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Temporal organization of narrative recall is present but attenuated in adults with hippocampal amnesia

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Abstract

Studies of the impact of brain injury on memory processes often focus on the quantity and episodic richness of those recollections. Here, we argue that the organization of one's recollections offers critical insights into the impact of brain injury on functional memory. It is well-established in studies of word list memory that free recall of unrelated words exhibits a clear temporal organization. This *temporal contiguity effect* refers to the fact that the order in which word lists are recalled reflects the original presentation order. Little is known, however, about the organization of recall for semantically rich materials, nor how recall organization is impacted by hippocampal damage and memory impairment. The present research is the first study, to our knowledge, of temporal organization in semantically rich narratives in three groups: (1) Adults with bilateral hippocampal damage and severe declarative memory impairment, (2) adults with bilateral ventromedial prefrontal cortex (vmPFC) damage and no memory impairment, and (3) demographically matched non-brain-injured comparison participants. We find that although the narrative recall of adults with bilateral hippocampal damage reflected the temporal order in which those narratives were experienced above chance levels, their temporal contiguity effect was significantly attenuated relative to comparison groups. In contrast, individuals with vmPFC damage did not differ from non-brain-injured comparison participants in temporal contiguity. This pattern of group differences yields insights into the cognitive and neural systems that support the use of temporal organization in recall. These data provide evidence that the retrieval of temporal context in narrative recall is hippocampal-dependent, whereas damage to the vmPFC does not impair the temporal organization of narrative recall. This evidence of limited but demonstrable organization of memory in participants with hippocampal damage and amnesia speaks to the power of narrative structures in supporting meaningfully organized recall despite memory impairment.

KEYWORDS

amnesia, declarative memory, free recall, hippocampus, narratives, temporal contiguity

1 | INTRODUCTION

Our experience of the world at the moment is shaped by the ability to recall from memory our past experiences. Consider that recall of one

detail from memory can facilitate remembrance of other, related memories. For example, recalling a detail about one beach vacation may bring to mind a semantically related detail from a different beach vacation, or a temporally proximal detail such as a work event that

occurred after your return from the beach. Empirical approaches to recall often employ paradigms in which participants are asked to study a list of words and then are asked to recall as many of those words as possible under different conditions of interest. Whereas some paradigms focus on the quantity of what can be recalled under different conditions of interest (e.g., Godden & Baddeley, 1975; Pezdek & Prull, 1993), other approaches examine the organization of recall by analyzing the order in which items are recalled (e.g., Healey et al., 2018; Kahana, 1996; Polyn et al., 2009).

The aim of the present research is to examine the organization of recall in individuals with and without hippocampal damage to gain insight into the role of the hippocampus in temporal organization and the impact of memory impairment on not just the quantity of what can be recalled, but on the tendency to organize what is recalled in a way that reflects how it was originally experienced.

1.1 | Organization of recall

Studies of recall organization typically employ paradigms where participants are asked to study a list of unrelated words, and then (typically after a few seconds or no delay), participants are asked to recall as many of the words as possible (Healey et al., 2018; Sederberg et al., 2010). Key findings in this literature include the demonstration of a strong temporal structure in recall; this *temporal contiguity effect* is robust in the recall of word lists, such that the order of recall strongly represents the order of presentation. When participants recall one word, the next word recalled is most likely to come from a temporally proximal position in the study order. A prominent explanation of this phenomenon is that when a given word is recalled, the context in which that word was encoded is recalled as well. This encoding context is most similar to words that were studied in close temporal proximity to the recalled word, thus promoting subsequent recall of other words close to the recalled word in study order (Howard & Kahana, 2002; Polyn et al., 2009). The processes by which context is encoded during study and then used to guide memory retrieval are hypothesized to reflect an automatic process rather than a strategic control of output order at test. The evidence for this point stems from the fact that the temporal contiguity effect is consistently observed across paradigms, including varied list lengths (Cortis Mack et al., 2015), with delays before test (Howard & Kahana, 1999), with self-paced presentation rates (Nguyen & McDaniel, 2015), and across populations (e.g., people of varying ages; Kahana et al., 2002; Lehmann & Hasselhorn, 2010), adults with schizophrenia (Polyn et al., 2015), adults with ADHD (Gibson et al., 2019); for discussion, see Healey et al. (2018).

It is worth noting that this body of work examines the organization participants exhibit in *free recall*, not the ability of participants to recall in a specific order when instructed to do so. Thus, assessing temporal contiguity is not a matter of judging how accurate participants are in recall, but to examine how participants organize recall in a way that is typically associated with greater amounts of information being accurately recalled (Sederberg et al., 2010). The temporal

contiguity effect however can be somewhat tied to primacy and recency effects (the tendency for participants to recall more from the beginning and end of a list, respectively), but the temporal contiguity effect is not solely driven by these patterns (Healey et al., 2018; Hintzman, 2016).¹ The finding that participants organize recalls temporally even when not prompted to consider study order suggests that temporal contiguity is an emergent property of recall.

A popular method of quantifying the magnitude of this temporal contiguity effect is to transform each participant's recall sequence into *lag-conditional response probabilities* (lag-CRP). For a given recall sequence, one first calculates the lag transition for each recall (excluding the first recalled word), where the lag transition is the difference in presentation order between two sequential recalls (e.g., if a person first recalled the fifth word on the list, and then next recalled the sixth word on the list, the lag transition for that second-recalled word would be a lag transition of +1). The possible lag values range from \pm (list length - 1). For example, if a study list is seven items long, the possible lags to be made are from -6 to +6. From all possible lag transitions, we can compute the conditional response probability (CRP). Each CRP value is the probability of making a given lag transition conditional on how often that lag transition could have been made (Kahana, 1996). Thus, for lag +1, we count up how often participants made a +1 lag transition in their recall series and divide it by how many times a lag +1 transition could have been made. This denominator value of when a transition could have been made is determined by list length and previously recalled items (e.g., you cannot make a +1 lag transition after recalling the seventh item if the eighth item has already been recalled or if the list is only seven items long). If the typical temporal contiguity effect is present, this analysis will show a tendency to make smaller absolute lag transitions (e.g., making more -1/+1 compared to -5/+5 transitions) and forward asymmetry (e.g., +1 is more probable than -1). Thus, after successfully recalling a single word, participants are most likely to move forward from one position to the next word they saw in the study.

