This is the author's final version. This article has been accepted for publication in the Journal of Cognitive Neuroscience.

Medial temporal lobe amnesia is associated with a deficit in recovering temporal context

Daniela J. Palombo^{1,2*#}, Joseph M. Di Lascio^{3,4*}, Marc W. Howard³ and Mieke Verfaellie^{1,2}

¹ VA Boston Healthcare System

² Department of Psychiatry, Boston University School of Medicine

³ Center for Memory and Brain, Department of Psychological and Brain Sciences, Boston University

⁴ Graduate Program for Neuroscience, Boston University School of Medicine

* The order of these authors was determined by a coin flip.

[#]Daniela J. Palombo is now an Assistant Professor at the University of British Columbia (Department of Psychology).

ABSTRACT

Medial temporal lobe (MTL) lesions are associated with severe impairments in episodic memory. In the framework of the Temporal Context Model (TCM), the hypothesized mechanism for episodic memory is the reinstatement of a prior experienced context (i.e., “jump back in time”), which relies upon the MTL (Howard, Fotedar, Datey, & Hasselmo, 2005). This hypothesis has proven difficult to test in amnesia due to floor-level performance by patients in recall tasks. To circumvent this issue, in the present study we used a “looped-list” format, in which a set of verbal stimuli was presented multiple times in a consistent order. This allowed for comparison of statistical properties such as probability of first recall and lag conditional response probability (lag-CRP) between amnesic patients and healthy controls. Results revealed that the lag-CRP, but not the probability of first recall, is altered in amnesia, suggesting a selective disruption of temporal contiguity. To further characterize the results, we fit a scale-invariant version of TCM (Howard, Shankar, Aue, & Criss, 2015) to the probability of first recall and lag-CRP curves. The modeling results suggested that the deficit in temporal contiguity in amnesia is best described as a failure to recover temporal context. These results provide the first direct evidence for an impairment in a jump-back-in-time mechanism in patients with MTL amnesia.

Keywords: amnesia, episodic memory, hippocampus, temporal contiguity

INTRODUCTION

Episodic memory is the ability to vividly bring to mind past events bound to a spatial and temporal context (Tulving, 1983). According to Tulving, this type of memory entails a form of mental time travel, in that it allows one to revisit in their mind's eye a previously experienced event. A striking impairment in this ability to re-experience the past is evident in patients with amnesia (Reed & Squire, 1998; Scoville & Milner, 1957), particularly in those with medial temporal lobe (MTL) lesions. Accordingly, such patients have been described as living in a 'permanent present' (Corkin, 2013). Yet, the mechanism underlying this impairment remains poorly understood.

In recent years, an influential class of models, namely Temporal Context Models (TCM; Healey & Kahana, 2016; Howard & Kahana, 2002; Polyn, Norman, & Kahana, 2009; Sederberg, Howard, & Kahana, 2008; Siegel & Kahana, 2014a) have offered a potential mechanism that can support episodic memory in normal cognition. These models have been constrained by a ubiquitous finding in episodic memory tasks, particularly in free recall tasks, which require participants to bring back to mind items studied in a word list. In such tasks, participants tend to recall together words that were presented closely in time in the study list, a phenomenon referred to as the temporal contiguity effect (Kahana, 1996). TCM postulates that episodic recall is mediated by a contextual representation that gradually evolves over time and provides an episodic retrieval cue in free recall tasks. According to this framework, the current, "time-of-test" context serves as a cue to drive recall of recently encoded list items; recent items are favored over earlier list items in recall because their encoding context most closely matches the time-of-test context. Once a recent item is recalled, it partially resets the temporal context to the state in which the item was encoded. This in turn, serves as a retrieval cue for recall of neighboring items on the list. This recovery of prior temporal context information can be understood as a computational implementation of a "jump back in time" that corresponds to Tulving's notion of mental time travel (Tulving, 1985).

Notably, TCM provides an explanation for the characteristic asymmetry of the temporal contiguity effect, as reflected in curves that plot response probability as a function of temporal lag, i.e., the lag-conditional response probability (lag-CRP) curve (Figure 1a): Given that the temporal context associated with recall of item n will be similar to the context associated with both items $n-1$ and $n+1$, the jump-back in time generates a symmetric retrieval cue for nearby items (Figure 1b). In addition to temporal and environmental features of the encoding episode, contextual representations also include thoughts and associations evoked by studied items themselves. Because the information caused by the word at serial position n is not part of the temporal context of words that precede it, recovery of this item information can only cause a contiguity effect in the forward direction, as shown in Figure 1b. That is, thoughts that arise during the encoding of item n will still be available in the temporal context at encoding of $n+1$, but cannot be available at $n-1$, as they had not yet occurred. By appropriately weighting these two symmetric and forward-asymmetric factors one can generate lag-CRP curves that provide a good description of empirical data (e.g., Howard, Kahana, & Wingfield, 2006; Polyn et al., 2009; Sederberg et al., 2008).

Critically, such a “jump-back-in-time” mechanism has recently been postulated as an account for episodic memory deficits in amnesia, and in particular, for the performance of amnesic patients in free recall tasks. This account elaborates and extends earlier models of amnesia that focused on the distinction between an intact short-term memory store and impaired long-term memory store (Baddeley & Warrington, 1970; Carlesimo, Marfia, Loasses, & Caltagirone, 1996; Warrington, 1982). A classic observation, favoring such a dual-store account of amnesia, is that in tasks of immediate free recall (IFR), in which there is no delay between study and test, amnesic patients are grossly impaired at recalling items from the early and middle portions of the list (presumed to be due to an impairment in long-term memory), yet show an intact recency effect, i.e., intact recall for end-of-list items (presumed to be due to intact short-term memory; e.g., Baddeley & Warrington, 1970; Carlesimo et al., 1996;

Talmi, Caplan, Richards, & Moscovitch, 2015). However, Talmi et al. (2015) offered evidence that is difficult to explain with a dual-store account. They assessed patients' performance in a continual-distractor free recall (CDFR) task, in which a brief distractor task is interposed after presentation of each word, including the last. Although the authors found the expected severe impairment in overall recall performance, critically, they also showed evidence for a robust recency effect.¹ Under the assumption that the distractor task displaces recent items from short-term memory, these findings cannot be explained by simply appealing to an intact short-term store in amnesic patients. Instead, Talmi et al. postulated that amnesics' performance can be understood as reflecting (1) impaired formation and/or retrieval of temporal context associations, which leads to an overall impairment in free recall; and (2) intact ability to use the current (time-of-test) context to recall end-of-list items, which accounts for the intact recency effect in CDFR. This account depends on the property of TCM that temporal context changes gradually over a broad range of time scales (Howard et al., 2015), a notion incompatible with a sharp distinction between a short- and long-term memory store.

