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Determinants of autobiographical memory in patients with unilateral temporal lobe epilepsy or excisions☆

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ABSTRACT

Patients with unilateral temporal lobe epilepsy from hippocampal origin and patients with unilateral surgical excision of an epileptic focus located in the medial temporal lobe were compared to healthy controls on a version of the Autobiographical Interview (AI) adapted to assess memory for event-specific and generic personal episodes. For both types of episodes, patients with unilateral (left and right) temporal lobe epilepsy or excision (TLE) reported fewer *internal details*, which are bits of information pertaining to the recollected episode. The source of this deficit was mainly the paucity of perceptual information about the personal episodes, but temporal and spatial information was also deficient. Information about the episode's story elements was preserved in both AM conditions. Participants were also tested on a script generation task to assess retrieval of semantic information. Patients with TLE excision, but not pre-surgical patients, reported significantly fewer actions per script in comparison to controls, suggesting that the temporal neocortex is more involved than mesial temporal structures in recall of this type of information. Together, these results indicate that the hippocampus is essential to the recollection of sensory perceptual aspects of past experiences. Detailed story elements and gist information, as collected during the AI and the script generation task, respectively, are more resilient to hippocampal damage. The similarity of the impairment between the event-specific and the generic memory conditions also suggests that temporal specificity is not a key determinant of hippocampal engagement in autobiographical retrieval.

Autobiographical memory (AM) represents knowledge about facts and events that concern an individual. Theorists have classified AM according to dimensions such as *temporal specificity*, which refers to how precisely a memory is bound in time (e.g. a single afternoon versus a life-period or a relative's name), and *recollective or re-experiential qualities*, which allow one to re-experience an event in a vivid, richly-detailed manner (Brewer, 1986, 1996; Conway, 1996; Conway & Pleydell-Pearce, 2000). In his seminal work on recollection, Tulving (1985) emphasized that retrieval of experiential detail was a critical feature separating recollective experience from familiarity. Although temporal context could certainly be postulated as a core attribute of recollected events, there is nothing in Tulving's original formulation that specifies that recollection must refer to a single instance versus a 'blended' experience; that is, whether Proust's madeleine evokes a particular prior experience or a conjunction of similar experiences (see also Neisser, 1981). In either case, according to Tulving, the re-experiencing is akin to mental time travel. Here, we examine Tulving's key construct of retrieval of episodic detail in the context of normal and disordered autobiographical memory.

A considerable amount of evidence indicates that the hippocampus plays a central role in AM, but the nature of its role is debated. Multiple Trace Theory (MTT) was formulated to explain variability in retrograde amnesia for different types of memories seen in association with hippocampal damage (Nadel & Moscovitch, 1997). This theory stipulates that the hippocampus is involved in the encoding and subsequent retrieval of memory for personal episodes, or event-specific AM. MTT suggests that when event-specific AM is encoded in a defined spatial and temporal context, it forms a hippocampal trace. The hippocampus supports the recollection of event-specific AM by reactivating the trace and retrieving the memory along with detailed contextual information. MTT also stipulates that forms of declarative memories that are not temporally specific and lack contextual information, also known as semantic memories, can be supported by other neural structures, and thus retrieved without a functioning hippocampus (Moscovitch et al., 2005; Nadel

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& Moscovitch, 1997). Examples of semantic memories include facts about one-self (e.g. I grew up in Rimouski) and general knowledge (e.g. Luanda is in Angola).

In support of MTT, there are many studies demonstrating that patients with damage to the medial temporal area, which includes the hippocampus and related structures, show a deficit in memory for personal episodes but relatively preserved memory for autobiographical facts and other semantic information (Addis, Moscovitch, & McAndrews, 2007; Cipolotti et al., 2001; Gilboa et al., 2005; Graham & Hodges, 1997; Rosenbaum, McKinnon, Levine, & Moscovitch, 2004; Rosenbaum et al., 2005, 2008; Steinvorth, Levine, & Corkin, 2005; Vargha-Khadem et al., 1997; Viskontas, McAndrews, & Moscovitch, 2000; Voltzenlogel et al., 2006). Evidence from functional neuroimaging also indicates that the hippocampus is consistently activated during event-specific AM retrieval (Addis, McIntosh, Moscovitch, Crawley, & McAndrews, 2004; Addis, Moscovitch, Crawley, & McAndrews, 2004; Denkova, Botzung, Scheiber, & Manning, 2006; Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004; Maguire & Mummery, 1999; Maguire, Henson, Mummery, & Frith, 2001; Maguire & Frith, 2003; Piolino et al., 2004; Ryan et al., 2001; Steinvorth, Corkin, & Halgren 2006; Vandekerckhove, Markowitsh, Mertens, & Woermann, 2005; also see Maguire, 2001; Svoboda, McKinnon, & Levine, 2006 for reviews).

