Fast Memory Integration Facilitated by Schema Consistency

Qiong Zhang [a,e,] *, **Vencislav Popov** [b,e,]*, **Griffin E. Koch** [c,d,e], **Regina C. Calloway** [c,d], **Marc N. Coutanche** [c,d,e]
{qiongz,vpopov}@cmu.edu, {griffinkoch, rcc36, marc.coutanche}@pitt.edu
[a] Machine Learning Department, [b] Department of Psychology, Carnegie Mellon University, Pittsburgh, PA 15213
[c] Learning Research & Development Center, [d] Department of Psychology, University of Pittsburgh, Pittsburgh, PA 15260
[e] Center for Neural Basis of Cognition, Pittsburgh, PA 15213

Abstract

Many everyday decisions are based not only on memories of direct experiences, but on memories that are integrated across multiple distinct experiences. Sometimes memory integration between existing memories and newly learnt information occurs rapidly, without requiring inference during the decision. It is known that prior knowledge (i.e. schema) affects the initial acquisition, and consolidation, of memories. In this study, we explore the effect of schema on the integration of acquired memories between paired associates (e.g. integrating A-B and B-C into A-B-C) that were schema consistent or inconsistent, as confirmed with a latent semantic analysis of text corpora. We find that enabling fast learning, by using material that is consistent with a schema, allows for fast memory integration. These behavioral results are consistent with predictions generated from neuroscientific hypotheses suggesting that an existing schema might enable neocortical learning that is distinct from a more explicit hippocampus-mediated integration of new information.

Keywords: Schema; Memory integration; Integrative encoding; Complementary learning system

Introduction

Memory is essential in guiding everyday decisions. These decisions are not only based on memories of direct experiences, but also rely on knowledge generalized across multiple distinct events. One process that supports such generalization is memory integration. Effective memory integration transforms distinct, but overlapping past experiences into a cohesive representation (Eichenbaum, 2000; Gluck & Myers, 1993), on which one can base novel judgments later (Zeithamova, Dominick, & Preston, 2012). These novel memory decisions can be supported either by direct integration during the encoding of overlapping elements (i.e., “integrative encoding”; Shohamy & Wagner, 2008) or by inferring the relations between elements during retrieval (i.e., “logical inference”; Bunsey and Eichenbaum, 1996; Dusek &Eichenbaum, 1997; Greene, Gross, Elsinger, & Rao, 2006). Research has suggested that prior knowledge (i.e. schema consistency or semantic relatedness) facilitates the initial acquisition, and consolidation, of memories (Sommer, 2017; Tse et al., 2007, 2011;). As both relations and schema impact how information is learned, here we investigate how the presence of a relevant schema affects the subsequent integration of overlapping acquired memories.

Memory integration is most commonly examined with the associative inference paradigm. In this task, participants learn separate events with overlapping components (e.g., A-B and B-C), and later have to infer the relations between elements that have not been experienced together but are indirectly associated (e.g., A-C; Myers et al., 2003; Preston, Shrager, Dudukovic, & Gabrieli, 2004; Shohamy & Wagner, 2008). Two different mechanisms have been proposed to explain how participants make such indirect inferences. The first mechanism, integrative encoding, is a fast method of memory integration that takes place during encoding, possibly through dynamic shifts between encoding and retrieval states of the hippocampus. This proposed mechanism is supported by experimental studies (Shohamy & Wagner, 2008), and is consistent with computational theories (Hasselmo & McClelland, 1999; Hasselmo, Schnell, & Barkai, 1995). The second mechanism, logical inference, does not involve directly encoding an integrated memory (i.e., A-C), and instead infers the relationship between A and C after retrieving separate memories of A-B and B-C (Dusek & Eichenbaum, 1997; Greene et al., 2006).

