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# The Temporal Unraveling of Autobiographical Memory Narratives in Patients With Temporal Lobe Epilepsy or Excisions

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**ABSTRACT: Medial temporal lobe epilepsy (TLE), a condition known to affect the integrity and function of medial temporal lobe structures such as the hippocampus, has been shown to disrupt memory for real-life episodes. Here, patients with unilateral TLE, patients who received a unilateral temporal lobe resection to cure TLE, and healthy controls produced free narratives of autobiographical memories (AMs). To assess *temporal resolution*, narratives were segmented into bits of information, or details, which were classified according to how precisely they could be located within the time course of the AM. Categories included details corresponding to the entire AM, to parts or subevents within the AM, and to actions taking place within seconds to minutes. The number of details per category was tallied and compared between patients and controls. *Temporal order* was assessed by determining the correct (internally consistent) chronological order of the sequence of events within the narrative. Results indicate that while patients' memory for the parts or subevents of personal episodes was intact, as was their temporal order, their memory for the minute-by-minute unraveling of the episode was impaired. We believe this loss of temporally specific details may contribute to the reduced vividness of AM recollection in TLE patients. Our findings provide further evidence that patients with hippocampal damage retrieve *skeletal* AMs for which the gist of the memory is maintained, but the specific details are lost. © 2010 Wiley-Liss, Inc.**

**KEY WORDS: hippocampus; autonoetic consciousness; episodic memory; temporal sequences; temporal resolution**

## INTRODUCTION

Medial temporal lobe structures, such as the hippocampus, are known to play a lasting role in autobiographical memory (AM) (Scoville and Milner, 1957; Maguire, 2001). In patients with hippocampal damage, the recollection of personal episodes is impaired (Vargha-Khadem et al., 1997; Kopelman et al., 1999; Viskontas et al., 2000; Kirwan et al., 2008), and the effective connectivity between the hippocampus and other brain structures that form an AM retrieval network is much reduced during AM retrieval (Maguire et al., 2001; Addis et al., 2007a). In this article, we examine temporal coherence among the elements of the memory to gain a fuller appreciation of the nature of the recollection deficit in patients with MTL damage.

Cumulative evidence indicates that hippocampal damage leads to an AM deficit best characterized by a loss of detail. When producing free narratives of personal episodes, patients with hippocampal damage report fewer narrative elements that depict the event, in comparison to healthy controls (Steinvorth et al., 2005; Rosenbaum et al., 2005, 2008; Addis et al., 2007a). Patients' subjective memory reexperiencing of the event is also less vivid (Noulhiane et al., 2008). In a previous analysis (St-Laurent et al., 2009), we showed how patients with unilateral medial temporal lobe epilepsy (TLE), who have hippocampal damage (either on the left or on the right), produce narratives that are especially impoverished in perceptual elements. Although our patients were unimpaired at describing what took place over the course of the event, they failed to report multisensory details (e.g., sounds, smells, physical attributes of the environment, location of objects and people in relation to them, etc.) that allow the rich, life-like reexperiencing of the memory. A reduction in the number of details and overall spatial coherence has also been observed in descriptions of imaginary scenes that likely were never experienced in patients with hippocampal amnesia (Hassabis and Maguire, 2007; Hassabis et al., 2007). These data suggest that hippocampal damage leads to an impaired capacity to integrate visuospatial information into complex, coherent constructs. This deficit seems to be the result of a diminished capacity to retain and conjure up vivid details, paired with an impaired capacity to organize these details together into a coherent scene or construct (Rosenbaum et al., 2009).

Although we know that hippocampal damage disrupts the spatial and perceptual properties of AM, less is known about the impact of hippocampal damage on the temporal aspects of AM. Hassabis and Maguire (2007) have coined the terms *microtime* and *macrotime* to refer to two different timescales relevant to AM. Whether the hippocampus plays a role in AM's macrotime, the temporal location of the memory along one's life time line, is debated (Moscovitch et al., 2005; Hassabis and Maguire, 2007; Kirwan et al., 2008). In a previous analysis (St-Laurent et al., 2009),

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we compared the memory for personal events with specific macrotime (single, unique AMs), to memory for events with fuzzier macrotime (generic personal events that repeated themselves on several occasions). Both AMs types showed an identical pattern of deficit in patients with hippocampal damage, suggesting that the hippocampus is not sensitive to the specificity with which AM is located along a macrotime line. In comparison, the goal of the current analysis was to assess whether the hippocampus is sensitive to AM's microtime, the minute-by-minute unraveling of an event. Microtime is considered an intrinsic property of the event, as it allows the different memory elements to be replayed in a chronological order (Eichenbaum, 2004; Hassabis and Maguire, 2007). We assessed whether damage to the hippocampus affects how AM details are organized along the time line of the event itself.

We reanalyzed AM narratives collected in patients with unilateral medial temporal lobe epilepsy or excisions (together referred to as TLE) and age- and education-matched healthy controls (St-Laurent et al., 2009). These narratives were collected following the guidelines of Levine et al. (2002)'s Autobiographical Interview (AI). With the current analysis, we assessed whether the specificity with which AM details could be located within the time course of the AM, what we call *temporal resolution*, determines their vulnerability to MTL damage. We developed a scoring system categorizing AM details according to their temporal resolution. The memory elements that took place at a very specific time during the AM (e.g., my father sneezed twice as he entered the room), the memory elements that stretched over a longer time period (e.g., we had dinner, then we talked for a while), and the memory elements that applied to the entire duration of the event (e.g., it was in Florida) were tallied, and the number of details recalled by TLE patients was compared with those recalled by healthy matched controls.

One of our aims was to determine whether MTL damage reduces the temporal fine-grain of AM, by affecting details of high temporal resolution disproportionately from details of lower resolution. Because details of high temporal resolution are concrete and specific, they are likely to contribute to the vivid reexperiencing of AM in one's mind's eye. With this analysis, we assessed whether a loss of temporal resolution is among the factors contributing to the loss of AM vividness observed in TLE patients (Steinvorth et al., 2005; Rosenbaum et al., 2005, 2008; Addis et al., 2007a), along with the documented loss of perceptual details.

Our second goal was to determine whether MTL damage disrupts the temporal order in which AM details are recollected. The literature suggests that the hippocampus may play a role in memory for sequential information. For example, rats with hippocampal lesions fail to discriminate between different locations based on the relative order in which they were visited (Chiba et al., 1994). Electrophysiological evidence also reveals that rat hippocampal place cells' activity reflects the sequential order in which they fire when the animal runs through their place fields in a learned environment, a sequential replay that can be observed, both in the awake and sleep state (Foster and Wilson, 2006, 2007; Ji and Wilson, 2007).

In humans, McAndrews and Milner (1991) showed that patients with unilateral temporal lobe excisions are unimpaired at making relative recency decisions about sequentially presented objects, although portions of the hippocampus were resected only in half the patients. However, Hopkins et al. (2004) reported that patients with hypoxic hippocampal lesions are impaired at learning sequences of spatial locations. Also, neuroimaging evidence indicates that the hippocampus is activated by the detection of sequence violations and during the encoding of overlapping sequences of face stimuli (Kumaran and Maguire, 2006a,b).

In the context of AM, functional neuroimaging reveals how the hippocampus is activated when people make judgments about the temporal order in which they took photographs when these were taken within a short, but not within a longer time interval from one another (St Jacques et al., 2008). A recent study by Thaiss and Petrides (2008) has also demonstrated that, in comparison to healthy controls, unilateral TLE patients are impaired at ordering events in time during the free recall of week-old AMs; patients also used temporal organization strategies less spontaneously than healthy controls. Taken together, evidence suggests that information about the temporal structure of AM is supported by the medial temporal lobe, especially the hippocampus.

For the current study, we assessed whether each of the AM's details were narrated in their chronological order. The number of breaks in chronology was tallied and compared between TLE patients and their controls in a manner analogous to the Thaiss and Petrides (2008) study. An external rater also rated the *temporal coherence* of AM on a four-point scale. High ratings were given to narratives with a clear beginning and end, which progressed smoothly while respecting chronology and were rich in details located specifically along the AM's time line. Based on the literature, we expected to observe more breaks in chronology and lower temporal coherence ratings in TLE patients in comparison to controls.

