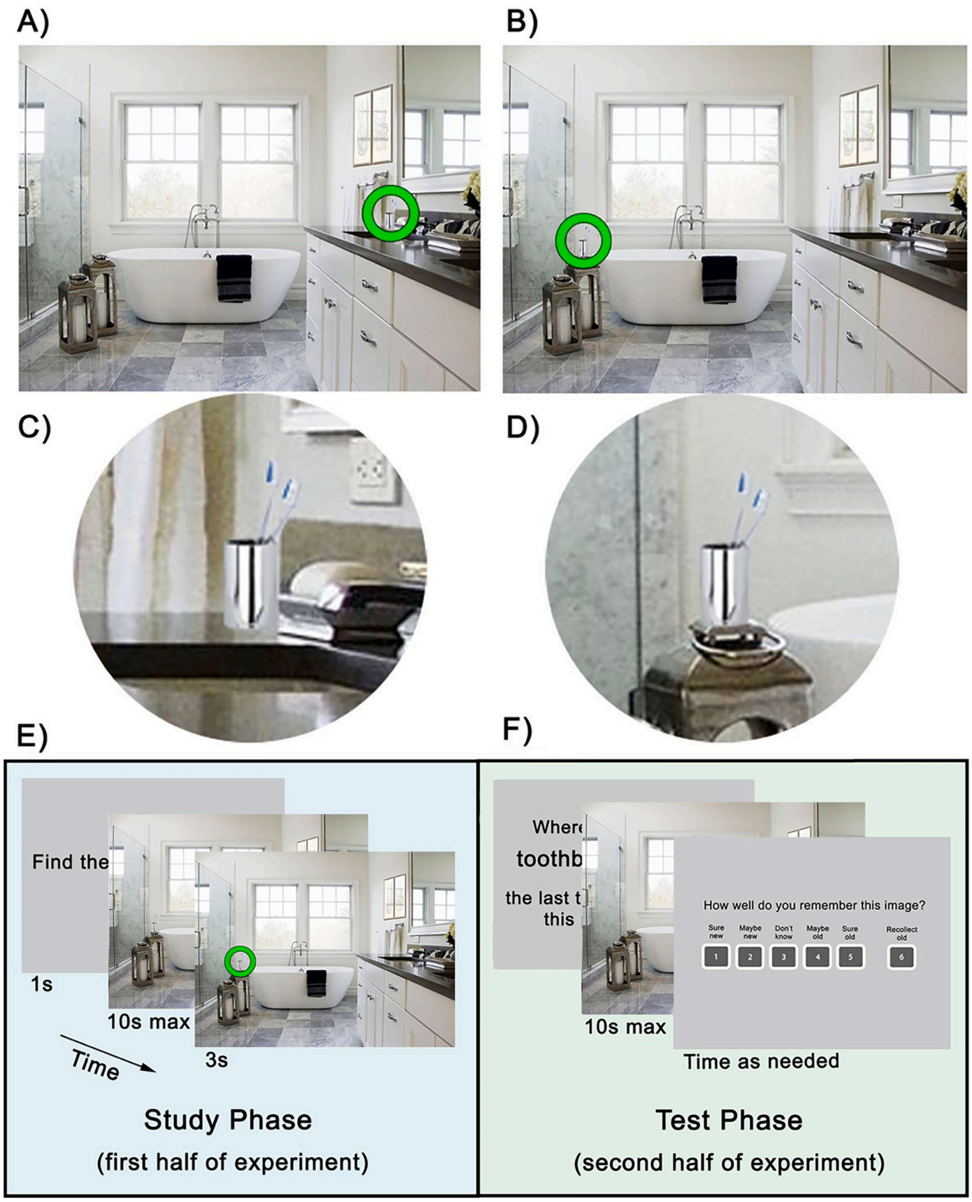

Fig. 1. Sample stimuli and procedure. A) The congruent version of a sample scene, with the target object (toothbrush cup) next to the sink. The ring appeared around the target after participants clicked on the scene in the study phase. B) The incongruent version of the scene. C) Closeup of the target object in the congruent scene (for visualization only; this was not part of the experiment). D) Closeup of the target object in the incongruent scene. E) The trial sequence in the study phase, which consisted of 60 scenes presented two times each (120 trials). In each trial, a target probe appeared (e.g., "Find the toothbrush cup"), followed by the scene with target object. Participants were required to click on the target object within 10s. After clicking or after 10s, whichever occurred first, a ring appeared around the target for 3s. F) The trial sequence in the test phase, which consisted of 80 scenes (80 trials). A target probe appeared, followed by the scene without the target object, and participants were given 10s to click on the scene location that they thought had contained the target when the scene was presented in the study phase. After 10s or clicking, whichever occurred first, participants gave a confidence-based recognition memory response for the scene.

and schema information may trade off or compete in the magnitude of their influence on behavior. For example, when participants are searching for objects in scenes, repetition-related improvements in search speed are greater when objects are in random locations compared to schema-consistent locations (Võ & Wolfe, 2013); moreover, across repeated presentations, some participants are able to learn to search for hidden targets in locations that are inconsistent with semantic expectations (Rehrig, Cheng, McMahan, & Shome, 2021). Although these studies did not directly assess participants' episodic memory, the results suggest that stronger episodic memory may reduce reliance on schema information. In addition, in an eyetracking study, we found that attention in scenes was less driven by semantic information when participants' familiarity with the scenes was stronger (Ramey, Yonelinas, & Henderson, 2020). Although the latter study did not examine schemas directly, the results suggest that semantic knowledge may interact with memory such that its influence decreases when memory strength increases.

The present study aimed to directly address the question of how schema knowledge interacts with episodic memory strength to influence behavioral performance, operationalized as spatial memory decisions. To do this, we examined the impact of spatial schema knowledge and recognition memory strength for scenes on the ability to remember where a target object was located in a previously viewed scene. First, participants searched for target objects in scenes during an initial study phase. Half the scenes contained the target object in a schema-congruent location (e.g., toothbrush next to sink), and half contained the target object in a schema-incongruent location (e.g., toothbrush next to bathtub; see Fig. 1). During a subsequent test phase, participants were shown a mixture of new and studied scenes that did not contain the target object and were asked to indicate the precise location that had contained the target object during the study phase. To examine the joint effects of schema congruency and memory strength for the scenes on spatial accuracy, we had participants make a recognition memory response on a confidence-based scale that allowed us to examine familiarity strength, recollection, and unconscious memory for the scenes (Ramey, Yonelinas, & Henderson, 2019). If memory is able to down-weight the use of schema knowledge, then schema congruency effects on spatial recall should decrease in magnitude as familiarity confidence increases. In addition to providing familiarity confidence, participants indicated if the scenes were confidently recognized *and* were accompanied by an ability to remember specific details about the study event (i.e., recollection; e.g., Tulving, 1982, 1985). Recollect responses have been interpreted to reflect either a distinct hippocampus-based recollection process, or extremely high levels of episodic memory strength (e.g., see Eichenbaum, Yonelinas, & Ranganath, 2007; Wixted, 2007; Yonelinas, 2002). In either case, if stronger episodic memory decreases the use of schema knowledge, then the schema congruency effects should be smallest for the recollect responses. Lastly, the confidence scale also allowed us to assess whether unconscious memory modulated the effects of schema congruency on spatial accuracy. Unconscious memory was indexed by comparing performance on new scenes to performance on scenes that had been studied but that participants were highly confident were new (i.e., high-confidence misses; Ramey et al., 2019; Ramey, Henderson, & Yonelinas, 2020). That is, because performance in forgotten old scenes could reflect either unconscious memory or a complete lack of memory (e.g., not paying attention to the scene at study), comparison to a baseline of new scenes is required to assess whether old scenes that were forgotten still contained some trace of unconscious memory. We also replicated the initial experiment in a separate sample to assess the robustness of the results.

