

The nature of recollection across months and years and after medial temporal lobe damage

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We studied the narrative recollections of memory-impaired patients with medial temporal lobe (MTL) damage who took a 25-min guided walk during which 11 planned events occurred. The recollections of the patients, recorded directly after the walk, were compared with the recollections of controls tested directly after the walk (C1), after one month (C2), or after 2.6 years (C3). With respect to memory for the walk, the narrative recollections of the patients were impoverished compared with C1 but resembled the recollections of volunteers tested after long delays (C2 and C3). In addition, how language was used by the patients in their recollections resembled how language was used by groups C2 and C3 (higher-frequency words, less concrete words, fewer nouns, more adverbs, more pronouns, and more indefinite articles). These findings appear to reflect how individuals, either memory-impaired patients or controls, typically speak about the past when memory is weak and lacks detail and need not have special implications about language use and MTL function beyond the domain of memory. A notable exception to the similarity between patient narratives and the narratives of C2 and C3 was that the control groups reported the events of the walk in correct chronological order, whereas the order in which patients reported events bore no relationship to the order in which events occurred. We suggest that the MTL is especially important for accessing global information about events and the relationships among their elements.

hippocampus | language | forgetting | autobiographical memory

The hippocampus is important for the formation of declarative memory (1–3). In humans, bilateral damage to the hippocampus is associated with moderately severe anterograde amnesia and temporally limited retrograde amnesia (4). When damage extends into the adjacent cortical regions that lie along the parahippocampal gyrus, the memory impairment is more severe, as in the well-studied patients H.M. and E.P. (5, 6). In many respects, the memory performance of hippocampal patients resembles the performance of healthy individuals whose memories are weak as the result of being tested after long retention intervals (7). The memory impairment is circumscribed and occurs against a background of intact performance in a variety of perceptual and cognitive tasks: visual discrimination among stimuli with a high degree of feature overlap (8, 9), spatial perception (10–13), spatial imagery (14), map reading and navigation (15, 16), and semantic knowledge (e.g., long-established knowledge about the identity and function of common objects) (17).

Patients with hippocampal damage also succeed at tests of language function. They detected and explained linguistic ambiguity in sentences as well as controls (18), and they obtained normal scores for grammar and form in their spoken narratives (17). However, other studies have described situations where hippocampal patients use language differently than healthy volunteers (19). For example, hippocampal patients have been reported to use fewer definite articles in their discourse (20), higher-frequency words, and words with lower imageability (21) and to exhibit poorer narrative coherence (i.e., poorer continuity and organization in narratives) (22, 23). These irregularities in the use of language could reflect impaired cognitive functions other than memory that are supported by the hippocampus.

Alternatively, they could reflect how narratives typically come to be constructed when memory is weak and has lost detail, whether in memory-impaired patients or in healthy individuals tested after a long retention interval.

Early studies by Bartlett (24) described how memories become impoverished and fragmented over time. This work involved retention intervals as long as 10 y, although it was based largely on single subjects and qualitative accounts of recollection. Using Bartlett's original material (the "War of the Ghosts" story), Bergman and Roediger (25) replicated the earlier work, documenting omissions, intrusions, and distortions across an interval of 6 mo. Studies of "flashbulb memories" (i.e., memories of surprising and shocking events) have also described loss of detail and inaccuracy across intervals up to 3 y (26, 27). Across time, verbatim recall is often replaced by memory for the gist of what happened, and even the gist can be forgotten (28, 29). While these studies document the amount of forgetting and reorganization that can occur across long time periods, there have been few, if any, studies of how language itself changes as memory is tested at different times after learning.

We have examined the narrative recollections of memory-impaired patients with medial temporal lobe lesions (the MTL group) who took a guided 25-min walk during which 11 planned events occurred (Fig. 1). The MTL group had lesions limited to the hippocampus ($n = 4$) or larger MTL lesions ($n = 1$). We compared the recollections of the patients to the recollections of volunteers tested as long as 2.6 y after the walk. We first examined the accuracy of the recollections, the number of details that described episodic memories about the events of the walk, and the richness of these details. Next, we counted the number of words used to report the details and examined several characteristics of the content words (nouns, adjectives, verbs, adverbs): their frequency, concreteness, and imageability. We also calculated the percentage of each type of

Significance

When memory-impaired patients with medial temporal lobe (MTL) damage recollected the events of a guided walk, their memory was not only impoverished and lacking in detail but was also characterized by peculiarities in language use. However, as time passed after learning (up to 2.6 years), the recollections of healthy volunteers came to exhibit many of the same features with respect to both the richness of memory and language use. Thus, the characteristics of patient recollections appeared as a consequence of weak memory. The patients differed markedly from controls tested after long delays in that they reported events of the walk in a haphazard order. The results illuminate the nature of memory impairment and the function of the MTL.