MTT predicts that the detailed recollection of event-specific AM depends on the hippocampus whereas semantic memories, whether public or personal, can be mediated by extra-hippocampal structures. However, MTT's predictions are less firm when it comes to AM for events experienced repeatedly, or generic AM. Generic AM is a form of AM that shares some but not all characteristics of event-specific AM. Although generic AM lacks the temporal specificity of event-related AM, relevant contextual information can be recovered and, consequently, this form of memories can be vividly recollected (Brewer, 1986, 1996, but see Conway, 2001). For example, the memory of a weekly meeting can contain details about the people usually present, the perceptual qualities of the meeting room, or the order in which things would usually take place over the course of the event. MTT suggests that the repeated encoding of an event could lead to the formation of multiple traces that may render the memory for this event more resilient to hippocampal damage. However, empirical evidence is needed to establish whether generic AM is supported by the hippocampus to the same extent as event-specific AM, or whether AM becomes hippocampally independent if experienced repeatedly.

Previous attempts at comparing the neural correlates of event-specific and generic AM have been sparse. Levine et al. (2004) designed a paradigm for a prospective memory study that exposed participants to their own tape-recorded narratives of event-specific and generic autobiographical episodes. Although no hippocampal activity was observed in either condition, several regions including the bilateral parahippocampal cortex distinguished between these two types of AM. Addis and colleagues (Addis et al., 2004a,b) also compared the neural correlates of event-specific versus generic AMs using functional MRI. They showed that the hippocampus was equally activated by the two conditions, suggesting it was insensitive to the difference in temporal specificity between event-specific and generic AM (Addis et al., 2004a). Instead, hippocampal activity was positively correlated with other characteristics that reflected contextual information, such as self-rated perceptual details (vividness), emotionality, and personal significance.

For this study, we adopted a lesion approach to compare the role played by the hippocampus in event-specific AM and generic AM. We compared both types of AM in patients with unilateral medial temporal lobe epilepsy and patients who had undergone unilateral surgical excision of an epileptic focus within the temporal lobe (including the hippocampus). A significant number of patients with unilateral temporal lobe epilepsy typically suffer from seizure-induced medial temporal sclerosis (MTS), which results in observable hippocampal atrophy in the epileptogenic hemisphere. Patients were compared to neurologically intact matched controls. Our goal was to extend MTT, by establishing whether it is temporal specificity or the amount of contextual information that makes AM hippocampally dependant. Our goal was also to address one of the key questions about hippocampal function: is it implicated only in memory acquired over unique episodes or does it also support the remembrance of contextual details acquired over multiple episodes?

Patients and controls were tested on a version of the Autobiographical Interview (AI) (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002) adapted to assess both generic and event-specific AM. The original version of the AI, which was designed to assess memory for single personal episodes, was used in the event-specific AM condition. Importantly, patients with medial temporal lobe damage which includes the hippocampus have been shown to be impaired on this task (Addis et al., 2007a; McKinnon et al., 2008; Rosenbaum et al., 2004, 2008; Steinvorth et al., 2005). Also, previous evidence from this clinical population has shown that patients with temporal lobe excision and patients with MTS and epilepsy awaiting the same surgery show an equivalent event-specific AM impairment (Viskontas et al., 2000), giving us confidence that both types of patients could be merged into a single clinical group. In the generic AM condition, a modified version of the interview was used to assess memory for personal events that were repeated at least 10 times. We also used a script generation task adapted from Godbout and Doyon (1995) as a control task. We elected to use the script task to control for the contribution of semantic memory, narrative skills and verbal fluency of performance on our adapted version of the AI.

1. Methods

1.1. Participants

All participants gave their informed consent in accordance with a protocol approved by the research ethics board of the University Health Network. Fourteen patients with left temporal lobe epilepsy or temporal lobe excision (LTLE) (10 pre-surgery, 3 male), and 11 patients with right temporal lobe epilepsy or temporal lobe excision (RTLE) (6 pre-surgery, 5 male) were recruited through the Epilepsy Program of Toronto Western Hospital. All patients were diagnosed with epilepsy from unilateral hippocampal origin, except for one pre-surgical RTLE patient in whom an independent left temporal focus was also observed. This participant's performance was indistinguishable from other TLE patients on the AI and the script generation task, 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.