2. Method

2.1. Participants

One-hundred and fifty undergraduate students successfully completed the experiment for course credit. Participants were required to pass pre-experimental attention checks to ensure they had read and understood the instructions. A sample size of 120 participants was needed to provide 95% power to detect the most relevant previously observed effect, which we obtained in a prior study (i.e., the interaction between familiarity strength and semantic meaning in influencing attention; Ramey, Yonelinas, & Henderson, 2020). We selected a final sample size of 150 participants to ensure that we would have adequate power even after potential exclusions. Participants were removed from analysis for technical issues or for failing to properly complete the task; specifically, due to clicking on the objects during the study phase less than 90% of the time (6 participants), quickly pressing a key to get through the recognition response phase (4 participants), or having atypical mouse coordinates that did not conform to the typical browser output (e.g., from using a tablet rather than computer; 7 participants). A total of 17 participants' data was removed, such that the sample used in analysis consisted of 133 participants.

The replication sample consisted of 60 undergraduate students who did not participate in the first experiment. The sample size was selected to provide 80% power to detect the familiarity strength effect in the first experiment. One participant was excluded for having atypical mouse coordinates, such that the final sample consisted of 59 participants. The experimental stimuli and procedure used in the replication sample were identical to the original experiment.

2.2. Apparatus

The study was conducted online using Javascript via JSpsych, which allows for accurate, high-speed presentation timing and response recording (de Leeuw, 2015). Participants were instructed to use a computer with a browser size of at least 800 × 600px. The experiment would not begin if a participant's browser size was less than 800 × 600px but allowed them to continue once they expanded it sufficiently; this requirement precluded use of a phone. Participants were able to see their cursor throughout the experiment.

2.3. Stimuli

Stimuli were 80 photographs of real-world scenes. All scenes were presented in colour at a resolution of 800×600 pixels. Of these 80 scenes, 60 were presented at study and test (i.e., old scenes), and 20 were presented only at test (i.e., new scenes). We included more old scenes than new scenes to ensure that an adequate number of old scenes were recognized at each level of confidence for analysis. Stimulus presentation was counterbalanced, such that the scenes appeared in different conditions (i.e., presented at both study and test, or used as a new lure during test) for different participants to mitigate stimulus effects.

Five scene categories were used, and a single type of target object was used for each category. The categories and targets consisted of kitchens (target: frying pan), dining rooms (target: wine glass), bedrooms (target: alarm clock), living rooms (target: coffee mug), and bathrooms (target: toothbrush cup). Eight different object exemplars were used per category, such that the visual features of the target object varied across different scenes within a category. In each scene, only one exemplar of the target object was present, and this was kept consistent across presentations. For example, in each living room scene, there was only one coffee mug present. Importantly, for a given scene viewed by a given participant, the target was always visually identical and in the same location across repeated viewings.

Two versions of each scene were created using Adobe Photoshop (Fig. 1A-D): one with the target object in a schema-consistent location (i.e., *congruent* scene), and one with the target in an unexpected location (i.e., *incongruent* scene). The congruent location was consistent across all scenes in a category, such that targets were placed relative to larger objects with which the target objects co-occur with high probability in daily life (Boettcher, Draschkow, Dienhart, & Võ, 2018). Specifically, in bathroom scenes, the toothbrush cups were located next to sinks; in dining room scenes, the wine glasses were located on tables (within arm's reach of a chair); in kitchen scenes, the pans were on stove burners; in bedroom scenes, the alarm clocks were on night stands; and in living room scenes, the coffee mugs were on coffee tables. In incongruent scenes, on the other hand, the objects were arbitrarily placed in unexpected but physically plausible locations (i.e., on floors, shelves, chairs, etc. rather than floating).

Scene congruency was manipulated within-subjects such that each participant was presented with half incongruent scenes and half congruent scenes. The congruent and incongruent versions of the scenes were also counterbalanced such that half of the participants saw the congruent version of a given scene, whereas the other half saw the incongruent version of that same scene. Importantly, a given scene was always congruent or incongruent within a given counterbalance, such that the target was always in the same place in a scene viewed across multiple repetitions by a given participant.

2.4. Procedure

The experiment lasted approximately 45 min and consisted of a study phase followed by a test phase (Fig. 1E-F). There was a 2-min break between the study and test phases. Before each phase, participants were given instructions as well as practice trials to familiarize them with the procedure. Participants were given a break midway through each phase. All procedures were approved by the University of California, Davis Institutional Review Board.

2.4.1. Study phase

Participants were told that they would be searching for and clicking on target objects and were asked to try to remember the scene and object locations for a later memory test. During the study phase, participants were presented with 60 unique scenes that were each repeated twice, for a total of 120 trials. The repetitions were randomly intermixed throughout the study phase, with the requirement that the same scene did not appear twice in a row. In each trial, participants were first given a 1s probe alerting them to the target object they would need to search for. For example, for dining room scenes, the probe was "Find the wine glass." After the probe, the scene appeared, and participants had 10s to click on the target object in the scene. After clicking on the scene, or after 10s had elapsed, a green ring appeared around the target object and remained for 3s to allow participants to encode the scene (Fig. 1A-B).

2.4.2. Test phase

In the test phase, participants were asked to recall where the target object had been located in each scene when they had seen it during the study phase, and to provide a confidence-based recognition memory judgment for each scene. Participants were told that even if they thought that a scene was new (i.e., not presented in the study phase), they should make their best guess for where the target object might have been if it had in fact been in the study phase—that is, if their recognition memory had failed and it actually was an old scene. The test phase included 80 scenes, 60 of which were presented in the study phase and 20 of which were new lures. Each scene was presented once, for a total of 80 test trials. Each trial began with a 1s target probe (e.g., "where was the wine glass the last time you saw this picture?"), followed by the presentation of a scene without its target object, and participants were given 10s to click on the location in the scene where they remembered having seen the target object in the study phase. After clicking, or after 10s elapsed, a recognition memory response scale appeared and participants were given time as needed to respond.