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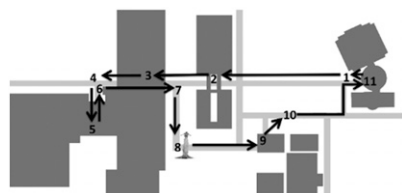


Fig. 1. Map indicating where 11 planned events occurred during a 25-min guided walk: 1: Discard cup. 2: Find change in vending machine. 3: View portraits. 4: Point out coffee cart. 5: Find book in library. 6: Receive bike lock. 7: Lock bike. 8: View statue. 9: Buy banana. 10: Tie shoes. 11: Drink from fountain. Sidewalks are light gray. Buildings are dark gray. Arrows indicate the path taken during the walk. Also see *Materials and Methods*. Reprinted from ref. 30.

content word, as well as the percentage of pronouns, definite articles, and indefinite articles among the words and phrases used to report the details. We also examined the temporal order in which the events of the walk were reported and the coherence of the narratives. In this way, we asked how the narrative recollections of the patients resembled and differed from the narratives of healthy volunteers tested after long delays.

Results

Events Remembered. Memory for the events of the walk declined as time passed. Fig. 2*A* shows the number of events referred to during the 6-min narratives (8.8, 8.0, and 5.7 events for C1, C2, and C3, respectively). Fig. 2*B* shows the scores on a 40-item, two-alternative test about the events of the walk (84.4, 73.6, 66.1% correct). For both measures, C3 (tested 2.6 y after the walk) performed more poorly than C1 (tested directly after the walk) ($t[6] > 3.4$, $P < 0.02$). Note, however, that even 2.6 y after the walk, participants remembered a good deal of material. For example, the 66.1% correct score on the 40-question test by C3 was well above the 46.8% score obtained by participants who took the same test without having taken the walk ($t[15] = 5.1$, $P < 0.001$). Fig. 2 also shows that the MTL group (tested directly after the walk) performed worse on both tests than C1 (6.6 in Fig. 2*A*; 65.0% in Fig. 2*B*; $t[11] > 2.9$, $P < 0.02$; t test for unequal variance) but similarly to the C2 and C3 groups tested after delays ($t[10] < 1.7$, $P > 0.10$).

Words Spoken and Details Recollected. The groups also spoke fewer total words during their 6-min narratives as time passed (574.3, 492.6, and 435.9 words for C1, C2, and C3, respectively; C1 vs. C3, $t[6] = 2.59$, $P < 0.05$). Again, the MTL group (489.6 words) spoke about as many words as the C2 and C3 groups tested after delays ($t[10] < 0.60$, $P > 0.10$). The groups differed even more with respect to how many words in the narratives actually described events from the walk (i.e., episodic details). Fig. 3*A* shows that for C1, 442.5 words (78% of the total) were in the service of describing episodes from the walk, whereas the number was only 277.0 for C2 (59% of total), 180.0 for C3

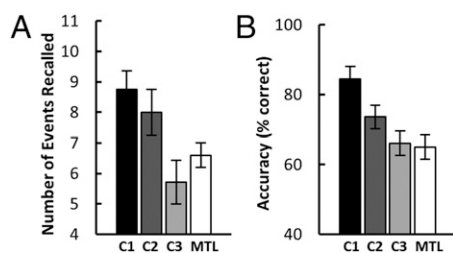


Fig. 2. Mean number of events referred to by each group during 6-min narrative recollections about the walk (*A*). Performance on 40 two-alternative, forced-choice questions about the events of the walk (*B*). C1 ($n = 8$), controls tested directly after the walk. C2 ($n = 7$), controls tested 1 mo after the walk. C3 ($n = 7$), controls from the C1 group tested 2.6 y after the walk. MTL ($n = 5$), patients with medial temporal lobe lesions.

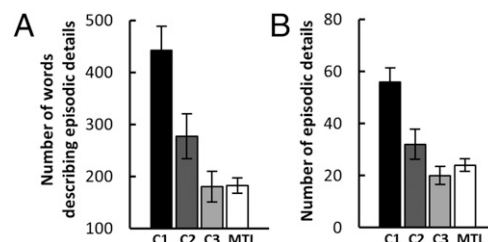


Fig. 3. Mean number of words in the 6-min narrative recollections used to report accurate episodic details about the walk (*A*). Mean number of accurate episodic details about the walk reported by each group in the 6-min narrative recollections (*B*). Groups are as in Fig. 2.

(40% of total), and 182.6 for MTL (42% of total) (C1 vs. C3, $t[6] = 4.97$, $P < 0.01$; MTL vs. C2 and C3, $t[10] < 2.1$, $P > 0.10$; MTL vs. C1, $t[8] = 5.43$, $P < 0.001$; t test for unequal variance). Thus, the participants in the C1 group, tested directly after the walk, used more words in their 6-min narratives to describe episodes from the walk than did the other groups. In addition, their narratives were efficient in that most of their words were used to describe episodes. The other groups used fewer words to describe episodes from the walk and their narratives were inefficient. Many of the words were parts of repetitions, bits of semantic details, and irrelevant comments.

Consistent with these differences in the number of words spoken, the groups differed markedly in how many accurate episodic details they reported (Fig. 3*B*). C1 reported 56 details, considerably more than the 20 details reported by C3 ($t[6] = 6.43$, $P < 0.001$). The MTL group recollected 24 details, fewer than C1 ($t[11] = 4.42$, $P < 0.001$) but similar to the number of details recollected by C2 (32 details) and C3 (20 details) (MTL vs. C2 and C3, $t[10] < 1.25$, $P > 0.10$). The following analyses were based on the words that appeared in the sentences and phrases that described these episodic details.