The lag-CRP curve is a great way to visualize the temporal contiguity effect for a group of participants, however to best measure individual use of temporal organization, researchers often compute *temporal organization scores*, a percentile value that quantifies the degree to which a given recall was organized temporally (Polyn et al., 2009). Temporal organization scores are computed by taking the lag values between each sequential recall and assigning them percentile scores for how temporally contiguous they are. For example, if a participant sees the following list of words: APPLE, HOUSE, BIRD, CACTUS, and they recall HOUSE, followed by BIRD (+1 lag), that would be the most temporally contiguous transition they could have made from HOUSE. Then if you move from BIRD to APPLE (-2 lag), this transition would earn a lower percentile rank. The final temporal organization score would reflect the average of these two transitions (and any others made). Temporal organization scores range from 0 to

¹We compute and report serial position information regarding this data set and explain why it is not considered in the interpretation of our results in Data S1.

1, with scores significantly greater than .5 reflecting recalls that are organized temporally (where a chance organization would be .5).

It is now well-established that the recall of a string of studied, unrelated items reflects the temporal organization with which that material was studied. However, a notable limitation of the generalizability of the current literature on this temporal contiguity effect is that most studies of recall organization are dependent on word list paradigms (Hintzman, 2016). While some recent findings attempt to explore the role of temporal organization in the recall of more naturalistic material (i.e., news stories in Uitvlugt & Healey, 2019; autobiographical memories in Diamond & Levine, 2020), relatively little is known about the extent to which organization of the recall of more semantically rich and internally structured material reflects primarily temporal organization or some other type of organizational scheme. For example, Uitvlugt and Healey (2019) found that when participants were asked to recall news stories from the last few months or years, they tended to recall stories that occurred within a few days of each other, even when controlling for semantic relationships among the stories. Likewise, Diamond and Levine (2020) asked participants to view a guided tour of the artwork and then attempt to recall the experience in detail 2 or 7 days later. They report a typical temporal contiguity effect, with peaks at lag ± 1 and temporal organization scores significantly greater than chance ($p < .001$). This leaves the question of is temporal contiguity only an emergent property of recall in this limited paradigm or does it generalize to the type of recalling we do in everyday life.

1.2 | Hippocampal contributions to recall and recall organization

While the temporal contiguity effect is ubiquitous, the *degree* to which recall from memory exhibits temporal organization varies across paradigms and populations. One relevant factor is memory performance (Sederberg et al., 2010). In a meta-analysis of nine word-list experiments conducted with non-brain-injured participants, Sederberg et al. found that temporal organization scores positively correlated with memory performance, suggesting that adult participants who recalled more words were more likely to have organized their recalls temporally. It is worth noting that while the two may be correlated, measures of temporal contiguity are not inherently dependent on how much is recalled, thus it is not necessary that if one participant recalls less, they must have less temporal organization.² This finding points to a potential relationship between quantity and organization in recall performance and is consistent with theoretical arguments that the retrieval of temporal contexts during free recall that results in temporal contiguity effects is dependent on the hippocampus (Howard et al., 2005).

The hippocampal-dependent declarative memory system is broadly understood to play a critical role in the formation and retrieval of new and enduring memories of experiences. Critically, this memory system supports the binding of the elements of an experienced event (e.g., time, place, people, objects) in a way that supports the flexible, relational, and context-sensitive use of these representations in the future (Davachi, 2006; Eichenbaum & Cohen, 2001; Konkel et al., 2008; Ranganath, 2010). Individuals with damage to the hippocampus exhibit deficits in the ability to recall information from memory (Cohen & Eichenbaum, 1993; Eichenbaum & Cohen, 2001). Moreover, individuals with hippocampal amnesia exhibit deficits in relational memory even when retention intervals are brief (Hannula et al., 2006; Rubin et al., 2011).

Recall that a leading explanation of the temporal organization of word-list recall rests on the idea that relations are encoded between studied items and the temporally instantiated contexts that they appear in, increasing the likelihood that items in close temporal proximity will be recalled together (Howard & Kahana, 2002; Polyn et al., 2009). The key role for hippocampus in the creation and use of relational memories (Cohen & Eichenbaum, 1993; Eichenbaum & Cohen, 2001; Rubin & Cohen, 2017) would therefore suggest that the influence of temporal context on recall should be a hippocampal-dependent process (Eichenbaum, 2017). Prior work has examined hippocampal contributions to memory for temporal relationships using explicit temporal order tasks, where participants are either asked to freely recall items in the order that they were studied in or are asked to take a list of items and move them into the order that they were studied in (Shimamura et al., 1990; St. Jacques et al., 2008; Dulas et al., 2022). These tasks share the property that participants are explicitly asked to remember the order items were studied in. However, this work differs from the free recall paradigms used to examine temporal contiguity, where any observed temporal organization of a participant's recall is spontaneous, rather than requested. Thus, while the hippocampus has been implicated in tasks where individuals are explicitly trying to utilize temporal order, it is less studied how the hippocampus may underscore implicit organization utilizing temporal context.

Inspired by models which posit a central role for hippocampus in the retrieval of temporal contexts in the temporal organization of recall (Howard et al., 2005), Palombo et al. (2019) modeled the temporal organization of word list recall in individuals with amnesia due to damage to the medial temporal lobe (MTL) including the hippocampus, and healthy comparison participants. To overcome the methodological challenge of measuring temporal contiguity in persons with memory impairment, Palombo et al. presented participants with the same word lists multiple times in the same order. After seeing a list four times, participants were asked to immediately recall the words. As expected, adults with MTL damage recalled fewer words than comparison participants. Critically, Palombo et al. also observed a different pattern of lag-CRP in participants with amnesia (exhibited by a significant interaction between $|\text{Lag}|$ and Group) that was indicative of less temporal organization. Computational modeling of the recall data revealed that including a parameter in the model responsible for the recovery of temporal context during recall which varied across groups (healthy

²For example, if a subject recalls only 3 of 10 items, they can still have a completely temporally organized recall. If they recall only the last three items and do so in order (item 8, 9, 10), this would yield a temporal organization score of 1. In contrast, a complete recall (10 of 10 items) can be recalled in an order that is no more temporally organized than chance (recalling item 3, 6, 10, 8, 4, 1, 9, 5, 2, 7 would be complete but yield a temporal organization score of .35, which is not significantly greater than chance (.5)).

non-brain-injured adults and individuals with MTL damage) provided the best fit to the data. This model estimated that individuals with MTL damage exhibited a lag-CRP curve with a smaller peak. The authors theorize that this attenuated temporal contiguity effect in amnesia is due to an inability to reinstate earlier contexts, a problem akin to an inability to “jump back in time” (Palombo et al., 2019).