At the neural level, research has highlighted the role of the hippocampal system in supporting both mechanisms. During integrative encoding, related prior experiences that overlap with the newly encoded information are reactivated in the hippocampus (Schlichting & Preston, 2015). Memory integration then takes place at the time of learning, supported by the integration of new experiences into existing memory networks by the hippocampus (Shohamy & Wagner, 2008; Zeithamova & Preston, 2010). Evidence for this comes from both non-human animal and human studies. Animal studies have demonstrated that the hippocampus can encode similarities between distinct events (Eichenbaum et al., 1999; Singer et al., 2010; Wood, Dudchenko, & Eichenbaum, 1999;), and can reactivate traces of prior events, when learning new information (Karlsson & Frank, 2009). In humans, hippocampal activity during encoding predicts subsequent performance in memory integration (Shohamy & Wagner, 2008; Schlichting, Zeithamova, & Preston, 2014). Similarly, it has been suggested that the hippocampus also supports the flexible retrieval of component memories (A-B and B-C) during logical inference (Greene et al., 2006; Heckers et al. 2004; Preston et al., 2004). In addition to the hippocampus, the medial prefrontal cortex (mPFC) demonstrates neural representational changes that are consistent with individual memories being integrated during encoding (Schlichting, Mumford, & Preston, 2015). Coupled with the medial

---

* QZ and VP contributed equally and should be considered co-first authors

temporal lobe during retrieval, the mPFC also supports memory integration through logical inference in which multiple memories are recalled and flexibly recombined (Zeithamova & Preston, 2010).

Most neuroscientific research on the associative inference task has focused on the role of the hippocampal system because the standard view in the field has been that neocortical learning occurs more slowly than the typical delays used in this paradigm. For example, according to the complementary learning systems theory (Marr, Willshaw, & McNaughton, 1991; McClelland, McNaughton, & O'Reilly, 1995), the brain keeps two separate memory stores to avoid interference between new information and existing memories. Initial learning takes place in the temporal store supported by the hippocampus. Through system consolidation involving both time and sleep, newly learnt information gradually transfers to a more permanent store supported by the neocortex (Born & Wilhelm, 2012; Frankland & Bontempi, 2005; Zola-Morgan & Squire, 1990). This standard view suggests that integrating A and C into one representation shortly after learning A-B and B-C is still strongly dependent on the hippocampal system.

However, recent findings suggest that system-level consolidation can take place rapidly. Newly learnt information that is consistent with pre-existing knowledge (i.e. schema) becomes independent of the hippocampus (Sommer, 2017; Tse et al., 2007, 2011;), with the mPFC shown to mediate the encoding (Bein, Reggev & Maril, 2014; van Kesteren, Ruiter, Fernandez, & Henson, 2012; van Kesteren et al., 2013). This effect was also supported by recent simulations under the complementary learning systems theory, in which assimilating schema-consistent knowledge occurred rapidly and without interference with existing neocortical representations (McClelland, 2013). Recent studies have also shown that word-concept associations can become rapidly integrated into lexical memory if related knowledge is accessed during encoding through a "fast mapping" procedure (Coutanche & Thompson-Schill, 2014; Coutanche & Thompson-Schill, 2015). This rapid integration draws on neocortical systems (Merhav, Karni, & Gilboa, 2015), without requiring the hippocampus (Sharon, Moscovitch, & Gilboa, 2011), and might share mechanisms with the rapid learning that is induced by a schema (Coutanche & Thompson-Schill, 2015).

Motivated by such neural evidence, in this study, we examined the role of schema in facilitating rapid memory integration in an associative inference task at the behavioral level. We report findings from participants who learned person-location associative word pairs, with some pairs that are schema-consistent (e.g. teacher-classroom, classroom-student) and others that are schema-inconsistent (e.g. baker-theater, theater-hiker). Our first goal was to examine the overall degree of memory integration by testing associative inference (e.g., "Were teacher and student linked in this experiment?") depending on schema consistency. Our second goal was to examine the degree to which integration is due to integrative encoding versus logical inference in each condition, by testing two levels of memory integration. In addition to generalizing A-B and B-C to A-C (i.e., 1-link integration), we also test generalizing A-B, B-C and C-D to A-D (i.e., 2-link integration). If participants respond to overlapping associations based on integrative encoding, their response times (i.e., RTs) should reflect a direct retrieval that is independent of the number of links. Alternatively, if participants respond based on logical inference, RTs should be dependent on the number of links, as the inference process involves cognitively traversing each link.