Memory strength was measured by asking participants to rate memory confidence for each scene on a 6-point scale during the recognition judgment (Yonelinas, 2002). Note that participants' memory confidence for the background scene was probed, not their confidence in their memory for the target location. Participants were told that if they could consciously recollect some qualitative aspect of the initial learning event, such as what they thought about when the scene was encountered earlier, they should respond "Recollect old (6);" otherwise, they rated their memory confidence by responding "I'm sure it's old (5)," "Maybe it's old (4)," "I don't know (3)," "Maybe it's new (2)," or "I'm sure it's new (1)." Importantly, participants were instructed that a "sure old" response was equal in confidence to a "recollect old" response, such that the only difference between them was that at least one specific detail of the learning event was remembered in recollected scenes. Participants were instructed and tested on how to use this scale prior to beginning the test phase.

2.5. Data reduction and analysis

The primary outcome of interest was *target distance:* the Euclidean distance between the location clicked by participants during the spatial recall portion of the test phase and the actual location of the target object when the scene was presented in the study phase. This was measured in pixels between the mouse position during the click, recorded in terms of coordinates on the 800x600px scene, and the center of the target object. Reaction time during the study phase search task was also examined.

The effects of episodic memory were examined by comparing the target distance values between scenes given different recognition responses. Specifically, memory was compared across familiarity-based responses (1–5) to assess familiarity strength, and between recollected and "sure old" responses (6 versus 5) to assess recollection. In order to examine unconscious memory, performance needs to be compared to a memoryless baseline. To do this, we also computed target distance in scenes that were new. Given that new scenes were never presented with a target object, they were not inherently congruent or incongruent and therefore did not have a true target location. Whether a new scene was classified as congruent or incongruent—and therefore, which target location was used for computing target distance—was determined by the condition in which participants in the opposite counterbalance saw the scene during study (i.e., if participants in counterbalance 1 saw the target as congruent in a scene at study, that scene was considered to be congruent in counterbalance 2 in which participants saw it as a new scene). Thus, to measure target distance in new scenes, we calculated the distance between the clicked location in the test phase and the target location when it was shown in the study phase for participants in the other counterbalance. Participants' clicks on new scenes represented their best guess for where the target object might have been located based on their schema knowledge and their knowledge of the experiment. From a participant's point of view, these new scenes were equivalent to old scenes that they had forgotten seeing (i.e., high-confidence misses), but without any potential contribution of unconscious memory. To assess effects of unconscious memory, we compared target distance between scenes that were old but forgotten (i.e., "sure new" responses), and scenes that were truly new.

All statistical analyses besides those using new scenes were conducted using linear mixed effects models with random intercepts of subject and image, which allowed us to harness trial-by-trial (i.e., within-subjects) data while controlling for individual differences and stimulus effects. The models were estimated using the lmerTest package in R (Kuznetsova, Brockhoff, & Christensen, 2017), and were fit using maximum likelihood. The degrees of freedom and *t* values used were output by the linear mixed effects model for the variables of interest. The degrees of freedom were computed using the Satterthwaite approximation, and were rounded to the nearest integer in the manuscript. For analyses using new scenes, standard linear regression was used because the measure was calculated between subjects (i.e., comparing performance between subjects who saw a given scene as a new scene and those who saw it as an old scene). Effect sizes were calculated as a standardized regression coefficient (β) for continuous variables, and Cohen's *d* for categorical variables.

3. Results

First, to visualize spatial memory accuracy, we plotted target location recall heatmaps for each condition (see Fig. 2A-B.). Each heatmap illustrates the distribution of recalled locations for scenes in that condition, normalized across the included scenes such that the center of the heatmap represents the location of the target object. Heatmaps for schema-congruent and incongruent scenes were plotted for each type of recognition response (i.e., studied scenes given a recognition response of "recollect," "sure old," "maybe old," "don't know," "maybe new," and "sure new"). The proportion of trials that were given each type of recognition response is presented in Table 1. In addition, as a baseline measure to assess participants' ability to guess the location of objects within a scene in the absence of any memory, we also plotted heatmaps for new (i.e., nonstudied) scenes (Fig. 2A). The heatmaps of new scenes