Although simulation work supports the notion that the deficit of amnesic patients can be understood as a failure to encode and/or retrieve temporal context (Sederberg et al., 2008; but see Davelaar, Goshen-Gottstein, Ashkenazi, Haarmann, & Usher, 2005), this hypothesis has not been directly tested. Doing so requires assessment of temporal contiguity—the signature of the jump-back-in-time mechanism underlying TCM—in patients with amnesia. However, there is an obvious methodological challenge: Because the lag-CRP depends on transitions between words, it is extremely

¹ In earlier work, Carlesimo et al. (1996) reported intact recency performance in amnesia in IFR, but the recency effect was attenuated relative to controls in CDFR, as would be predicted by a dual-store model. However, Talmi et al. (2015) critically noted that the amnesia impairment in CDFR in Carlesimo et al. may simply reflect an overall reduction in performance across all serial positions. Accordingly, because the recency slopes appeared similar in amnesic patients and controls, it was suggested that the recency effect might in fact be intact. This possibility was confirmed in Talmi et al.: When only considering the first recalled item (i.e., probability of first recall) in CDFR, amnesic patients were just as likely as controls to sample from the last items in the study list, suggesting that both groups had equivalent access to end-of-list items.

difficult to measure in patients whose performance is close to floor and who therefore do not generate sufficient successive correct recalls.

In the present study, we use a “looped-list” format in which participants see a list of sequentially presented words. Instead of terminating after the last word (as in standard free recall tasks), the list seamlessly loops around to the first word in multiple cycles. In this way, each word is presented many times and their temporal relationships are preserved and reinforced with each cycle through the list. That is, although environmental features most likely vary with each repetition cycle, thoughts and associations brought to mind by each study item—a critical part of the unfolding temporal context—get reinforced across repetitions. One can implement this idea at an operational level by allowing repetitions of a word to cause strengthened context-to-item associations. As we show below, this novel methodological technique was successful in boosting free recall performance in MTL amnesia, enabling measurement of the lag-CRP in such patients. Combined with computational modeling, we were able to characterize for the first time temporal contiguity effects in amnesia. Critically, if amnesia reflects a failure to recover temporal context (i.e., a jump back in time), then the lag-CRP curve should be flattened in comparison to controls. That is, the symmetric component corresponding to the jump-back-in-time mechanism should be compromised, which would result in a change in the *shape* of the lag-CRP curve that can be detected with the computational model. Because the patients in this study have lesions localized to the MTL, any specific impairments shed light on the neural basis of a jump-back-in-time mechanism and the computational function of the MTL.

MATERIALS AND METHODS

Participants

Patients. Ten patients with amnesia (3 women) secondary to MTL damage participated in the study (see Table 1 for demographic and neuropsychological data). Each patient’s neuropsychological profile indicated severe impairment that was limited to the domain of memory. Etiology of amnesia

included hypoxic-ischemic injury secondary to either cardiac or respiratory arrest (n=6), stroke (n=2), encephalitis (n=1), and status epilepticus followed by left temporal lobectomy (n=1). One patient with hypoxic injury secondary to respiratory arrest was excluded because she was unable to maintain focus during the task and her performance was characterized by many extra-list intrusions, reflecting the incorporation of background stimuli into her recall.

Lesions for 7 of the remaining patients are presented in Figure 2, either on MRI or CT images. Two patients (P01, P02), who had suffered from cardiac arrest, could not be scanned due to medical contraindications and are thus not included in the figure. MTL pathology for these patients was inferred based on etiology and neuropsychological profile.

Of the patients with available scans, for 4 patients (P03, P04, P07, P08), lesions within the MTL were restricted to the hippocampus, 1 patient (P06) had a lesion that included the hippocampus and MTL cortices, and 1 patient (P09) had a lesion that extended beyond the MTL into anterolateral temporal neocortex. For the patient whose etiology was encephalitis (P05), clinical MRI was acquired but only in the acute phase of the illness, with no visible lesions observed on T1-weighted images. However, T2-flair images demonstrated bilateral hyperintensities in the hippocampus and MTL cortices (as well as the anterior insula). As shown in Table 1, medial temporal volumetric data for the hippocampus and MTL cortices was available for 5 of the 9 patients (P03, P04, P07, P08, P09), using methodology reported elsewhere (Kan, Giovanello, Schnyer, Makris, & Verfaellie, 2007).

Healthy Controls. Sixteen healthy control participants (7 women) were matched to the patient group in age (57.9 ± 7.5 years), education (14.8 ± 2.5 years) and verbal IQ (105.7 ± 10.2), which was assessed with the Wechsler Adult Intelligence Scale-III (WAIS-III; Wechsler, 1997). All participants provided informed consent in accordance with the Institutional Review Boards at Boston University and the VA Boston Healthcare System.

Materials and Procedure

One hundred and twenty easy-to-pronounce nouns of high frequency (mean = 133.5) and high concreteness (mean = 492.5) were selected from the MRC Psycholinguistic normative database (websites.psychology.uwa.edu.au/school/MRCDatabase/mrc2.html). All words contained 2 syllables, and were between 4-10 letters long (mean = 6.2). Nouns that could also be considered as verbs were not used.

Twelve word lists, each containing 10 words, were constructed such that each list consisted of no more than two words starting with the same letter of the alphabet and such that lists were well matched overall in terms of mean frequency, concreteness and number of letters. *Within* list, words were quasi-randomized, such that words starting with the same letter of the alphabet did not appear back-to-back. The 12 lists used are shown in the Appendix.

Participants were randomly assigned 9 of the 12 lists over 3 sessions. Although the within-list order was fixed for all participants, the order in which the lists were presented was randomized both across and within session for each participant.² As noted earlier, to boost the overall number of items recalled, each list repeated four times, in the same order, with a seamless transition across the repeated lists (referred to as the “looped-list” format as noted above).

Figure 3 depicts a schematic of the paradigm. In each session, for each list, participants were given the following instructions: *“You are going to see a series of words displayed on the screen one after another. I want you to read each word out loud and try to remember as many words as you can because I will ask you to recall them. It may seem like a long list, but the same words will repeat multiple times so just do your best to remember as many as you can.”* Each word was presented for 1200 msec in the center of the screen in uppercase black Arial font, size 18, on a white background, followed

²Whereas the majority of participants were administered 9 lists that were divided equally over 3 sessions (3-3-3), a small subset of participants deviated from this list prescription due to time constraints or technical issues (i.e., computer malfunction). To ensure all participants received 9 lists, this subset of participants were either given an extra list in a subsequent session, or were tested in a 4th session. This included 3 patients (2-4-3; 3-2-3-1; 3-1-3-2) and 4 controls (3-2-2-2; 3-3-2-1; 3-3-2-1; 3-3-2-1).

by a 1600 msec intertrial interval (ITI), which was comprised of a blank screen. Immediately following the presentation of the final word, “recall the words” was printed on the screen in blue font (Arial, size 18), which the experimenter read aloud. The experimenter recorded participant responses on a sheet of paper, in the exact order they were recalled; repetitions and intrusions were also recorded. Each list was separated by an unrelated task.