Methods

Participants

Thirty-five participants (17 females; mean (M) age = 20.7 years, standard deviation (sd) = 3.0; English speakers without a learning or attentional disorder) contributed to the study. Informed consent was obtained for each participant prior to beginning the study. Upon completion, participants were compensated through course credit or payment for their time. The University of Pittsburgh Institutional Review Board approved all procedures. Eight participants were excluded from the analysis – five participants did not reach criterion for at least half of the studied pairs (see Procedure); three participants showed chance performance during forced-choice testing. Exclusion criteria were established prior to the start of data collection.

Materials

To test the effects of schema consistency on memory integration, we implemented a 2 (schema consistency: consistent vs. inconsistent) x 2 (linked pairs: one-link integration vs. two-link integration) within-subjects design. Schema consistency in the present study is based on the association between a person (e.g., teacher) and a location (e.g., classroom). Within the experiment, one 'set' consists of three word-pair associations in each schema condition (e.g. schema consistent: teacher-classroom, classroom-student, student-dormitory; schema inconsistent: baker-mountain, mountain-principal, principal-circus). There are ten sets within each schema condition, resulting in 60 unique word-pair associations to be studied. Word pairs are trained in the study phase of the experiment.

Latent semantic analysis (http://lsa.colorado.edu/) was used to confirm schema consistency. LSA can be used to measure word associations based on their co-occurrence within large corpora (Landauer & Dumais, 1997). LSA values range from -1 to 1, with higher values indicating stronger semantic associations. Word pairs in the schema-consistent condition (μ = .42, SE = .04) had higher LSA scores than word pairs in the schema-inconsistent condition (μ = .06 , SE = .01; $t(58) = 8.59$, $p < .001$).

Procedure

Study Phase Study phase of the experiment started with a learning task, where participants were presented with two words (a person and a location) and instructed to remember the pairing. To help them remember the words, participants had to decide how likely it would be to see the person/profession in the paired location, on a 4-point scale (very likely, somewhat likely, somewhat unlikely, very unlikely). Each trial began with a fixation cross presented in the middle of the screen for 0.5 s., followed by the word pair, which remained on the screen for 3.5 s. regardless of when participants responded.

In the second task during the study phase, participants performed multiple drop-out cycles of cued-recall of all studied pairs. In each cycle, participants were presented with all cue words (one of the words they had previously studied) in a random order, and asked to type in the word that had been paired with each cue. Participants were presented with the first letter of the correctly matching word, and had five seconds to type the remaining letters. After typing in a word, participants were shown the correct answer paired with the cue word (regardless of accuracy), to enable restudying. In the case when participants typed an incorrect word as the match for the cue word, the cue word was added to the end of the list and was tested again following the presentation of all other cue words. This continued until all pairs were correctly recalled, thus concluding one learning cycle. The task completed once each pair had been recalled correctly three consecutive times without drop-out.

At the end of the study phase, there was a distractor task, where participants played a game of Tetris (http://www.freetetris.org/game.php) for 15 minutes. This distractor task allowed us to eliminate the recently learned information from working memory, and to prevent rehearsal of the word pairs.

Test Phase During the test phase, on each trial participants saw three words, a cue word on top and two choices on the bottom. Participants completed a forced-choice task by selecting which of the two words on the bottom had been associated with the cue word within the experiment – either because they were studied together or because they were indirectly connected by studied pairs. To prevent participants from responding solely based on schema consistency in the schema consistent condition, the foil was selected to be as strongly semantically related to the cue (μ = .28, SE = .02), as was the correct answer (μ = .27, SE = .02). E.g., if the cue was "teacher" and the correct answer was "classroom" the distractor was "school". Words from the schema inconsistent condition served as foils for the schema consistent condition and vice versa. Therefore, all words in the forced-choice recognition task were encountered in the study phase, and participants could not respond based on familiarity alone.

Participants were instructed to answer as quickly and as accurately as possible, as both factors would increase the amount of points they earned for the task. The points (later displayed to the participants) were helpful for keeping participants motivated, without causing additional learning during the test phase (because the point-feedback was not provided on the basis of individual trials). There were two ways in which correct words could be associated with the cue word: i) direct associations occurred when the two words (i.e. A-B) had been previously studied; ii) indirect associations occurred when words had been learned, but never directly paired together (i.e. A-C, since previously learned A-B and B-C). Participants were not required to make the distinction between direct and indirect associations, but instead simply selected which word was in some way associated with the cue word. After selecting a word, participants were asked to indicate their confidence in their answer on a 3-point scale (guess, probably, sure). After 10 trials, participants were shown a screen with the number of points they had accrued up to that point and could rest if needed, before beginning a new set of trials.

