

# Learning and remembering real-world events after medial temporal lobe damage

Adam J. O. Dede<sup>a,b</sup>, Jennifer C. Frascino<sup>a,c</sup>, John T. Wixted<sup>b</sup>, and Larry R. Squire<sup>a,b,c,d,1</sup>

<sup>a</sup>Veterans Affairs San Diego Healthcare System, San Diego, CA 92161; <sup>b</sup>Department of Psychology, University of California, San Diego, La Jolla, CA 92093; <sup>c</sup>Department of Psychiatry, University of California, San Diego, La Jolla, CA 92093; and <sup>d</sup>Department of Neurosciences, University of California, San Diego, La Jolla, CA 92093

Contributed by Larry R. Squire, October 13, 2016 (sent for review May 10, 2016; reviewed by Howard Eichenbaum and Joseph R. Manns)

**The hippocampus is important for autobiographical memory, but its role is unclear. In the study, patients with hippocampal damage and controls were taken on a 25-min walk on the University of California, San Diego, campus during which 11 planned events occurred. Memory was tested directly after the walk. In addition, a second group of controls took the same walk and were tested after 1 mo. Patients with hippocampal damage remembered fewer details than controls tested directly after the walk but remembered a similar number of details as controls tested after 1 mo. Notably, the details that were reported by patients had the characteristics of episodic recollection and included references to particular places and events. Patients exhibited no special difficulty remembering spatial details in comparison with nonspatial details. Last, whereas both control groups tended to recall the events of the walk in chronological order, the order in which patients recalled the events was unrelated to the order in which they occurred. The findings illuminate the role of the hippocampus in autobiographical memory and in the spatial and nonspatial aspects of episodic recollection.**

hippocampus | prospective memory | autobiographical memory

Autobiographical memory represents the experiences of our lives and provides our sense of self. We can reexperience events from the past, and we can imagine events in the future. Without this faculty, our conscious life would be a series of unconnected moments.

The severely amnesic patient K.C. cannot remember a single personal event from his life and cannot describe what he did yesterday or what he might do tomorrow (1). K.C.'s amnesia was caused by a closed-head injury, which damaged the hippocampus and adjacent cortex, as well as regions of the frontal and parietal lobes (2). Although the extent of K.C.'s lesions makes it difficult to relate his impairment to anatomy, other work has studied autobiographical memory in patients with more circumscribed damage.

A number of studies have identified the hippocampus as an important structure for autobiographical memory (3–5), but its role remains unclear. Some findings emphasize its function in forming new memories about both events and facts (episodic and semantic memory) (6). Other studies suggest that the hippocampus is particularly important for the episodic content of autobiographical memory (e.g., time, place, and perceptual information) and that, as a result, patients with hippocampal damage must rely on semantic memory alone (7). Still other work suggests that the hippocampus is especially important for spatial cognition and that impaired autobiographical memory after hippocampal damage is due to a difficulty in constructing spatially coherent scenes (8).

Here, we describe a different approach to the study of autobiographical memory and hippocampal function. Patients with hippocampal damage and healthy volunteers were taken individually on a 25-min walk on the University of California, San Diego, campus during which 11 planned events occurred (Fig. 1). Directly after the walk, participants were asked for 6-min, narrative descriptions of what they could remember. Next, they constructed 1-min narratives in response to prompts about each of

the 11 events. Last, they were given 40 two-alternative, forced-choice questions about particular details of the walk. In this way, we assessed the accuracy and quality of memory for real-world events. Specifically, we evaluated whether and to what extent participants could recollect episodic content. We also evaluated the quantity of spatial and nonspatial content and the temporal organization of the narratives. To determine whether impairments exhibited by the patients reflect a qualitatively distinct deficit or a normal feature of weak memory, we also tested a second group of volunteers who took the same walk but were tested only after an interval of 1 mo.

## Results

**Six-Minute Narratives About the Walk.** The patients with hippocampal lesions (H) recalled fewer accurate episodic details about the walk than the control-1 (CON-1) group [ $t(10) = 3.9, P < 0.01$ ] and about the same number of details overall as the control-2 (CON-2) group tested after 1 mo [ $t(9) < 1.0, P > 0.2$ ] (Table 1). Fig. 2 shows that, except for details about time (which were rare in all groups), the H patients recalled fewer details than the CON-1 group in each category (event, space, and perception) [ $t_s(10) > 2.3, P_s < 0.05$ ], and they recalled about the same number of details in each category as the CON-2 group ( $P_s > 0.1$ ). The single patient with large medial temporal lobe (MTL) lesions performed more poorly than the patients with hippocampal lesions [Table 1;  $t(3) = 6.6, P < 0.05$ ]. Note that the hippocampal patients and the MTL patient had no more difficulty reporting spatial details about the walk than other kinds of details (Fig. 2A). Thus, the hippocampal patients scored 1.6, 1.5, and 1.3 SDs below the CON-1 mean for details in each category (event, space, and perception).