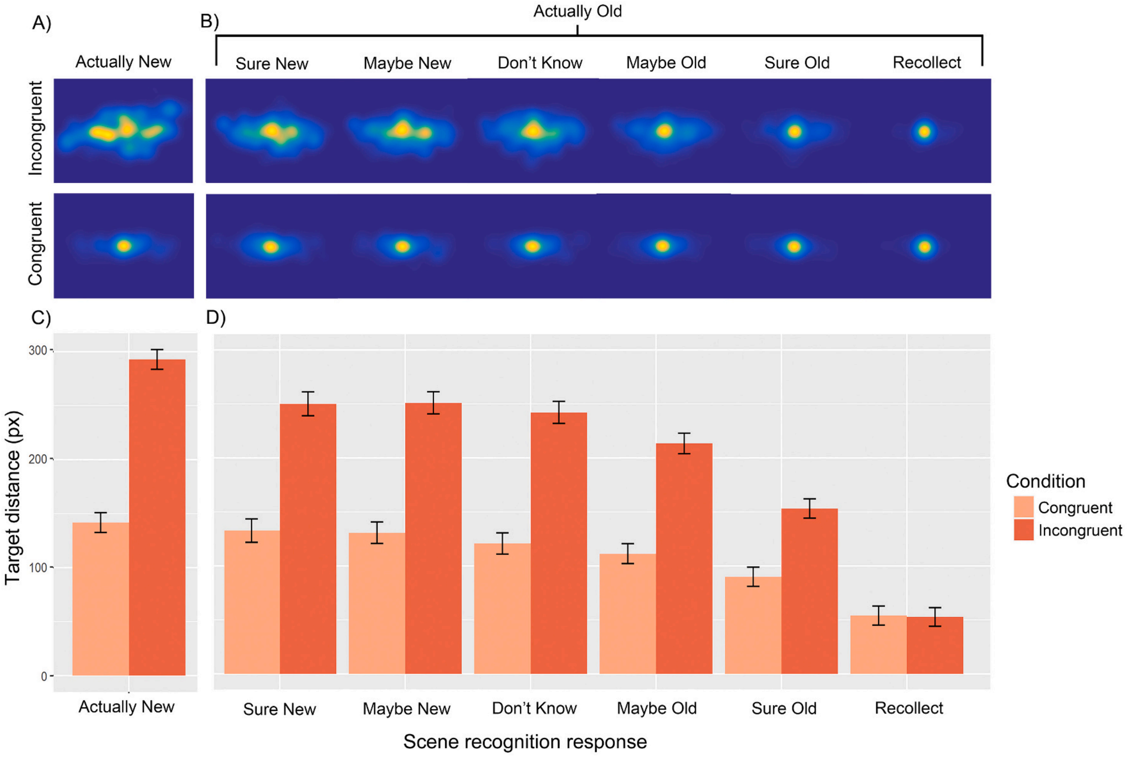

Fig. 2. Object location memory for schema-congruent and incongruent target objects in new scenes (A) and old scenes (B). Each heat map illustrates the distribution of recalled locations for the objects, normalized such that the center of the heatmap represents the location of the target object. Thus, heatmaps tightly focused on the center-point—as in the recollected scenes—indicate high spatial accuracy, whereas more distributed heatmaps indicate poorer spatial accuracy. C and D) Spatial memory accuracy measured as the distance between the recalled location and the studied object location (i.e., target distance). Higher values indicate lower accuracy. To control for subject and image effects, the least-squares means derived from a linear mixed effects model with random effects of subject and image are plotted, and the error bars represent the standard error of these estimated means from the model.

Table 1
Recognition response proportions for each scene type.

	"Sure new"	"Maybe new"	"Don't know"	"Maybe old"	"Sure old"	"Recollect old"
Old Scenes	7%	10%	11%	16%	24%	32%
New Scenes	37%	28%	14%	12%	5%	3%

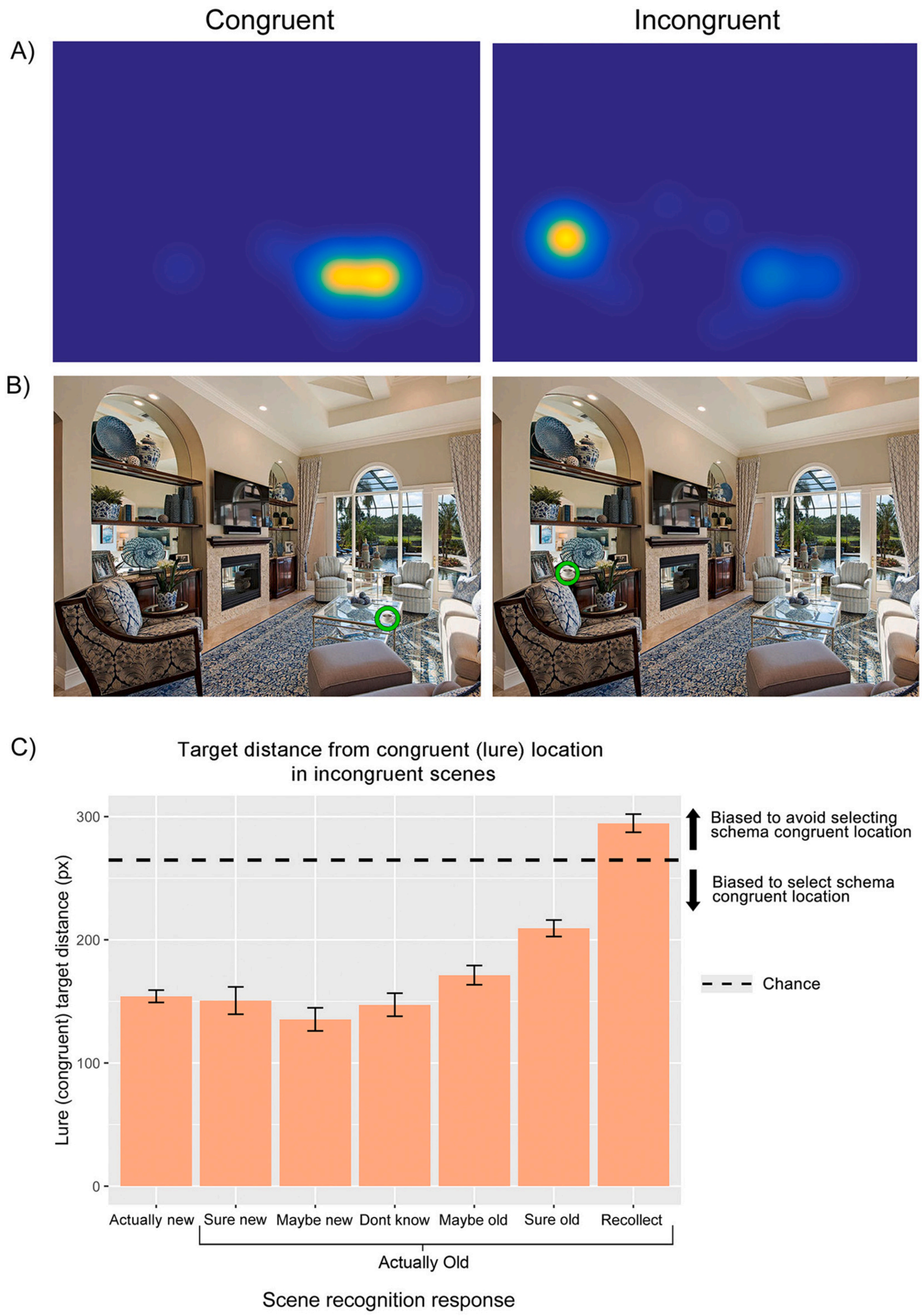

Fig. 3. The effect of memory on spatial recall errors for incongruent scenes. A) Example of the effect of schema congruency on spatial accuracy. The heatmaps are smoothed aggregate density maps of the click locations made on the congruent and incongruent version of the same scene. For example, the congruent heatmap includes the test phase click location from each participant who saw the congruent version of the scene. The incongruent heatmap suggests that many of the errors in these trials were due to participants erroneously choosing the congruent region. B) The congruent and incongruent versions of the scene. The target is circled for each case. C) Distance between the recalled object location and the schema-congruent location for objects studied in an incongruent location, plotted for each type of recognition response. Trials that were correctly recalled (i.e., <25 pixels from the studied location) have been excluded. The dashed line represents chance performance, which is the average distance between the recalled locations and a randomly selected target location. Values below the chance line indicate that participants' selected locations were more likely than chance to be near the schema-congruent region, and indicate that errors on those incongruent scenes may be driven by schema bias. Values above the chance line, as in the recollect responses, indicate that the selected locations were less likely than chance to be near a schema congruent region; this suggests that errors in these trials were not driven by schema bias. To control for subject and image effects, the least-squares means derived from a linear mixed effects model with random effects of subject and image are plotted, and the error bars represent the standard error of these estimated means from the model.

were based on the recalled locations relative to the object locations for those same scenes in the opposite counterbalance, in which participants had seen the scene at study; a new scene's designation as congruent or incongruent was therefore determined by the condition in which it was presented in the opposite counterbalance.