Analyses

Scoring. For each participant, we tallied the average number of (1) words correctly recalled; (2) repetitions; and (3) intrusions. For analyses pertaining to lag-CRPs (see below), whereas repetitions were considered, intrusions were not included in the analyses.

Conditional response probability (lag-CRP). The lag-CRP enables one to measure the effect of temporal contiguity on recall sequences (Healey & Kahana, 2016; Kahana, 1996; Sederberg et al., 2008). The goal of the lag-CRP is to estimate the probability that after recalling the word from serial position i the next word recalled comes from serial position $i + \text{lag}$. The variable lag can take on both positive and negative values. To be concrete, suppose the participant had just recalled the word PUPIL from a list that included the words ABSENCE HOLLOW PUPIL RIVER DARLING. In this case, a recall transition from PUPIL to RIVER would be associated with a lag of +1 whereas a recall transition from PUPIL to ABSENCE would be associated with a lag of -2. In computing the lag-CRP one observes the number of times transitions of a particular lag occurred divided by the number of times that transitions of that lag could have occurred as a correct recall.

In this experiment, repetitions in the list cause lag to be a circular variable. For instance, the seventh item in the list follows the first item in the list by lag +6 but also precedes it by lag -4. In these analyses we used the lag with the smallest absolute value. Because lag +/- 5 is ambiguous, we only included points out to +/- 4 in the lag-CRP analyses.

Computational Modeling.

Modeling framework. Because it is already well-known that amnesic patients recall fewer items overall than control participants, in this study we took the approach of constructing a minimal model that would enable us to characterize and compare temporal retrieval effects across groups. Recent work has developed a scale-invariant representation of temporal context (Shankar & Howard, 2012) that aligns well with the firing properties of neurons recorded in the MTL (MacDonald, Lepage, Eden, & Eichenbaum, 2011) and can account for a range of behavioral findings, including scale-invariant recency and contiguity effects in free recall (Howard et al., 2015). This approach leads to simple analytic expressions for temporal retrieval effects. Following a model for recency and contiguity effects (Howard et al., 2015), herein dubbed Scale Invariant Temporal History (SITH), we used the following expressions to estimate the probability of first recall (PFR):

$$P_{FR}(n) = \frac{(d+nD)^{-b}}{\sum_{m=1}^l (d+mD)^{-b}} \quad (1)$$

where m is the summation index used to integrate across serial positions in the denominator, n is the serial position, d is the delay between study and recall, D is the presentation rate, b is the sensitivity of the Luce choice rule, with an enhancement factor of φ at the first serial position. In this experiment, taking into account the looped-list format, the lag-CRP is given by:

$$p_n = [\gamma(n)^{-1} + (\gamma + \gamma_f)(l - n)^{-1} + c]^b \quad (2)$$

$$p_{-n} = [(\gamma + \gamma_f)(n)^{-1} + \gamma(l - n)^{-1} + c]^b \quad (3)$$

where n is a lag from 1 to 4 and l is the number of unique items in the list. Equation 2 describes the lag-CRP in the forward direction; Equation 3 describes the lag-CRP in the backward direction. The parameter c represents the presence of noise, with larger values diminishing the relative differences between points, b is again the sensitivity of the Luce choice rule, γ is the degree of contextual reinstatement (or jump back in time), and γ_f controls the strength of simple forward associations. The expressions in Eqs. 2-3 have two terms. The term weighted by $+\gamma_f$ is the degree to which the previously recalled word overlaps with the scale-invariant temporal context of the potentially retrieved item (both parameters appear because the list loops). The term weighted by γ is due to recovery of the previous state of scale-invariant temporal context.

This simple formulation has the ability to describe a broad range of lag-CRP curves (Figure 1b). If there is no jump back in time, i.e., if $\gamma_f > 0$ but $\gamma = 0$, then the model generates a lag-CRP that is asymmetric and provides only forward-going temporal associations (Figure 1b, dashed line). If the lag-CRP was only dependent on a jump back in time, i.e., if $\gamma_f = 0$ but $\gamma > 0$, the model generates a purely symmetric lag-CRP (Figure 1b, dotted line). If the temporal noise c is very large relative to the other components, the model generates no contiguity effect at all (Figure 1b, solid curve). The canonical asymmetric shape of the empirical lag-CRP can be achieved by assigning moderate values to the symmetric and asymmetric components of activation (Figure 4, see also Howard et al., 2015).

Parameter estimation. The TCM-SITH model has 7 parameters, 4 of which affect the PFR, and 4 of which affect the CRP (one is shared by both calculations). All calculations were performed with $d = 1$ and $D = 1$. The other parameters were chosen by quasi-Newton minimization (L-BFGS-B) of the goodness of fit value of both PFR and lag-CRP points to minimize:

$$\sum_i \frac{(m_i - o_i)^2}{\sigma_i} \quad (4)$$

where m_i is the model's predicted value at point i , o_i is the observed value and σ_i is the standard error of the mean. The shape of the PFR was affected by the value of ϕ . The shape of the lag-CRP was governed by γ , γ_t , and c . To control for possible differences in the empirical data due to output position effects, we normalized the sum of probabilities in the lag-CRP to be the same as that of the behavioral data separately for each group.

Under the assumption that the model generated the data, we would expect Eq. 4 to be distributed like chi-squared with a number of degrees of freedom equal to one minus the number of data points minus the number of free parameters. It is straightforward to compare nested models because the expected difference in the goodness of fit statistic should be equal to chi-squared with degrees of freedom equal to the difference in number of parameters between the two models.

In order to test hypotheses about parameters that account for the difference between groups we evaluated nested models. The parameters of each model were estimated independently. The models differed in which parameters were allowed to vary across groups. For instance, to evaluate the effect of γ we compared a base model in which all parameters were shared across group to a model in which only γ was allowed to vary between patients and controls. We evaluated nested models with all possible permutations of parameter variation, e.g., only γ varies across groups; γ and c vary; γ_t , ϕ , and c vary, et cetera, except that we did not ever allow the Luce choice exponent b to vary across groups.