Finally, participants were tested on a script generation task adapted from Godbout and Doyon (1995), for which they listed actions that people usually perform over the course of familiar activities, in the order in which these actions usually take place. Results for the script task have been reported elsewhere (St-Laurent et al., 2009). We used this task to assess whether temporal organization was respected when our participants narrated well-learned events that were neither episodic nor autobiographical.

## MATERIALS AND METHODS

### Participants

The controls and patients whose data are reported here have been described previously by St-Laurent et al. (2009). Participants were recruited and tested according to a protocol approved by Toronto's University Health Network (UHN)

*TABLE 1.*

*Demographic and Neuropsychological Characteristics of Control, LTLE, and RTLE Participants*

| | Control, ($n$ = 20) | LTLE, ($n$ = 14) | RTLE, ($n$ = 11) |
|---|---|---|---|
| Mean age in years (SD) | 39.15 (8.70) | 43.79 (6.97) | 37.00 (8.06) |
| Gender: male/female | 9/11 | 3/11 | 5/6 |
| Years of education (SD) | 16.15 (2.66) | 14.93 (3.27) | 15.36 (3.72) |
| Surgical status: presurgery/postsurgery | N/A | 10/4 | 6/5 |
| Handedness: right/left | N/A | 9/5 | 11/0 |
| Language representation: left/right[a] | N/A | 11/3 | 11/0 |
| Mean WASI full-scale IQ (SD) | N/A | 95.79 (10.97) | 96.91 (13.58) |
| RAVLT: Mean standardized total recall score (SD)[b] | N/A | −0.19 (0.91) | 0.16 (0.75) |
| RVDLT: Mean standardized total recall score (SD)[c] | N/A | −2.00 (1.67) | −2.87 (1.46) |

[a]Nondominant hemispheric language representation was determined with fMRI or a WADA test.
[b]Raw scores were converted into $z$ scores based on norms from Selnes et al. (1991).
[c]Raw scores were converted into $z$ scores based on norms from Strauss and Spreen (1991).
IQ, intellectual quotient; L, left; N/A, not applicable; R, right; RAVTL, Rey Auditory Verbal Learning Test; RVDLT, Rey Visual Design Learning Test; SD, standard deviation; TLE, temporal lobe epilepsy or excisions; WASI, Wechsler Abbreviated Scale of Intelligence (1999).

Research Ethics Board. Table 1 contains the demographic information about the participants and standardized neuropsychological test scores for the patients. All participants were fluent or native English speakers.

TLE patients were recruited through the Epilepsy Program of Toronto Western Hospital. All patients were diagnosed with epilepsy from unilateral hippocampal origin, except for one presurgical patient with right TLE (RTLE) in whom an independent left temporal focus was also observed, even though the majority of his seizures originated from the right hemisphere. This participant's performance was indistinguishable from other TLE patients, so we elected to include him. The temporal lobe excision consisted in the removal of the amygdala, of 2–4 cm from the hippocampus and parahippocampal gyrus and of 4–6 cm along the lateral convexity of the middle, inferior, and fusiform gyri of the temporal lobe.

All of the patients who had undergone surgery were seizure-free postoperatively, except for one RTLE patient whose ablated epileptogenic cyst had regrown since his surgery. Three left TLE (LTLE) patients (two presurgery, one postsurgery) had a small lesion in their occipital cortex. Other patients showed no damage to portions of the brain other than the medial temporal area that was unrelated to either seizure activity or to a temporal lobe excision. In neurologically intact adults, the right hippocampus is slightly larger than the left (Pruessner et al., 2001; Kallai et al., 2005; Tanskanen et al., 2005). This hippocampal asymmetry, as assessed with a composite measure of hippocampal width, was significantly exaggerated in our presurgery LTLE patients and significantly reduced in our presurgery RTLE patients in comparison to a group of healthy controls (St-Laurent et al., 2009). This result indicates a pattern of hippocampal atrophy, an indicator of medial temporal sclerosis, which is consistent with seizure lateralization in our presurgery patients.

Healthy controls were recruited among staff members at the Toronto Western Hospital and through online and newspaper advertisement. Exclusion criteria consisted of a history of neurological (tumor, epilepsy, concussion, cyst, meningitis, stroke, congenital disease) or psychiatric (depression, schizophrenia) disorder. Controls were matched to patients for age, gender, and years of education.

## Task Administration

The task administration has been described previously by St-Laurent et al. (2009) and was adapted from Levine et al.'s (2002) AI. Briefly, participants retrieved two AMs for single, unique episodes (event-specific AMs), and two AMs for episodes that repeated themselves at least ten times (generic AMs); event-specific and generic AMs were collected in an ABBA, BAAB fashion. Generic AMs were not included in the current analysis because they were deemed inadequate for our purpose. Highly temporally specific memory elements, such as details of conversations and sequences of actions, are unlikely to be repeated across repeated instances of an event. Thus, by their very nature, generic AMs would lack the temporal resolution necessary to address our research question.

For the event-specific AM condition, the participants selected a personal event that lasted from a few minutes to a few hours, and which took place at least a year ago, but no more than 10 years ago. The experimenter verified that the AM fit the study's criteria, and the participants were instructed to narrate the AM in as much detail as they could retrieve. When the narration came to a natural end, participants were probed to report additional details in a nonspecific manner (e.g., "Is there anything else you can tell me about this event?"). The task ended when probing failed to elicit further details. After each AM was narrated in this manner, a semistructured interview covering different aspects of the event was also administered (Levine et al.,

2002), but these data were not included in the current analysis. Participants' narratives were audio-taped.

## Task Scoring

Audiotaped memory narratives were transcribed into word documents by an external person and were made anonymous by MPM. MSTL, who also conducted the interviews, separated the AMs into details. Out of the 90 transcripts included in the dataset (two transcripts for each of the 45 participants), 31 were scored by MT (15 controls, 11 LTLE, 5 RTLE), 29 were scored by MSL (14 controls, 7 LTLE, 8 RTLE), and 30 were scored by both MT and MSL (11 controls, 10 LTLE, 9 RTLE). The dataset presented in the results sections includes 29 protocols scored by MSL and 61 protocols scored by MT; MT was blind to the identity of the participants (controls or patients). To assess interrater reliability, intraclass correlations (two-way mixed-effects model; McGraw and Wong, 1996) were also conducted on the 30 protocols scored by both scorers. These correlations are reported in the Results section.

During scoring, details were classified either as internal or external, according to a definition introduced by Levine et al. (2002). Internal details reflected information that pertained to the main event described, such as the people present, the events that took place over the course of the episode, the physical setting and other perceptual elements associated with the event, the time and location at which the episode took place, the different thoughts and emotions experienced by the narrator over the course of the event, etc. External details, by comparison, reflected information that did not pertain directly to the narrated event, such as general knowledge or long-standing opinions, information about an unrelated episode, or reflections about the event (e.g., "now that I think about it, it was rather silly of me to say that.") The repetition of internal information was also considered external. Table 2 includes examples of details from each category.

Results of a previous analysis performed on this dataset, for which AM details were also classified as internal or external, have been reported elsewhere. Because of our emphasis on the narration of the actions and events that took place during the AM, we elected to resegment the memories into larger details. For example, in the previous analysis, a detail was counted for each piece of perceptual information (e.g., I saw a large, black, furry dog = three details). Here, perceptual information that pertained to the same object was considered a single detail if it was acquired simultaneously (e.g., I saw a large, black, furry dog = one detail). A slightly coarser segmentation accounts for the discrepancies between the absolute number of internal and external details reported here, and those reported by St-Laurent et al. (2009).