Richness of Episodic Detail. Given that the number of details available about the events of the walk declined with the passage of time, it is not surprising that the quality of the recollections also declined. The richness score (Fig. 4) is intended to indicate the episodic quality of the recollections that were produced about each event. Across events, the mean richness score (0–6) of the sentences and phrases describing episodic details was 4.05, 3.67, and 3.34 for C1, C2, and C3, respectively (C1 vs. C3, $t[6] = 2.78$, $P < 0.05$). The score for the MTL group (3.10) was lower than the scores for C1 and C2 ($t > 2.7$, $P < 0.05$) but similar to the C3 score ($t[10] = 1.04$, $P > 0.10$).

Properties of Content Words. We next examined the content words (nouns, adjectives, verbs, and adverbs) that appeared within the sentences and phrases that described episodic details. Fig. 5 shows scores for word frequency and ratings for the concreteness and imageability of the content words. As time passed after the walk, participants used higher-frequency words (Fig. 5*A*), less concrete words (Fig. 5*B*), and less imageable words (Fig. 5*C*). For word frequency (Fig. 5*A*), the scores were 162, 203, and 287 for C1, C2, and C3, respectively (C1 vs. C2, $t[13] = 2.37$, $P < 0.05$; C1 vs. C3, $t[6] = 7.72$, $P < 0.001$).

The word frequency score for the MTL group (260) was similar to the scores obtained by the control groups tested after delays. Thus, the frequency of words used by the MTL group was higher than that of C1 ($t[11] = 4.47$, $P < 0.001$), marginally higher than that of C2 ($t[10] = 2.14$, $P < 0.06$), and most similar to that of C3 ($t[10] = 0.86$, $P > 0.10$). For concreteness (Fig. 5*B*), the ratings were 428, 410, and 394 for C1, C2, and C3, respectively (C1 vs. C2, $t[13] = 2.13$, $P < 0.09$; C1 vs. C3, $t[6] = 3.72$, $P < 0.01$). The concreteness rating for the MTL group (414) was most similar to that of the control groups tested after delays (C2 and C3 vs. MTL, $t[10] < 1.80$, $P > 0.10$). However, the MTL rating in this case did not differ significantly from that of C1 ($t[11] = 1.32$, $P > 0.10$). For imageability (Fig. 5*C*), the ratings were 443, 432, and 415 for C1, C2, and C3, respectively (C1 vs. C2, $t[13] = 1.93$, $P < 0.08$; C1 vs. C3, $t[6] = 3.68$, $P < 0.01$). The imageability rating for the MTL group (441) was marginally

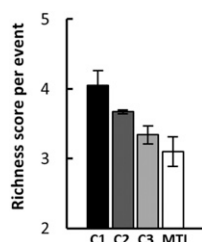


Fig. 4. Mean richness of the episodic details describing each event in 6-min narrative recollections about the walk. Richness was rated on a 0–6 scale (see *Materials and Methods*). Groups are as in Fig. 2.

higher than that of C3 ($t[10] = 2.18, P = 0.054$) and not measurably different from those of the other groups ($t < 0.99, P > 0.34$).

Across groups, nouns accounted for 38.1% of the content words used to describe episodic details, verbs accounted for 25.5%, adverbs accounted for 18.8%, and adjectives accounted for 17.5%. As time passed after the walk, the use of nouns and adverbs changed (Fig. 6), but there were not systematic changes in the use of verbs or adjectives. Specifically, nouns appeared less frequently in the narratives as time passed, and adverbs appeared more frequently. The percentage of nouns was 41.8, 36.0, 38.3, and 36.6 for C1, C2, C3, and MTL, respectively (C1 vs. C2, $t[13] = 2.64$, $P < 0.05$; C1 vs. C3, $t[6] = 2.37$, $P < 0.06$). The MTL group used nouns at about the same frequency as the groups tested after delays ($t < 0.5$, $P > 0.65$), although not significantly less frequently than C1 ($t[11] = 1.60$, $P = 0.14$). For adverbs, the percentages were 16.6, 17.6, 22.1, and 18.9 (C1 vs. C3, $t[6] = 4.00$, $P < 0.01$; C2 vs. C3, $t[12] = 2.28$, $P < 0.05$). The MTL group used adverbs at about the same frequency as the groups tested after delays ($t < 1.5$, $P > 0.16$) and more frequently than C1 ($t[11] = 2.27$, $P < 0.05$). For verbs, the percentages were 24.0, 30.4, 25.2, and 22.5. For adjectives, the percentages were 17.6, 16.0, 14.5, and 22.1.

Pronouns. Fig. 7A shows the percentage of pronouns that appeared among the words in the sentences and phrases that described episodic details. The percentages were 12.7, 18.4, 17.7, and 18.3 for C1, C2, C3, and MTL, respectively. C1, tested directly after the walk, used about 30% fewer pronouns than the MTL group or the groups tested after delays ($t > 3.4$, $P < 0.001$). The MTL group, C2, and C3 used pronouns with similar frequency.