There were 100 test trials: 60 containing studied pairs and 40 containing linked pairs. In order to gather more observations, the testing was repeated 4 times, where each cycle contained the 100 trials we described in a novel random order each time.

Results

We analyzed the accuracies, confidence ratings, and RTs via logistic and linear mixed-effects regression models (Baayen, Davidson, & Bates, 2008). We excluded incorrect responses from analyses of confidence ratings and RTs (6-30%, depending on the condition). Random effects were determined through restricted likelihood ratio tests and all final models included varying intercepts for subjects and individual word pairs (i.e., different subjects and items differ in their overall accuracy and RT estimates), as well as varying slopes by subject for the effect of schema consistency (i.e., the models account for how much differences in schema consistency varies across subjects). We inferred the significance of each effect based on likelihood ratio tests and AIC comparisons of the regression models that contained the effect in question with identical models that lacked this contrast.

The effect of schema on learning associations

During the study phase, initial learning differed between schema-consistent pairs and schema-inconsistent pairs. Schema-consistent word pairs were correctly recalled more often on their first presentation in each cued-recall cycle (Figure 1a; ΔAIC = -34, $\chi2$ (1) = 35.82, $p < .001$). Schema-consistent pairs were also recalled faster (Figure 1b; ΔAIC = -26, $\chi2$ (1) = 27.62, $p < .001$) and with higher accuracy throughout the study phase (Figure 1c; ΔAIC = -37, $\chi2$ (1) = 38.97, $p < .001$), though memory for the pairs was saturated in both conditions by the end of learning. This is evident by the subsequent forced-choice recognition performance for studied word pairs (Figure 3), which were recognized equally accurately (ΔAIC = -0.7, $\chi2$ (1) = 2.69, $p = .101$)

and with similar confidence (ΔAIC = 0.8, χ2 (1) = 0.229, p = .632) regardless of schema consistency. Schema-consistent pairs were recognized slightly faster than schema-inconsistent pairs, but the effect did not reach significance (ΔAIC = -1, χ2 (1) = 3.41, p = .065). In summary, while it took longer to learn schema-inconsistent pairs to criterion, post-learning recognition accuracy, speed and confidence did not differ as a function of schema consistency.

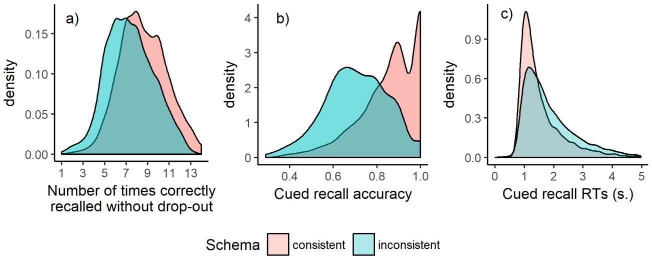

Figure 1: Cued-recall performance during learning: a) distribution of the number of cued-recall cycles on which each pair was recalled correctly on the first presentation (i.e. without further drop-out); b) distribution of cued-recall accuracy for each pair averaged over learning cycles; c) distribution of RTs for correct cued-recall of each pair.

The effect of schema on memory integration

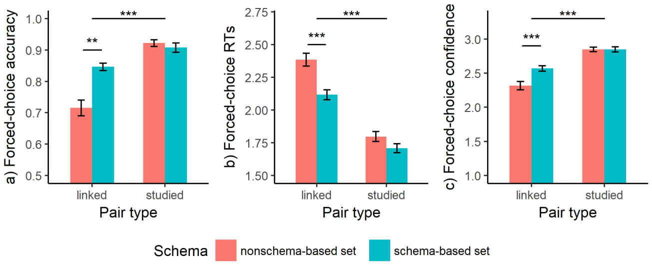

Figure 2: Forced choice a) accuracy, b) RTs (in s.) and c) confidence for studied and linked pairs depending on whether they were part of a schema. ** p < .01, *** p < .001