Internal details were further differentiated between temporally precise and temporally indefinite details. Temporally precise details were bits of information reflecting events that took place at a specific moment within the time course of the narrated episode. For example, if a participant described a wedding reception, the arrival of the groom and bride, the toast, the dinner, and the dance would each be categorized as temporally precise details. On the other hand, temporally indefinite details reflected bits of information that pertained to the entire duration of the episode. The geographical location, the date, the people present, and the physical attribute of the room in which the episode took place are examples of temporally indefinite internal details (see Table 2). Note that context could sometimes determine whether a detail (e.g., "We went to my favorite restaurant") was coded as temporally indefinite (e.g., if the entire event took place at that restaurant) or temporally precise (e.g., if the event was an evening where people went for dinner, then went to the movie, etc).

*TABLE 2.*

*Examples From Each Scoring Category*

| Category | Example |
|---|---|
| **INTERNAL** | |
| **Temporally precise** | |
| Higher order | We went to the gym first |
| | She talked to us for a while |
| | We drove there |
| | I cleaned up the kitchen |
| Clustered | We heard the thunder |
| | She told him she didn't care |
| | Laurie pinched my arm |
| | I replaced it on the Shelf |
| **Temporally indefinite** | |
| | It was a Wednesday |
| | We were at a bar on St-Denis |
| | I remember feeling sick that day |
| | He was wearing that shirt I like |
| **EXTERNAL** | |
| **Other** | I forget how we got there |
| | That's my mother's name |
| | I just love orange Pekoe, you know? |
| | I guess I shouldn't have done that |

Temporally precise details were further categorized into higher order and clustered details, depending on their level of temporal resolution. Higher order details reflect the gist of the event: they correspond to the major parts, or subepisodes, of the main episode. Higher order details are abstract: they are not easily visualized, and they do not correspond to concrete, specific actions. Instead, it is assumed that a series of concrete actions take place within each of these subepisodes. For example, if the main episode was a wedding reception, "we had dinner" would be a higher order detail. It is assumed that people found their seats, sat down, ate different courses, drank, and had conversation over the course of "dinner" (see Table 2).

On the other hand, clustered details reflect concrete, specific actions that can be easily visualized. They tend to organize into clusters, which are cohesive sequences of short-lasting events rapidly succeeding each other in time. Details are considered parts of a cluster if they take place within seconds to minutes following the previous detail from that cluster. The best example of a cluster is the detailed reiteration of a conversation.

(e.g., "She said, "you look awful!," to which I answered, "so do you!" We just started to laugh."). By definition, clustered details are always preceded by a higher order detail, which sets the context of the cluster (e.g., "We spent a day at the beach (HO). We arrived there (C), parked the car (C), picked up our things (C), and headed straight for the changing rooms (C) while my parents carried the picnic (C)"). Thus, the very first detail of a cluster is always categorized as a higher order detail. For each narrative, the number of clusters was tallied, and the mean cluster size, or the mean number of clustered details per cluster, was also calculated.

If a higher order detail was not narrated in the order in which it took place over the course of the event, it was considered a sequencing error. A sequencing error was tallied if the last temporal detail narrated *before* a higher order detail had clearly taken place *after* the higher order detail within the time course of the episode (e.g., "This guy was bleeding on the floor (HO), and the bouncers were just standing there laughing (HO). And I remember the ambulance people would not come into the bar (HO). So yeah, one of the bouncers called an ambulance (HO, Sequ. Err.)."). Also, a sequencing error was counted whenever it could not be implied from the narrative that the last temporal detail narrated before a higher order detail had taken place before the higher order detail over the time course of the episode (e.g., "I danced with my husband at some point (HO). What else happened? (External) Oh, I danced with my nephews and nieces (HO, Sequ. Err.). And they served that weird dessert I didn't really like (HO, Sequ. Err.). That's all I can remember (External)."). Sequencing errors were also tallied for clustered details. If two details were considered to have happened simultaneously, no error was counted (e.g., "I walk into the living room (HO), my daughter is holding the cat (C) while the dog is barking at them (C), jumping up and down (C)." An error was only counted if a clustered detail was preceded in the narration by another clustered detail that had clearly taken place later within the time course of the episode.

### Temporal Coherence Ratings

We wanted to assess the overall impression of coherence and temporal organization given by narratives produced by patients and controls. An external rater blind to the identity of the participants rated the memory narratives for their temporal coherence, on a scale of 0–3. A score of "0" was given to narratives with very few internal details or to narratives for which most of the internal details could not be located within the time frame of the narrative. A score of "1" was given to narratives for which there was a beginning and an end, but for which most of the internal details were not specific in time or were not narrated in the order in which they took place. A score of "2" was given to narratives for which most details could be located within the time course of the event, but for which the narration was slightly patchy, jumping in time from one event to the next without continuity. Finally, a score of "3" was given to highly structured narratives for which most details could be clearly located within the time course of the event, and which described the event from beginning to end without missing any parts, giving a clear sense of continuity. Examples of AMs rated as 0, 1, 2, and 3 are available online in the supplementary materials section.

### Script Generation

The script generation task administered here, which was adapted from Godbout and Doyon (1995), has been described elsewhere (St-Laurent et al., 2009). Participants were tested on this task after completing the AI. Our goal was to assess patients' semantic memory retrieval, narrative skills, and verbal fluency, with a task that was not autobiographical.

Participants were requested to list as many actions as they could think of that people generally carried out during the course of the four familiar activities (eating at a restaurant, washing dishes, shopping for groceries, and washing clothes—in a randomized order), in the order in which these actions took place. Participants were told that enumerating between 10 and 20 actions was adequate, but they were not bound to that range. There was no time limit. All responses were audio-taped and transcribed by an external typist.

The total number of actions was tabulated per script, and as a total score per participant. Sequencing errors (action not reported in the order in which it usually occurs during the activity), irrelevant intrusions (action that did not belong to the script), and perseveration errors (action repeated within the script) (Godbout and Doyon, 1995) were also tabulated. Perseveration errors were not counted as actions.

## RESULTS

### Script Generation

Three control participants were not tested on this task because of lack of time. Results for the script generation task have been reported elsewhere in more detail (St-Laurent et al., 2009). Briefly, the LTLE, RTLE, and control groups did not differ in terms of number of actions reported (one-way ANOVA: $F_{(2,\ 39)} = 1.797$, $P = 0.179$; partial $\text{Eta}^2 = 0.084$). Also, a series of one-way ANOVAs indicated that the two patient groups did not differ from the controls in terms of sequencing errors ($F_{(2,\ 39)} = 1.491$, $P = 0.238$), intrusions ($F_{(2,\ 39)} = 1.468$, $P = 0.243$), and perseveration errors ($F_{(2,\ 39)} = 1.395$, $P = 0.260$). Thus, patients' narration of familiar scripts were as well structured as those of controls, with all groups making very few errors (see Table 3).

### Interrater Reliability

Intraclass correlations for single measures (two-way mixed model; McGraw and Wong, 1996) were calculated between scores obtained by the two scorers for each detail category on

*TABLE 3.*

*Performance on the Script Generation Task*

| | CTL | LTLE | RTLE |
|---|---|---|---|
| | | Mean (SD) | |
| Numbers of actions | 19.75 (6.59) | 18.80 (6.89) | 15.39 (3.57) |
| Sequencing errors | 0.82 (0.78) | 1.09 (0.86) | 0.57 (0.53) |
| Perseveration errors | 1.43 (1.36) | 2.25 (1.97) | 1.45 (0.78) |
| Intrusions | 0.12 (0.22) | 0.38 (0.62) | 0.28 (0.34) |

30 memory narratives. Coefficients for each detail category are reported in Table 4.

## Internal and External Details

An analysis of the number of internal and external details performed on this dataset has been reported previously (St-Laurent et al., 2009). While the absolute number of internal and external details reported here are lower than those reported in the previous analysis, the pattern of results is unchanged. Figure 1 (top) illustrates the number of internal and external details tallied for the controls and TLE patients (left and right). A two-way ANOVA with repeated measures over detail categories (internal vs. external details) revealed a significant main effect of detail category ($F_{(1,\ 43)} = 38.595$, $P < 0.001$). A post hoc paired-sample *t*-test revealed that participants reported significantly fewer external details than internal details ($t_{(44)} = 5.669$, $P < 0.001$). We also observed a significant main effect of group ($F_{(1,\ 43)} = 4.535$, $P < 0.05$), and a significant group × detail category interaction effect ($F_{(1,\ 43)} = 5.940$, $P < 0.05$). Follow-up independent sample *t*-tests revealed that TLE patients reported significantly fewer internal details than did controls ($t_{(43)} = 2.485$, $P < 0.05$), while they did not differ from controls for external details ($t_{(43)} = 0.923$, $P = 0.361$). The left and right TLE patient groups did not differ significantly from each other for internal details ($t_{(23)} = 0.316$, $P = 0.754$), and neither did the pre and postsurgery patients ($t_{(23)} = 0.834$, $P = 0.413$).