The findings from Palombo et al. (2019) offer empirical support for the claim that the hippocampus makes key contributions to the retrieval of temporal contexts that manifest in the temporal organization of word-list recall (Howard et al., 2005). Yet, recalling a list of unrelated words is unlike many of the memory activities of daily living for which we encode and retrieve meaningful, structured, and personally relevant information, potentially limiting the generalizability of these findings to cognition in everyday life (Hintzman, 2016). One alternative material to examine temporal organization in more realistic stimuli is to leverage narratives. Previous work has shown that adults with hippocampal damage and amnesia are capable of both generating (Race et al., 2011) and retelling (Kurczek & Duff, 2011) stories. A body of research exists looking at the coherence of narrative generation and retellings in adults with amnesia (Kurczek & Duff, 2011; Race et al., 2015; Rosenbaum et al., 2009; St-Laurent et al., 2011). Coherence refers to how linguistically tied two adjacent utterances are, for example, does a dietetic pronoun have a clear unambiguous referent established in a prior referent. Measures of coherence sometimes involve an assessment of temporal order, but this is always constrained to a predicted order based on themes and semantics. For example, Rosenbaum et al. (2009) examined the coherence of commonly known stories such as fairy tales and myths. The researchers then judged the retellings by examining differences in the order of these retellings compared to a set order the researchers believed made thematic sense. Thus, the temporal organization judgment here is tied to the expected thematic flow, which differs from classic temporal contiguity literature that has an exact story order established by presentation order. It is probable that coherence and temporal order are correlated, as it is more likely to have a coherent story if it is told in order. However, temporal order as a function solely of the original presentation order, not an implied correct or thematic order, has not been measured for narrative retelling in adults with amnesia.

1.3 | The present research

The present study is a re-analysis of data described in our earlier work (Hilverman et al., 2018). The original analysis of the data set examined the role of the hippocampal declarative memory system in integrating co-occurring information from speech and gesture in immediate retellings of narratives. That analysis found that individuals with bilateral hippocampal damage and amnesia recalled fewer narrative details than non-brain-injured comparison participants, and a brain damage comparison group with bilateral damage to the ventromedial prefrontal cortex (vmPFC). However, despite recalling fewer story details than the two comparison groups, individuals with amnesia were more likely to report unique information from gestures in their narrative

retellings, suggesting that hippocampal declarative memory is not necessary for binding speech and gesture for immediate comprehension of spoken narrative.

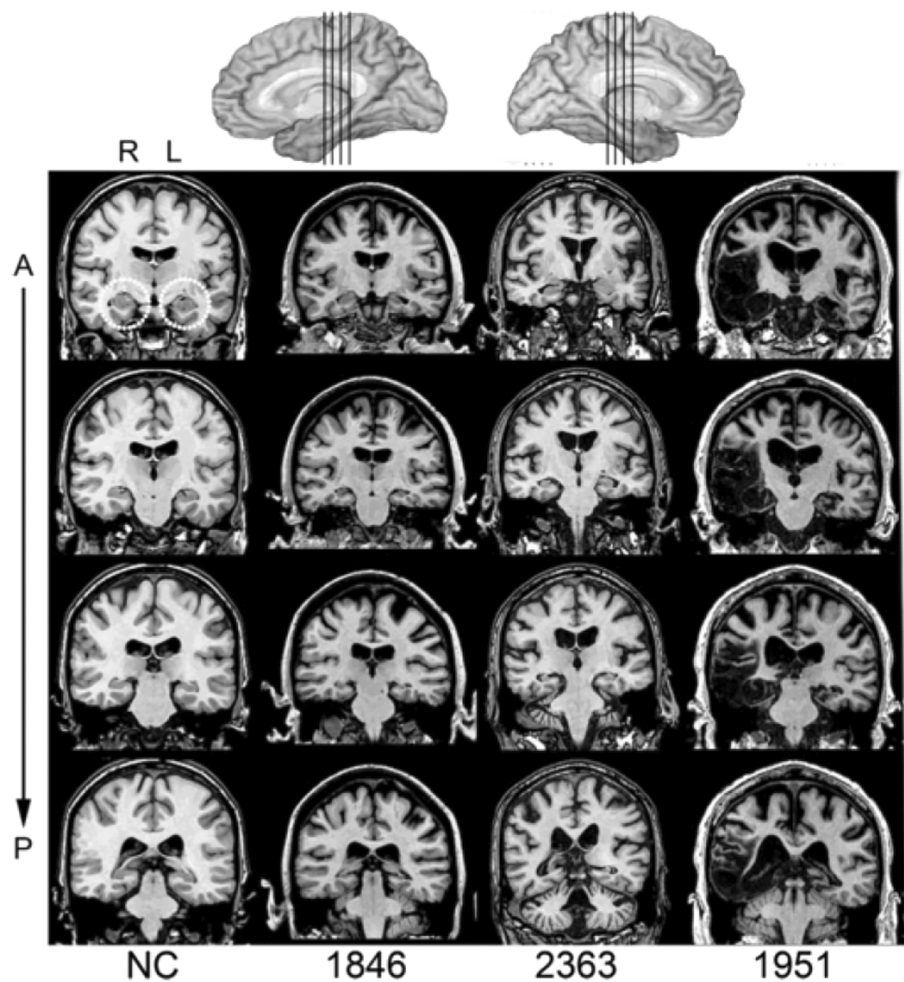
This study leverages this rich data set to examine the novel question of the impact of hippocampal damage on the temporal organization of narrative retellings. The analyses reported here are exploratory in nature and were not planned prior to the collection of data. The aim of the present research is to understand how adults with hippocampal amnesia organize their recalls of narratives. There were two goals for this work: First, we aimed to assess temporal contiguity using materials—narratives—which have an internal structure and which, unlike word lists, are more representative of the types of material one might recall in everyday settings. Second, we examined if temporal contiguity is diminished in adults with hippocampal amnesia in these complex materials. Finally, while our primary focus here is on the role of the hippocampus in the temporal organization of narrative retellings, we also analyze the data of the brain-damaged comparison group from the original data set (Hilverman et al., 2018). A brain-damaged comparison group allows us to make claims about hippocampal specificity in performance as opposed to capturing the effects of brain damage more broadly. Individuals with bilateral vmPFC damage are an ideal comparison group because they do not have damage to the medial temporal lobes or hippocampus, and they do not have memory impairments. However, studying temporal contiguity in patients with vmPFC damage is of additional interest given the links in the literature between frontal lobe damage and deficits in narrative organization and temporal processing and memory (e.g., Coelho, 2002; Shimamura et al., 1990; Zalla et al., 2002).