The patients (H and MTL) also recalled more inaccurate details than CON-1 and fewer unverifiable details (Table 1), but these differences did not reach significance ( $P < 0.08$  for inaccurate

## Significance

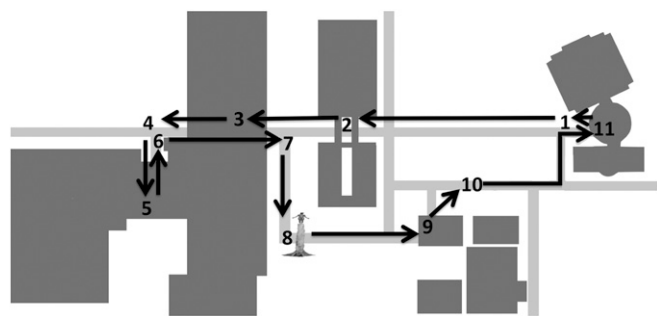
We explored the role of the medial temporal lobe (MTL) in remembering recent events. Patients with MTL damage and healthy controls were taken on a walk during which 11 planned events occurred. Patients remembered fewer details about the events than controls. Nevertheless, the details made reference to particular places and events from the walk. In addition, patients were similarly impaired across different kinds of content (spatial and nonspatial). Last, the patients were particularly impaired at remembering the temporal order in which the events occurred. The findings illuminate the role of the MTL in memory for real-world events and in the spatial and nonspatial aspects of recollection.

Author contributions: A.J.O.D., J.C.F., J.T.W., and L.R.S. designed research; A.J.O.D. and J.C.F. performed research; A.J.O.D. analyzed data; and A.J.O.D. and L.R.S. wrote the paper.

Reviewers: H.E., Center for Memory and Brain, Boston University; and J.R.M., Emory University.

The authors declare no conflict of interest.

<sup>1</sup>To whom correspondence should be addressed. Email: lsquire@ucsd.edu.



**Fig. 1.** Map of 11 events that occurred during a 25-min guided walk. 1: discard a cup. 2: find change in a vending machine. 3: view portraits of department chairs. 4: point out coffee cart. 5: find book on the second floor of the library. 6: receive bike lock from student. 7: lock up bike. 8: view statue. 9: buy banana in cafe. 10: stop to tie shoes. 11: drink from water fountain. Sidewalks are light gray. Buildings are dark gray. Arrows indicate the path taken during the walk.

details;  $P > 0.2$  for unverifiable details). It was also the case that patients repeated themselves more during narrative construction than did CON-1 [ $t(10) = 2.4$ ,  $P < 0.05$ ] (Fig. 2B).

To assess memory for the temporal order in which the events had occurred, we plotted the order in which the 11 events of the walk were described. Fig. 3A provides this information for the H and MTL patients (combined) and for CON-1. The CON-1 group described events approximately in the order in which they had occurred ( $r = 0.95$ ,  $P < 0.05$ ). By contrast, the order in which patients described events was unrelated to the order in which they had occurred ( $r = -0.47$ ,  $P > 0.2$ ). Fig. 3B shows corresponding data for CON-2 in comparison with the data for CON-1. Group CON-2, like CON-1, described events in the order they had occurred ( $r = 0.91$ ,  $P < 0.05$ ).

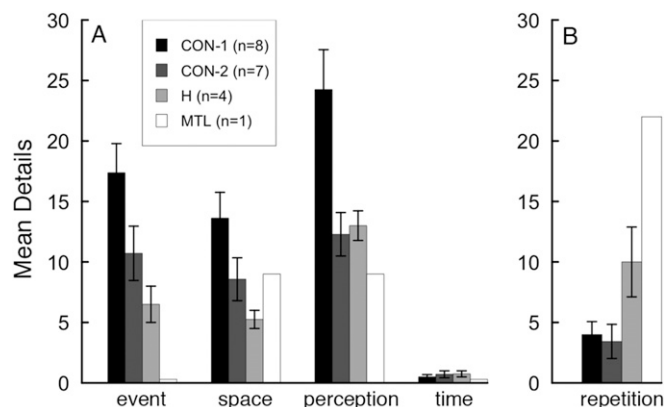
**One-Minute Narratives About Each of the 11 Events.** Fig. 4 shows the number of accurate details that were recalled during 1 min in response to prompts about each event of the walk. Patients with hippocampal lesions retrieved significantly fewer details than CON-1 about every event ( $P_s < 0.05$ ), except event 11 (the drink). The events that were most memorable for CON-1 were also the most memorable events for the patients (Fig. 5) ( $r = 0.81$ ,  $P < 0.05$ ).