An examination of Fig. 2B shows that spatial accuracy for the target locations improved with unconscious memory, $p = .003$, familiarity strength, $p < .0001$, and recollection, $p < .0001$, and that spatial accuracy was generally better for congruent than incongruent scenes (i.e., more tightly focused recall heatmaps for schema-congruent than incongruent scenes), $p < .0001$. Importantly, this congruency effect was dependent on the type of memory participants had for the scenes: Unconscious memory reduced the congruency effect compared to new scenes ("sure new" old scenes versus new scenes), and the congruency effect weakened further with increasing familiarity strength ("sure new" through "sure old" scenes). Perhaps surprisingly, for recollected scenes, the congruency effect was eliminated entirely such that spatial accuracy was similar for schema-congruent and incongruent scenes.

These effects were analyzed by examining the distance between the recalled location and the actual target location (i.e., "target distance"; Fig. 2C-D). For recollected scenes, target distance did not differ between schema-congruent and incongruent scenes, $t(10271) = 0.23$, $p = .82$, $d = 0.004$, indicating that schema congruency had no significant effect on spatial accuracy for scenes that were recollected. Analysis using Bayes factors provided substantial evidence for the null hypothesis ($BF_{10} = 0.16$)[1] that there was no schema congruency effect within recollected scenes. Moreover, a direct comparison of performance in the recollected scenes and the high-confidence familiar scenes (i.e., "sure old" scenes) revealed a significant interaction such that the effect of schema congruency on target distance was larger for scenes recognized on the basis of familiarity compared to those judged to be recollected, $t(4292) = 7.68$, $p < .0001$, $d = 0.23$.

To probe the relationship between episodic familiarity strength and schema knowledge, we examined whether the linear gradient of familiarity-based responses (i.e., "sure new" through "sure old" responses) interacted with congruency to predict target distance. We found that as familiarity strength increased, the effect of schema congruency on target distance decreased, $\beta = -0.12$, $t(5242) = -4.97$, $p < .0001$. These results indicate that although schema congruency effects were present in familiar scenes ($p < .0001$), they were weaker for more familiar items.

To examine the impact of schema congruency under conditions in which there was no contribution of memory, we examined target distance for new, non-studied scenes, and found that spatial accuracy was significantly greater for schema-congruent than incongruent scenes, $t(2551) = 21.21$, $p < .0001$, $d = 0.84$. Moreover, a direct comparison of old scenes that could only have unconscious memory (i.e., old scenes receiving a "sure new" response) with truly new scenes revealed that there was a significant interaction such that the schema congruency effect was larger for new scenes compared to unconsciously recognized old scenes, $t(3096) = 2.84$, $p = .005$, $d = 0.1$. This indicates that even in the absence of conscious memory, schema congruency effects on spatial accuracy are reduced by unconscious memory for a previously viewed scene. Overall, the results thus far indicate that schema congruency has its largest effects on spatial accuracy when memory for the scenes is weakest.

To better characterize the effects of schema congruency on spatial accuracy, we further examined the recalled locations in schema-incongruent scenes across all memory responses. We found that when participants made a spatial location error, they did not select a location randomly, but rather they often incorrectly recalled that the object had been in the schema-congruent location. For example, Fig. 3A-B shows the distribution of recalled locations for one of the scenes when the object was in the schema-congruent or schema-incongruent location, respectively. For the congruent condition, the average recalled location was quite close to the target location. For the incongruent condition, most recalled locations were close to the target location, but there was also a tendency to falsely recall that the object had been in the congruent location. To quantify this latter effect, we calculated a new target distance measure for each incongruent scene by measuring the distance between the clicked location in the test phase and the target location from the *congruent* version of that scene (i.e., *lure target distance*). Importantly, the included participants had never actually seen the congruent version of these scenes in the study phase. As a baseline against which to compare these lure target distance values, we also calculated target distance values between the clicked locations and randomly selected target locations from other scenes; the final baseline value was the average value over 100 iterations of this process. Lure target distance values that are lower than this baseline would imply above-chance likelihood of clicking near the lure location; that is, participants would be more likely to click near the lure location than any other incorrect location. This would indicate a semantic bias towards the congruent—but incorrect—location.

For the analysis, we only used trials in which participants did not successfully click within 25px of the incongruent location (but note that all results outlined below were significant to $p < .001$ when all trials were used). We found that participants were more likely than chance to click near the lure, congruent location in new scenes, $p < .0001$, and in all old scenes that were not recollected, $ps < 0.004$ (Fig. 3C). This indicates that in incongruent new scenes, and in incongruent old scenes that were forgotten or familiar, participants' spatial accuracy was reduced in part due to semantic bias towards the schema-congruent location. In contrast, in recollected incongruent scenes, participants were less likely than chance to falsely recall the lure congruent location, $t(923) = -4.09$, $p < .0001$, $d = -0.27$. This suggests that even when spatial memory failed in recollected scenes (i.e., was >25px from the target location), participants were able to recollect that a target was not in a congruent location—thus sparing them from incorrect semantic bias. In other words, participants' recollection may have eliminated congruent locations as possible locations, thus improving their performance even when they did not remember the incongruent target location per se. Together, these results suggest not only that schema knowledge may actively undermine spatial memory performance in incongruent scenes, but that strong episodic memory—particularly recollection—protects against this effect.

Although the results of the current study were quite robust in that the interactions between schema congruency and episodic memory were highly significant, we wished to determine whether the results would replicate, so we conducted a second experiment with a different group of participants using the same method (Fig. 4). Importantly, the pattern of results was found to replicate in this second experiment (compare Fig. 2 to Fig. 4), and all of the significant results reported above were replicated. Specifically, the effect of congruency was significantly reduced due to unconscious memory (i.e., in "sure new" old scenes compared to new scenes), $t(1315) = -2.44$, $p = .015$, $d = -0.14$. Schema congruency effects also decreased as familiarity strength increased, $\beta = -0.16$, $t(2110) = -4.10$, $p < .0001$. Furthermore, there was no congruency effect in recollected scenes, $t(4455) = -0.32$, $p = .75$, $d = -0.01$, and recollection uniquely protected from bias towards congruent regions, $t(382) = 2.66$, $p = .008$, $d = 0.27$.

We also reran the main analyses in both experiments controlling for study phase viewing time, as well as controlling for slight differences in the distribution of target locations between conditions, and found that the same pattern of results was obtained (see Appendix). Furthermore, in the Appendix, we include additional analyses of search speed in the study phase, as well as participant-rated congruency scores to validate the congruency manipulations.

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[1] By convention, a $BF_{10} < 0.33$ indicates substantial evidence for the null hypothesis (Jeffreys, 1961).