Forced-choice performance in the recognition test of "linked" pairs (A-C or A-D for A-B, B-C, C-D) revealed that there was greater memory integration for pairs that were in schema-consistent sets. Participants were more accurate (Figure 2a, ΔAIC = -8, χ2 (1) = 10.6, p = < .01), faster (Figure 2b, ΔAIC = -14, χ2 (1) = 15.68, p < .001) and more confident (Figure 2c, ΔAIC = -59, χ2 (1) = 65.49, p < .001) in judging that pairs had been linked, when they were part of a schema. This is despite accuracy and confidence of studied pairs being saturated by the end of the study phase. In summary, all three measures of forced-choice performance (accuracy, RTs and confidence) indicate that schema-consistent linked pairs were better integrated during study. Could the differences in forced-choice performance for linked pairs be explained by the speed of learning (i.e., the number of study trials to reach criterion)? Memory integration involves reactivating traces for related information (Karlsson and Frank, 2009; Shohamy and Wagner, 2008) and since schema-consistent pairs were learned faster and earlier during the study, they might be easier to reactivate and integrate. To test this explanation, we included the average accuracy and RTs for each same-set word pair for each participant, as predictors and by-subject random slopes in the mixed-effects regression model. Memory integration was better when the component pairs were learned more quickly during study – average cued recall accuracy for studied pairs predicted subsequent forced-choice accuracy (ΔAIC = -10, χ2 (1) =12.387, p < .001) and confidence ratings (ΔAIC = -23, χ2 (1) =24.65, p < .001) for linked pairs in the set, and the cued recall RTs of studied pairs predicted forced-choice RTs for linked pairs in the set (ΔAIC = -4, χ2 (1) =6.21, p = .013). Importantly, the differences between schema-consistent and schema-inconsistent pairs that we outlined above remained significant even after accounting for the learning rate of each pair (all p < .01), suggesting that learning rate was not driving this effect.

The effect of schema on integrative encoding

Table 1: Forced-choice performance

Condition	Accuracy	RTs (ms.)	Confidence
Schema consistent			
Links: 1	0.88	2064	2.79
Links: 2	0.81	2163	2.61
Difference	**0.07**	**-99**	**0.18**
Schema inconsistent			
Links: 1	0.79	2268	2.67
Links: 2	0.65	2485	2.30
Difference	**0.14**	**-217**	**0.37**

In the last section, we presented evidence that schema-consistent pairs experience more memory integration. This section further looks into the extent of fast memory integration (i.e. integrative encoding). All three measures of forced-choice performance indicate there was more integrative encoding for schema-consistent pairs. The extent of integrative encoding during memory integration is reflected in the independence of accuracy, RTs and confidence from the number of links among the linked pairs. If participants depended more on logical inference to judge the pairs, then accuracy, RTs, and confidence should have been worse when they had to cognitively traverse more links to connect the words. Table 1 shows that the number of links impacted all measures twice as much for schema-inconsistent, than schema-consistent, pairs. The mixed effects regression models confirmed a significant main effect of number of links on accuracy (ΔAIC = -26, χ2 (1) = 28.56, p < .001), RTs (ΔAIC = -19, χ2 (1) =21.15, p < .001) and confidence (ΔAIC = -22, χ2 (1) = 24.30, p < .001). The effect of number of links interacted significantly with schema consistency for RTs (ΔAIC = -3, χ2 (1) = 5.04, p = .025) and confidence (ΔAIC = -7, χ2 (1) = 8.94, p = .003), but not accuracy (ΔAIC = 0.7, χ2 (1) = 1.26, p = .261). With the impact of the number of links on RT larger in the schema-inconsistent condition than the schema-consistent condition, we can conclude that memory integration requires more integrative encoding in the schema-consistent condition, while decisions in the schema-inconsistent condition depend more on logical inference.

General Discussion

We have conducted a study in which participants learned pairs of words with overlapping content (A-B, B-C, C-D) during a study phase. Shortly after a distraction task, participants judged whether two elements were indirectly linked during the study phase (A-C or A-D). We varied the relation of word pairs to be either schema-consistent or schema-inconsistent. The results of this study confirmed our hypothesis that schema not only affects the initial learning of word associations, but also affects performance during ilater memory integration (even after accounting for differences in initial learning rate). In addition, the data suggest that schema consistency facilitates integrative encoding through a weaker dependency of inference RTs, accuracy, and confidence, on the number of links that connected the two words during study.