Unlike in the 6-min narratives, the hippocampal patients retrieved marginally fewer accurate details overall than CON-2 (3.9 vs. 5.4 details per event,  $P = 0.06$ ). This finding appeared to depend on differences in how well the two groups remembered the more salient events that appear to the right in Fig. 4. To confirm this observation, events were divided into two groups: the five events best remembered by CON-1 and the five events least remembered. Whereas the scores of the hippocampal patients matched the scores of the CON-2 group for the least remembered events, the patients remembered the salient events

**Table 1. Total details**

Group	Accurate	Inaccurate	Unverifiable
CON-1	56 (5.3)	4 (1.1)	10 (4.5)
CON-2	32 (5.8)	4 (1.4)	7 (3.6)
H	26 (2.7)	10 (6.2)	5 (2.3)
MTL	18	8	5

Mean number of accurate, inaccurate, and unverifiable details produced by each group during a 6-min narrative description of the walk. SEs are in parentheses. CON-1, controls tested directly after the walk. CON-2, controls tested 1 mo after the walk. H, patients with hippocampal lesions. MTL, a patient with large medial temporal lobe lesions.



**Fig. 2.** Number of accurate details produced during a 6-min narrative description of events that occurred during a 25-min walk. (A) Details were assigned to one of four categories according to their content. (B) The number of details that were repeated during the narrative. CON-1, controls tested directly after the walk. CON-2, controls tested 1 mo after the walk. H, patients with hippocampal lesions. MTL, a patient with large medial temporal lobe lesions. Error bars show SEM.

less well than the CON-2 group [interaction of group by salience:  $F(1,9) = 9.4$ ,  $P < 0.05$ ].

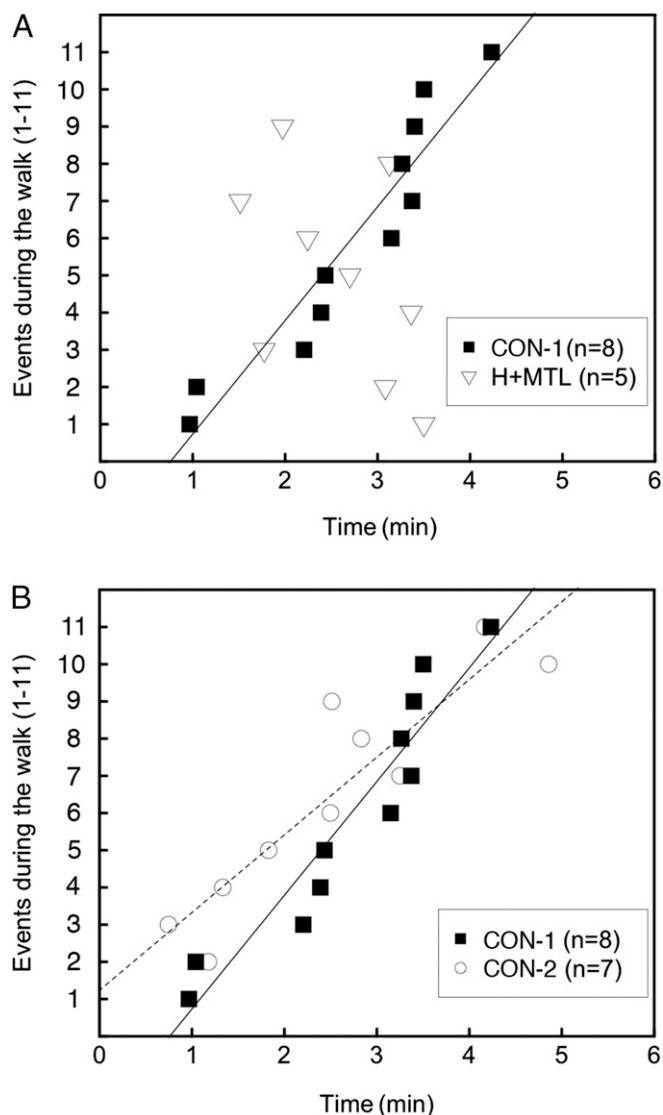
As with the 6-min narratives, we evaluated performance in each content category averaged across all events (event, space, and perception). (Time details were rare and were not counted;  $< 0.1$  detail per event in each group). The H group recalled fewer event and perception details than CON-1 [ $z(10) > 3.0$ ,  $P_s < 0.05$ ] and marginally fewer space details;  $P < 0.1$ . The CON-1 group produced an average of 2.9, 1.4, and 4.4 accurate details per event in the event, space, and perception categories, respectively. For the H group, the corresponding values were 1.4, 0.6, and 1.9 details, and for CON-2 the values were 1.6, 1.4, and 2.4 details. The H group scored 2.7, 1.2, and 1.3 SDs below the CON-1 mean in the event, space, and perception categories, respectively.