Information was obtained from the patients' medical chart following their consent. All of the patients who had undergone surgery were seizure-free post-operatively, except for one RTLE patient whose ablated epileptogenic cyst had re-grown since his surgery. Three LTLE patients (2 pre-surgery and 1 post-surgery) 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. Five out of nine pre-surgery LTLE patients and three out of six pre-surgery RTLE patients were diagnosed with medial temporal sclerosis by a radiologist according to clinical criteria (atrophy on T1-weighted MRI scans and gliosis on T2-weighted MRI scans).

In order to characterize hippocampal atrophy in our pre-surgery patients as a function of their epileptogenic hemisphere, we took a linear measurement of hippocampal width (Gao et al., 2003) on pre-surgery patients' MRI scans (except for one RTLE case for whom scans were unavailable), which we compared to measurements obtained from a group of healthy controls (the healthy control measurements have been reported previously by Addis et al., 2007a). The control group was composed of 14 right-handed adults (six male) who ranged in age between 24 and 56 years old ($M = 34.14$, S.D. = 10.76). Their age did not differ significantly from RTLE and LTLE patients groups (Mann–Whitney U-test: $U = 33.50$, $p = .482$, and $U = 32.50$, $p = .054$, respectively). Images were either acquired with a 3 or a 1.5 T GE MR system using a three-dimensional T1 weighted sequence (FOV = 200–256; 60–148 axial slices, 1–2.6 mm thick).

For each hemisphere, we used ANALYZE AVW Software (Biomedical Imaging Resource, Mayo Foundation, Rochester, MN) to reconstruct a slice four slices above

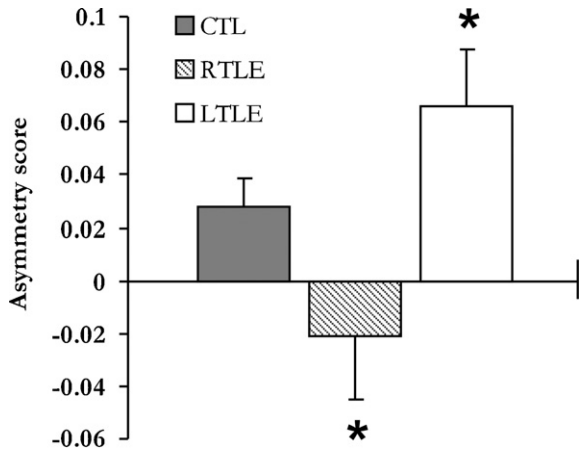

Fig. 1. Hippocampal asymmetry score. Asymmetry scores for the pre-surgery LTLE and RTLE patients, and a group of healthy controls. The asymmetry score is calculated by subtracting the composite score for the left hippocampus from the composite score for the right hippocampus. The composite score is the sum of hippocampal widths measured at four different points along the long hippocampal axis, and adjusted for intracranial width for each participant. The bars indicate the standard error of the mean for each group. Significant differences relative to the control group are indicated by an asterisk. *Note*: $^{*}p < .05$.

the one passing through the inter-collicular sulcus (ICS), along the long axis of the hippocampus (adapted from Gao et al., 2003 by Addis et al., 2007a). Along this slice, hippocampal width was measured at the anterior and the posterior boundaries of the midbrain, at the midpoint between these two boundaries, and at the point between these two boundaries where the hippocampus was the thinnest. These four measurements were summed up into a composite score, which was divided by intracranial width (the distance between the most lateral points on the left and right temporal cortices in the same slice) to account for overall brain size and to correct for differences in voxel width between scans. An intraclass correlation (two-way mixed-effects model; McGraw & Wong, 1996) calculated from 16 composite scores (eight individuals × 2 hippocampi) obtained by two independent raters revealed a coefficient of .873 ($p < .001$).[1]

Asymmetry scores were calculated by subtracting the left composite score from the right composite score for each participant. Asymmetry scores are plotted in Fig. 1 for the pre-surgery LTLE and RTLE patients and for the healthy controls. The asymmetry score was significantly greater for the LTLE patients than for the controls (Mann–Whitney *U*-test: $U = 34.00$, $p = .034$, one-tailed), while it was significantly reduced for RTLE patients in comparison to controls (Mann–Whitney *U*-test: $U = 18.00$, $p = .024$, one-tailed). Our control group's positive asymmetry score is consistent with evidence that the right hippocampus is slightly larger than the left in healthy adults (Kallai et al., 2005; Pruessner, Collin, Pruessner, & Evans, 2001; Tanskanen et al., 2005).