RESULTS

As expected, controls recalled significantly more words than patients across sessions (proportion recalled, mean $\pm$ standard deviation; controls: 0.80 ± 0.09 ; patients: 0.52 ± 0.04), $t(23) = 8.57$, $p = 1.30 \times 10^{-8}$, but the groups did not significantly differ in the number of repetitions (controls: 0.77 ± 0.43 ; patients: 0.49 ± 0.60), $t(23) = 1.30$, nor the number of intrusions (controls: 0.12 ± 0.12 ; patients: 0.25 ± 0.21), $t(23) = -1.88$.

Traditional analyses of temporal retrieval effects

Serial position curves. As seen in Figure 5a, amnesic patients recalled fewer items at each serial position than controls. The ANOVA of probability of recall as a function of serial position showed a main effect of group, $F(1,230) = 162.07$, $p = 1.87\text{e-}28$, which reflects lower overall levels of recall in patients. There was a significant effect of serial position, $F(9,230) = 12.13$, $p = 1.22\text{e-}15$, reflecting the well-established primacy and recency effects, but no interaction between group and serial position, $F(9,230) = 1.32$.

Probability of first recall (PFR). Figure 5b shows the probability that patients and controls initiated free recall with each serial position. The ANOVA of probability of first recall as a function of serial position showed a main effect of serial position, $F(9,230) = 36.55$, $p = 1.07\text{e-}39$. The main effect of serial position is apparently a consequence of an elevated probability of initiating recall with the first item on the list (a primacy effect), and to initiate recall from the end of the list (a recency effect). Although, numerically, patients' first recall was less likely to come from the first position, there was no interaction of group and serial position, $F(9,230) = 1.51$. Because the PFR is normalized to one for each participant, it is not possible to test for a main effect of group.

To more fully characterize the effects of recency, we examined only serial positions after the first one. This analysis again revealed a main effect of serial position, $F(8,207) = 10.30$, $p = 4.25\text{e-}12$; neither the main effect of group, $F(1,207) = 2.12$, nor the interaction of group and serial position, $F(8,207) = 0.33$, was significant, indicating that there is no evidence for a disruption of the recency effect in the probability of first recall in amnesic patients. The lack of group differences in the recency effect supports the conclusion that the rate of contextual drift, namely the change in temporal context as a function of time, did not vary between patients and controls.

Conditional response probability (lag-CRP). Figure 5c shows the lag-CRP curves for patients and controls. We conducted an ANOVA of the lag-CRP results with group (patient vs control), $|\text{lag}|$ (1:4) and direction (forward vs backward) as factors. We found main effects of group, $F(1,184) = 6.86$, p

= .01; direction, $F(1,184) = 10.29$, $p = .0016$, and $|\text{lag}|$, $F(3,184) = 34.65$, $p = 8.40\text{e-}18$. There was no interaction effect of group and direction, $F(1,184) = 0.0011$, nor of group, $|\text{lag}|$, and direction, $F(3,184) = 0.69$. As expected based on previous work showing an asymmetry in the CRP, we found an interaction of $|\text{lag}|$ and direction, $F(3,184) = 17.35$, $p = 5.8\text{e-}10$. Critically, we found an interaction of group and $|\text{lag}|$, $F(3,184) = 4.55$, $p = .0042$, indicating that the effect of temporal contiguity on the trajectory of memory retrievals through time was disrupted in amnesic patients. The modeling presented below sheds additional light on the nature of the disruption in the contiguity effect in amnesia.³

TCM-SITH Modeling results

We started with a base model with five free parameters to model the probability of first recall and the lag-CRP. The parameter b controls the exponent in the Luce choice rule (see eq. 2) and affects both the PFR and the CRP. The parameters d , which controls the effective delay before recall begins, D , which controls the presentation rate, and ϕ , which controls the magnitude of the primacy effect, only have an effect on the PFR; d and D were fixed to 1. Three parameters, c , γ_f and γ affect the shape of the lag-CRP curve.

The strategy we adopted was to first fit the PFR and CRP curves for patients and controls with a single set of five parameters, b , ϕ , c , γ_f and γ . In order to assess the effects of group, we compared models with separate values of various parameters for patients and controls. To the extent that this model fits better than the nested base model, we can infer that the parameter allowed to vary across groups captured some of the variance attributable to amnesia.

The best-fitting base model gave values of $b = 1.55$, $\phi = 79.71$, $c = 22.99$, $\gamma_f = 16.66$, and $\gamma = 8.34$. The fit of the base model, $\text{chi-squared}(30) = 75.64$, deviated from chance ($p = 8.20\text{e-}6$). However,

³We note that although the lag-CRP curve in the patients appears non-monotonic for negative lags, when we fit these data with a polynomial model, the quadratic component was not statistically reliable, $F(1,1) = 6.69$. Nonetheless, we speculate that this trend is a consequence of the looped list format: In the absence of strong backward associations (as in the patients), one would expect that the CRP at lag -1 would be smaller than the CRP at lag -2 because -2 is closer in the forward direction.

the primary function of modeling here is to provide a way to characterize differences in the temporal retrieval abilities of amnesic patients compared to controls and to determine which model parameters best describe that change.

Model-based analysis of the PFR. Based on prior work (Carlesimo et al., 1996; Kesner & Novak, 1982) we asked whether amnesic patients had a disrupted primacy effect by comparing the base model to a model in which ϕ was allowed to vary separately for amnesic patients and controls. The best fitting parameters of this model were $b = 1.47$, $c = 27.47$, $\gamma_f = 21.67$, $\gamma = 15.67$, with $\phi = 90.90$ for controls and $\phi = 49.78$ for patients. This model provided a marginally superior fit to the base model, chi-squared(1) = 3.41, $p = 0.0648$. This is consistent with prior work showing a disruption of primacy in MTL amnesia.

Model-based analysis of the lag-CRP. In order to determine what model components best described the disruption of the contiguity effect in MTL amnesia, we fit a range of models examining the effect of allowing γ , γ_f , and c to vary across groups. Allowing γ_f , the parameter responsible for the forward asymmetry in the lag-CRP, to vary across groups did not reliably improve the fit over the base model, chi-squared(1) = 2.29. Allowing c to vary across groups, resulting in an overall decrease in the temporal contiguity effect, did not improve the fit, chi-squared(1) = 1.24. Critically, allowing γ , the parameter responsible for recovery of temporal context, to vary across groups provided a dramatic improvement in the fit, chi-squared(1) = 13.18, $p = 0.00028$, with best fitting parameters $b = 1.50$, $\phi = 74.05$, $c = 27.61$, $\gamma_f = 20.38$, control $\gamma = 36.55$, and patient $\gamma = 4.68$. Note that for controls the fit settled on roughly similar values for γ and γ_f , with γ about twice as large as γ_f . However, for amnesic patients the fit settled on value of γ that was much lower than for control patients; this value was also about four times less than the value of γ_f . Allowing c or γ_f to vary across groups in addition to γ did not improve the fit over the model in which γ was allowed to vary, both chi-squared(1) = 0.74. These results suggest that

the change in the temporal contiguity effect observed in amnesic patients was well-described by a selective disruption in the recovery of temporal context.