Extend the effect of schema to memory integration

It is known that schema affects the initial acquisition, and consolidation, of memories (Alba & Hasher, 1983). New information can undergo system-level consolidation (with hippocampal independence) very rapidly when facilitated by a schema (Tse et al., 2007). In fact, even among patients with medial temporal lobe (MTL) damage, intact prior knowledge structures can support learning new episodic information that is consistent with schemas (Kan, Alexander, & Verfaellie, 2009). In contrast, damage to the mPFC is associated with reduced ability to integrate incoming information (Schnider, 2003). Recent neural imaging studies in a healthy population have further verified that schema-consistent knowledge is mediated by mPFC, and is integrated with neocortex rapidly, while schema-inconsistent knowledge is mediated by the MTL (van Kesteren et al., 2012; van Kesteren et al., 2013). These differences in initial acquisition and consolidation of new memories motivated us to investigate differences in behavioral markers of memory integration in our current study.

In particular, we observed not only enhanced learning of word pairs facilitated by schema, but also enhanced memory integration, in the form of improved recognition of schema-consistent linked pairs. This enhanced memory integration occurred despite both schema-consistent and inconsistent studied pairs being learned to the same criterion and recognized equally well during the test phase. In addition, the facilitation in memory integration is almost immediate during the encoding stage, rather than occurring (through logical inference) during the retrieval of initially learnt word pairs. When combined, these results suggest that schema plays a key role in fast integration of new information with existing memories.

Potential mechanism of fast memory integration

Given the differential involvement of the hippocampus or neocortex based on the use of schema (van Kesteren et al., 2012; van Kesteren et al., 2013), we hypothesize that the facilitation effect we observed might reflect different mechanisms of memory integration performed by the hippocampus and neocortex. In the hippocampus, fast memory integration is facilitated by dynamic shifts between encoding and retrieval states. Encoding of a new but overlapping event can reactivate a previous event that has mismatching details (Karlsson & Frank, 2009; Shohamy & Wagner, 2008). In the neocortex, mPFC demonstrates neural representational changes that are consistent with integrative encoding (Schlichting et al., 2015).

Fast encoding that bypasses the hippocampal system is possible when the new information is consistent with schema (Tse et al., 2007, 2011), with the mPFC shown to mediate the encoding (van Kesteren et al., 2012; van Kesteren et al., 2013). We observed greater (fast) memory integration for schema-consistent pairings, which might draw on generalization mechanisms that are more efficiently implemented in the neocortex than in the hippocampus.

Further implications and future directions

The current study suggests an alternative mechanism that can support integrative encoding. While the currently investigated question was motivated by results and proposed mechanisms at the neural level, it cannot directly test competing neural theories. Nevertheless, the finding that schema consistency facilitates memory integration, and particularly integrative encoding, is novel and highly informative at the psychological/behavioral level. Furthermore, it suggests venues for future neuroimaging research. In particular, based on these behavioral results, we propose that when there is rapid system-level consolidation facilitated by schema, memories can also undergo fast memory integration. Given the short interval between our study and test phases, it is likely that the learnt material had not become completely independent of the hippocampus, even under the effect of schema. The resulting integrative encoding is therefore likely supported by both the hippocampus and neocortex, or from an interaction between the two. Future neural imaging studies with high spatial resolution in different cortical and sub-cortical areas would be beneficial to make this distinction. Further neural imaging studies might also use neural activity during the encoding stage to predict later memory integration performance.

Acknowledgments

We thank John Paulus, Kimberly Hoover and Chao Wu for their assistance with the study.

References

Alba, J. W., & Hasher, L. (1983). Is memory schematic?. *Psychological Bulletin*, *93*(2), 203.

Born, J., & Wilhelm, I. (2012). System consolidation of memory during sleep. *Psychological Research*, *76*(2), 192-203.

Bunsey, M., & Eichenbaum, H. (1996). Conservation of hippocampal memory function in rats and humans. *Nature, 379*(6562), 255.

Coutanche, M. N., & Thompson-Schill, S. L. (2014). Fast mapping rapidly integrates information into existing memory networks. *Journal of Experimental Psychology: General*, *143*(6), 2296-2303.