All patients were fluent or native English speakers. All RTLE patients were right handed and had language lateralized to the left hemisphere. Five LTLE patients were left handed (1 post-surgery and 4 pre-surgery). Three LTLE patients (1 post-surgery and 2 pre-surgery) had language representation in the right hemisphere according to fMRI or to a WADA test. Table 1 contains demographic information about the participants, and neuropsychological test scores for the patients.

Controls: 19 healthy controls (8 male) were recruited among staff members at the Toronto Western Hospital, and through on-line and newspaper advertisement. These healthy controls were different individuals from the controls whose hippocampal width is presented above. Exclusion criteria comprised history of neurological (tumour, epilepsy, concussion, cyst, meningitis, stroke, congenital disease) or psychiatric (depression, schizophrenia) disorder. All controls were fluent or native English speakers. Controls were matched to patients for age, gender and years of education.

1.2. Script generation

1.2.1. Administration

Participants were tested on an adapted version of a script generation task developed by Godbout and Doyon (1995), following their completion of the AI. This task was selected to assess patients' capacity to produce a memory narrative that was not autobiographical, and that lacked specific contextual information. We elected to use this task to control for skills that may have contributed to performance on the AI, such as semantic memory retrieval, narrative skills and verbal fluency. Evidence linking semantic memory to some of the temporal lobe structures resected in our post-surgery patients (Cosentino, Chute, Libon, Moore, & Grossman, 2006; Henry & Crawford, 2004; Patterson, Nestor, & Rogers, 2007) also motivated this choice.

Participants were instructed to describe four familiar activities: eating at a restaurant, washing dishes, shopping for groceries and washing clothes. These four activities were selected from a list of activities likely to be familiar to most participants (Godbout and Doyon, 1995). The order in which each of the activities was assessed was randomized for each participant. Participants were requested to list as many actions as they could think of that people generally carried out during the course of the activity, in the order in which these actions took place. Participants were explicitly instructed to list actions reflecting what they thought people generally did, and not what reflected their particular habits. They were told that between 10 and 20 actions would be adequate, but that they were not bound to that range. There was no time limit and all responses were audiotaped.

1.2.2. Scoring

Participants' taped protocols were transcribed. Responses were broken down into different *actions* by the person who administered the test (MSL). For each participant, the total number of actions was tabulated per script, and as a total score per participant. Sequencing errors, irrelevant intrusions and perseveration errors as defined by Godbout and Doyon (1995) were tabulated in the same fashion. A sequencing error was counted when an action was not reported in the order in which it usually occurs during the course of the activity. An irrelevant intrusion was counted for each action that did not belong into the script. A perseveration error was counted when the same action was repeated. Three additional categories were also added to the original scoring system: *idiosyncratic errors* were calculated whenever participants reported actions that reflected their own particular habits and could not be generalized to others. *Other errors* where counted whenever participants made comments that could not be considered actions per se. Finally, *alternative actions* were scored when more than one option was offered as parts of the script (e.g. "The person can either hand dry the dishes [one action] or leave it to dry on the dish rack [one action, alternative]"). While sequencing errors, irrelevant intrusions, idiosyncratic errors and alternative actions were counted as actions, perseverative errors and other errors were not. Fig. 2 offers an example of a script scored according to the method described here.

1.3. Autobiographical interview

1.3.1. Administration

The original version of the Autobiographical Interview (Levine et al., 2002) was modified for the purpose of this study. Participants described memories of personal episodes that were either event-specific or generic; two Event-Specific and two Generic autobiographical memories (AMs) were assessed, for a total of four AMs per participant. Event-Specific and Generic AMs were collected following either an *ABBA* or a *BAAB* order, which was alternated between consecutive participants. A list of suggestions of Event-Specific and Generic AMs was made available to the participants. For the Event-Specific AMs condition, participants were instructed to describe episodes that took place a single time, sometime between a year ago and 10 years ago, and that lasted from a few minutes to a few hours. For the Generic AMs condition, participants were instructed to select repeated events of the same type that always took place in the same context and in the same spatial location (e.g. a bi-weekly salsa class at the neighbourhood studio, commuting to a specific job, babysitting the same family, Friday dinner at your in-laws, going to a favorite club

Table 1
Demographic and neuropsychological characteristics of Control, LTLE and RTLE participants.