2 | METHODS

2.1 | Participants

HC group: Four individuals (one female, three male) with hippocampal amnesia (HC) participated. All individuals with amnesia had non-progressive bilateral hippocampal (HC) lesions and severe declarative memory impairments. Three experienced anoxic/hypoxic episodes (1846, 2363, 2563) resulting in bilateral hippocampal damage. The fourth individual contracted herpes simplex encephalitis (1951). Bilateral hippocampal damage and significantly reduced hippocampal volumes were confirmed by structural MRI for three of the four individuals. Hippocampal damage for individual 2563 was confirmed by computerized tomography because he wears a pacemaker and is unable to undergo MRI examination. The three anoxic participants had no damage to the lateral temporal lobes or anterior temporal lobes. Participant 1951 had more extensive bilateral MTL damage affecting the hippocampus, amygdala, and surrounding cortices (Figure 1). Neuropsychological testing revealed a severe and selective impairment in declarative memory ($M = 65.5$; Wechsler Memory Scale-III General Memory Index) while measures of verbal IQ, vocabulary, and semantic knowledge were within the normal range as

FIGURE 1 Magnetic resonance scans of hippocampal patients. Images are coronal slices through four points along the hippocampus from T1-weighted scans. Volume changes can be noted in the hippocampal region for Patients 1846 and 2363 and significant bilateral MTL damage including the hippocampus can be noted in Patient 1951. A, anterior; L, left; NC, non-injured comparison brain; P, posterior; R, right.



measured by standardized tests (Table 1). The participants with amnesia also performed normally on experimental measures of non-declarative or procedural memory (Cavaco et al., 2011).

vmPFC group: Four brain-damaged comparison participants (three female, one male) with non-progressive bilateral damage to the ventromedial prefrontal cortex (vmPFC) participated. Etiologies of vmPFC damage were meningioma resection and sub-arachnoid hemorrhage/anterior communicating artery aneurism. vmPFC participants had no damage to the medial temporal lobe and exhibited no declarative memory impairment. Like the individuals with amnesia, the vmPFC group performed in the normal range on neuropsychological tests of intelligence and language. In critical contrast to the individuals with amnesia, the vmPFC group performed within normal limits on standardized tests of declarative memory (Table 1).

NC group: 20 non-brain-injured comparison (NC) participants (9 female, 11 male) participated. NC participants were screened to rule out diagnoses and medications that can interfere with cognition (e.g., neurological or psychiatric conditions, developmental or learning disorders, untreated diabetes or sleep apnea). NC participants were matched to both the HC and vmPFC groups on sex, age, and educational attainment. NC participants were 61.0 years old, on average, and had 15.9 years of education, on average. Demographic matching

of NCs to the participants with brain lesions reduces between group variability and increases statistical power to detect differences across groups, as our sample size was necessarily small due to the rare incidence of hippocampal amnesia.

2.2 | Procedure

A female adult native English speaker narrated four stories about a man named Carl who experienced a string of bad luck (see Appendix A). Each story was about 30 s long, consisted of six sentences, and contained 10–12 details that were later examined for recall. The narrator produced four gestures during the story: two redundant gestures conveying overlapping information with speech (e.g., a circle gesture on the phrase “big googly eye”) and two complementary gestures conveying unique information not present in speech (e.g., a picking gesture on the phrase “he got a flower”). These gestures were critical for the primary analysis examining speech-gesture integration in Hilverman et al., 2018, but do not factor into the present analysis. Each participant viewed the four stories on a laptop screen. While the video played, a picture displaying a scene from the story was also present on the screen. Immediately after each video

TABLE 1 Demographic, neuroanatomical, and neuropsychological characteristics of the HC and vmPFC groups.

Participant	Demographic characteristics				Neuropsychological scores												
	Sex	Age	Hand.	Edu.	Etiology	Damage	Anatomical		Intelligence			Memory				Language	
							HC volume	HC volume	WAIS-III FSIQ	WAIS-III Vocab	WAIS-III Info	WMS-III GMI	AVLT Delay	CFT Delay	BNT	TT	
1846	F	58	R	14	Anoxia	Bilateral HC	-4.23	84	8	8	8	57	3	6	43	41	
2363	M	58	R	18	Anoxia	Bilateral HC	-2.64	98	10	13	73	0	0	58	44		
2563	M	59	L	16	Anoxia	Bilateral HC	N/A	102	12	12	75	1	7	52	44		
1951	M	62	R	16	HSE	Bilateral HC + MTL	-8.10	106	9	11	57	2	4	49	44		
HC mean		59.3		16			-5.0	97.5	9.8	11	65.5*	1.5	4.3	50.5	43.3		
vmPFC mean		69.5		13			N/A	115.5	N/A	N/A	116.3	N/A	N/A	57	43.8		

Note: Demographic, neuroanatomical, and neuropsychological characteristics of participants with hippocampal amnesia and vmPFC damage; Volumetric data are z-scores as measured through high resolution volumetric MRI and compared to a matched healthy comparison group (Allen et al., 2006; Buchanan et al., 2005). Bolded scores are impaired as defined as two or more standard deviations below normative data. * = *t* tests reveal that groups differed statistically on the WMS-III GMI ($p = .0002$) but not on the WAIS-III FSIQ ($p = 0.16$), BNT ($p = .12$), or TT ($p = .56$).

Abbreviations: + MTL, damage extending into the greater medial temporal lobes; AVLT, auditory verbal learning test, 15 min delay score; BNT, Boston Naming Test; CFT, complex figure test, recall score; Edu., years of completed education; Hand., handedness; HC, hippocampus; HSE, herpes simplex encephalitis; N/A, no available data; TT, token test; vmPFC, ventromedial prefrontal cortex; WAIS-III FSIQ, Wechsler Adult Intelligence Scale-III Full Scale Intelligence Quotient; WMS-III GMI, Wechsler Memory Scale-III General Memory Index.