Hippocampal patients produced more inaccurate details than CON-1 [1.6 vs. 0.5 details per event;  $t(10) = 3.4$ ,  $P < 0.05$ ] and about the same number of inaccurate details as CON-2 (1.6 vs. 1.1 details per event;  $P > 0.1$ ). Participants reported few unverifiable details during the 1-min narratives (range of means across groups = 0.6–1.5 details per event; no between-group differences,  $P_s > 0.1$ ).

We also asked whether the patients had difficulty connecting remembered details to the appropriate events. That is, did patients mix details between events more frequently than controls? Accordingly, for the 1-min narratives we counted how often participants reported details about events other than the event being asked about. The hippocampal patients did this only rarely, numerically less often than the CON-1 group (0.2 times per event vs. 0.3 times per event).

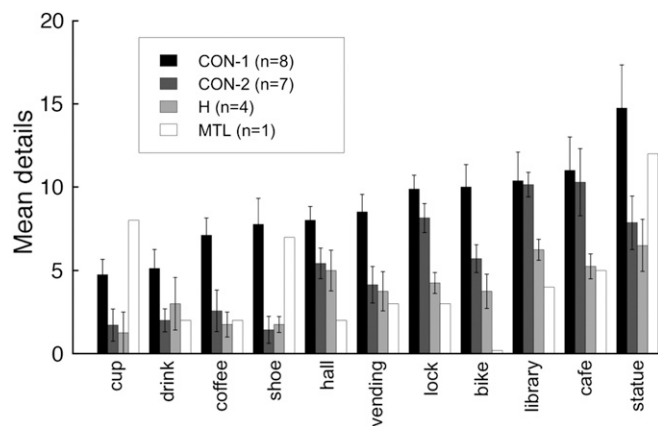
Performance of the patient with large MTL lesions was variable. Whereas he produced fewer details per event overall than CON-1 (4.4 vs. 8.8), he nevertheless did well describing three of the events (cup, shoe, and statue). However, he often appeared to remember only a fragment about an event and then generated a narrative consisting of plausible guesses and far-fetched comments (in reference to the statue: “It wasn’t a covered wagon”). In addition, his narratives included more than twice as many inaccurate details as the narratives of any other group (3.3 per event), he repeated himself frequently (Fig. 2B), and he frequently incorporated remarks about events other than the event he was asked about (four times more often than any other group).

**Two-Alternative, Forced-Choice Questions About the Walk.** Fig. 6 shows the results for the two-alternative, forced-choice test. Overall, patients with hippocampal lesions performed more



**Fig. 3.** The data points show when, on average, the events from the walk were described during the 6-min narratives. The two control groups tended to describe events in the order that they occurred. The order in which the patients described events was unrelated to the order in which the events occurred. Lines represent significant fits to the data. (A) The patients described only 9 of the 11 events, and no patient described events 10 and 11. Black squares: CON-1, controls tested directly after the walk. Open triangles: H, patients with hippocampal lesions plus MTL, a patient with large medial temporal lobe lesions. (B) CON-1 (black squares) together with controls tested 1 mo after the walk (CON-2, open circles). The CON-2 group described only 10 of the 11 events, and no CON-2 described event 1.

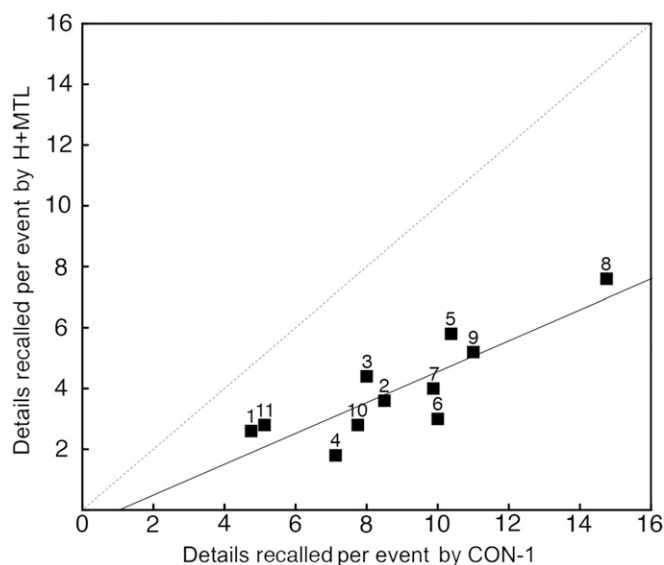
poorly than CON-1 [ $t(10) = 2.4, P < 0.05$ ] and performed similarly to CON-2 ( $P > 0.2$ ). The hippocampal patients performed poorly in all content categories. In the case of questions about time, the average score of the patients was good, but they did not score above chance levels (due to high variability). Their scores were 2.1, 1.4, and 2.5 SDs below the CON-1 mean for questions about events, space, and perception, respectively. Thus, although the hippocampal patients obtained a low score on questions about space, relative to CON-1 they performed no worse on questions about space than on other types of questions. It is also notable that the patient with large MTL lesions performed poorly overall, but did well on questions about space.