	Control ($n = 19$)[a]	LTLE ($n = 14$)	RTLE ($n = 11$)
Mean age in years (S.D.)	39.47 (8.81)	43.79 (6.97)	37.00 (8.06)
Years of edu. (S.D.)	16.11(2.73)	14.93 (3.27)	15.36 (3.72)
Mean WASI F.S. IQ (S.D.)	N/A	95.79 (10.97)	96.91 (13.58)
Mean RAVLT (S.D.)[b]	N/A	−0.19 (0.91)	0.16 (0.75)
Mean RAVLT (S.D.)[c]	N/A	−2.00 (1.67)	−2.87 (1.46)

[a] One control participant (male) was excluded from the Generic AM condition (AI).

[b] Raw total recall scores were converted into *z* scores based on norms from Selnes et al. (1991).

[c] Raw total recall scores were converted into *z* scores based on norms from Strauss and Spreen (1991).

Note: edu. = education; F.S. IQ = Full Scale Intellectual Quotient; L = left; N/A = not applicable; R = right; RAVTL = Rey Auditory-Verbal Learning Test; RVDLT = Rey Visual Design Learning Test; S.D. = standard deviation; TLE = temporal lobe epilepsy or excisions; WASI = Wechsler Abbreviated Scale of Intelligence (1999).

[1] The intraclass correlation coefficient obtained here is lower than coefficients originally reported by Gao et al. (2003). Importantly, our sample size was smaller, and our measurements were performed on young and middle-aged individuals, a group that is potentially more homogenous than Gao et al.'s (2003) population of older adults.

Activity – Washing Clothes

OK, well I live in a six-plex on the ground floor (O) and so I just have to go down one or two steps at…to the laundry room (1, Id) and…and put the clothes in the washer…(2) this sounds so simple…(O) and start the machine (3) and then I go back upstairs (4) and my ears are so sensitive from my […] that I can actually hear when the softener…(O) I can either tell, I can either tell…the next floor up I can tell when somebody is doing their laundry because I can hear the water… (O) that's good actually because I can go down and put softener in (5, Id) and then I go and do so (P) and then after about half an hour I go down (6). And put the clothes in the dryer (7) and I'll check in about half an hour which is… (8, Id) these dryers…it's a brand new…too much heat… (O) you wouldn't go the whole time (O). So I'll check it maybe in 20 minutes or so… (P) there might be like just one or two things that aren't dry…(9). So sometimes I'll wait until half an hour (10, Id, A) and I know everything is already dry… The machine actually goes for 50 minutes (O) but I always put it on a gentle…not on the highest, like about in the middle, (11, Id, SE) because it just gets too hot. (O) So then clothes out (12) and if there are any shirts or stuff that you don't want to get too wrinkled you can certainly put them on the top (13) and take the basket up (14) and it is all done. (O) Well, then, not quite then, (O) then the folding comes…(15) put them away and… (16) that's it, I'm done (O).

Fig. 2. Example of a script scored according to a system adapted from Godbout and Doyon (1995). The script is for "washing clothes". Numbers are given to each counted action. *Note*: A = alternative action; Id = idiosyncratic error; O = other unclassifiable comments; P = perseverance error; SE = sequencing error.

or restaurant, walking a child to pre-school, etc.). Generic episodes needed to have been repeated a minimum of 10 times (no maximum) within the last 10 years. Also, they could not have occurred during the previous year to control for the possibility that memory for the most recent episode would be too fresh in the mind such that participants would rely on that specific episode to describe the generic case. Every instance of the repeated event also needed to be limited in time from a few minutes to a few hours, in a manner analogous to the event-specific episodes. The recency of AM was assessed based on participants' self-report. For Generic AMs, recency was defined as the last time a repeated event took place; the number of repetitions was inferred from the frequency of repetition and the time period over which an event took place, also based on self-report. In the rare occasion when a participant failed to come up with episodes fitting these time windows, the date rule was ignored (see Section 2).

The interview was divided up into three conditions: Free Recall, General Probe, and Specific Probe (Levine et al., 2002). During Free Recall, participants were instructed to describe the episode of their choice in as much details as possible, which they did without interruption. The General Probe condition was administered immediately after Free Recall came to a natural end; the investigator would probe the participant to report supplemental details about the episode, in a non-specific manner (e.g. "Is there anything else you can remember about this event?"). Together, Free Recall and General Probe are referred to as the Recall condition.

After Recall was administered for all four AMs, the Specific Probe condition was then administered for each memory in the order in which they had been previously collected. The Specific Probe condition is a semi-structured interview that consists in a series of questions covering five main aspects of the memory: when the event took place, where it took place, the things that happened over the course of the event, what the participant perceived (e.g. visual, auditory or olfactory information), and what the participant thought or felt. Interviews were audiotaped for transcription and scoring.