Because allowing ϕ to vary across groups produced a marginally significant improvement in the fit and because prior work has shown an impairment in primacy in MTL amnesic patients, we also compared models in which ϕ was allowed to vary across groups along with the various parameters that affect the shape of the lag-CRP curve. We found that the model with ϕ and γ allowed to vary across groups provided the best fit, with a reliable improvement over the base model with no parameters varying across groups, $\chi^2(2) = 16.8$, $p = 0.00023$, with best fitting parameters $b = 1.43$, $c = 27.49$, $\gamma_f = 22.17$, control $\gamma = 40.95$ and $\phi = 85.37$, and patient $\gamma = 4.98$ and $\phi = 45.89$; see Figure 6 for PFR (Figure 6a) and lag-CRP curves (Figure 6b) generated by this model. Again, note that for controls the fit settled on roughly similar values for γ and γ_f with γ a bit less than two times greater than γ_f . However, for amnesic patients the fit settled on a value of γ about eight times less than the control patients and about four times less than the value of γ_f . The best-fitting parameters also showed that patients had lower values of ϕ than did controls. Allowing both ϕ and γ_f to vary across groups did not result in a reliable improvement over the base model, $\chi^2(2) = 5.79$. Likewise, allowing both ϕ and c to vary across groups did not result in a reliable improvement over the base model, $\chi^2(2) = 4.72$. Allowing γ_f or c to vary across groups in addition to ϕ and γ did not improve the fit, both $\chi^2(1) = .56$. The evidence from the modeling work supports the hypothesis that the disruption in the temporal contiguity effect in amnesic patients with MTL lesions is attributable to a deficit in the recovery of temporal context (i.e., a failure to jump back in time).

DISCUSSION

In this study we examined free recall in amnesic patients and control participants using a looped-list format in which a set of verbal stimuli was presented multiple times in a consistent order. This procedure allowed us not only to examine participants' overall level of recall, but also to evaluate for the

first time the temporal retrieval characteristics of their recall performance. Traditional statistics, complemented by a descriptive free recall model (Howard et al., 2015),⁴ show that amnesic patients, in addition to having reduced recall, have a disrupted temporal contiguity effect. By contrast, amnesic patients' first recall (i.e., PFR) was as likely as that of controls to be sampled from end-of-list items, suggesting that test context can serve as an effective cue for recall.

Our study allowed a direct test of the interpretation Talmi et al. (2015) offered for their finding of intact recency effects in amnesia in CDFR. By using a looped-list format, we were able to bring amnesics' recall to a level where one can meaningfully measure recall sequences⁵. This made possible for the first time examination of temporal contiguity effects in amnesia. Consistent with the notion that the recall impairment in amnesia can be understood as a disruption in the formation and/or recovery of item-context representations, our lag-CRP results, coupled with the computational modeling results (i.e., a reduction in γ), demonstrate that patients were unable to reinstate the temporal context in which an

⁴ In this study we used a minimal model to estimate the probability of first recall and temporal contiguity effects as measured by the lag-CRP. Other free recall models use a more detailed approach in which the entire sequence of recalls is estimated (Polyn et al., 2009; Sederberg et al., 2008). This detailed modeling approach has been successfully applied to studies of reconsolidation (Sederberg, Gershman, Polyn, & Norman, 2011), learning (Lohnas, Polyn, & Kahana, 2015), spacing (Siegel & Kahana, 2014b), aging (Healey & Kahana, 2016; Kahana, 1996), and emotion (Talmi, Lohnas, & Daw, 2017). There are costs and benefits to the simpler, more descriptive approach compared to the more detailed approach. For instance, a detailed model of free recall requires estimation of many more free parameters (e.g., the Sederberg et al., 2008 model used 12 free parameters). On the other hand, the simpler approach used in this paper does not generate an entire recall sequence, making it difficult to evaluate changes in the serial position curve, which aggregate over the entire sequence of recalls. Insofar as there was no interaction of group and serial position in the current study, this is probably not a major cost. Moreover, both the more descriptive (Howard & Kahana, 2002) and more detailed approach (Healey & Kahana, 2016) have been applied to the study of aging, yielding similar results. This experience suggests that the simple model used here is sufficient for understanding the qualitative pattern of results in amnesic patients.

⁵ It should be noted that repeating the study items (i.e., the looped-list format) leads to somewhat different patterns of free performance relative to the standard (immediate) free recall condition used in prior work (e.g., Howard & Kahana, 1999). Indeed, in the present study, the primacy effect appears more robust (and the recency effect attenuated) relative to the standard condition, although we did not compare these approaches directly. Nonetheless, a relatively large primacy effect is not atypical in free recall studies, especially those that have a relatively slow presentation rate (e.g., Glanzer & Cunitz, 1966).

item was encoded, thus rendering unavailable a critical cue for the recall of neighboring items. Taken together with the finding that patients were able to use test context as an effective cue for the recall of end of list items, our results suggest a selective deficit in the ability to jump back in time.

Evidence for such a jump-back-in-time mechanism is not limited to free recall; findings provide support for a similar mechanism in other episodic memory tasks that make high demands on recollection, including high-confidence recognition memory (Folkerts, Rutishauser, & Howard, 2018; Schwartz, Howard, Jing, & Kahana, 2005) and cued recall (Davis, Geller, Rizzuto, & Kahana, 2008). We propose that the impairment in a jump-back-in-time mechanism observed in the present study provides a framework for understanding recollection deficits in amnesia that extend beyond those observed in free recall. In this regard, although an impairment in the reinstatement of temporal context may be apparent particularly in tasks that measure temporal aspects of behavior (Dede, Frascino, Wixted, & Squire, 2016; Palombo & Verfaellie, 2017), deficits need not be limited as such. That is, retrieval of temporal context provides a vehicle for the reinstatement of event-specific information, be it temporal (Hirst & Volpe, 1982; Shimamura, Janowsky, & Squire, 1990), spatial (Cave & Squire, 1991; Kumaran et al., 2007) or semantic (Giovanello, Verfaellie, & Keane, 2003; Yonelinas et al., 2002), all of which are vulnerable in amnesia. Notably, such an impairment in the retrieval of temporal context would not impact memory judgments based on familiarity, given that such judgments are devoid of contextual information. As such, our findings are consistent with dual-process models that postulate a dissociation between recollection and familiarity in amnesia (Yonelinas, 2002). However, we note that the modeling approach used here does not allow us to conclude that the deficit in temporal context in amnesia is *causally* linked to their impairment in overall recall.