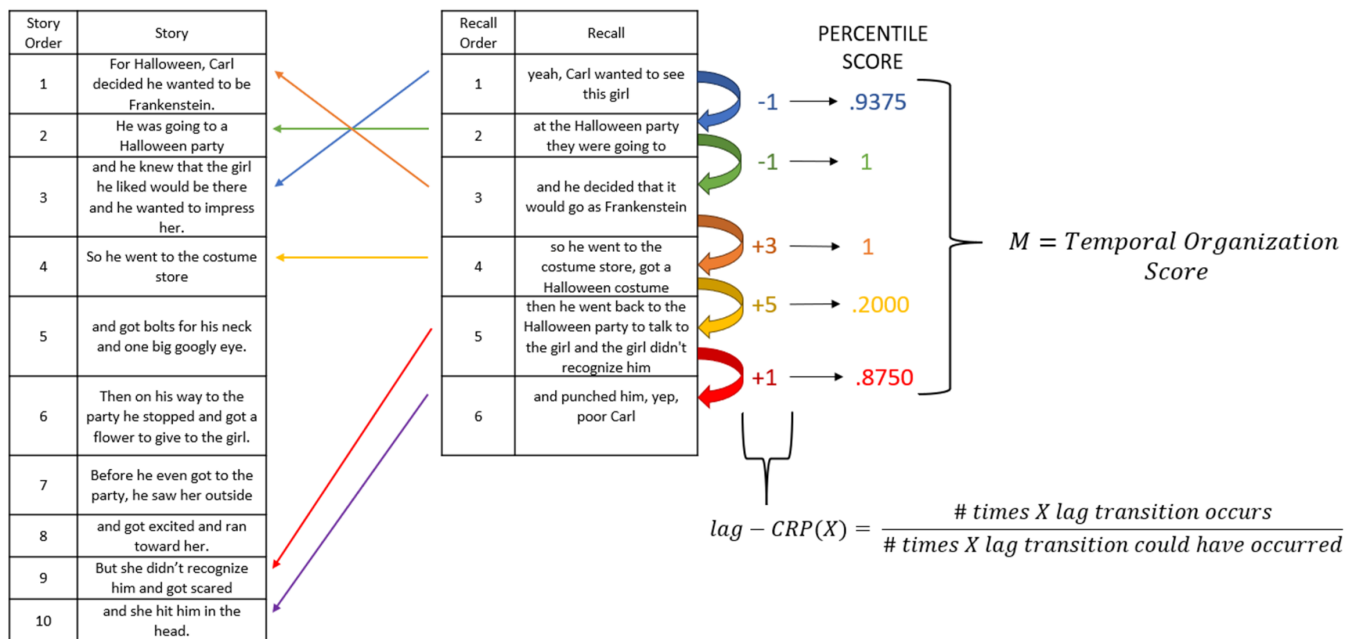


FIGURE 2 Example of temporal coding and analysis for narrative recall. The left table shows the story in the order participants heard it. The middle table shows the way one participant recalled that story. The arrows show which recall details matched which story details. The curved arrows show the lag transitions made each time they recall a new detail based on the change in story order. Percentile scores are hypothetical examples of how each lag transition could be turned into a percentile rank. The average of these percentile scores is the temporal organization score. The lag-CRP value for each lag value (X) is computed by dividing the number of times that lag transition occurs by the number of times that lag transition could have been made.

ended, the video disappeared leaving only the picture cue on the screen (see Appendix A). Participants were then prompted to retell what happened in that particular story. The experimenter listened attentively during each retelling, providing occasional backchannel encouragement (e.g., mmhmm). The task was free recall, and participants were allowed to recall the material in any order.

2.3 | Coding

By Hilverman et al. (2018), each retelling was scored for the number of story details recalled. We added additional coding to record the order in which those details were recalled for each story. The maximum recall for each story was 10–12 details. Recall order was coded as 1 – N number of details recalled for each story. By comparing the order in which story details were presented by the narrator and the order in which story details were retold by the participants, we examined the temporal organization of narrative recall across the three participant groups (Figure 2).

3 | RESULTS

The data for both analyses (lag-conditional response probability and temporal organization scores) were fit with mixed effects models. We used the buildmer function (Voeten, 2019) in R (version 4.2.1), to

identify a parsimonious random effects structure (Matuschek et al., 2017) for the model. The results of the buildmer function indicated that all random effects should be removed from models, which would be equivalent to linear regression. Due to an a priori interest in variability by persons, we elected to maintain random intercepts for participants. Note that the participant-intercept estimates for the lag-conditional response probability analysis were at zero and the model returned a singularity warning. The results of the participant-intercept model for this analysis are therefore equivalent to the buildmer-identified linear model.

3.1 | Lag-conditional response probability

To assess temporal contiguity in the narrative recalls, we first computed lag-CRP values. Lag refers to the difference in study position between two sequential recalls. For example, if a participant first recalls the third story detail they heard followed by the fifth story detail they heard, they made a lag +2 transition (see Figure 2). For each trial, we compute the lag values for each pair of details recalled. Then a conditional response probability is computed for each lag value. This is the probability that a participant made a given lag transition conditional on all possible transitions (Kahana, 1996). Possible transitions are constrained by the overall length of the list (or in the present case, the length of the narrative in terms of number of details) that is being recalled (in this experiment, 10 or 12 details) and

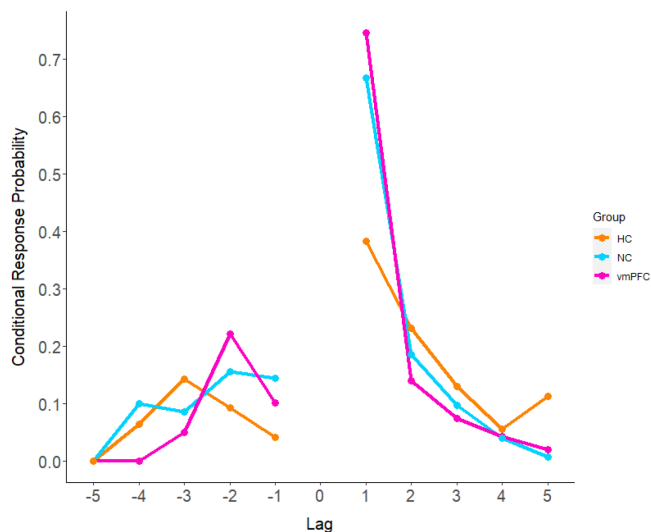


FIGURE 3 Lag-conditional response probabilities plotted for each group (HC = adults with hippocampal amnesia, NC = non-brain-injured comparison participants, vmPFC = adults with vmPFC damage).

previous transitions that have been made in that recall sequence. Thus, each possible lag value will have a CRP value—the conditional probability of that transition occurring. The possible lag values range from ± 5 (list length -1) but most temporal contiguity work focuses on ± 5 , as values further from 0 are only possible with longer lists and become less interpretable. The lag-conditional response probability values for the data split by group are displayed in Figure 3.

The data were fit in a multilevel model with random intercepts for participant and fixed effects for Group (adults with hippocampal amnesia compared to non-brain-injured comparison participants and to adults with vmPFC damage) Absolute Lag ($|1|$, $|2|$, $|3|$, $|4|$, $|5|$) and Direction (positive or negative) and with conditional response probability as the dependent measure (Table 2). Each participant contributed four sets of probabilities, one for each story. This analysis approach was modeled after previous work assessing lag-CRP with ANOVAs of $|Lag|$ and Direction (Howard et al., 2009; Palombo et al., 2019). The results of the multilevel model indicated that the main effects of $|Lag|$, $p = .002$, and Direction, $p < .001$, were qualified by a $|Lag|$ by Direction interaction, $p = .012$. Inspection of the data revealed a preference for shorter lag transitions over longer ones, and this preference for short lags was more pronounced in the positive direction. These findings are broadly consistent with prior findings of greater conditional-response probability values for smaller absolute lag values and a pattern of forward asymmetry that make up the temporal contiguity effect in both typical word lists (Bouffard et al., 2018; Healey et al., 2018; Howard & Kahana, 2002; Kahana, 1996; McDaniel et al., 2011) and more complex materials (Cutler et al., 2019; Diamond & Levine, 2020; Uitvlugt & Healey, 2019).