1.3.2. Scoring

The audiotapes were transcribed. The transcripts were scored by MSL, who also conducted the interviews. MSL was trained to achieve high inter-rater reliability with an extensively trained scorer on a set of practice event-specific memories. A different external rater who was blind to the identity of the participants scored 15 of the Generic AMs collected for this study. Intraclass correlations (two-way mixed-effects model; McGraw & Wong, 1996) conducted on MSL's and the external scorer's protocols are reported in the results section.

Narratives were segmented into parcels or *details*, which were then classified into different categories. For both the Event-Specific and the Generic AM conditions, details were tallied for the Recall condition alone, and as a composite score for the Recall and the Specific Probe conditions. The Specific Probe condition was not analyzed separately because it built on the information provided during Recall.

The details categorization system differed slightly for Event-Specific and for Generic AMs. Event-Specific AMs were scored according to the original AI (Levine et al., 2002). All details were either classified as INTERNAL or EXTERNAL. INTERNAL details pertained directly to the main episode described; they were further divided into the following five categories: EVENT (what happened), TIME (when it happened), PLACE (where it happened), PERCEPTUAL (things that were seen, heard, smelled, felt or tasted), and EMOTION/THOUGHT (thoughts or emotions experienced over the course of the episode).

EXTERNAL details were those that did not directly pertain to the episode being described. They were further divided into the following categories: details that pertained to event-specific episodes tangential or unrelated to the main episode described, SEMANTIC, REPETITIONS, and OTHER details. SEMANTIC details were details that reflected information that was either not bound to a spatio-temporal context (e.g. opinions, general knowledge), or information that pertained to repeated or extended episodes (e.g. "my family did not speak English when we arrived in Canada"). REPETITIONS were counted whenever information was repeated, and across testing conditions: a detail mentioned during Recall was categorized as a REPETITION if it was mentioned again during the Specific Probe condition. OTHER details were pieces of information that did not correspond to any other details category, such as retrospective comments about an event, or comments on one's memory (e.g. "I cannot remember what happened after that"). Table 2 provides examples of details from the main categories.

Generic AMs were scored using a modification of Levine et al. (2002)'s system. Details were classified into three main categories: INTERNAL UNIQUE details, INTERNAL GENERIC details, and EXTERNAL details. INTERNAL UNIQUE details pertained to only a single or a few specific instances of the generic episode (e.g. "once the instructor brought cake for everyone"). Details from this category were excluded from the final analysis. INTERNAL GENERIC details pertained to all, most, or a significant number of instances of the generic episode; the category was further divided into five categories analogous to the original scoring system's: EVENT (what would usually happen), TIME (when it would usually happen), PLACE (where it would usually happen), PERCEPTUAL (things that were usually seen, heard, felt, smelled or tasted), and EMOTION/THOUGHT (thoughts or feelings usually experienced over the course of the event).

EXTERNAL details included the same three categories as for the event-specific episodes: SEMANTIC, REPETITION, and OTHER. Again, SEMANTIC details were not bound to a spatio-temporal context, or were more loosely bound to a spatio-temporal context than INTERNAL UNIQUE and INTERNAL GENERIC details. For example, "My favorite colour is blue" is SEMANTIC, while "The walls of the classroom where the class took place were blue" is INTERNAL GENERIC (PERCEPTUAL). EXTERNAL details also included details pertaining to a generic episode other than the main generic episode described, and details pertaining to an event-specific episode that was not a unique instance of the main generic episode. Table 2 provides examples of details from the main categories.

Table 2
Examples from scoring categories.

Event-Specific AM details		Generic AM details	
Internal		Internal Generic	
Event	My brother was there	Event	My friend would usually come
	He dropped the gold coin		First thing I'd get was a coffee
	We played poker		It was an advanced salsa class
	It was her birthday party		Half the department would be there
	She got really mad		He would get frustrated at times
Time	It started at 8	Time	The meeting started at 8
	It was in January		It was usually held in March
	That was 3 years ago		We met every 2 weeks
	It happened on a Tuesday		It was on Tuesdays
Place	We were at a bar on St-Denis	Place	We'd meet at the Eaton Center
	We sat at the back of the room		We'd wait by the south doors
	I walked into a convenience store		I sat the back of the bus
	That was in Romania		That's when I was still in Brazil
Perceptual	She was a brunctte	Perceptual	The walls were beige
	The band was loud		She would always speak loudly
	My palms were sweaty		It would quickly become painful
	The sun was bright		It echoed in the room
	It tasted like soap		I would feel really full after that
Thought	I was trilled	Thought	I would be excited to be there
	I felt incredibly calm		My mind would start to wander
	He reminded me of my uncle		I'd feel serene after the workout
	The concert was just plain bad		I was interested most of the time
	I was flustered		I would feel a strong connection
External		External	
Semantic	He's greek	Semantic	My mom bakes the best chocolate cookies
	Their trains are on time		They don't trust their currency
	She's an aggressive player		His dad is a bad driver
	We kept dating for another month		I was a student
	They were mostly feeding on noodles		They are from Calgary
	I hate sushi		She has allergies
Other	I cant remember now	Other	That's all I remember
	It's quite vivid in my mind		Crazy story, hey?
	Looking back, I don't know what I was thinking		What were we saying?
	It's a great memory		I cant remember if she was there
	I could tell you a lot more about this		Now was it at 7 or at 8?