**Fig. 4.** Number of accurate details produced in 1-min narratives when participants were asked about each event separately in response to a prompt. The data are arranged according to how well the CON-1 group remembered each event. CON-1, controls tested directly after the walk. CON-2, controls tested 1 mo after the walk. H, patients with hippocampal lesions. MTL, a patient with large medial temporal lobe lesions. Error bars show SEM.

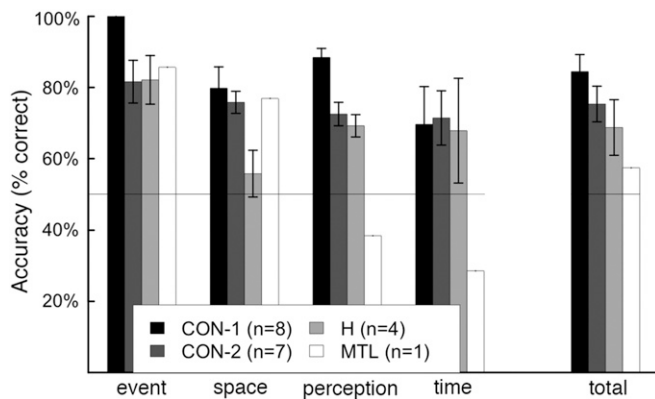
### Discussion

Patients with hippocampal damage remembered fewer details than controls about 11 events that occurred during a guided walk on the university campus. This impairment was evident in 6-min narratives that participants constructed about the walk, directly after returning to the laboratory (Fig. 2). Patients also recalled fewer details than controls in prompted 1-min narratives about each of the 11 events (Fig. 4), and they performed poorly on 40 two-alternative, forced-choice questions about specific details



**Fig. 5.** Details recalled during 1-min narratives about each event in response to a prompt (also see Fig. 4). The events best remembered by CON-1 were also the events best remembered by the H and MTL patients. The numbers identify each event (Fig. 1). The scatter plot shows the mean number of accurate details per event produced by the patients as a function of the mean number of details produced by the patients as a function of the mean number of details produced by CON-1. For example, CON-1 recalled 7.1 details about event 4 (coffee cart) and 10.4 details about event 5 (library). The patients recalled 1.8 and 6.2 details about these same two events. CON-1, controls tested directly after the walk. H, patients with hippocampal lesions. MTL, a patient with large medial temporal lobe lesions.





**Fig. 6.** Performance on a test of 40 two-alternative, forced-choice questions about the events from the walk. There were four types of questions, querying different types of information. CON-1, controls tested directly after the walk. CON-2, controls tested 1 mo after the walk. H, patients with hippocampal lesions. MTL, a patient with large medial temporal lobe lesions. Error bars show SEM. Horizontal line represents chance performance.

from the walk (Fig. 6). In many respects, performance of the patients resembled the performance of a group (CON-2) that was tested 1 mo after the walk. Thus, in their 6-min narratives, patients recalled about the same number of total details as the CON-2 group (Table 1), and they recalled a similar number of details in each content category (event, space, perception, and time) (Fig. 2). However, in one respect, patient performance differed sharply from the performance of either the CON-1 or CON-2 groups. Whereas both control groups tended to recall the events of the walk in the order that they occurred, the order in which patients recalled the events was unrelated to the order in which the events occurred (Fig. 3).

Despite their memory impairment, the patients did remember a significant number of event, space, and perception details in both the 6-min (Fig. 2) and 1-min narratives. These details had the characteristics of episodic recollections and included references to particular places and events. For example, G.W. remembered that the bicycle “had a light on the front.” L.J. remembered that the books in the library had been “further down on the shelf, and it seems like they were white.” In addition, the events that were most memorable for the controls were also most memorable for the patients (Fig. 5), suggesting that patients and controls experienced the salience of the events similarly.