The Group comparisons were both significant, however, this effect alone cannot be interpreted, as differences in total conditional response probabilities alone (without consideration for $|Lag|$ or Direction) is meaningless. However, both Group comparisons also

significantly interact with $|Lag|$ ($ps < .005$). We probe this interaction by looking at the Group comparisons at each of the 5 $|Lag|$ values. We find that at $Lag = |1|$, both Group comparisons are significant. This means that the group with amnesia were significantly less likely to make $Lag |1|$ transitions than both the group with vmPFC damage ($\beta = .21, p = .002$) and the non-brain-injured comparison group ($\beta = .25, p = .006$). No Group differences were observed at $Lag |2|$, $|3|$, or $|4|$, but at $Lag |5|$ we see that the group with amnesia differs from the non-brain-injured comparison group. Here we see that the group with amnesia are significantly more likely to make $lag |5|$ transitions than the non-brain-injured comparison group ($\beta = .06, p = .003$). Thus, it appears our group with amnesia is more likely to make longer, rather than shorter, lag transitions compared to the other two groups measured. These two differences at $Lag |1|$ and $Lag |5|$ are not necessarily independent—when a participant fails to make a short lag transition, they must instead make longer transitions. This unfortunately does mean that the $|Lag|$ factor cannot be viewed as truly independent—a limitation noted by earlier work (Howard et al., 2009). These group comparisons do not significantly interact with direction nor were there three-way interactions with $|Lag|$ and Direction ($ps > .1$). We reran this model with the non-brain-injured group as the reference category so that we could assess if the group with vmPFC damage significantly differed from them in temporal organization. This model revealed no Group difference ($\beta = .00, p < .738$) nor a difference when interacting with $|Lag|$, Direction, or both ($ps > .6$).

It is worth noting that participant 1951 differs from the other three individuals with amnesia in lesion size (e.g., extensive bilateral MTL damage vs. more restricted hippocampal damage) and etiology (e.g., HSE vs. anoxia). For this reason, we reran our analyses with this individual removed from our sample. When participant 1951 was excluded from the analysis, the patterns of significance remained the same. The group differences interacted with the $|Lag|$ effect ($|Lag|*Group$ (HC vs. NC): $\beta = -.04, p = .018$, $|Lag|*Group$ (HC vs. vmPFC): $\beta = -.05, p = .025$). Once again, probing these interactions showed that the group with amnesia was less likely to make $Lag = |1|$ transitions than the group with vmPFC damage ($\beta = -.22, p = .026$) and the non-brain-injured group ($\beta = -.18, p = .019$) and more likely to make $Lag = |5|$ transitions than the non-brain-injured group ($\beta = .03, p = .042$). Thus, participant 1951's more severe impairments are not the sole driver of the effects found above.

3.2 | Temporal organization scores

To quantify the overall temporal contiguity in the narrative recalls we computed temporal organization scores. These scores are a single percentile value per recall that quantifies temporal contiguity in that given recall. A score at 1 reflects perfect temporal organization, while values closer to 0.5 suggest an order that is no more temporally organized than chance (Polyn et al., 2009). These percentile scores are the average of the percentile scores computed for each lag transition that was made as participants recalled each detail. It is worth noting that this measure of temporal organization is not a reflection of memory

TABLE 2 Results of multilevel model. Data include 4 trials from each of 28 participants (4 with hippocampal amnesia (HC), 4 with vmPFC damage, and 20 non-injured comparison participants (NC)). Since the random intercept for Participant is 0, the inclusion of this term is inconsequential, and thus the model is functionally the same as linear model.

Fixed effects	Estimate	SE	t-value	p-value
(Intercept)	0.25	0.04	5.90	<.001
Lag	-0.04	0.01	3.05	.002
Direction	0.31	0.08	3.7	<.001
Group (HC vs. NC)	0.17	0.05	3.7	<.001
Group (HC vs. vmPFC)	0.19	0.07	3.05	.002
Lag *Direction	-0.07	0.03	2.51	.012
Lag * Group (HC vs. NC)	-0.05	0.01	3.39	<.001
Lag * Group (HC vs. vmPFC)	-0.06	0.02	2.91	.004
Direction* Group (HC vs. NC)	0.13	0.09	1.46	.146
Direction* Group (HC vs. vmPFC)	0.16	0.12	1.30	.194
Lag * Direction* Group (HC vs. NC)	-0.05	0.03	1.64	.102
Lag * Direction* Group (HC vs. vmPFC)	-0.05	0.04	1.21	.226
Random effects	Variance	SD		
Participant	0	0		

Note: The values were bolded to indicate these fixed effects were significant (p -values less than .05).

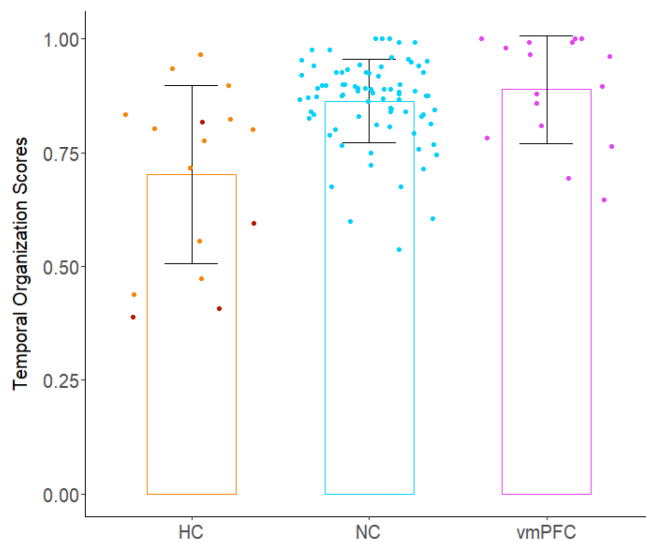


FIGURE 4 The average temporal organization scores of each group. Standard deviations are the error bars and individual trial scores are the points. Participant 1951's data are shown in red. HC, adults with hippocampal amnesia; NC, non-brain-injured comparison participants; vmPFC, adults with vmPFC damage.

accuracy. If Participant A recalls 10 details and Participant B recalls 2 details but both participants only make +1 lag transitions (recalling each detail in the same order they heard them), they would both have a temporal organization score of 1. Thus, temporal organization scores reflect only how organized a recall is, not how complete or accurate it is. A temporal organization score was computed for each of 112 recall trials in the data set (each participant had four trials—one immediate recall of each of four stories). Temporal organization scores can only be computed if there are at least two successful recalls for a given trial, but this was always the case for this data set (Figure 4).