*TABLE 4.*

*Interrater Reliability: Intraclass Correlation Coefficients*

| Details category | Coeff. |
|---|---|
| Internal | 0.986 |
| Temp. indefinite | 0.918 |
| Temp. precise | 0.978 |
| Higher order | 0.807 |
| Clustered | 0.831 |
| Numb. clusters | 0.754 |
| Mean cluster size | 0.795 |
| External | 0.953 |
| Repetition | 0.918 |
| Other | 0.962 |

Note: Intraclass correlation coefficients are calculated between the main scorer's (MT) and the external scorer's (MSL) ratings.
Coeff. = Coefficient; Numb. = Number of, Temp. = Temporal.

## Temporally Precise and Temporally Indefinite Details

Figure 1 (middle) illustrates the number of temporally precise and temporally indefinite details tallied for the controls and TLE patients (left and right). A two-way ANOVA with repeated measure over detail type (temporally precise and temporally indefinite details) revealed a significant main effect from the detail category ($F_{(1,\ 43)} = 36.277$, $P < 0.001$). Paired-

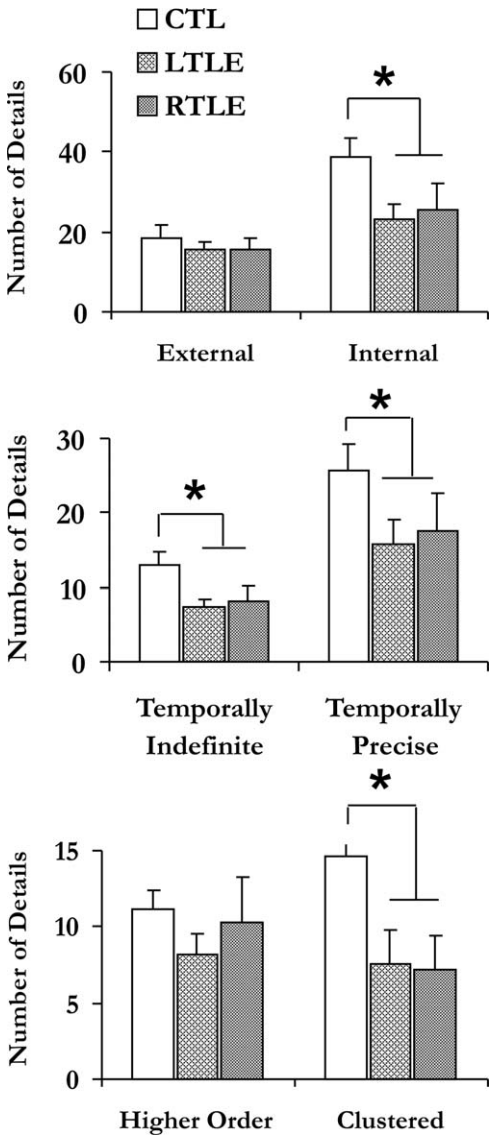


**FIGURE 1. Mean number of details per category for the controls and the two patient groups. Top: Internal and external details; Middle: temporally precise and temporally indefinite details; Bottom: higher order and clustered details. Details are averaged over two AMs for each participant. The bars indicate the standard error of the mean for each group. Significant differences from the control group are indicated by an asterisk. Note: *$P < 0.05$.**

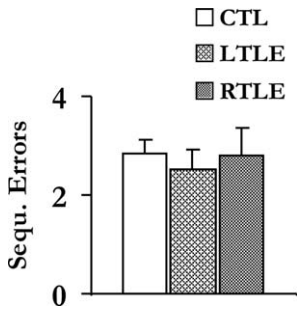


**FIGURE 2. Sequential errors. Mean number of higher order details that were not narrated in a chronological order for the controls and the two patient groups. Errors are averaged over two AMs for each participant. The bars indicate the standard error of the mean for each group. There was no significant group difference in the number of sequential errors committed.**

sample *t*-tests revealed that participants reported significantly fewer temporally indefinite details in comparison to temporally precise details ($t_{(44)} = 5.915$, $P < 0.001$). We also observed a significant main effect of group ($F_{(1, 43)} = 6.174$, $P < 0.05$). The group × details category interaction effect was not significant ($F_{(1, 43)} = 1.282$, $P = 0.264$). Follow-up independent sample *t*-tests revealed that controls reported significantly more temporally precise ($t_{(43)} = 2.102$, $P < 0.05$) and temporally indefinite ($t_{(43)} = 2.575$, $P < 0.05$) details than do TLE patients. That is, patients reported fewer actions and events that took place at a specific time within the AM, but they also reported fewer details that pertained to the entire duration of the event. The left and right TLE patient groups did not differ significantly from one another for the number of temporally precise ($t_{(23)} = 0.295$, $P = 0.771$) and temporally indefinite ($t_{(23)} = 0.266$, $P = 0.793$) details. Also, there was no significant difference between the pre and postsurgery patients for the number of temporally precise ($t_{(23)} = 0.740$, $P = 0.467$) and temporally indefinite ($t_{(23)} = 0.801$, $P = 0.431$) details produced.

## Higher Order and Clustered Details

Figure 1 (bottom) illustrates the number of higher order and clustered details tallied for the controls and TLE patients (left and right). A two-way ANOVA with repeated measure over detail category (higher order and clustered details) revealed a significant main effect of group ($F_{(1, 43)} = 4.420$, $P < 0.05$) and a significant group × detail category interaction effect ($F_{(1, 43)} = 4.380$, $P < 0.05$). The main effect of detail category was not significant ($F_{(1, 43)} = 0.547$, $P = 0.463$). Post hoc independent sample *t*-tests revealed that patients reported fewer clustered details than do controls ($t_{(43)} = 2.457$, $P < 0.05$); however, the two groups did not differ significantly for the number of higher order details ($t_{(43)} = 1.005$, $P = 0.321$). In other words, patients' reduction in clustered details accounts for their reduction in temporally precise details. The left and right TLE patient groups did not differ significantly from one another for the number of clustered details ($t_{(23)} = 0.121$, $P = 0.905$), and neither did the pre and postsurgery patients ($t_{(23)} = 0.698$, $P = 0.492$).

## Sequencing Errors

Figure 2 illustrates the mean number of higher order details for which a sequencing error was committed for the patient and control groups. A higher order sequencing error was counted whenever a higher order detail was not narrated in the order in which it took place within the time course of an event. An independent sample *t*-test failed to reveal a significant difference in higher order sequencing errors between the patients and controls ($t_{(43)} = 0.386$, $P = 0.702$). For clustered details, sequencing errors were also tallied when details were not narrated in order, but so few errors were committed that no further analyses were conducted; one control participant committed one error for each of the two AM, and another control participant committed one error on a single AM).

## Number of Clusters and Mean Cluster Size

The number of cohesive series of clustered details, or clusters, was tallied per participant. Figure 3 illustrates the mean number of clusters (left), and the mean cluster size (mean number of details per cluster; right) for the controls and patients. Independent sample *t*-tests failed to reveal a significant difference in the number of clusters produced by patients and controls ($t_{(43)} = 1.429$, $P = 0.160$), but indicated how patients' mean cluster size was significantly lower than that of controls ($t_{(43)} = 2.972$, $P < 0.01$). An analysis of covariance (ANCOVA) comparing patients and controls for mean cluster size, and using the number of external details as a covariate, was also significant ($F_{(1, 42)} = 8.090$, $P < 0.01$), ruling out a possible concern that the group difference was accounted for by a systematic difference in verbal output between the two groups. The left and right TLE patients did not differ significantly from one another in terms of mean cluster size ($t_{(23)} = 0.544$, $P = 0.592$), and neither did the pre and postsurgery patients ($t_{(23)} = 1.519$, $P = 0.143$).