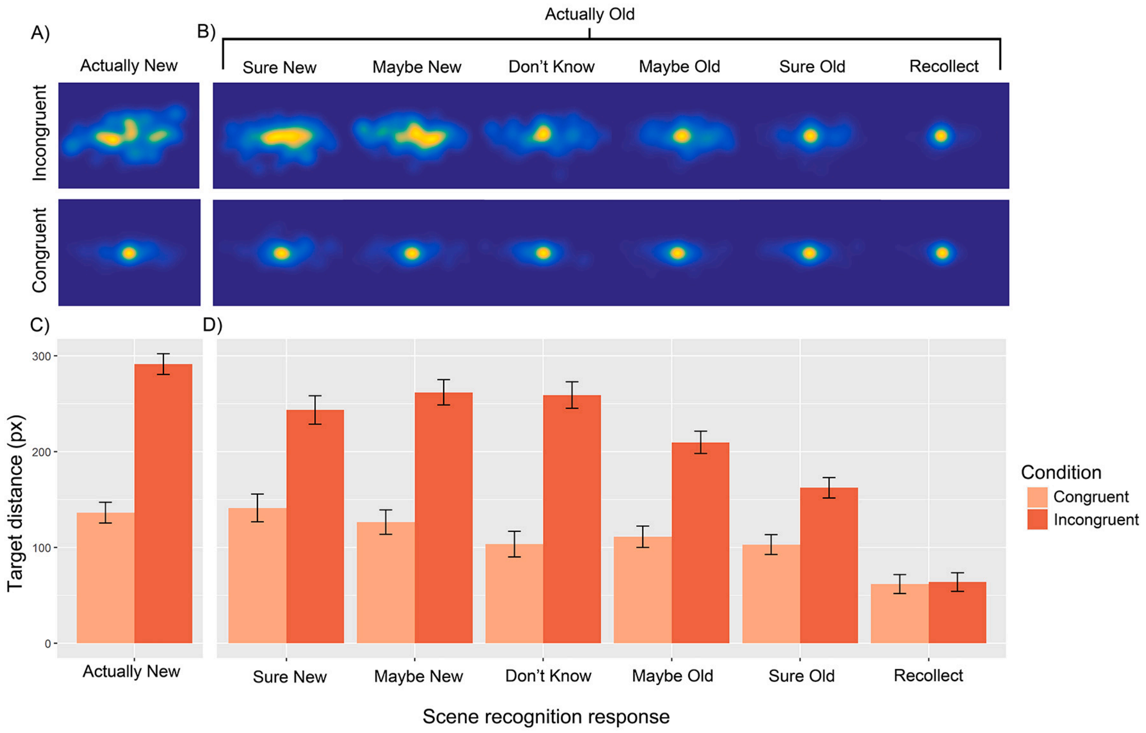

Fig. 4. Replication experiment data, showing object location memory for schema-congruent and incongruent target objects in new scenes (A) and old scenes (B). Each heat map illustrates the distribution of recalled locations for the scenes, normalized such that the center of the heatmap represents the location of the target object. Thus, heatmaps tightly focused on the center-point —as in the recollect responses—indicate high spatial accuracy, whereas more distributed heatmaps indicate poorer spatial accuracy. C and D) Spatial accuracy measured as the distance between the recalled location and the studied object location. To control for subject and image effects, the least-squares means derived from a linear mixed effects model with random effects of subject and image are plotted, and the error bars represent the standard error of these estimated means from the model.

4. Discussion

In the present study, we examined how different recognition memory processes interact with schema knowledge to influence spatial memory decisions. Participants first searched scenes for a target object that was in either a schema-congruent or a schema-incongruent location. In a subsequent spatial recall phase, participants indicated where in each scene they thought the target object had been located in the earlier search task. In addition, they gave a confidence-based recognition memory judgment for each scene that allowed us to isolate recollection, familiarity, and unconscious memory. We found a robust schema congruency effect such that spatial recall was more accurate for objects in congruent than incongruent locations. Importantly, the magnitude of this effect decreased as memory strength for the scenes increased. That is, the congruency effect was largest in new scenes, decreased with unconscious memory, decreased further with familiarity confidence, and was absent entirely for recollected scenes. In addition, poorer spatial memory performance in incongruent scenes reflected a tendency to falsely recall the target as having been in a schema-congruent location, but only in scenes that were not recollected: When recollection occurred, participants were significantly biased *against* selecting the congruent locations—even when they did not remember the correct incongruent location—suggesting that recollection is able to oppose the effects of schema bias even when the precise location is not remembered.

These results indicate that the influence of schema information on behavior is dependent on episodic memory strength and type. Given that most current models of how schemas contribute to memory decisions characterize memory as a single, or largely undifferentiated, construct, our findings suggest that an important next step for such models will be to consider how variations in memory modulate the strength of schema influences. Moreover, our finding that recollection appeared to allow participants to remember that an object was schema-incongruent fits well with recent Bayesian models that incorporate multiple levels of category information (Hemmer & Steyvers, 2009). Specifically, it appears that at least two levels of schema or category information were incorporated into memory decisions in our experiment: first, pre-experimental schema knowledge of where objects tend to be found in the environment, and second, category knowledge for whether an object was located in a congruent or incongruent region during initial scene viewing. Thus, it may be that recollection, specifically, allowed participants to remember whether a studied object was in the “congruent” category of scenes or the “incongruent” category of scenes, and therefore allowed participants to override bias by pre-experimental schema information even when they did not remember the target location. Further experiments are needed to directly test this possibility, but if memory can in fact down-weight some types of schema information while increasing the use of others, it would constitute another clear future consideration for models of memory.

The extent to which schema information is incorporated into memory decisions may depend upon the precision of information provided by memory. That is, prior work has indicated that recollection provides high-precision spatial information, whereas familiarity provides low-precision, gist-like spatial information (Kolarik et al., 2016; Kolarik, Baer, Shahlaie, Yonelinas, & Ekstrom, 2018). Object location predictions provided by schema knowledge, on the other hand, are typically diffuse and probabilistic rather than precise (Biederman, 1981; Huttenlocher et al., 1991; Torralba, Oliva, Castelhano, & Henderson, 2006). Therefore, when high-precision recollection is available, these precise representations may be prioritized over schema predictions, in line with what has been assumed by some models of memory (Huttenlocher et al., 1991; Persaud & Hemmer, 2016). Similarly, because familiarity and presumably unconscious memory provide some degree of precision that is above and beyond the probabilistic spatial information supported by schema knowledge, schematic spatial predictions may be down-weighted in favor of these more deterministic memory predictions. If this account is correct, it should be possible to modify the outcome of schema-memory competition by varying the relative precision of the spatial information supported by each. For example, schema knowledge may be more heavily weighted if it supports precise spatial information (e.g., the location of a door handle vs. the location of a cellphone) as indicated by Hemmer and Steyvers (2009), whereas recollection may be more heavily weighted if it provides more precise information (e.g., when I attend to where I place my phone vs. attending to other aspects of the ongoing episode). Future experiments directly examining this possibility may be well-poised to further our understanding of memory-schema interactions.