Coutanche, M. N., & Thompson-Schill, S. L. (2015). Rapid consolidation of new knowledge in adulthood via fast mapping. *Trends in Cognitive Sciences*, *19*(9), 486-488.

Dusek, J. A., & Eichenbaum, H. (1997). The hippocampus and memory for orderly stimulus relations. *Proceedings of the National Academy of Sciences*, *94*(13), 7109-7114.

Eichenbaum, H. (2000). A cortical–hippocampal system for declarative memory. *Nature Reviews Neuroscience*, *1*(1), 41-50.

Eichenbaum, H., Dudchenko, P., Wood, E., Shapiro, M., & Tanila, H. (1999). The hippocampus, memory, and place cells: is it spatial memory or a memory space? Neuron *23*, 209–226.

Frankland, P. W., & Bontempi, B. (2005). The organization of recent and remote memories. *Nature Reviews Neuroscience*, *6*(2), 119-130.

Gluck, M. A., & Myers, C. E. (1993). Hippocampal mediation of stimulus representation: A computational theory. *Hippocampus*, *3*(4), 491-516.

Greene, A. J., Gross, W. L., Elsinger, C. L., & Rao, S. M. (2006). An FMRI analysis of the human hippocampus: inference, context, and task awareness. *Journal of Cognitive Neuroscience*, *18*(7), 1156-1173.

Hasselmo, M. E., & McClelland, J. L. (1999). Neural models of memory. *Current opinion in neurobiology*, *9*(2), 184-188.

Hasselmo, M. E., Schnell, E., & Barkai, E. (1995). Dynamics of learning and recall at excitatory recurrent synapses and cholinergic modulation in rat hippocampal region CA3. *Journal of Neuroscience*, *15*(7), 5249-5262.

Heckers, S., Zalesak, M., Weiss, A. P., Ditman, T., & Titone, D. (2004). Hippocampal activation during transitive inference in humans. *Hippocampus*, *14*(2), 153-162.

Hupbach, A., Gomez, R., Hardt, O., & Nadel, L. (2007). Reconsolidation of episodic memories: a subtle reminder triggers integration of new information. *Learning & Memory*, *14*(1-2), 47-53.

Kan, I. P., Alexander, M. P., & Verfaellie, M. (2009). Contribution of prior semantic knowledge to new episodic learning in amnesia. *Journal of Cognitive Neuroscience*, *21*(5), 938-944.

Karlsson, M. P., and Frank, L. M. (2009). Awake replay of remote experiences in the hippocampus. *Nat. Neurosci. 12*, 913–918.

Kuhl, B. A., Shah, A. T., Dubrow, S., and Wagner, A. D. (2010). Resistance to forgetting associated with hippocampus-mediated reactivation during new learning. *Nat. Neurosci. 13*, 501–506.

Kumaran, D., & Maguire, E. A. (2006). An unexpected sequence of events: mismatch detection in the human hippocampus. *PLoS biology*, *4*(12), e424.

Landauer, T. K., & Dumais, S. T. (1997). A solution to Plato's problem: The latent semantic analysis theory of acquisition, induction, and representation of knowledge. *Psychological Review, 104*(2), 211-240.

Marr, D., Willshaw, D., & McNaughton, B. (1991). Simple memory: a theory for archicortex. In From the Retina to the Neocortex (pp. 59-128). Birkhäuser Boston.

McClelland, J. L. (2013). Incorporating rapid neocortical learning of new schema-consistent information into complementary learning systems theory. *Journal of Experimental Psychology: General*, *142*(4), 1190.

McClelland, J. L., McNaughton, B. L., & O'reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory. *Psychological review*, *102*(3), 419.

McClelland, J. L., & Rogers, T. T. (2003). The parallel distributed processing approach to semantic cognition. *Nature Reviews Neuroscience*, *4*(4), 310-322.

McKenzie, S., & Eichenbaum, H. (2011). Consolidation and reconsolidation: two lives of memories? *Neuron*, *71*(2), 224-233.

Merhav, M., Karni, A., & Gilboa, A. (2015). Not all declarative memories are created equal: fast mapping as a direct route to cortical declarative representations. *Neuroimage*, *117*, 80-92.