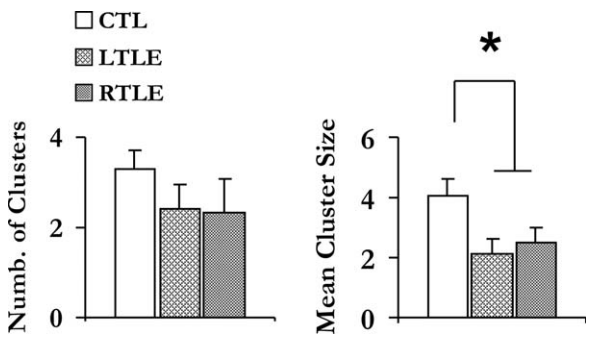


**FIGURE 3. Left: mean number of clusters per AM, for the controls and the two patient groups. Right: mean cluster size (mean number of clustered details per AM) for the controls and the two patient groups. The bars indicate the standard error of the mean for each group. Significant differences from the control group are indicated by an asterisk. Note: *$P < 0.05$.**

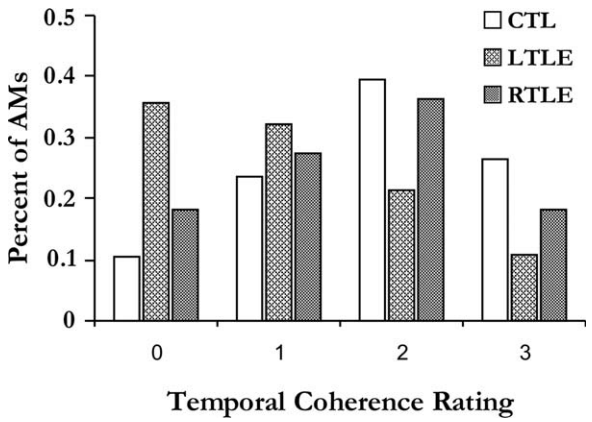


**FIGURE 4. Distribution of temporal coherence ratings. Percentage of AMs from each group (control, LTLE, and RTLE) divided according to their temporal coherence rating, on a scale from 0 to 3.**

## Temporal Coherence Ratings

Temporal coherence ratings are missing for one control participant whose data were collected after our external rater became unavailable. Figure 4 illustrates the distribution of the temporal coherence ratings attributed to patients and controls' AMs. A nonparametric statistical comparison between LTLE patients and the controls revealed group differences for temporal coherence ratings (Kruskal-Wallis test; $\chi^2 = 8.067$, $P < 0.05$). Follow-up nonparametric comparisons revealed that LTLE patients' AMs were rated significantly lower than those of controls (Mann-Whitney $U = 62.500$, $P < 0.01$), while RTLE patients' AMs did not differ from those of controls (Mann-Whitney $U = 77.50$, $P = 0.250$). LTLE patients' AMs were rated lower than those of RTLE patients, although this trend was not significant (Mann-Whitney $U = 43.500$, $P = 0.066$).

# DISCUSSION

Damage to the MTL, particularly to the hippocampus, disrupts the detailed recollection of rich autobiographical episodes (Moscovitch et al., 2000; Rosenbaum et al., 2005, 2008; Steinvorth et al., 2005; Addis et al., 2007a). Our investigation of the temporal organization of memory for autobiographical events revealed an added temporal dimension to this deficit. Ratings of the memories' temporal coherence, which reflects a global impression of correct chronology, temporal resolution, and temporal continuity, were lower for the memories of LTLE patients than for those for RTLE patients and controls. Importantly, our patients' normal performance on a script generation task indicates that this result was not mediated by an impairment in verbal output or narrative structure. To characterize this temporal coherence deficit more precisely, we conducted analyses on two aspects of temporal processing: temporal resolution and temporal order. We observed that both left and right TLE patients' memories lacked temporal resolution while demonstrating intact temporal order.

## The MTL and Temporal Resolution

We showed that temporally precise details, which took place at specific time points over the course of the AM, were reduced in TLE patients. These details corresponded mostly to the storyline of the AM, to what took place over the course of the event. A previous analysis of this dataset revealed a nonsignificant trend for TLE patients to report fewer details about the AM's storyline (*event* details), when these details were simply tallied regardless of their temporal resolution (St-Laurent et al., 2009). Here, we observed that temporally precise clustered details, which depicted the minute-by-minute unraveling of the episode (e.g., she reached for the phone, but I grabbed it first), were significantly reduced in our patients. In contrast, we did not observe a group difference in the number of temporally precise higher order details, which corresponded to coarser segments of the AM (e.g., we had dinner, then we went to see a play). In other words, our patients were unimpaired at recollecting the gist or the outline of the episode, but their memory lacked the fine-grained temporal resolution.

A closer look at the organization of clustered details revealed that TLE patients and controls produced an equivalent number of clusters. However, the mean number of details per Cluster was reduced for the patients, indicating that their clusters contained fewer concrete, imageable details than those of controls. It is interesting to note that reduction in cluster size in patients with MTL lesions is also found on tests of semantic fluency that have no temporal component or narrative structure (Troyer et al., 1998). This correspondence between different tests suggests that cluster size may reflect the outcome of a fundamental process to which the medial temporal lobe contributes. Taking Rosen et al.'s (2005) proposal that cluster size reflects working memory capacity, and in the light of recent observations that the hippocampus contributes to working memory (Hannula and Ranganath, 2008), one can speculate that our patients' reduced cluster size could reflect a working memory deficit. However, with the current paradigm, we could not address whether our patients were impaired at integrating memory details into clusters, or whether they simply lacked these memory details to begin with.

We would also like to emphasize that scores obtained on each AM measure were indistinguishable between pre and postsurgery patients. While postsurgery patients have unilateral damage that includes the hippocampus, the amygdala and the medial and lateral temporal cortices, presurgery patients' lesions are mostly restricted to the hippocampus. Our patients, however, have long-standing seizures (mean years = 33.96, SD = 11.44), and we cannot rule out the possibility of more widespread damage or functional reorganization in the neural circuitry supporting their AM. For example, white matter abnormalities have been reported in the fornix, the cingulum, the genu of the corpus callosum, and other structures outside the

medial temporal lobe in patients with epilepsy of hippocampal origin (Arfanakis et al., 2002; Gross et al., 2006; Concha et al., 2009). In addition, some recent findings suggest the possibility of functional reorganization of short-term associative memory in patients with MTS and longstanding seizures in that they show reduced deficits following TLE surgery relative to patients with other structural lesions and shorter duration of epilepsy (Braun et al., 2008). Because our patients' seizures are longstanding, it is conceivable that functional reorganization may have influenced their performance on our task. However, evidence that the effective connectivity between the hippocampus and other regions activated during AM retrieval is drastically reduced in presurgery TLE patients (Addis et al., 2007a) suggests that their AM deficit reflects a disengagement between the hippocampus and the rest of the AM retrieval network rather than an incorporation of *compensatory* regions.

It is undoubtedly the case that the memory for temporally precise autobiographical details is supported by a network whose activity is disrupted in our patients and within which the hippocampus proper plays a central role. This network may extend to include areas such as the parahippocampal region, which seems to be involved in memory for temporal context (Ekstrom and Bookheimer, 2007; Eichenbaum and Lipton, 2008). However, the presence of extrahippocampal medial temporal damage in postsurgery patients clearly fails to worsen performance on our task, suggesting that lesions restricted primarily to the hippocampus are sufficient to induce the kind of deficit we observed in our patients.

In sum, our results add to our understanding of the role played by the hippocampus in AM by revealing how the most precisely time-bound story elements are most vulnerable to hippocampal damage and cannot be salvaged by relying on compensatory mechanisms. While the AM deficit following damage to the hippocampus has been characterized in terms of preserved gist and loss of details before (Rosenbaum et al., 2009; St-Laurent et al., 2009), this is the first time a gist vs. details type of deficit is revealed in the context of the AM's microtemporal (Hassabis and Maguire, 2007) properties.