The group average temporal organization scores were compared to a chance level of .5 using one-sample t tests. All three group

TABLE 3 The average temporal organization scores for each group (standard deviations in parentheses) and comparison to chance (one sample t test comparing average to value of .5).

Group	Average (SD)	Compared to chance (.5)
Amnesia	.701 (.195)	$t(15) = 4.12, p < .001$
Non-injured comparison	.863 (.092)	$t(79) = 35.30, p < .001$
vmPFC	.889 (.118)	$t(15) = 13.16, p < .001$

averages were significantly greater than .5, suggesting that on average, the recalls from each group were all influenced by temporal organization (Table 3). To compare groups, we fit a multilevel model with random intercepts for participants (Variance = 0.002, Standard Deviation = 0.05). The model revealed that the group with amnesia had significantly lower temporal organization scores than the group with vmPFC damage ($\beta = .19, p = .001$), and the non-brain-injured comparison group ($\beta = .16, p < .001$) (See Figure 4). Rerunning the model with the non-brain-injured comparison group as the reference group allows us to compare the vmPFC group to them. We see here that these two groups do not differ in temporal organization scores ($\beta = .03, p < .519$).

To understand whether these findings were driven by participant 1951, who has more extensive medial temporal lobe damage, we repeated these analyses with this individual removed from the data set. With participant 1951 excluded, the pattern of results was unchanged. The group with amnesia exhibited temporal organization scores that were above chance ($t(11) = 5.00, p < .001$), but significantly attenuated compared to the vmPFC group ($\beta = .14, p = .009$), and the non-injured comparison group ($\beta = .11, p = .009$).

4 | CONCLUSIONS

Adults with hippocampal amnesia organized their recall of narratives temporally, despite deficits in declarative memory. This temporal

contiguity effect was, however, attenuated in comparison to non-brain-injured comparison participants and adults with vmPFC damage as measured by both Lag-conditional response probabilities and temporal organization scores. The amnesia participants in this study exhibited organization of recall representative of the typical temporal contiguity effect, with an average temporal organization score that was significantly greater than chance, and the most probable lag transitions being |1|. Despite these successes, the average temporal organization scores for participants with amnesia was significantly lower than that of the other two groups, and participants with amnesia were less likely to make |1| lag transitions compared to the other two groups. Taken together, these analyses provide evidence for limited but demonstrable temporal organization of memory despite bilateral hippocampal damage and profound declarative memory deficits. Our findings go beyond prior evidence of impaired temporal contiguity following hippocampal damage in the recall of looped word lists (Palombo et al., 2019), in demonstrating evidence of temporal organization that was not completely eliminated in more naturalistic materials. Individuals with amnesia recalled recently experienced narratives in a way that reflects the temporal structure of the narrative, despite recalling overall fewer details.

This exploratory analysis contributes to two different lines of questioning that have yet to be fully resolved. First, our findings contribute to a growing body of work exploring how recall of more naturalistic stimuli are subject to temporal contiguity. The analyses used in this study, computation of temporal organization scores and lag-CRP, were originally designed to investigate recall of word lists (Kahana, 1996; Polyn et al., 2009). The experience of studying a list of words differs in many ways from the experiences we have in daily life. Semantic and causal relationships of ordinary experiences like walks on the beach and watching a movie co-vary with temporal organization of the elements therein. The fact that investigations of temporal organization in recall largely focus on unstructured word lists has been noted as a limitation for generalization of temporal contiguity to other areas of cognition (Hintzman, 2016). The present research differs from prior work in that we examined the perception and recall of narratives which have an internal semantic structure which is more representative of information encountered in daily life. To the best of our knowledge, an analysis of temporal contiguity in narrative recall has only appeared once before in the literature (Cutler et al., 2019). The results of the present research suggest that these traditional tools for assessing temporal contiguity can usefully characterize the temporal contiguity that emerges in the recall of more structured, meaningfully related material.

The second contribution of this work is that our analyses add nuance to our understanding of how temporal organization is utilized by adults with hippocampal amnesia. Previously, the only prior work examining temporal contiguity in adults with amnesia concluded that the temporal contiguity effect was disrupted for these individuals (Palombo et al., 2019). In this prior work, the authors found that presenting a looped word list to adults with amnesia yielded a lag-CRP curve that was less representative of the temporal contiguity effect compared to what is typically observed in non-brain-injured adults. In

line with this work, we found similar results—when recalling recently experienced and previously unfamiliar narratives, participants with amnesia showed less temporal organization. However, here we observe that while the temporal contiguity effect was attenuated in adults with hippocampal amnesia, this effect was significantly greater than chance despite a profound memory impairment. These results align with prior work in patients with MTL damage that has shown that even when fewer details of previously known fairytales are recalled, patients with MTL damage still tend to recall them in a thematic order (Verfaellie et al., 2014). Thus, we can conclude that participants who have amnesia resulting from damage to the hippocampus show a similar pattern to healthy patients in the way they organize free recalls, but that the degree of organization is attenuated. Is the hippocampus necessary for temporal organization in recall? If we consider demonstrating any intact organization as evidence of a lack of necessity, then no. We can conclude that the hippocampus contributes to but is not strictly necessary for temporal organization in recall. Alternatively, if we consider necessity as demonstrated when there is any significant deviation from the performance of non-brain-injured comparison participants, then yes. We would conclude that the hippocampus is necessary to achieve the level of temporal organization observed in non-brain-injured adults.

Beyond understanding the neural correlates of the temporal contiguity effect, the present findings also point to narrative recall as a useful paradigm for studying mechanics of everyday memory in individuals with memory impairment. For example, Kovner et al. (1983) found that building narratives around word lists can boost recall of these word lists for adults with amnesia. In prior work on adults with hippocampal amnesia, the researchers utilized a looped word list to boost overall rates of recall (Palombo et al., 2019). While the latter approach solves the problem of trying to analyze temporal contiguity with too few successful recalls, it does not address the greater question of how temporal contiguity endures outside of a word list paradigm. Instead, the present work leverages narratives to boost overall rates of recall, as narratives are a type of stimuli that participants with amnesia are able to generate (Race et al., 2011), to facilitate better free recall of words (Kovner et al., 1983).