Whereas our findings provide support for an impairment in temporal context in amnesia—an explanation postulated by Talmi et al., (2015) to account for findings that are incompatible with a dual-store explanation—it should be noted that our study was not designed to adjudicate between single- and

dual-store (e.g., Atkinson & Shiffrin, 1968; Davelaar et al., 2005) interpretations of amnesia. A direct comparison of the two classes of models would require measurement of the recency and contiguity effects across a broader range of time scales, including CDFR and delayed free recall.

In addition to shedding light on the nature of the episodic memory impairment in amnesia, our results link the proposed temporal context mechanism to the MTL. This result fits into a growing body of work suggesting a role for the MTL in the recovery of temporal context in the service of episodic memory. A recent study by Goyal et al. (2018) examined the effects of stimulation within the MTL (i.e., entorhinal cortex and hippocampus) on free recall in patients with temporal lobe epilepsy. They found that stimulation of the MTL impaired overall recall but also disrupted the temporal contiguity effect. Notably, a robust disruption in the temporal contiguity effect was observed in the backward direction. Likewise, in our study, as shown in Figure 5c, patients showed no evidence for a backwards temporal contiguity effect, a pattern described by the modeling results as a disruption in the ability to recover temporal context.

Complementing the above behavioral evidence, there is a growing body of neurophysiological evidence in animals and humans that directly links temporal context to neural activity in the MTL (see Howard, 2017 for a recent review). If the state of temporal context corresponds to active neurons in the MTL, and if one could directly observe those neurons, the computational model used here predicts that 1) the set of neurons active at any moment should change gradually with the passage of time; and 2) an episodic memory should result in recovery of a preceding state of gradually changing temporal context. Indeed, in animal work, there is strong evidence that the set of neurons active in the hippocampus changes gradually over a broad range of time from seconds to minutes, and even across days (Cai et al., 2016; Mau et al., 2018; Rubin, Geva, Sheintuch, & Ziv, 2015). Moreover, human neurophysiological studies demonstrate that the gradually changing state of temporal context is recovered when information is remembered. Folkerts et al. (2018) measured single neurons from the MTL of human epilepsy patients

during an item recognition task. Mirroring prior animal studies, the activity of populations of neurons in the MTL changed gradually over time during study of the list. In addition, when a studied item presented at test was remembered with high confidence, the set of active neurons recovered the gradually changing ensemble state that was present just before and after the item was initially studied. Critically, this neural jump back in time was not observed when the item was not remembered with high confidence. These results from single unit recordings add to findings from human electrocorticography recordings during free recall (Manning, Polyn, Baltuch, Litt, & Kahana, 2011) and cued recall (Yaffe et al., 2014), and provide strong evidence that the brain recovers a gradually changing temporal context signal during episodic recall tasks. Moreover, outside the domain of laboratory experiences, fMRI results show that memories from participants' real world experience are organized in the hippocampus along temporal (as well as spatial) dimensions (Nielson, Smith, Sreekumar, Dennis, & Sederberg, 2015).

The findings in this paper provide a critical link between an emerging literature on the role of temporal context reinstatement in episodic memory and well-established deficits in free recall in patients with MTL lesions by providing a mechanistic framework for understanding such deficits. By combining behavioral results from a novel methodological approach with a computational modeling framework of a well-characterized laboratory memory task, we demonstrate that amnesia is associated with a failure to jump back in time, precisely the signature that Tulving (1985) envisioned when characterizing episodic memory as mental time travel.

Table 1

Patients	Etiology	Age	Edu	WAIS III		WMS III			Volume Loss (%)	
				VIQ	WMI	GM	VD	AD	Hippocampal	Subhippocampal
P01	Hypoxic-Ischemic	65	16	100	88	86	78	83	N/A	N/A
P02	Hypoxic-Ischemic	63	17	131	126	86	78	86	N/A	N/A
P03	Stroke	50	20	111	99	60	65	58	43%	-
P04	Hypoxic-Ischemic	59	14	106	115	59	72	52	22%	-
P05	Encephalitis	73	13	99	104	49	56	58	N/A	N/A
P06	Hypoxic-Ischemic	65	12	88	75	52	56	55	N/A	N/A
P07	Hypoxic-Ischemic	47	12	103	95	59	68	55	46%	-
P08	Stroke	62	18	117	88	67	75	55	62%	-
P09	Status Epilepticus	52	16	93	94	49	53	52	63%	60% ^a
	+ Left Temporal Lobectomy									
									70%	-

Note: Age, age in years; Edu, education in years; WAIS-III, Wechsler Adult Intelligence Scale-III; WMS-III, Wechsler Memory Scale-III; VIQ, verbal intelligence quotient; WMI, working memory index; N/A, not available. ^aVolume loss in left anterior parahippocampal gyrus (i.e., entorhinal cortex, medial portion of the temporal pole, and the medial portion of perirhinal cortex; (see Kan et al., 2007 for methodology).

Figures

Figure 1. a) The temporal contiguity effect in free recall. Lag-CRP average from 20 experiments (Kahana, Howard, & Polyn, 2008). The lag-CRP estimates the probability of making a recall transition from serial position n to serial position $n + \text{lag}$. The lag-CRP shows two robust properties. First, the curve is peaked around zero, in both the forward and backward directions indicating that there is an increased tendency to recall nearby words together in free recall. Second, the curve is more pronounced in the forward direction than in the backward direction. This asymmetry is extremely robust in free recall studies. **b)** Three components affect the shape of the lag-CRP curve in TCM-SITH. These components differentially contribute to the activation of items nearby in the list to the one just recalled. The solid line represents the case with no temporal information; the dashed line represents the case with only simple associations evoked by the recalled item; the dotted line represents the case with only recovery of the context in which the recalled item was encoded.

Figure 2. Structural MRI and CT scans depicting medial temporal lobe (MTL) lesions for 8 of the 10 amnesic participants (see Method). The left side of the brain is displayed on the right side of the image. T1-weighted MRI images depict lesions for P03, P04, P07, P08, and P09 in the coronal and axial plane. T2-Flair MRI images depict lesion locations for P05 in the axial plane. CT slices show lesion location for P06 in the axial plane.

Figure 3. Trial and coding structure for the free recall task for one looped list (list 1, see Appendix). **a)** At study, participants saw the same list repeat in a seamless fashion four times (only two cycles shown). **b)** At test, participants immediately recalled the words. For calculating lag-CRP curves, each transition between words was assigned a positive or negative value, depending on the order of recall and the shortest possible lag between the words. For example, if a participant recalled “motor” followed by “center”, the lag was coded as -1 , which represents a *backward* transition. If a participant recalled “center” followed by “column”, the lag was coded as $+3$, which represents a *forward* transition.