## The MTL, Temporal Specificity, and Vividness

Previous work depicting the AM deficit observed following hippocampal damage as a function of the AM's temporal properties has been based on much coarser time scales. Among such scales are Conway's (1996, 2001) hierarchical model of AM, which classifies AM according to temporal specificity, and stipulates that memory for unique personal episodes (e.g., last week's lab meeting) is embedded into memory for extended and repeated episodes (e.g., our weekly lab meetings), which itself is embedded into memory for life periods (e.g., post doc years in a specific lab). Research has shown that memory for unique episodes is especially vulnerable to hippocampal damage, while memory for personal semantics, which includes information about life periods, is more resilient (Nadel and Moscovitch, 1997; Vargha-Khadem et al., 1997; Viskontas et al., 2000). Although these results have been interpreted as an indication that temporally specific AMs are more readily disrupted by hippocampal damage (Nadel and Moscovitch, 1997), recent work has shown that the number of details, the vividness, and the perceptual qualities of AM, rather than its temporal qualities, are what dictates hippocampal involvement. For example, memory for detail-rich generic personal events (events repeated multiple times) (St-Laurent et al., 2009), the construction of never-experienced scenes (Hassabis et al., 2007), and the imagining of future events (Addis et al., 2007b), have all been shown to involve the hippocampus to the same extent as memory for detail-rich unique past episodes (Moscovitch, 2008).

A parallel can be drawn between this literature and our results. We showed, on a microtime scale, that the most precisely time-bound story elements, which are embedded into less temporally precise story elements, are most vulnerable to medial temporal lobe damage. These results could be interpreted as an indication that temporal specificity renders AM details dependent on hippocampal integrity. Alternatively, it could be the concreteness and imageability of temporally precise details that renders them vulnerable to hippocampal damage.

This second interpretation is supported by our finding that the number of temporally indefinite details is also reduced in our patients. Temporally indefinite details applied to the entire duration of the AM and included information about the type of event described (e.g., it was a wedding reception; we went to the movie), the location (e.g., it was somewhere in the distillery district; I was at the mall), the time (e.g., it was a Wednesday afternoon; it was last July; it happened 20 years ago), the people present (e.g., My mother and I went to a concert; both my brothers were present) and the general feel of the event (e.g., I had a great time!; It was really scary). More importantly, a large portion of temporally indefinite details corresponded to information depicting the perceptual characteristics of the event, such as visual scene elements (e.g., we could see the garden by the window; we sat under a tree), colors (e.g., the walls were bright green; his shirt had brown stains), sounds (e.g., the concert was loud; I could hear chatter; we could hear the sea), smells (e.g., the room was stuffy; her perfume was strong), etc. While the current analysis did not distinguish systematically between these different types of details, a previous analysis performed on this dataset revealed that TLE patients were grossly impaired at recollecting perceptual details (St-Laurent et al., 2009). We suspect that the deficit in temporally indefinite details we are observing is at least partially accounted for by a loss of perceptual details, which would be consistent with evidence that a loss of hippocampal function impairs the retrieval of rich visuospatial information (Hassabis et al., 2007; Hirshhorn et al., 2009).

Thus, our impression is that the hippocampus is not sensitive to temporal specificity per se. Rather, we believe that our patients' AM deficit is best characterized as a paucity of the kind of details most likely to contribute to the richness or vividness of AM recollection: perceptual and visuospatial details, and concrete time-specific story elements. These results support the notion that the hippocampus plays a role in the rich reexperienc-

ing of past personal episodes (Moscovitch, 2006, 2008), a defining feature of Tulving's (1972) concept of episodic memory.

## The MTL and Temporal Order

Interestingly, the number of sequencing errors tallied for both categories of time-specific details (higher order and clustered details) was negligible, and did not differ between patients and controls. Additionally, the number of sequencing errors observed during the script generation task was minimal, and did not show group differences. Together, our results indicate that medial temporal damage does not disrupt the capacity to order scripts and personal memory narratives chronologically.

This finding is at odds with some of the literature reporting hippocampal involvement in memory for sequences, both in humans and animals. For example, neuroimaging studies have reported an increase in hippocampal activation during the encoding and the retrieval of sequences of arbitrary stimuli (Kumaran and Maguire, 2006a,b), and during recency judgements about events following each other closely in time (St Jacques et al., 2008). Hippocampal lesions have also been shown to disrupt recency judgements (Chiba et al., 1994; but see McAndrews and Milner, 1991), as well as the acquisition and the disambiguation of sequences (Agster et al., 2002; Fortin et al., 2002; Hopkins et al., 2004).

Key differences in paradigms might explain the discrepancy between our negative finding and the literature. First, most tasks assessing memory for sequences have a strong associative component due to the arbitrary nature of the association between the stimuli forming the sequence (e.g., Chiba et al., 1994; Kumaran and Maguire, 2006a,b). In contrast, the AMs produced by our participants were organized into narratives with a logical, causal structure, with one event leading to the next. It has been shown that a forward narration order facilitates the recall of stories and autobiographical events, suggesting that AMs may naturally be structured as forward sequences (Anderson and Conway, 1993; Radvansky et al., 2005). Real-world semantic and personal knowledge may also support the organization of AM details into sequentially structured stories (e.g., people know they arrive at a party before they leave, etc). Since memory for real-world semantics is resilient to medial temporal lobe damage (see Moscovitch et al., 2005, for a review), it may have contributed to the proper ordering of our patients' AMs.

Second, memory for sequences is typically assessed using forced-choice paradigms in the literature (e.g., McAndrews and Milner, 1991; Fortin et al., 2002; St Jacques et al., 2008). In such tasks, errors are an unavoidable consequence of failure to recall the sequence, whereas in our free-recall paradigms, participants may simply omit details that cannot be integrated into the order of the narrative. Thus, we cannot rule out that our patients' AM performance reflects a poor memory for sequences. Evidence that our patients' AMs were rated as more patchy than those of controls and that patients remembered fewer details per cluster than controls could both be interpreted as a failure to encode or retrieve long, cohesive sequences of AM details. However, with the current paradigm, we cannot determine whether our patients' performance reflects a failure to integrate details into coherent sequences, or whether they simply cannot retrieve sufficient numbers of details to form proper sequences. For the time being, the lack of an increase in sequencing errors in our patients leads us to conclude that their AM deficit reflects a paucity of details, leaving it to future work to determine whether this paucity is mediated by a deficient memory for sequences.

Crucially, our results are at odds with a similar study showing a disruption in the temporal ordering of AM details during free recall in patients with unilateral medial temporal lobe excision (Thaiss and Petrides, 2008). In that study, fewer TLE patients than healthy controls adopted temporal ordering strategies spontaneously when listing activities they performed over a 2-day period, as determined by a blind external rater. Also, a comparison between a diary entry describing the original order in which these activities took place and the remembered order for these activities which was provided a week later clearly showed that sequencing errors were more prominent in TLE patients' narratives.

There are a number of factors that may underlie this discrepancy. First, unlike Thaiss and Petrides's (2008), our paradigm did not allow us to verify the accuracy of our participants' narratives. While Thaiss and Petrides (2008) compared the order in which activities were listed from memory to the order in which they occurred, we compared the order in which AM details were narrated to the order in which the participants remembered these details had taken place. For our task, as long as participants recalled AM details according to the order in which they thought the event took place, no sequencing error was counted. Thus, while our patients' narratives appeared to describe an event chronologically (from beginning to end), we cannot rule out that this chronology was more distorted than that provided by the controls, an issue that deserves further investigation. Nonetheless, we did not replicate Thaiss and Petrides' (2008) finding that TLE patients used a temporal ordering strategy less spontaneously than controls. While our patients' memories were rated as more patchy and less cohesive by an external rater, their memory details were retrieved in a forward sequence (whether or not this sequence was an accurate depiction of the original event's order).