Myers, C. E., Shohamy, D., Gluck, M. A., Grossman, S., Kluger, A., Ferris, S., ... & Schwartz, R. (2003). Dissociating hippocampal versus basal ganglia contributions to learning and transfer. *Journal of Cognitive Neuroscience*, *15*(2), 185-193.

Nadel, L., & Hardt, O. (2011). Update on memory systems and processes. *Neuropsychopharmacology*, *36*(1), 251-273.

Nadel, L., Hupbach, A., Gomez, R., & Newman-Smith, K. (2012). Memory formation, consolidation and transformation. *Neuroscience & Biobehavioral Reviews*, *36*(7), 1640-1645.

Peirce, JW (2007) PsychoPy - Psychophysics software in Python. *Journal of Neuroscience Methods*, *162*(1-2), 8-13.

Peirce, J.W. (2009) Generating stimuli for neuroscience using PsychoPy. *Frontiers in Neuroinformatics*, 2:10.

Preston, A. R., Shrager, Y., Dudukovic, N. M., & Gabrieli, J. D. (2004). Hippocampal contribution to the novel use of relational information in declarative memory. *Hippocampus*, *14*(2), 148-152.

Schlichting, M. L., Mumford, J. A., & Preston, A. R. (2015). Learning-related representational changes reveal dissociable integration and separation signatures in the hippocampus and prefrontal cortex. *Nature communications*, *6*, 8151.

Schlichting, M. L., & Preston, A. R. (2015). Memory integration: neural mechanisms and implications for behavior. *Current Opinion in Behavioral Sciences*, *1*, 1–8.

Schlichting, M. L., Zeithamova, D., & Preston, A. R. (2014). CA1 subfield contributions to memory integration and inference. *Hippocampus*, *24*(10), 1248-1260.

Schnider, A. (2003). Spontaneous confabulation and the adaptation of thought to ongoing reality. *Nature Reviews Neuroscience*, *4*(8), 662-671.

Sharon, T., Moscovitch, M., & Gilboa, A. (2011). Rapid neocortical acquisition of long-term arbitrary associations independent of the hippocampus. *Proceedings of the National Academy of Sciences*, *108*(3), 1146-1151.

Shohamy, D., & Wagner, A. D. (2008). Integrating memories in the human brain: hippocampal-midbrain encoding of overlapping events. Neuron, *60*(2), 378-389.

Singer, A. C., Karlsson, M. P., Nathe, A. R., Carr, M. F., and Frank, L. M. (2010). Experience-dependent development of coordinated hippocampal spatial activity representing the similarity of related locations. *J. Neurosci. 30*, 11586–11604.

Sommer, T. (2017). The emergence of knowledge and how it supports the memory for novel related information. Cerebral Cortex, *27*(3), 1906-1921.

Tse, D., Langston, R. F., Kakeyama, M., Bethus, I., Spooner, P. A., Wood, E. R., ... & Morris, R. G. (2007). Schemas and memory consolidation. *Science*, *316*(5821), 76-82.

van Kesteren, M. T., Beul, S. F., Takashima, A., Henson, R. N., Ruiter, D. J., & Fernández, G. (2013). Differential roles for medial prefrontal and medial temporal cortices in schema-dependent encoding: from congruent to incongruent. *Neuropsychologia*, *51*(12), 2352-2359.

van Kesteren, M. T., Ruiter, D. J., Fernández, G., & Henson, R. N. (2012). How schema and novelty augment memory formation. Trends in neurosciences, *35*(4), 211-219.

Wood, E. R., Dudchenko, P. A., & Eichenbaum, H. (1999). The global record of memory in hippocampal neuronal activity. *Nature*, *397*, 613–616.

Zeithamova, D., Dominick, A. L., & Preston, A. R. (2012). Hippocampal and ventral medial prefrontal activation during retrieval-mediated learning supports novel inference. *Neuron*, *75*(1), 168-179.

Zeithamova, D., & Preston, A. R. (2010). Flexible memories: differential roles for medial temporal lobe and prefrontal cortex in cross-episode binding. *Journal of Neuroscience*, *30*(44), 14676-14684.

Zola-Morgan, S., & Squire, L. R. (1990). The neuropsychology of memory. *Annals of the New York Academy of Sciences*, *608*(1), 434-456.