The behavior of our patients was distinct from that observed with the densely amnesic patient K.C. (1) and others like him, who cannot remember any personal events (patient D.R.B. in 9, patient R.F.R. in 10, and patient G.T. in 11). If damage to the hippocampus were the cause of such a severe condition, then our patients’ narratives should have been devoid of episodic content, lacking specificity about the events of the walk. Their narratives,

to the extent they could remember, should have amounted to a collection of factual statements related to what was seen on the walk. However, the narratives produced by our patients contained vivid episodic content. Accordingly, our results are at odds with the idea that the hippocampus is specifically necessary for the episodic content of recollection (7). The difference between our patients and more severely impaired patients (e.g., K.C.) likely depends on differences in the locus and extent of their brain damage. Indeed, patient K.C. and all of the patients cited above have damage that extends beyond the MTL to involve other regions, especially in frontal and lateral temporal cortex (also see 2, 12).

The question arises whether the capacity for episodic recall reflects partially preserved hippocampal function in patients with a reduction in hippocampal volume averaging only 45%. This possibility seems unlikely for two reasons. First, even patient G.P., who has virtually no detectable hippocampus, was capable of some episodic recollection. Second, for two different patients, neurohistology revealed complete loss of hippocampal neurons despite only partial reduction in hippocampal volume (13). Thus, partial hippocampal volume loss in memory-impaired patients can reflect complete hippocampal dysfunction.

The impairment exhibited by the patients was evident to a similar degree in three of the four content categories: event, space, and perception (Fig. 2). Notably, patients exhibited no special difficulty in the production of spatial content, not in the 6-min narratives and not in the 1-min narratives. Indeed, every patient provided some accurate and specific spatial details. For example, K.E., when describing the student with the bike lock (event 6), accurately remembered: “he was walking west, and we were going east.” G.W. accurately reported that there were “muffins on the counter next to the bananas” (event 9). Even G.P., with large MTL lesions, accurately reported that the statue had been “8 to 10 feet high. . . water was coming out of the top.” In addition, on the 40-item test, the patients had no more difficulty, in comparison with CON-1, with the questions that asked about space than with questions about other features of the events (Fig. 6). Taken together, our results provide little support for the idea that the hippocampus has a special role in constructing spatial scenes or in recollecting spatial details from memory. We also inspected the spatial details produced by the patients in light of the distinction between allocentric (viewpoint-independent) information and egocentric (viewpoint-dependent) information. Although we found many details difficult to classify, both kinds of details were reported (for allocentric, see examples above; for egocentric, G.W. remembered: “I was. . . up ahead of her”).

The patients produced few intrusions from events other than the one being asked about during 1-min narratives. This observation suggests that the patients were able to organize the details from the walk into distinct coherent events. By contrast, they differed markedly from controls in that they did not (in the 6-min narratives) describe events in the same sequence in which they had occurred (Fig. 3A). Even controls tested after 1 mo still

**Table 2. Characteristics of memory-impaired patients**

Patient	Age, y	Education, y	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 below 50. IQ score for D.A. is from the Wechsler Adult Intelligence Scale-IV.

recalled events in approximately chronological order (Fig. 3B). Thus, difficulty with temporal order information was not a simple consequence of weak memory.

We suggest that the inability of the patients to remember the temporal sequence of the walk reflected their inability to bridge temporal gaps between discrete events. The same difficulty might explain why patients did poorly at remembering events 5, 6, and 9, which were salient but also extended in time. Specifically, the gaps between events would have challenged working memory capacity (14). For each event, working memory was engaged anew, overwriting any representation in working memory of the previous event and regardless of the temporal separation between the two events. Accordingly, it would have been difficult to link separate events, except by relying on long-term memory. The patients with hippocampal damage would have been disadvantaged because they could not have used long-term memory to learn about the order of events as they proceeded along the walk. Similar findings have been reported for rats with hippocampal lesions in a sequence-learning task (15).

Note that this finding is not evidence for a selective impairment in memory for temporal information. Rather, we suggest that patients would have been especially impaired on any test that assessed “global” information about the relationship between events (temporal, spatial, or perceptual relationships). In contrast, for tests that assess “local” information about individual events (and most of our tests did), the information could initially have been acquired within working memory. The information would then be available for transfer to long-term memory to the extent that long-term memory can be established after hippocampal damage. Importantly, as indicated in Figs. 2, 4, and 6, patients with hippocampal damage retain some ability to learn about events, locations, and other material.

In summary, patients with damage to the MTL learned and remembered fewer details about real-world events than controls when testing occurred directly after the events occurred. In many respects, the patients performed similarly to controls tested after a delay of 1 mo (Figs. 2 and 4). Despite their impairment, patients recalled many accurate and specific episodic details about events of the walk. They also remembered details from all content categories (Fig. 2), and there was no evidence of a special difficulty reporting spatial content about the events. By contrast, patients were strikingly deficient at remembering the temporal sequence in which events occurred during the walk (Fig. 3A). The latter result suggests that the hippocampus is particularly important for bridging gaps between events and discovering relationships between separate events (temporal, spatial, or perceptual).