Articles. We next examined the percentage of definite (the) and indefinite (a, an) articles that appeared among the words in the sentences and phrases that described episodic details. For definite articles (Fig. 7B), the percentages tended to decrease as time passed after the walk (5.0, 4.8, 4.4, and 6.1 for C1, C2, C3, and MTL, respectively). For indefinite articles (Fig. 7C), the percentages tended to increase (2.0, 2.9, 3.9, and 2.8) (C1 vs. C2, $t[13] = 2.11$, $P < 0.054$; C1 vs. C3, $t[6] = 2.28$, $P < 0.063$). We considered the possibility that these trends represent a meaningful feature of normal forgetting.

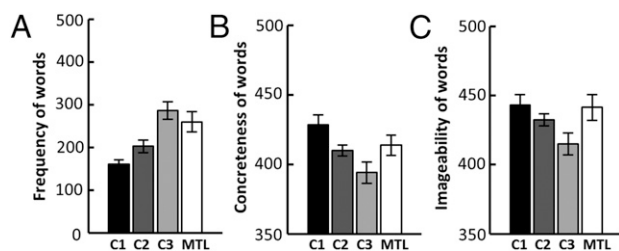


Fig. 5. Characteristics of the content words (nouns, adjectives, verbs, adverbs) used to report accurate episodic details in the 6-min narrative recollections about the walk. (A) Word frequency of the content words. (B) Concreteness of the words. (C) Imageability of the words. Word frequency is based on a corpus of 190,000 words. Concreteness and imageability are based on ratings (100–700): see *Materials and Methods*. Groups are as in Fig. 2.

Thus, one might suppose that, as time passes after a learning event, the word “a” or “an” might often substitute for “the” as memory becomes less precise. For example, one might initially say “I remember the library” but later say “I remember a library.” We found some support for this idea in a two-way, repeated measures ANOVA, where one factor was time (C1 tested directly after the walk vs. C3 tested 2.6 y after the walk) and the other factor was article type (definite vs. indefinite). The ANOVA yielded an effect of article type ($F[1,12] = 6.23, P < 0.05$) and, notably, a marginal interaction of time \times article type ($F[1,12] = 3.42, P = 0.09$). The MTL group, like the other groups, used fewer indefinite articles than definite articles, but the scores of the MTL group did not differ significantly from the scores of any other group ($t < 1.38, P > 0.19$).

Temporal Order of Event Memory. Fig. 8 shows when each event of the walk was mentioned during the course of the 6-min narrative recollections. Note that the number of events mentioned varied from group to group (Fig. 2*A*), and only one participant (in C1) referred to all of the events. As reported previously (30), the C1 and C2 groups described events approximately in the order that the events occurred (Fig. 8*A* and *B*). In contrast, the order in which the MTL group described events (Fig. 8*D*) was unrelated to the order in which the events occurred. In the present study, we found that even participants tested 2.6 y after the walk (C3) described events close to the order in which they had occurred (Fig. 8*C*). Indeed, C3 related events in the proper order despite the fact that this group referred to fewer events in their narratives than did the MTL group (5.7 vs. 6.6, Fig. 2*A*) and remembered fewer details (20 vs. 24 details, Fig. 3*B*).

Narrative Coherence. Fig. 9 shows the coherence score for the 6-min narratives based on ratings of how well a narrative was oriented in space and time (context), the extent to which actions were reported in a sensible order (chronology), and the extent to which participants remained on topic and told a coherent story (theme). The overall coherence score declined with the passage of time after the walk (2.13, 1.86, and 1.74 for C1, C2, and C3, respectively; C1 vs. C3, $t[6] = 3.672$, $P = 0.01$). This change in coherence score was due largely to the change in chronology scores as time passed (2.69, 2.14, and 2.07 for C1, C2, and C3, respectively; C1 vs. C3, $t[6] = 3.667$, $P = 0.01$). The scores for context were low because of the few references to time and were virtually the same across the three control groups (1.13, 1.00, 1.07). The scores for theme declined a little with time (2.56, 2.43, 2.07), but the difference between groups did not reach significance (C1 vs. C3, $t[6] = 1.99$, $P = 0.09$). Note that the theme score would be affected by a poor chronology score because a lack of temporal order affects the ability to tell a coherent story that stays on topic and provides an ending.

The MTL group obtained a coherence score much lower than the other groups (MTL vs. each control group, $t > 3.39$, $P < 0.01$). This finding was due largely to the poor chronology score for the MTL group (0.80; MTL vs. each control group, $t > 3.43$, $P < 0.01$). The MTL group obtained the same score as the other groups on the context measure (1.00). The MTL score for theme (1.70) was also

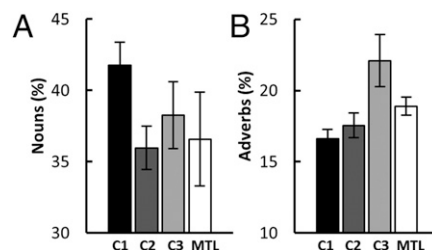


Fig. 6. Percentage of nouns among the words used to report accurate episodic details in the 6-min narrative recollections about the walk (A). Percentage of adverbs used to report accurate episodic details in the 6-min narrative recollections about the walk (B). Groups are as in Fig. 2.