Second, important differences exist between the types of memories tested in the two studies. While Thaiss and Petrides's (2008) participants were requested to list week-old memories selected by the experimenter from a diary completed by the participant, our participants narrated self-selected memories that were at least a year old. The AMs described by Thaiss and Petrides's (2008) participants were both more recent and more trivial than those of our participants, with the most commonly described events involving watching television, cooking a meal, eating, or doing household chores (Thaiss and Petrides, 2008, Supplementary Material). It is unlikely that memory for most of these events would be preserved over long intervals and could be retrieved a year later as rich and distinct memories. On the other hand, our participant's memories were clearly of this type. They also carried more personal significance (e.g., the

day I met my future wife; my near-death experience; the day I quit my job), and corresponded more closely to what Neisser et al. (1996) called *socially motivated narratives*, which are personal events worth rehearsing and telling others. Because the memories retrieved by our patients were more likely to have such a narrative structure than those of Thaiss and Petrides (2008), it is possible that participants were more likely to adopt spontaneously a temporal ordering strategy at retrieval, as when telling a story (Radvansky et al., 2005).

In sum, our results do not provide evidence for the hypothesis that medial temporal damage interferes with the temporal ordering of AM narratives. Instead, TLE patients produced narratives that were as temporally structured as those of controls, only not as precise. While we cannot establish whether our patients' memory for the AM's order is as faithful to reality as the controls' memory, we clearly showed that our patients are unimpaired at producing narratives that respect what they remember to be the chronological order of the event, indicating that the general temporal ordering processes at play when narrating an AM from beginning to end are intact following medial temporal damage. What is deficient is the number of elements of the narrative that reduce its temporal precision.

### The MTL and Laterality

Although the sample sizes were small for analysis of laterality effects, we did not observe differences in performance between left and right TLE patients on our measures of temporal resolution or sequencing. The absence of a laterality effect is consistent with previous findings that medial temporal damage to either hemisphere leads to comparable deficits in AM (Viskontas et al., 2000; Addis, 2005; Noulhiane et al., 2008), but see (Voltzenlogel et al., 2006). While it is likely that each hemisphere contributes to AM in a special way, as suggested by some of the functional neuroimaging studies of AM (Addis et al., 2004), the complex and multidimensional nature of AM has made it difficult to reveal laterality effects in behavioral studies.

Surprisingly, a laterality effect was revealed for the temporal coherence ratings of our patients' narratives. While narratives of RTLE patients were rated similar to those of controls, LTLE patients' narratives were given significantly lower coherence scores. This rating reflected a global characterization of the "flow" of the AM narrative and thus our LTLE patients' narratives were perceived as "patchy" in comparison to the other groups. These findings likely relate to the observations that patients with left TLE show subtle impairments in spontaneous speech and narrative discourse (Field et al., 2000; Bartha et al., 2005) rather than signaling a deficit specific to the coherence of AM narratives.

## CONCLUSION

We have demonstrated that damage to medial temporal structures that includes the hippocampus reduces the temporal resolution of memory for autobiographical episodes. Our results give partial support to claims that microtime, or the minute-by-minute temporal unraveling of AM, depends on the MTL and, likely, the hippocampus in particular (Hassabis and Maguire, 2007). MTL damage resulted in a deficit in which story elements located precisely along the time line of an AM were disrupted, while story elements corresponding to larger chunks of times were preserved. Interestingly, hippocampal damage did not disrupt our patients' capacity to retrieve memory details in a temporally ordered fashion, suggesting that the hippocampus is not essential to the chronological narration of the types of AMs sampled here. In accord with our previous findings regarding the role of the hippocampus in retrieval of perceptual detail, it also plays a central role in memory for details of high temporal resolution, possibly due to their concreteness, their imageability, their high contextual specificity, or a combination of these factors.

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## REFERENCES

Addis DR. 2005. Investigating the engagement of the hippocampus and related structures during autobiographical memory retrieval in healthy individuals and temporal lobe epilepsy patients. Thesis. Toronto, Canada: University of Toronto.

Addis DR, Moscovitch M, Crawley AP, McAndrews MP. 2004. Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. Hippocampus 14:752–762.

Addis DR, Moscovitch M, McAndrews MP. 2007a. Consequences of hippocampal damage across the autobiographical memory network in left temporal lobe epilepsy. Brain 130 (Pt 9):2327–2342.

Addis DR, Wong AT, Schacter DL. 2007b. Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. Neuropsychologia 45:1363–1377.

Agster KL, Fortin NJ, Eichenbaum H. 2002. The hippocampus and disambiguation of overlapping sequences. J Neurosci 22:5760–5768.

Anderson SJ, Conway MA. 1993. Investigating the structure of autoboigraphical memories. J Exp Psychol: Learn Mem Cogn 19:1178–1196.

Arfanakis K, Hermann BP, Rogers BP, Carew JD, Seidenberg M, Meyerand ME. 2002. Diffusion tensor MRI in temporal lobe epilepsy. Magn Reson Imag 20:511–519.

Bartha L, Benke T, Bauer G, Trinka E. 2005. Interictal language functions in temporal lobe epilepsy. J Neurol Neurosurg Psychiatry 76:808–814.

Braun M, Finke C, Ostendorf F, Lehmann TN, Hoffmann KT, Ploner CJ. 2008. Reorganization of associative memory in humans with long-standing hippocampal damage. Brain 131:2742–2750.

Chiba AA, Kesner RP, Reynolds AM. 1994. Memory for spatial location as a function of temporal lag in rats: Role of hippocampus and medial prefrontal cortex. Behav Neural Biol 61:123–131.

Concha L, Beaulieu C, Collins DL, Gross DW. 2009. White-matter diffusion abnormalities in temporal-lobe epilepsy with and without mesial temporal sclerosis. J Neurol Neurosurg Psychiatry 80:312–319.

Conway MA. 1996. Autobiographical memory. In: Bjork EL, Bjork RA, editors. Memory. Handbook of Perception and Cognition, 2nd ed. San Diego, CA: Academic Press. pp 165–194.

Conway MA. 2001. Sensory-perceptual episodic memory and its context: Autobiographical memory. Philos Trans R Soc Lond B Biol Sci 356:1375–1384.

Eichenbaum H. 2004. Hippocampus: Cognitive processes and neural representations that underlie declarative memory. Neuron 44:109–120.

Eichenbaum H, Lipton PA. 2008. Towards a functional organization of the medial temporal lobe memory system: Role of the parahippocampal and medial entorhinal cortical areas. Hippocampus 18:1314–1324.

Ekstrom AD, Bookheimer SY. 2007. Spatial and temporal episodic memory retrieval recruit dissociable functional networks in the human brain. Learn Mem 14:645–654.

Field SJ, Saling MM, Berkovic SF. 2000. Interictal discourse production in temporal lobe epilepsy. Brain Lang 74:213–222.

Fortin NJ, Agster KL, Eichenbaum HB. 2002. Critical role of the hippocampus in memory for sequences of events. Nat Neurosci 5:458–462.

Foster DJ, Wilson MA. 2006. Reverse replay of behavioural sequences in hippocampal place cells during the awake state. Nature 440:680–683.

Foster DJ, Wilson MA. 2007. Hippocampal theta sequences. Hippocampus 17:1093–1099.

Godbout L, Doyon J. 1995. Mental representation of knowledge following frontal-lobe or postrolandic lesions. Neuropsychologia 33: 1671–1696.

Gross DW, Concha L, Beaulieu C. 2006. Extratemporal white matter abnormalities in mesial temporal lobe epilepsy demonstrated with diffusion tensor imaging. Epilepsia 47:1360–1363.

Hannula DE, Ranganath C. 2008. Medial temporal lobe activity predicts successful relational memory binding. J Neurosci 28:116–124.

Hassabis D, Maguire EA. 2008. Deconstructing episodic memory with construction. Trends Cogn Sci 11:299–306.

Hassabis D, Kumaran D, Vann SD, Maguire EA. 2007. Patients with hippocampal amnesia cannot imagine new experiences. Proc Natl Acad Sci USA 104:1726–1731.

Hirshhorn M, Newman L, Moscovitch M. 2009. Detailed descriptions of routes travelled, but not map-like knowledge, correlates with tests of hippocampal function in older adults. In: Annual Cognitive Neuroscience Society Meeting, San Francisco, CA.