Another contribution of this work is that it further delineates the intact abilities of those with vmPFC damage. Recall that the patients with vmPFC did not have hippocampal or MTL damage and did not have memory impairment. In contrast to participants with hippocampal damage, the participants with vmPFC damage did not significantly differ in their temporal organization from the non-brain-injured comparison group. At first blush, this is a surprising finding, as frontal lobe damage is often associated with deficits in narrative organization, temporal processing and memory, and judgments of temporal order (e.g., Coelho, 2002; Milner et al., 1985; Shimamura et al., 1990; Zalla et al., 2002). Closer examination of lesion specificity across studies, however, suggests that lateral prefrontal lesions may be more predictive of deficits in narrative organization and temporal processing impairments than ventromedial prefrontal lesions. Findings from Shimamura et al. (1990), who found that individuals with frontal lobe damage were significantly worse at an explicit temporal ordering task

of 15 words than a non-brain-injured comparison group, are often cited as evidence for the link between the frontal lobes to temporal order processing. However, of the six patients they studied, four had unilateral lesions (two right, two left) but there were no analyses of regional specificity within the frontal lobes. More recent work has linked damage to the dorsolateral prefrontal cortex with deficits in narrative organization (e.g., content, coherence, cohesion; Coelho et al., 2012; Karaduman et al., 2017) although there is inconsistency across studies on the presence of deficits associated with damage to the left or right dorsolateral prefrontal cortex. In contrast, individuals with bilateral ventromedial prefrontal cortex damage do not have impairments in narrative organization as measured by discourse coherence and cohesion (i.e., the relatedness or continuity within and across utterances of a narrative) including in a story retelling task (Kurzcek & Duff, 2011). Interestingly, and in line with the findings of the present study, individuals with hippocampal amnesia (the same participants as in the current study) were impaired on measures of discourse coherence and cohesion in their narrative tellings (Kurzcek & Duff, 2011). While there are a number of differences across these study designs, taken together with the present results, it appears as though damage to the vmPFC is not associated with disruptions in temporal memory or organization of narrative stimuli as studied here.

The present work is, of course, not without limitations. These limitations include the fact that the work was exploratory in nature, and the analyses were applied to pre-existing data. In addition, the sample size for persons with hippocampal damage and with vmPFC damage are small due to the rarity of these participant populations. Yet despite these limitations, this work offers new insights into the nature of memory organization for meaningful and structured materials that are more typical of the sorts of things we may wish to remember on an everyday basis. By comparing non-brain-injured adult participants with two different groups of individuals with brain injury, persons with bilateral ventromedial prefrontal cortex damage, and persons with bilateral hippocampal damage, we were able to show that while all three groups demonstrated significant temporal organization in their recalls, the degree of organization was significantly attenuated in individuals with hippocampal damage. These findings offer key empirical support for theoretical proposals that the temporal contiguity effects that emerge as a result of the retrieval of temporal contexts during free recall are hippocampal-dependent. Finally, we wish to emphasize the importance of contextualizing the present evidence of limited but demonstrable organization of memory observed in persons with hippocampal damage and amnesia. Despite a profound memory impairment, these individuals not only successfully retrieved details of a recently-experienced narrative, but further, the way in which they retrieved those details reflected the order in which they were originally experienced at above-chance levels. This remarkable finding highlights the significance of studying cognitive processes in meaningful contexts that are typical of everyday life.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to report.

DATA AVAILABILITY STATEMENT

The data and analyses scripts are currently private but will be made public upon publication. The editors and reviewers may view the public data files at https://osf.io/wxyz/?view_only=6052374d641443d2becb151bc039dbb5.

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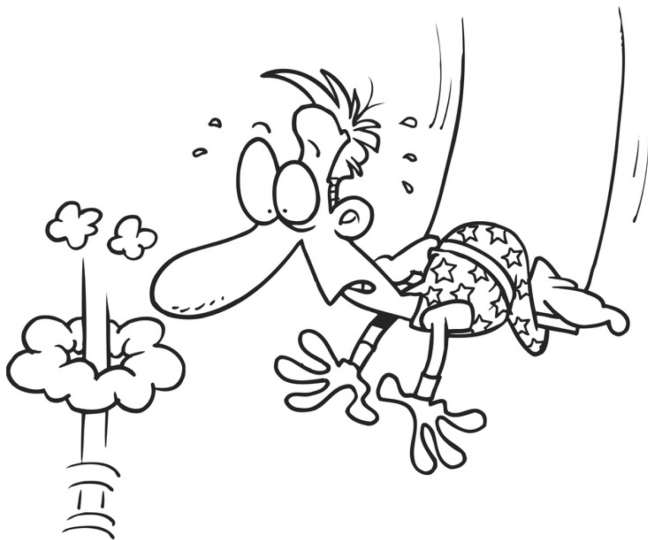
SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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APPENDIX A

A.1 | CARL STORIES



1. One day Carl decided he wanted to try his luck on the flying trapeze.
2. He went to the store and bought a new outfit covered in stars (**STARS**) that he thought would make him look like a professional.
3. Then he caught a ride (**HITCHHIKE/TAXI**) down to the nearby circus, to talk to the Ringmaster.
4. The Ringmaster was desperate for a trapeze artist and asked Carl to do his first show that very same night (**TONIGHT**).
5. But Carl didn't mention that he had never actually been on a trapeze before.
6. So as soon as Carl got up on the bar, he got scared and let go and flew off into the crowd (**FLIP, SOAR**).



1. Carl wanted to start a fire in his backyard so he got an ax to split wood.
2. All of his friends told him to get face protection (**GOGGLES, MASK**) but he didn't think he needed it.
3. He took the ax outside and wildly chopped at the wood (**AX SWING**).
4. His neighbor was watching and came over and asked if he'd chop some logs for her too.
5. So Carl got excited and chopped faster and faster (**AX SWING**).
6. And of course, when he least expected it, half of a log flew up and hit him in the face (**NOSE, FOREHEAD**).



1. Carl decided to try a new recipe for his friends when he had them over for dinner.
2. He searched and searched (**BOOK/COMPUTER**) for a new recipe to try and finally found one for meatballs.
3. He ground up meat himself and then formed the meat into balls (**BALL**).
4. When his friends come over, he starting cooking the meatballs (**OVEN/STOVE**).
5. Then he went in the other room and talked (**TALK**) to his friends.
6. But he forgot about the meatballs and when he went back into the kitchen they were burnt to a crisp.



1. For Halloween, Carl decided he wanted to be Frankenstein (**BOLTS**).
2. He was going to a Halloween party and he knew that the girl he liked would be there and he wanted to impress her.
3. So he went to the costume store and got bolts for his neck and one big goopy eye (**EYE**).
4. Then on his way to the party, he stopped and got a flower (**PICKED/CUT**) to give to the girl.
5. Before he even got to the party, he saw her outside and got excited and ran toward her.
6. But she didn't recognize him and got scared and she hit him (**PUNCH/SLAP**) in the head.