Figure 4. The simple descriptive model of free recall used here can account for the canonical shape of the temporal contiguity effect in free recall. We informally adjusted the parameters of the model to roughly replicate the lag-CRP curve shown in Figure 1a. Here, $\gamma = 0.3$, $\gamma_f = 0.3$, $b = 1.5$, and $c = 0.1$. Equivalent values of γ and γ_f provide a good description of the canonical shape.

Figure 5. a) Probability of recall, b) probability of first recall, and c) lag-CRP for controls (dashed) and patients (solid). The patients show a disrupted temporal contiguity effect in the lag-CRP. Error bars represent standard error of the mean.

Figure 6. Model fits for (a) Probability of first recall and (b) lag-CRP where the primacy enhancement factor ϕ and the magnitude of contextual reinstatement γ are allowed to vary across groups. The best-fitting model as determined by chi-squared goodness of fit described amnesic patients as having lower values for ϕ (controls: 85.4, patients: 45.9) and γ (controls: 41.0, patients: 4.98). These differences accounted for changes in the primacy effect and the temporal contiguity effect, respectively.

Acknowledgements

D.J.P. was supported by a postdoctoral fellowship from the Canadian Institutes of Health Research. J.M.D. and M.W.H. were supported by NSF IIS 1631460 and NIH R01EB022864, J.M.D. was also supported by NIH T90DA032484-05. M.V. is supported by a Senior Research Career Scientist Award from the Clinical Science Research and Development Service, Department of Veterans Affairs. We thank Rose Hopkins for assistance with data collection, and Zoran Tiganj for helpful conversations. The contents of this manuscript do not represent the view of the US Department of Veterans Affairs or the US Government.

Appendix

List 1	List 2	List 3	List 4	List 5	List 6	List 7	List 8	List 9	List 10	List 11	List 12
breakfast	captain	device	hotel	distance	island	husband	machine	poet	money	father	platform
column	estate	cattle	baby	student	budget	engine	woman	children	window	volume	brother
problem	summer	body	artist	product	circle	council	village	account	station	river	session
music	level	pattern	corner	winter	jury	symbol	fellow	party	unit	system	city
office	hero	market	service	metal	mother	water	payment	disease	event	minor	person
trial	marriage	evening	nature	nation	railroad	portion	signal	fashion	culture	title	concern
weather	paper	cousin	statement	series	career	background	degree	meeting	lady	hour	figure
rifle	valley	pressure	country	contract	surface	college	public	uncle	message	doctor	entrance
center	shoulder	forest	bedroom	number	novel	item	table	congress	coffee	angle	bottle
motor	question	story	leader	fire	dinner	army	letter	season	teacher	morning	income

REFERENCES

- Atkinson, R. C., & Shiffrin, R. M. (1968). Human Memory: A Proposed System and its Control Processes. In W. S. Kenneth & S. Janet Taylor (Eds.), *Psychology of Learning and Motivation* (Vol. Volume 2, pp. 89-195): Academic Press.
- Baddeley, A. D., & Warrington, E. K. (1970). Amnesia and the distinction between long- and short-term memory. *Journal of Verbal Learning and Verbal Behavior*, 9(2), 176-189.
- Cai, D. J., Aharoni, D., Shuman, T., Shobe, J., Biane, J., Song, W., et al. (2016). A shared neural ensemble links distinct contextual memories encoded close in time. *Nature*, 534(7605), 115-118.
- Carlesimo, G. A., Marfia, G. A., Loasses, A., & Caltagirone, C. (1996). Recency effect in anterograde amnesia: evidence for distinct memory stores underlying enhanced retrieval of terminal items in immediate and delayed recall paradigms. *Neuropsychologia*, 34(3), 177-184.
- Cave, C. B., & Squire, L. R. (1991). Equivalent impairment of spatial and nonspatial memory following damage to the human hippocampus. *Hippocampus*, 1(3), 329-340.
- Corkin, S. (2013). *Permanent Present Tense: The Unforgettable Life of the Amnesic Patient, H.M.*: Basic Books.
- Davelaar, E. J., Goshen-Gottstein, Y., Ashkenazi, A., Haarmann, H. J., & Usher, M. (2005). The demise of short-term memory revisited: empirical and computational investigations of recency effects. *Psychological Review*, 112(1), 3-42.
- Davis, O. C., Geller, A. S., Rizzuto, D. S., & Kahana, M. J. (2008). Temporal associative processes revealed by intrusions in paired-associate recall. *Psychonomic Bulletin & Review*, 15(1), 64-69.
- Dede, A. J., Frascino, J. C., Wixted, J. T., & Squire, L. R. (2016). Learning and remembering real-world events after medial temporal lobe damage. *Proceedings of the National Academy of Sciences*, 113(47), 13480-13485.
- Folkerts, S., Rutishauser, U., & Howard, M. W. (2018). Human Episodic Memory Retrieval Is Accompanied by a Neural Contiguity Effect. *Journal of Neuroscience*, 38(17), 4200-4211.
- Giovanello, K. S., Verfaellie, M., & Keane, M. M. (2003). Disproportionate deficit in associative recognition relative to item recognition in global amnesia. *Cognitive, Affective & Behavioral Neuroscience*, 3(3), 186-194.
- Glanzer, M., & Cunitz, A. R. (1966). Two storage mechanisms in free recall. *Journal of Verbal Learning & Verbal Behavior*, 5(4), 351-360.
- Goyal, A., Miller, J., Watrous, A. J., Lee, S. A., Coffey, T., Sperling, M. R., et al. (2018). Electrical Stimulation in Hippocampus and Entorhinal Cortex Impairs Spatial and Temporal Memory. *Journal of Neuroscience*, 38(19), 4471-4481.
- Healey, M. K., & Kahana, M. J. (2016). A four-component model of age-related memory change. *Psychological Review*, 123(1), 23-69.
- Hirst, W., & Volpe, B. T. (1982). Temporal order judgments with amnesia. *Brain and Cognition*, 1(3), 294-306.
- Howard, M. W. (2017). Temporal and spatial context in the mind and brain. *Current Opinion in Behavioral Sciences*, 17, 14-19.
- Howard, M. W., Fotedar, M. S., Datey, A. V., & Hasselmo, M. E. (2005). The temporal context model in spatial navigation and relational learning: toward a common explanation of medial temporal lobe function across domains. *Psychological Review*, 112(1), 75-116.