2. Results

2.1. Script generation

The LTLE, RTLE and control groups were compared for their performance on the script generation task. A one-way ANOVA over the mean number of actions comparing controls and the two patient groups did not reveal a significant difference between the groups ($F(2, 39) = 1.797$, $p = .179$; partial $Eta^2 = .084$).

A MANOVA over the number of errors and other action characteristics did not reveal significant group differences ($\Lambda = .736$, $F(12, 68) = .938$, $p = .515$). Groups did not differ significantly for the number of errors committed (sequencing: $F(2, 39) = 1.491$, $p = .238$; intrusion: $F(2, 39) = 1.468$, $p = .243$; perseverance: $F(2, 39) = 1.395$, $p = .260$). Groups also did not differ significantly for the mean number of idiosyncratic ($F(2, 39) = 2.868$, $p = .069$) or alternative actions ($F(2, 39) = 0.960$, $p = .392$), or for the mean number of other comments ($F(2, 39) = 2.418$, $p = .102$).

Despite the lack of a group effect in the mean number of actions produced, we considered it important to examine post-surgery patients separately given evidence linking semantic memory to some of the temporal cortical structures resected in these patients (e.g. Patterson et al., 2007). In order to maximize our statistical power, limited by our low number of post-surgery patients ($n = 9$), we performed planned orthogonal contrasts tailored to address whether post-surgery patients performed differently from pre-surgery patients and controls. A first contrast revealed that pre-surgery patients and controls produced significantly more actions than post-surgery patients ($t(39) = -2.205$, $p = 0.33$; see Fig. 3). A second contrast revealed that pre-surgical patients performed similarly to controls ($t(39) = 0.390$, $p = 0.698$). Post-surgery patients did not commit significantly more errors than controls or pre-surgery patients (data not shown).

2.2. Modified autobiographical interview

Data from one control participant were excluded from the analysis of the Generic AM condition because he failed to come up with generic memories; his data were also excluded from joint analyses of the Event-Specific and the Generic AM conditions. For the Event-Specific Condition, 7 out of 88 AMs failed to meet the time criteria (4 took place less than a year prior to the interview, and 3 took place more than 10 years prior to the interview). For the Generic AM condition, 6 AMs were less than a year old, and 3 were older than 10 years, out of 86 AMs. Two AMs occurred fewer than 10 times in a 10-year period. These AMs were not distinguishable from the others in terms of the number of details per category, and we elected to include them in the analysis.

The Specific Probe condition was included in the AI in order to provide participants with additional retrieval support compared to the Recall condition. Providing specific retrieval probes might be expected to benefit patients to a greater extent than controls if poor performance were merely a matter of spontaneously accessing event details (Levine et al., 2002). However, for both Event-Specific and Generic AMs, probing benefited the controls more than the TLE patients, so that group differences were magnified and not

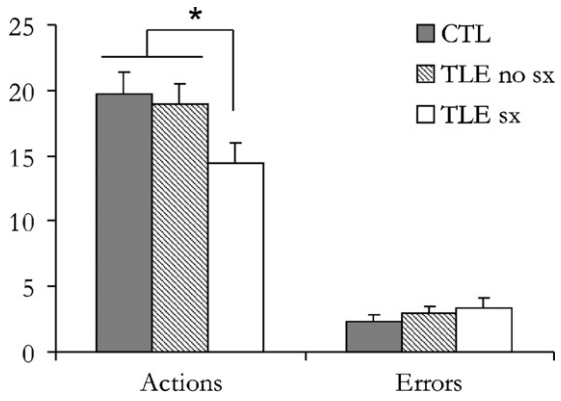

Fig. 3. Script generation. Mean number of actions and errors for four scripts. The composite error score is the sum of the sequencing errors (SE), irrelevant intrusions (Irr), and perseverance errors (P) averaged for each of the scripts. The scripts were: "washing dishes", "washing clothes", "eating at the restaurant" and "shopping for groceries". The bars indicate the standard error of the mean for each group: controls, pre-surgical TLE (left and right) and post-surgical TLE (left and right) patients. Significant group differences are indicated by an asterisk. *Note*: sx = medial temporal lobe surgical resection; $^{*}p < .05$.