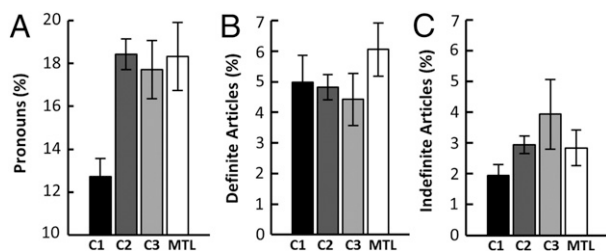


Fig. 7. Percentage of pronouns among the words used to report accurate episodic details in the 6-min narrative recollections (A). Percentage of definite articles used to report episodic details (B). Percentage of indefinite articles used to report episodic details (C). Groups are as in Fig. 2.

low, although not measurably different from the score of any control group ($t < 1.42$, $P > 0.17$).

Discussion

Healthy volunteers and memory-impaired patients recollected the events of a 25-min guided walk. They first generated 6-min narratives about the walk and then answered 40 questions. The patients were tested directly after the walk (MTL group). The volunteers were tested either directly after the walk (C1) or 1 mo after the walk (C2). In addition, seven of the eight participants in C1 were tested again 2.6 y after the walk (C3). As time passed after the walk, memory for the events of the walk weakened. The volunteers remembered fewer events (Fig. 2A), answered fewer questions about the walk correctly (Fig. 2B), spoke fewer words overall and fewer words that specifically described events (Fig. 3A), recalled fewer details about the walk (Fig. 3B), and generated narratives with lower richness scores (Fig. 4). We note that group C3, tested after 2.6 y, likely benefited from having also received the initial test (see ref. 25 for such a benefit of repeated testing). Still, C3 consistently performed more poorly than group C2.

The passage of time also affected the way in which words were used in the narratives as well as the organization of the narratives. Among the content words (nouns, adjectives, verbs, adverbs), volunteers used higher-frequency (i.e., more common) words as time passed (Fig. 5A), less concrete words (Fig. 5B), less imageable words (Fig. 5C), fewer nouns (Fig. 6A), and more adverbs (Fig. 6B). They

also used more pronouns (Fig. 7A) and tended to use indefinite articles in favor of definite articles (Fig. 7B and C). All of the volunteers reported events close to the order in which the events occurred, even 2.6 y after the walk (Fig. 8A–C), with small decreases in temporal precision across time ($r = 0.95$, $r = 0.91$, $r = 0.88$). Last, estimates of narrative coherence declined with time (Fig. 9). This score depends importantly on the ability to report events in proper temporal order, and across participants, it also correlated with estimates of richness ($r = 0.56$, $P < 0.01$). These findings, taken together, describe an effect of time on memory that resulted in briefer narratives that were less precise and lacked detail.

Patients in the MTL group also generated narratives that were imprecise and lacked detail. With respect to the content of memory (number of events referred to, number of questions answered correctly, number of words used, number of details recalled, and the richness of the narratives), the MTL group differed sharply from the C1 group and resembled the C3 group tested after 2.6 y (Figs. 2–4). With respect to language use, the MTL group also obtained scores similar to the scores of the volunteers tested after delays. Thus, the MTL group tended to use high-frequency words (Fig. 5A), less concrete words (Fig. 5B), fewer nouns (Fig. 6A), more adverbs (Fig. 6B), more pronouns (Fig. 7A), and more indefinite articles (Fig. 7C). Two clear exceptions to this pattern were that the MTL group was intact (and similar to C1) with respect to the imageability of the words in their narratives (Fig. 5C) and with respect to the use of definite articles (Fig. 7B).

The most striking finding in the narratives of the MTL patients was that the events of the walk were reported in a haphazard order that bore no relationship to the order in which the events actually occurred (Fig. 8D). Indeed, the MTL group performed far more poorly than even volunteers in group C3 tested after 2.6 y (Fig. 8C). In earlier work (30), we noted the poor temporal order memory of MTL patients in comparison with volunteers tested after a delay of 1 mo (C2). However, in that case, the MTL group also had marginally poorer fact memory than the C2 group (Figs. 2 and 3B). It therefore seemed possible that the temporal structure of narratives generated by volunteers might collapse at some longer interval after the walk, perhaps at a time when the fact memory of volunteers was as poor as the fact memory of the MTL group. However, this did not occur. The C3 group tested 2.6 y after the walk had good temporal order memory, far better than the MTL group, although fact memory for the walk itself was a little worse than in the MTL group (Figs. 2A and 3B). We suppose that the poor narrative coherence score obtained by the MTL group (Fig. 9) reflects this same difficulty in appreciating temporal order.