- Howard, M. W., & Kahana, M. J. (1999). Contextual variability and serial position effects in free recall. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 25(4), 923-941.
- Howard, M. W., & Kahana, M. J. (2002). A distributed representation of temporal context. *Journal of Mathematical Psychology*, 46, 269-299.
- Howard, M. W., Kahana, M. J., & Wingfield, A. (2006). Aging and contextual binding: modeling recency and lag recency effects with the temporal context model. *Psychonomic Bulletin & Review*, 13(3), 439-445.
- Howard, M. W., Shankar, K. H., Aue, W. R., & Criss, A. H. (2015). A distributed representation of internal time. *Psychological Review*, 122(1), 24-53.
- Kahana, M. J. (1996). Associative retrieval processes in free recall. *Memory & Cognition*, 24(1), 103-109.
- Kahana, M. J., Howard, M. W., & Polyn, S. M. (2008). Associative Retrieval Processes in Episodic Memory. *Psychology*, 3.
- Kan, I. P., Giovanello, K. S., Schnyer, D. M., Makris, N., & Verfaellie, M. (2007). Role of the medial temporal lobes in relational memory: Neuropsychological evidence from a cued recognition paradigm. *Neuropsychologia*, 45(11), 2589-2597.
- Kesner, R. P., & Novak, J. M. (1982). Serial position curve in rats: role of the dorsal hippocampus. *Science*, 218(4568), 173-175.
- Kumaran, D., Hassabis, D., Spiers, H. J., Vann, S. D., Vargha-Khadem, F., & Maguire, E. A. (2007). Impaired spatial and non-spatial configural learning in patients with hippocampal pathology. *Neuropsychologia*, 45(12), 2699-2711.
- Lohnas, L. J., Polyn, S. M., & Kahana, M. J. (2015). Expanding the scope of memory search: Modeling intralist and interlist effects in free recall. *Psychological Review*, 122(2), 337-363.
- MacDonald, C. J., Lepage, K. Q., Eden, U. T., & Eichenbaum, H. (2011). Hippocampal "time cells" bridge the gap in memory for discontinuous events. *Neuron*, 71(4), 737-749.
- Manning, J. R., Polyn, S. M., Baltuch, G. H., Litt, B., & Kahana, M. J. (2011). Oscillatory patterns in temporal lobe reveal context reinstatement during memory search. *Proceedings of the National Academy of Sciences*, 108(31), 12893-12897.
- Mau, W., Sullivan, D. W., Kinsky, N. R., Hasselmo, M. E., Howard, M. W., & Eichenbaum, H. (2018). The Same Hippocampal CA1 Population Simultaneously Codes Temporal Information over Multiple Timescales. *Current Biology*, 28(10), 1499-1508 e1494.
- Nielson, D. M., Smith, T. A., Sreekumar, V., Dennis, S., & Sederberg, P. B. (2015). Human hippocampus represents space and time during retrieval of real-world memories. *Proceedings of the National Academy of Sciences*, 112(35), 11078-11083.
- Palombo, D. J., & Verfaellie, M. (2017). Hippocampal contributions to memory for time: evidence from neuropsychological studies. *Current Opinion in Behavioral Sciences*, 17, 107-113.
- Polyn, S. M., Norman, K. A., & Kahana, M. J. (2009). A context maintenance and retrieval model of organizational processes in free recall. *Psychological Review*, 116(1), 129-156.
- Reed, J. M., & Squire, L. R. (1998). Retrograde amnesia for facts and events: findings from four new cases. *Journal of Neuroscience*, 18(10), 3943-3954.
- Rubin, A., Geva, N., Sheintuch, L., & Ziv, Y. (2015). Hippocampal ensemble dynamics timestamp events in long-term memory. *Elife*, 4.
- Schwartz, G., Howard, M. W., Jing, B., & Kahana, M. J. (2005). Shadows of the past: temporal retrieval effects in recognition memory. *Psychological Science*, 16(11), 898-904.
- Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery, and Psychiatry*, 20(1), 11-21.

- Sederberg, P. B., Gershman, S. J., Polyn, S. M., & Norman, K. A. (2011). Human memory reconsolidation can be explained using the temporal context model. *Psychonomic Bulletin & Review*, 18(3), 455-468.
- Sederberg, P. B., Howard, M. W., & Kahana, M. J. (2008). A context-based theory of recency and contiguity in free recall. *Psychological Review*, 115(4), 893-912.
- Shankar, K. H., & Howard, M. W. (2012). A scale-invariant internal representation of time. *Neural Computation*, 24(1), 134-193.
- Shimamura, A. P., Janowsky, J. S., & Squire, L. R. (1990). Memory for the temporal order of events in patients with frontal lobe lesions and amnesic patients. *Neuropsychologia*, 28(8), 803-813.
- Siegel, L. L., & Kahana, M. J. (2014a). A retrieved context account of spacing and repetition effects in free recall. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, 40(3), 755-764.
- Siegel, L. L., & Kahana, M. J. (2014b). A retrieved context account of spacing and repetition effects in free recall. *J Exp Psychol Learn Mem Cogn*, 40(3), 755-764.
- Talmi, D., Caplan, J. B., Richards, B., & Moscovitch, M. (2015). Long-Term Recency in Anterograde Amnesia. *PLoS One*, 10(6), e0124084.
- Talmi, D., Lohnas, L. J., & Daw, N. (2017). A retrieved context model of the emotional modulation of memory. *bioRxiv*.
- Tulving, E. (1983). *Elements of Episodic Memory*. New York: Oxford University Press.
- Tulving, E. (1985). Memory and consciousness. *Canadian Psychology*, 26(1), 1-12.
- Warrington, E. K. (1982). The double dissociation of short- and long-term memory deficits. In L. S. Cermak (Ed.), *Human memory and amnesia*. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Wechsler, D. (1997). *Wechsler Adult Intelligence Scale—Third Edition (WAIS-III) Administration and Scoring Manual*. San Antonio, TX: Harcourt Assessment.
- Yaffe, R. B., Kerr, M. S., Damera, S., Sarma, S. V., Inati, S. K., & Zaghoul, K. A. (2014). Reinstatement of distributed cortical oscillations occurs with precise spatiotemporal dynamics during successful memory retrieval. *Proceedings of the National Academy of Sciences*, 111(52), 18727-18732.
- Yonelinas, A. P. (2002). The Nature of Recollection and Familiarity: A Review of 30 Years of Research. *Journal of Memory and Language*, 46(3), 441-517.
- Yonelinas, A. P., Kroll, N. E., Quamme, J. R., Lazzara, M. M., Sauve, M. J., Widaman, K. F., et al. (2002). Effects of extensive temporal lobe damage or mild hypoxia on recollection and familiarity. *Nature Neuroscience*, 5(11), 1236-1241.