The present results also provide support for recent neural models proposing competitive interactions between episodic memory and schema knowledge (Gilboa & Marlatte, 2017; Sommer, 2017; van Kesteren et al., 2012; Wagner et al., 2015). These models suggest that during learning of arbitrary object-location associations, the episodic system—which is reliant on the hippocampus—is critical for binding objects to specific locations. However, when object locations are consistent with established spatial schemas, learning can be supported by a separate schema-learning system, which is reliant on the cortex and the ventromedial prefrontal cortex (vmPFC). These episodic memory and schema systems are assumed to be competitive and mutually inhibitory, as suggested by studies showing that learning schema-related knowledge is related to increased cortical and vmPFC activation and reduced hippocampal activity (for review see Gilboa & Marlatte, 2017). However, direct behavioral evidence that these systems compete has been lacking. To our knowledge, the current results are the first to provide such direct evidence.

The reduction of schema effects by memory was strongest for scenes that were recollected, but was also evident in familiar scenes such that the effect of schema congruency decreased as familiarity confidence increased. This indicates that both recollection and familiarity can compete with and effectively oppose the effects of schema knowledge when that knowledge is detrimental to performance. The competitive interaction models have not differentiated between recollection and familiarity-based memory, so the current results present new challenges to those models and suggest areas for further investigation. For example, the hippocampus plays a critical role in supporting recollection (Bastin et al., 2019; Eichenbaum et al., 2007 but see Wais, Wixted, Hopkins, & Squire, 2006), and therefore our finding that recollection can compete with schema knowledge supports the claim that the hippocampus and regions supporting schema knowledge may be mutually inhibitory in some circumstances (Gilboa & Marlatte, 2017; van Kesteren et al., 2012). However, medial temporal lobe regions outside the hippocampus such as the perirhinal cortex support familiarity (Aggleton & Brown, 1999; Eichenbaum et al., 2007). Thus, the current results suggest that schema-related regions may also be in direct competition with regions such as the perirhinal cortex, which has not yet been considered.

The schema congruency effects observed in the current study were smaller for unconsciously recognized scenes than for truly new scenes. That is, for studied scenes that participants were highly confident had not been studied, participants had better spatial recall, and congruency effects were smaller, than if the scenes had not been studied at all. These results suggest that even unconscious forms of memory can support memory for object locations. Interestingly, prior studies finding unconscious memory effects have typically used implicit measures such as eye movements and search speed (see Goujon, Didierjean, & Thorpe, 2015; Hannula & Greene, 2012; Ramey et al., 2019), but the present study points to a possible role of unconscious memory even in explicit spatial recall decisions. Moreover, utilizing the present paradigm in patient populations with medial temporal lobe damage may be particularly useful for informing the debates surrounding hippocampal involvement in unconscious memory for associations (Hannula & Greene, 2012).

In sum, it is clear that memory and schema knowledge simultaneously contribute to a wide variety of everyday behaviors, but how they are resolved to influence behavior has been a subject of debate (e.g., Gilboa & Marlatte, 2017). Although schemas and memory can synergistically enhance performance in some cases, schemas can also lead to systematic errors when they are inconsistent with individual past experiences. The current results show that the effects of schema knowledge can be effectively eliminated when memory provides strong episodic information, and point to clear ways to improve both cognitive and neural models of schema-memory interactions.

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Appendix A

A.1. Search speed in the study phase

On average, participants found the target in 99% of study trials in Experiment 1, and 99% of study trials in Experiment 2 as well. The mean search speed when the target was found was 2305 ms in Experiment 1, and 2250 ms in Experiment 2.

The average reaction time to click on the target in the first presentation of each scene in the study phase was significantly higher than the second study phase presentation, $p < .0001$. This difference remained when practice effects were controlled for by covarying when each scene was presented in the study phase (i.e., including a covariate of the ordinal trial number), $p < .0001$, indicating that much of the improvement in search speed was driven by episodic memory for target locations rather than general skill learning.

In addition to improvements from episodic memory, search speed benefitted from schema knowledge as well. Specifically, participants were significantly faster at finding congruent targets than incongruent targets in the study phase, $p < .0001$. We also examined whether there was an interaction between congruency and presentation (i.e., first versus second presentation), and found that the difference between congruent and incongruent scenes was smaller on the second presentation, $p < .0001$. That is, when episodic memory was available, schema congruency had less of an effect on search speed—consistent with our main results.

A.2. Study duration effects

In addition to examining search speed as a measure of performance, we also determined whether study duration influenced any of the effects obtained in the main results in the manuscript. Study duration was calculated as participants' total viewing duration for a scene in the study phase, summed across both presentations of a given scene. This duration included both search speed and the 3s encoding time that occurred once they found the target or search timed out (see Fig. 1E). First, we found that study duration was weakly positively related to test phase target distance across all scenes in Experiment 1, $p = .03$, but not in Experiment 2, $p = .47$. Second, we found that higher study duration was related to stronger subsequent memory in both experiments, $ps < 0.001$. However, the magnitude of this effect was relatively weak, as shown in Fig. A1. Importantly, including study duration as a covariate in our main analyses of congruency-memory interactions did not change the pattern of results: In both samples, when study duration was covaried, there was still no effect of congruency within recollected scenes, $ps > 0.74$, and the congruency effects still weakened as familiarity increased, $p < .0001$. (Note that we could not examine the unconscious memory effects with study duration, because there was no study duration for new scenes.)

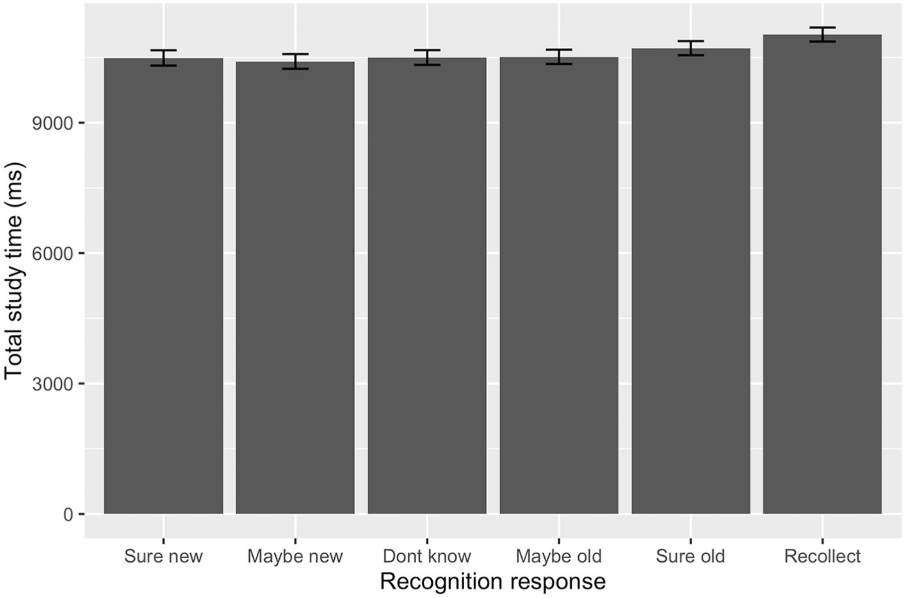

Fig. A1. Total study duration by memory response for old scenes.