The fact that the passage of time affected the use of language in narrative recollections is relevant to earlier studies describing abnormalities in language use by memory-impaired patients with hippocampal lesions. For example, reports that patients used fewer definite articles (20), higher-frequency words (21), and words with lower imageability (21) may reflect how patients typically speak when memory is weak and lacks detail. This idea was proposed by the earlier authors, and the present findings support it by showing directly that the use of language by memory-impaired patients matched in many respects the use of language by volunteers whose memory was weak as a result of being tested after a long delay. The

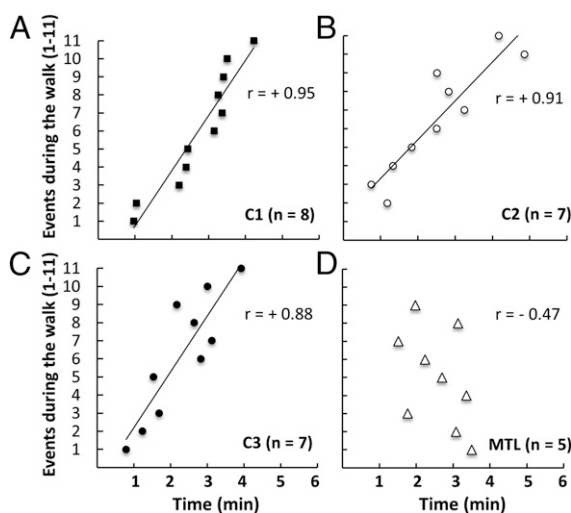


Fig. 8. The data points show when, on average, the events from the walk were referred to during the 6-min narratives. The control groups tended to describe events in the order that they occurred (A–C). The order in which the MTL patients mentioned events was unrelated to the order in which the events occurred (D). Lines represent significant fits to the data. No C2 described event 1. No C3 described event 4. No patient described events 10 and 11.

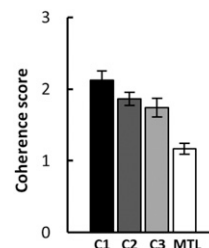


Fig. 9. Coherence of the 6-min narrative recollections based on ratings (0–3) for each of three characteristics of the narratives: context, chronology, and theme (see Materials and Methods). Groups are as in Fig. 2.

pronouns used by each participant by the total number of words used to report episodic details. Most pronouns were self-referential (41.8%: I, me, we, us, our) or referenced others (35.9%: he, she, it, him, her, they, them). The others (22.3%) were possessive (mine, yours, his, hers, its, ours, theirs), reflexive (myself, herself, ourselves, itself), relative (that, which, who, whom, what, whose), or indefinite (everybody, either, none, something).

Definite and Indefinite Articles. We also recorded within the 6-min narratives the number of articles that appeared within the sentences and phrases containing accurate episodic details. All definite (the) and indefinite (a, an) articles were counted. As with content words, the number of articles used by each participant was divided by the total number of words that each participant used to report episodic details.

Temporal Order of Event Memory. We used the audio recordings to note the time during the 6-min narratives when participants in C3 mentioned each event. The same data were presented previously for C1, C2, and the MTL patients (30) and are presented here as well. For events mentioned more than once, the times when the event was mentioned were averaged. In this way, we calculated the order in which events were reported.

Narrative Coherence. Narrative coherence is a measure of the quality of autobiographical memories (44) and was used in a recent study of memory-impaired patients (23). As in that study, we scored narrative coherence as a composite of three separate factors: context, chronology, and theme. Context refers to the extent to which a narrative was oriented in space and time. Chronology refers to the extent to which the actions in a narrative were reported in a sensible temporal order. Theme refers to the extent to which

participants remained on topic, reported details that were causally related to each other, and provided a resolution to the story. For each 6-min narrative, the sentences and phrases that contained episodic details provided the basis for a single score (0, 1, 2, or 3) on each of the three dimensions (context, chronology, and theme). The three scores were then averaged and averaged again across two raters to obtain a single coherence score for each participant (correlation across participants between the single scores of the two raters = 0.86). We expected measures of chronology, and to some extent theme, to overlap with our measure of temporal order of event memory. In addition, we expected the context measure to be influenced by the particular circumstances of the present study. Participants were instructed to remember a walk, so there should be ample references to places. However, because the narratives were directed to the experimenter, who had shared the walk, one might expect fewer references to time.

Data Analysis. To determine how healthy volunteers performed as time passed after the walk, we relied primarily on comparisons by paired *t* tests between the scores of seven (out of eight) participants in C1 and the same seven participants when they were tested again 2.6 y after the walk (C3). The fact that C1 and C3 involved the same individuals and C2 involved different individuals ruled out the use of ANOVAs and trend analyses that could have included all three groups (C1, C2, and C3). We compared the MTL patients to the control groups using two-sample *t* tests. In all figures, error bars denote SEM.

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Supporting Information (SI)

Participants. Five memory-impaired patients participated (Table S1), four with bilateral medial temporal lobe lesions limited to the hippocampus (the CA fields, dentate gyrus, and subicular complex) and one with larger medial temporal lobe lesions (the MTL group). For the five patients, the average score for delayed recall (30 min) of two short prose passages was 1.0 segments (25 segments per passage). The average score for delayed recall (10-15 min) of a complex diagram was 5.1 (maximum score = 36). Paired-associate learning of 10 unrelated noun-noun pairs summed across each of three successive trials was 3.0 pairs (30 pairs total). On these same tests, 11 healthy controls scored 20.2 for the prose passages, 18.3 for the diagram, and 24.1 for paired-associate learning (1).