Hopkins RO, Waldram K, Kesner RP. 2004. Sequences assessed by declarative and procedural tests of memory in amnesic patients with hippocampal damage. Neuropsychologia 42:1877–1886.

Ji D, Wilson MA. 2007. Coordinated memory replay in the visual cortex and hippocampus during sleep. Nat Neurosci 10:100–107.

Kallai J, Csathó A, Kövér F, Makány T, Nemes J, Horváth K, Kovács N, Manning JT, Nadel L, Nagy F. 2005. MRI-assessed volume of left and right hippocampi in females correlates with relative length of the second and fourth fingers (the 2D:4D ratio). Psychiatry Res 140:199–210.

Kirwan CB, Bayley PJ, Galvan VV, Squire LR. 2008. Detailed recollection of remote autobiographical memory after damage to the medial temporal lobe. Proc Natl Acad Sci USA 105:2676–2680.

Kopelman MD, Stanhope N, Kingsley D. 1999. Retrograde amnesia in patients with diencephalic, temporal lobe or frontal lesions. Neuropsychologia 37:939–958.

Kumaran D, Maguire EA. 2006a. The dynamics of hippocampal activation during encoding of overlapping sequences. Neuron 49:617–629.

Kumaran D, Maguire EA. 2006b. An unexpected sequence of events: Mismatch detection in the human hippocampus. PLoS Biol 4:e424

Levine B, Svoboda E, Hay JF, Winocur G, Moscovitch M. 2002. Aging and autobiographical memory: Dissociating episodic from semantic retrieval. Psychol Aging 17:677–689.

Maguire EA. 2001. Neuroimaging studies of autobiographical event memory. Philos Trans R Soc Lond B Biol Sci 356:1441–1451.

Maguire EA, Vargha-Khadem F, Mishkin M. 2001. The effects of bilateral hippocampal damage on fMRI regional activations and interactions during memory retrieval. Brain 124 (Pt 6):1156–1170.

McAndrews MP, Milner B. 1991. The frontal cortex and memory for temporal order. Neuropsychologia 29:849–859.

McGraw KO, Wong SP. 1996. Forming inferences about some intraclass correlation coefficients. Psychol Methods 1:30–46.

Moscovitch M. 2008. The hippocampus as a "stupid," domain-specific module: Implications for theories of recent and remote memory, and of imagination. Can J Exp Psychol 62:62–79.

Moscovitch M, Yaschyshyn L, Ziegler M, Nadel L. 2000. Remote episodic memory and retrograde amnesia: Was Endel Tulving right all along? In: Tulving E, editor. Memory, Consciousness and the Brain: The Tallinn Conference. Philadelphia, PA: Psychology Press/ Taylor & Francis. pp 331–345.

Moscovitch M, Rosenbaum RS, Gilboa A, Addis DR, Westmacott R, Grady C, McAndrews MP, Levine B, Black S, Winocur G, Nadel L. 2005. Functional neuroanatomy of remote episodic, semantic and spatial memory: A unified account based on multiple trace theory. J Anat 207:35–66.

Moscovitch M, Nadel L, Winocur G, Gilboa A, Rosenbaum RS. 2006. The cognitive neuroscience of remote episodic, semantic and spatial memory. Curr Opin Neurobiol 16:179–190.

Nadel L, Moscovitch M. 1997. Memory consolidation, retrograde amnesia and the hippocampal complex. Curr Opin Neurobiol 7:217–227.

Neisser U, Winograd E, Bergman ET, Schreiber CA, Palmer SE, Weldon MS. 1996. Remembering the earthquake: Direct experience vs. hearing the news. Memory 4:337–357.

Noulhiane M, Piolino P, Hasboun D, Clemenceau S, Baulac M, Samson S. 2008. Autonoetic consciousness in autobiographical memories after medial temporal lobe resection. Behav Neurol 19:19–22.

Pruessner JC, Collins DL, Pruessner M, Evans AC. 2001. Age and gender predict volume decline in the anterior and posterior hippocampus in early adulthood. J Neurosci 21:194–200.

Radvansky GA, Copeland DE, Zwaan RA. 2005. A novel study: Investigating the structure of narrative and autobiographical memories. Memory 13:796–814.

Rosen VM, Sunderland T, Levy J, Harwell A, McGee L, Hammond C, Bhupali D, Putnam K, Bergeson J, Lefkowitz C. 2005. Apolipoprotein E, category fluency: Evidence for reduced semantic access in healthy normal controls at risk for developing Alzheimer's disease. Neuropsychologia 43:647–658.

Rosenbaum RS, Kohler S, Schacter DL, Moscovitch M, Westmacott R, Black SE, Gao F, Tulving E. 2005. The case of K.C.: Contributions of a memory-impaired person to memory theory. Neuropsychologia 43:989–1021.

Rosenbaum RS, Moscovitch M, Foster JK, Schnyer DM, Gao F, Kovacevic N, Verfaellie M, Black SE, Levine B. 2008. Patterns of autobiographical memory loss in medial-temporal lobe amnesic patients. J Cogn Neurosci 20:1490–1506.

Rosenbaum RS, Gilboa A, Levine B, Winocur G, Moscovitch M. 2009. Amnesia as an impairment of detail generation and binding: Evidence from personal, fictional, and semantic narratives in K.C. Neuropsychologia 47:2181–2187.

Scoville WB, Milner B. 1957. Loss of recent memory after bilateral hippocampal lesions. J Neurol Neurosurg Psychiatry 20:11–21.

Selnes OA, Jacobson L, Machado AM, Becker JT, Wesch J, Miller EN, Visscher B, McArthur JC. 1991. Normative data for a brief neuropsychological screening battery. Perceptual and Motor Skills 73:539–550.

St Jacques P, Rubin DC, LaBar KS, Cabeza R. 2008. The short and long of it: Neural correlates of temporal-order memory for autobiographical events. J Cogn Neurosci 20:1327–1341.

St-Laurent M, Moscovitch M, Levine B, McAndrews MP. 2009. Determinants of autobiographical memory in patients with unilateral temporal lobe epilepsy or excisions. Neuropsychologia 47:2211–2221.

Steinvorth S, Levine B, Corkin S. 2005. Medial temporal lobe structures are needed to re-experience remote autobiographical memories: Evidence from HM, W.R. Neuropsychologia 43:479–496.

Strauss E, Spreen O, editors. 1991. Rey Visual Design Learning Test (RVDLT). In: A Compendium of Neuropsychological Tests. New York, NY: Oxford University Press. pp 168–176.

Tanskanen P, Veijola JM, Piipo UK, Haapea M, Miettunen JA, Pyhtinen J, Bullmore ET, Jones PB, Isohanni MK. 2005. Hippocampus and amygdala volumes in schizophrenia and other psychoses in the Northern Finland 1996 birth cohort. Schizophr Res 75:283–294.

Thaiss L, Petrides M. 2008. Autobiographical memory of the recent past following frontal cortex or temporal lobe excisions. Eur J Neurosci 28:829–840.

Troyer AK, Moscovitch M, Winocur G, Alexander MP, Stuss D. 1998. Clustering and switching on verbal fluency: The effects of focal frontal- and temporal-lobe lesions. Neuropsychologia 36:499–504.

Tulving E. 1972. Episodic and semantic memory. In: Tulving E, Donaldson W, editors. Organization of Memory. New York: Academic Press. pp 381–403.

Vargha-Khadem F, Gadian DG, Watkins KE, Connelly A, Van Paesschen W, Mishkin M. 1997. Differential effects of early hippocampal pathology on episodic and semantic memory. Science 277:376–380.

Viskontas IV, McAndrews MP, Moscovitch M. 2000. Remote episodic memory deficits in patients with unilateral temporal lobe epilepsy and excisions. J Neurosci 20:5853–5857.

Voltzenlogel V, Despres O, Vignal JP, Steinhoff BJ, Kehrli P, Manning L. 2006. Remote memory in temporal lobe epilepsy. Epilepsia 47:1329–1336.