## Materials and Methods

**Participants.** Five memory-impaired patients participated (Table 2), 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. 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 (13), 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 (16, 17). 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 (18). G.P. has an average bilateral reduction in hippocampal volume of 96%. The volume of the parahippocampal gyrus is reduced by 94%. Eight coronal magnetic resonance images from each patient, together with detailed description of the lesions, are presented elsewhere (19).

Two groups of healthy volunteers also participated. One group (CON-1) was tested directly after the walk ( $n = 8$ ; 1 female; mean age = 60.8 y; mean education = 13.8 y). The other group (CON-2) was tested 1 mo after the walk ( $n = 7$ ; 3 females; mean age = 64.1; mean education = 14.8 y). All procedures were approved by the Institutional Review Board at the University of California, San Diego, and participants gave written informed consent before participation.

**Procedure.** Each participant was taken for a 25-min walk on the campus of the University of California, San Diego. Before the walk, participants were told that their memory would be tested afterward for everything that occurred during the walk. However, they would not need to remember any part of conversations. A fixed order of 11 events occurred during the walks (Fig. 1). The experimenter was the “actor” for each event (she discarded the cup, found the book, etc.). The sixth event of the walk required a confederate, who provided a bike lock and asked that the experimenter lock his bike. The walks were scheduled at either 10:30 AM or 1:30 PM (not during class changes or lunch time) to standardize the background environment as much as possible.

Upon returning to the laboratory, patients and controls in the no-delay condition were tested for their memory of the walk. The procedure was identical for controls tested 1 mo later. Participants were first given up to 6 min to describe in as much detail as possible all that they could remember about the walk. The experimenter provided support during narrative construction by probing for detail (20, 21). Probes ranged from general (e.g., “Can you tell me any more details about what happened on the walk?”) to specific (e.g., “How close to the lock did you get?”; “Where was the water?”). The experimenter did not introduce information that had not been already provided by the participant.

Next, the experimenter provided a prompt for each of the 11 events of the walk (e.g., “What happened at the vending machine?”). In response to each prompt, participants were given up to 1 min to describe the event in as much detail as possible. The instructions emphasized that participants could repeat details they had already reported in the 6-min narrative.

Last, participants were asked 40 two-alternative, forced-choice questions about the 11 events of the walk. The questions followed the order in which the events had occurred. Before asking questions about a particular event, the event in question was first identified (e.g., The next few questions will be about the statue). Seven questions asked about the event itself (e.g., Did we find a quarter or a dime?). Thirteen questions asked for perceptual information (e.g., Were the doors to the building wooden or glass?). Thirteen questions asked for spatial information (e.g., What kind of vending machine was on the right: snack or drink?). Seven questions asked for temporal information (e.g., Did it take less than 30 s or more than 3 min to walk from the bike to the fountain?). All responses were recorded.

**Narrative Scoring.** Narratives were first partitioned into details as described previously (5, 21–24). Each detail was then scored as reflecting episodic memory, semantic memory, repetition, or remembered thoughts. Episodic details described aspects of specific events. Semantic details described facts that contextualized events. Participants produced few semantic details, perhaps because little context is needed when one describes recent events to someone who also experienced them. Mean semantic details (< 6.4 per group per narrative) were not considered further (e.g., “What’s the point of butterfly nets, because how often do you run into butterflies?”). Repetitions were details that repeated information from earlier in the narrative. Thoughts described introspective commentary (e.g., “I liked that place”) and were not analyzed further.

Next, following methods described in other studies (22–24), each episodic detail was categorized according to its content: event, space, time, or perception. Event details described persons or actions. Spatial details described places or spatial relationships between objects or persons. Time details described temporal information about an event (e.g., “It was real quick”). Perceptual details described objects, colors, weather, or other sensory information.

We then assessed the accuracy of each detail. Details were scored as “accurate” if they could be verified as having happened on the walk (e.g., “You found a quarter in the machine”). Details were scored as “inaccurate” if they did not happen on the walk [e.g., “We stopped at a Pepsi machine” (it was a snack machine)]. Details were scored as “unverifiable” if it was not

possible to determine their accuracy. The unverifiable details were usually unrelated to any of the 11 scheduled events and involved objects, actions, or pieces of conversation (e.g., "A girl walking on the path had red shoes").

A.D. partitioned the 6-min narratives into details and assigned them to content categories. A second person blind to group membership scored a randomly selected 32% of the data (two participants from each of the three groups, six participants total). Across participants and content ratings, the

correlation between scores was 0.92, and Cronbach's  $\alpha$  was 0.96. A.D. scored the 1-min narratives.