Patients G.W. and D.A. became amnesic in 2001 and 2011, respectively, following drug overdose and associated respiratory failure. Patient K.E. became amnesic in 2004 after an episode of ischemia associated with kidney failure and toxic shock syndrome. Patient L.J. (the only female) became amnesic in 1988 during a 6-mo period with no known precipitating event. Her memory impairment has been stable since that time. Patients K.E., L.J., G.W., and D.A. have an average bilateral reduction in hippocampal volume of 49%, 46%, 48%, and 35%, respectively. On the basis of findings from two patients (L.M. and W.H.) with similar bilateral volume loss in the hippocampus for whom detailed postmortem neurohistological information was obtained (2), the degree of volume loss in these four patients may reflect nearly complete loss of hippocampal neurons. The volume of the parahippocampal gyrus (including temporopolar, perirhinal, entorhinal, and parahippocampal cortices) is reduced by 11%, -17%, 10%, and -5% for K.E., L.J., G.W., and D.A., respectively. These values are based on published guidelines for identifying the boundaries of the parahippocampal

gyrus (3, 4). The negative values indicate instances where the volume was larger for a patient than for controls.

Patient G.P. has severe memory impairment resulting from viral encephalitis in 1987. His memory impairment is so severe that, during repeated testing over many weeks, he did not recognize that he had been tested before (5). G.P. has an average bilateral reduction in hippocampal volume of 96%. The volume of the parahippocampal gyrus is reduced by 94%. G.P. also has a reduction in the volume of the left temporal lobe (fusiform gyrus plus inferior, medial, and superior temporal gyri) of 24%. The right temporal lobe volume is reduced by only 6%. Eight coronal magnetic resonance images from each patient, together with detailed description of the lesions can be found in Figure S1.

Three groups of healthy volunteers also participated in the main experiment. One group (C1) was tested directly after the walk ($n = 8$; 1 female; mean age = 60.8 y; mean education = 13.8 y). A second group (C2) was tested 1 month after the walk ($n = 7$; 3 females; mean age = 64.1; mean education = 14.8 y). In addition, seven of the eight participants in C1 were tested again 2.6 years after the walk (C3, $n = 7$).

Table S1. Characteristics of memory-impaired patients

Patient	Age (years)	Education (years)	WAIS-III IQ	WMS-R				
				Attention	Verbal	Visual	General	Delay
D.A.	31	12	95	104	90	91	90	56
K.E.	73	13.5	108	114	64	84	72	55
L.J.	77	12	101	105	83	60	69	<50
G.W.	55	12	108	105	67	86	70	<50
G.P.	68	16	98	102	79	62	66	50

The Wechsler Adult Intelligence Scale (WAIS-III) and the Wechsler Memory Scale-Revised (WMS-R) yield mean scores of 100 in the normal population with a SD of 15. The WMS-R does not provide numerical scores for individuals who score < 50. The IQ score for D.A. is from the WAIS-IV.

Figure S1

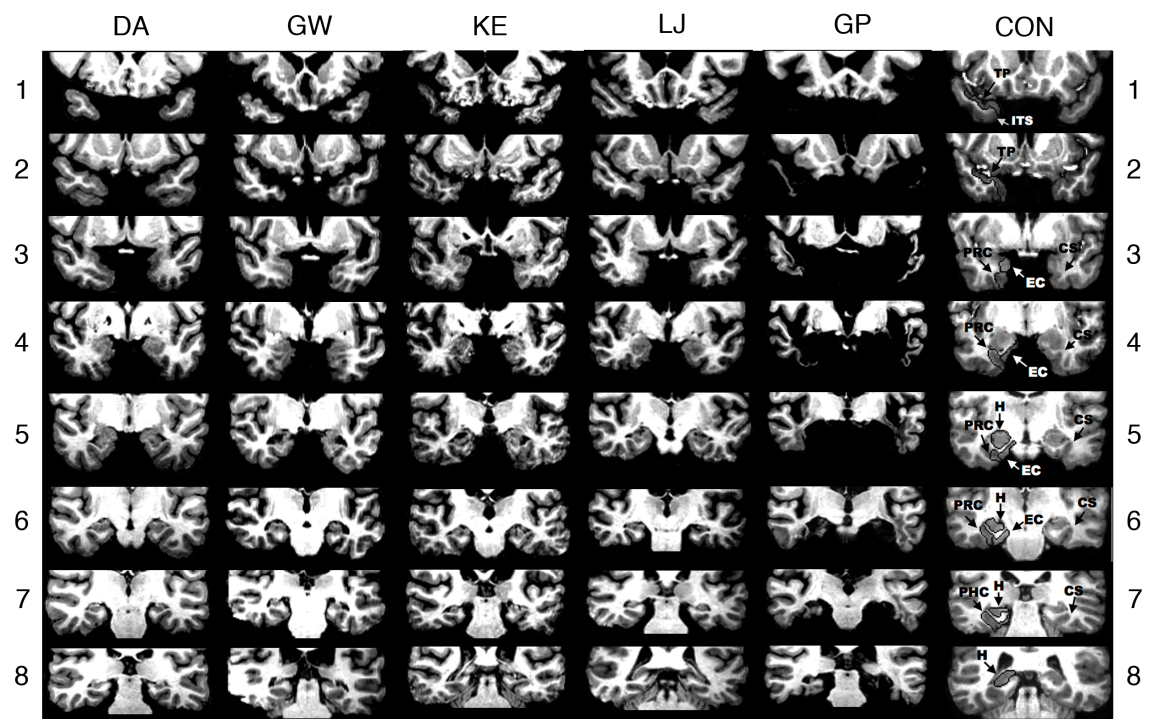


Figure S1. Series of eight T1-weighted coronal images of six patients are illustrated with limited hippocampal lesions (DA, GW, KE, and LJ), one patient with extensive medial temporal lobe damage (GP), and one control (CON). The sections proceed posteriorly in 7mm intervals from the temporopolar (TP) cortex in the top section. The left side of the brain is on the right side of each image.