A.3. Target distributions in congruent and incongruent scenes

When creating the scenes, we aimed to produce similar distributions of target locations across the two types of scenes (see Fig. A2 A-B). However, to ensure that any slight differences in target location distributions did not affect the present results, we re-ran the analyses using only scenes whose target location overlapped with a target location in a scene in the opposite condition. To do this, we eliminated from analysis all incongruent scenes in which the target was not overlapping with a target in a congruent scene. Similarly, we eliminated all congruent scenes in which the target was not overlapping with a target in an incongruent scene. Thus, all scenes were yoked to a scene in the opposite condition in terms of target location. After these exclusions, 57 of 80 incongruent scenes were retained for analysis, and 56 of 80 congruent scenes were retained. The resulting target distributions are shown in Fig. A2 C—D.

The same pattern of results was obtained as in the manuscript. Specifically, when reanalyzing the data from both experiments using only the yoked scenes, the congruency effect within recollected scenes was not significant ($ps > 0.36$), the familiarity strength effect was significant ($ps < 0.006$), and the unconscious memory effect was significant ($ps < 0.001$). For the schema bias analysis in incongruent scenes, the results were the same as those obtained in the manuscript for both experiments: Lure target distance in all non-recollected incongruent scenes was significantly below chance (i.e., biased to select the schema congruent region), $ps < 0.001$, whereas lure target distance in recollected incongruent scenes was significantly above chance (i.e., biased away from the congruent region, even when they didn't remember the correct target location), $ps < 0.0001$. These results indicate that the present findings were not driven by differences in the overall distribution of target locations between conditions.

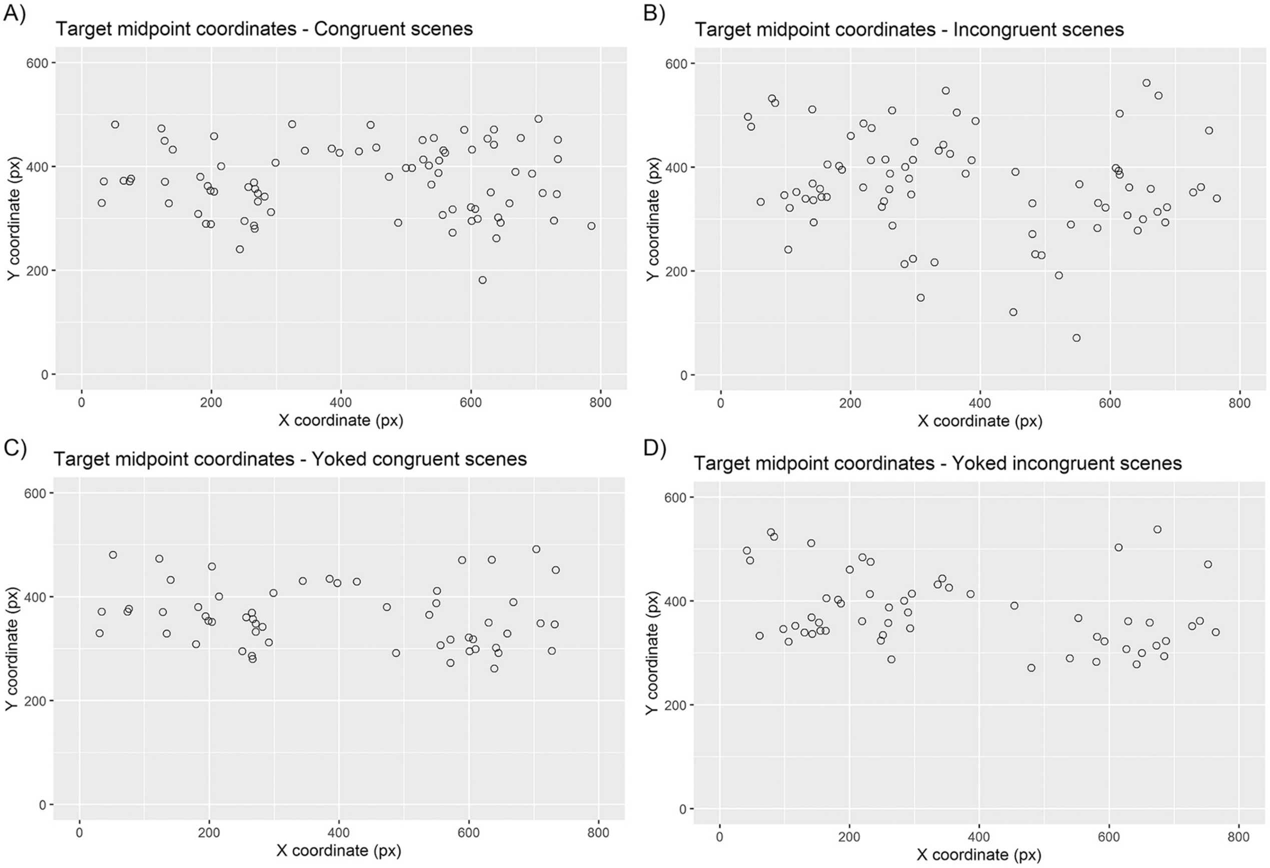

Fig. A2. Distributions of target locations. A) Distribution of the target locations in congruent scenes. B) Distribution of target locations in incongruent scenes. C) Distribution of target locations in the subset of congruent scenes that were yoked to the incongruent scenes, such that every target overlapped with at least one target location in the incongruent condition. D) Distribution of target locations in the subset of incongruent scenes that were yoked to the congruent scenes, such that every target overlapped with at least one target location in the congruent condition.

A.4. Continuous congruency scores

In the process of creating the scenes, we made a congruent and incongruent version of each scene. To validate the congruency manipulation, we also had a separate group of participants ($n = 25$) rate each scene for the congruency of its target object on a continuous scale. Specifically, participants were asked to rate how normal or unusual a target's location was on a 1–6 scale. These scores were averaged together to produce a congruency score for each scene. As expected, congruent scenes were rated as significantly more congruent than were incongruent scenes, $p < .0001$. These results verify that the congruency manipulation had the intended effect.

Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cognition.2022.105111.

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