**ACKNOWLEDGMENTS.** We thank Ryan Ward and Christine Smith for assistance. This work was supported by the Medical Research Service of the Department of Veterans Affairs (CX-000359-05A1), and National Institute of Mental Health Grant 24600.

1. Tulving E (1985) Memory and consciousness. *Can Psychol* 26(1):1–12.
2. Rosenbaum RS, et al. (2005) The case of K.C.: Contributions of a memory-impaired person to memory theory. *Neuropsychologia* 43(7):989–1021.
3. Kopelman MD, Bright P (2012) On remembering and forgetting our autobiographical pasts: Retrograde amnesia and Andrew Mayes's contribution to neuropsychological method. *Neuropsychologia* 50(13):2961–2972.
4. Moscovitch M, Nadel L, Winocur G, Gilboa A, Rosenbaum RS (2006) The cognitive neuroscience of remote episodic, semantic and spatial memory. *Curr Opin Neurobiol* 16(2):179–190.
5. Bayley PJ, Hopkins RO, Squire LR (2003) Successful recollection of remote autobiographical memories by amnesic patients with medial temporal lobe lesions. *Neuron* 38(1):135–144.
6. Squire LR (1992) Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychol Rev* 99(2):195–231.
7. Winocur G, Moscovitch M (2011) Memory transformation and systems consolidation. *J Int Neuropsychol Soc* 17(5):766–780.
8. Mullally SL, Intraub H, Maguire EA (2012) Attenuated boundary extension produces a paradoxical memory advantage in amnesic patients. *Curr Biol* 22(4):261–268.
9. Damasio AR, Eslinger PJ, Damasio H, Van Hoesen GW, Cornell S (1985) Multimodal amnesic syndrome following bilateral temporal and basal forebrain damage. *Arch Neurol* 42(3):252–259.
10. Warrington EK, McCarthy RA (1988) The fractionation of retrograde amnesia. *Brain Cogn* 7(2):184–200.
11. Bayley PJ, Gold JJ, Hopkins RO, Squire LR (2005) The neuroanatomy of remote memory. *Neuron* 46(5):799–810.
12. McCarthy RA, Kopelman MD, Warrington EK (2005) Remembering and forgetting of semantic knowledge in amnesia: A 16-year follow-up investigation of RFR. *Neuropsychologia* 43(3):356–372.
13. Rempel-Clover NL, Zola SM, Squire LR, Amaral DG (1996) Three cases of enduring memory impairment after bilateral damage limited to the hippocampal formation. *J Neurosci* 16(16):5233–5255.
14. Jeneson A, Squire LR (2011) Working memory, long-term memory, and medial temporal lobe function. *Learn Mem* 19(1):15–25.
15. Fortin NJ, Agster KL, Eichenbaum HB (2002) Critical role of the hippocampus in memory for sequences of events. *Nat Neurosci* 5(5):458–462.
16. Insausti R, et al. (1998) MR volumetric analysis of the human entorhinal, perirhinal, and temporopolar cortices. *AJNR Am J Neuroradiol* 19(4):659–671.
17. Frankó E, Insausti AM, Artacho-Pérola E, Insausti R, Chavoix C (2014) Identification of the human medial temporal lobe regions on magnetic resonance images. *Hum Brain Mapp* 35(1):248–256.
18. Bayley PJ, Frascino JC, Squire LR (2005) Robust habit learning in the absence of awareness and independent of the medial temporal lobe. *Nature* 436(7050):550–553.
19. Knutson AR, Hopkins RO, Squire LR (2013) A pencil rescues impaired performance on a visual discrimination task in patients with medial temporal lobe lesions. *Learn Mem* 20(11):607–610.
20. Kirwan CB, Bayley PJ, Galván VV, Squire LR (2008) Detailed recollection of remote autobiographical memory after damage to the medial temporal lobe. *Proc Natl Acad Sci USA* 105(7):2676–2680.
21. Levine B, Svoboda E, Hay JF, Winocur G, Moscovitch M (2002) Aging and autobiographical memory: Dissociating episodic from semantic retrieval. *Psychol Aging* 17(4):677–689.
22. Hassabis D, Kumaran D, Vann SD, Maguire EA (2007) Patients with hippocampal amnesia cannot imagine new experiences. *Proc Natl Acad Sci USA* 104(5):1726–1731.
23. Race E, Keane MM, Verfaellie M (2011) Medial temporal lobe damage causes deficits in episodic memory and episodic future thinking not attributable to deficits in narrative construction. *J Neurosci* 31(28):10262–10269.
24. Dede AJO, Wixted J, Hopkins RO, Squire LR (2016) Autobiographical memory, future imagining, and the medial temporal lobe. *Proc Natl Acad Sci USA* 113:13474–13479.