As described by ref (3), TP cortex extends medially from the inferotemporal sulcus (ITS) to the fundus of the TP sulcus. TP cortex extends rostrally from the tip of the temporal pole caudally to the limen insula (LI), which approximates the border between the TP cortex and perirhinal cortex (PRC). Caudal to TP cortex, the collateral sulcus (CS) is the most important structure for the identification of medial temporal lobe cortices. At its most rostral extent, the CS is surrounded entirely by PRC. Caudally, entorhinal cortex (EC) extends from the midpoint of the medial bank of the CS to the subiculum, while PRC extends laterally from the midpoint of the medial bank of the CS to the inferotemporal cortex. Two millimeters caudal to the disappearance of the gyrus intralimbicus of the hippocampus (H), the CS is surrounded by parahippocampal cortex (PHC). The caudal border of the posterior PHC is defined as lying 1.5mm posterior to the crus of the fornix at the point where the fimbria turns upwards to continue as the posterior pillars of the fornix and posterior to the pulvinar nucleus of the thalamus (4).

The top section (row 1) shows the TP cortex and the ITS in the control brain. None of the patients with limited hippocampal lesions have damage evident at this level. For GP, the TP cortex and lateral temporal cortex are missing bilaterally. The ITS is visible bilaterally at this level for patients GW and KE. For LJ, only the right ITS is visible. For DA, the ITS is not visible on either side at this level. The second section (row 2) shows TP cortex and the ITS in the control brain. The ITS and TP cortex is evident in all patients with limited hippocampal lesions at this level. None of the patients with limited hippocampal lesions has damage evident at this level. For GP, note that the portion of

the temporal lobe missing corresponds to TP cortex and also involves the lateral temporal lobe, especially on the left. The CS is visible, indicating the beginning of PRC, in patients KE (right side only). The third section (row 3) shows the CS and surrounding PRC and EC in the control brain. None of the patients with limited hippocampal lesions has damage evident at this level with the exception of KE, who has damage in the basal ganglia secondary to toxic shock syndrome (and to a lesser extent in row 4). For patient DA, the CS is not evident at this level and PRC is evident bilaterally. For patients GW, KE, and LJ, the PRC is evident on the left side, bounded by the LI and CS. On the right side, both EC and PRC are evident. For GP, no CS or surrounding tissue is evident, and damage to left lateral temporal lobe is evident. The fourth section (row 4) shows the anterior hippocampus and the adjacent PRC and EC in the control brain. At this level hippocampal damage is evident in patient DA. The hippocampus is not yet visible at this level in any of the other patients with limited hippocampal lesions. For DA, bilateral damage to the globus pallidus is evident at this level, presumably secondary to heroin overdose. No damage to the PRC or EC is evident for any of the patients at this level, except for GP who has no medial temporal lobe tissue at this level and who has damage to the left lateral temporal lobe. The fifth section (row 5) shows the hippocampus and the adjacent PRC and EC in the control brain. The CS and the surrounding PRC and EC appear normal in all patients at this level with the exception of GP, who has no medial temporal lobe tissue at this level and who exhibits some damage to left lateral temporal lobe. Damage is evident in the hippocampal region of all patients. The sixth section (row 6) shows the hippocampus and the adjacent PRC and EC in the control brain. Damage is evident in the hippocampal region for all patients at this level. The surrounding PRC and EC appear normal in all patients except GP, who has little normal medial temporal lobe tissue in either hemisphere. Both the PRC and EC are visible in all hippocampal patients bilaterally. The seventh section (row 7) shows the hippocampus and the CS,

surrounded by PHC in the control brain. Damage to the hippocampus is evident in all patients at this level. In all patients with damage limited to the hippocampus, the PHC is evident, but in patient DA the PRC is still visible on the right side. Patient GP has little normal medial temporal lobe tissue in either hemisphere. The eighth section (row 8) shows the hippocampus in the control brain. Bilateral hippocampal damage is evident in patients DA, GW, KE, and GP at this level. Patient LJ shows hippocampal damage only on the left side. PHC is no longer evident at this level in patients DA, KE, or LJ and PHC appears normal in patient GW. Patient GP has some spared PHC on the right at this level. The warping artifact in the right lateral temporal lobe of GW on this section did not interfere with the assessment of his damage. Posterior to this level, GP exhibits hippocampal damage and damage to the PHC. No damage is evident posterior to this level for any of the other patients. Reprinted from ref. (6).

Supporting Information References

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