reduced with retrieval support (for similar findings, see Levine et al., 2002; McKinnon et al., 2008; Rosenbaum et al., 2008). Because we observed a similar pattern of results following the Recall and the Recall + Specific Probe conditions, we only report analyses performed on the Recall + Specific Probe conditions for brevity. For both the Event-Specific and the Generic AM conditions, pre- and post-surgery TLE patients did not differ significantly from one another on any of the AI's details categories ($p = .182–.965$). For both AM conditions, left and right TLE patients also did not differ significantly on any of the details categories ($p = .062–.994$). In order to gain statistical power, we merged all TLE patients into a single patient group, which we compared to the controls. In the figures, TLE patients' performance on the AI is presented according to the laterality of their lesion, regardless of their surgery status.

2.2.1. Inter-rater reliability

For the Event-Specific AMs, intraclass correlation coefficients for the INTERNAL and the EXTERNAL details were .96 and .84, respectively (two-way mixed-effects model, single measures; McGraw & Wong, 1996). For the Generic AMs, consistency coefficients for INTERNAL UNIQUE, INTERNAL GENERIC, and EXTERNAL details were .97, .92, and .91, respectively. Intraclass correlations were also conducted on the details subcategories, and are reported in Table 3.

2.2.2. Event-Specific AMs: INTERNAL and EXTERNAL details

The mean number of INTERNAL and EXTERNAL details produced for the Event-Specific AM condition was compared between the controls and the TLE patients. A two-way ANOVA with repeated measure over detail category revealed a significant effect of group ($F(1, 42) = 4.262$, $p < .05$, partial $Eta^2 = .092$), a significant effect of detail category ($F(1, 42) = 30.678$, $p < .001$, partial $Eta^2 = .422$), and a significant group × detail category interaction effect ($F(1, 42) = 15.132$, $p < .001$, partial $Eta^2 = .265$). Planned comparisons revealed that, while patients reported significantly fewer INTERNAL details than controls ($t(42) = 3.940$, $p < .001$, Cohen's $d = 1.19$), the two groups produced similar numbers of EXTERNAL details ($t(42) = .347$, $p = .731$, Cohen's $d = 0.11$) (see Fig. 4).

2.2.3. Generic AMs: INTERNAL and EXTERNAL details

The mean number of INTERNAL GENERIC and EXTERNAL details reported for the Generic AM condition was compared between the controls and the TLE patients. INTERNAL UNIQUE details, which pertain only to specific instances of the repeated episode, were excluded from the analysis (Controls: $M = 13.11$, S.D. = 14.06; TLE: $M = 10.36$, S.D. = 7.86). A two-way ANOVA with repeated measure over detail category revealed a significant effect of detail category ($F(1, 41) = 40.628$, $p < .001$, partial $Eta^2 = .498$), and a significant group x detail category interaction effect ($F(1, 41) = 24.136$, $p < .001$, partial $Eta^2 = .371$), but the main group effect was not significant ($F(1, 41) = 2.124$, $p < .153$, partial $Eta^2 = .049$). Planned comparisons revealed that, while patients reported significantly fewer INTERNAL GENERIC details than controls ($t(41) = 3.925$, $p < .001$, Cohen's $d = 1.21$), the two groups produced similar numbers of EXTERNAL details ($t(41) = 1.068$, $p = .292$, Cohen's $d = 0.33$) (see Fig. 4).

2.2.4. INTERNAL details: Event-Specific and Generic AMs

In order to address whether TLE affects the two AM conditions equally, the mean number of INTERNAL details produced by each of the groups during the Event-Specific AM condition was compared to the mean number of INTERNAL GENERIC details produced by each of the groups during the Generic AM condition. Due to important differences in the inclusion criteria for EXTERNAL details between the Event-Specific and the Generic AM conditions, EXTERNAL details from the two AM conditions could not be compared in the same omnibus test, and were excluded from this analysis. For the Generic AM condition, INTERNAL UNIQUE details, which pertain only to specific instances of the repeated episode, were also excluded from the analysis. A two-way ANOVA with repeated measure over AM condition revealed a significant main effect of group ($F(1, 41) = 17.897$, $p < 0.001$), with patients

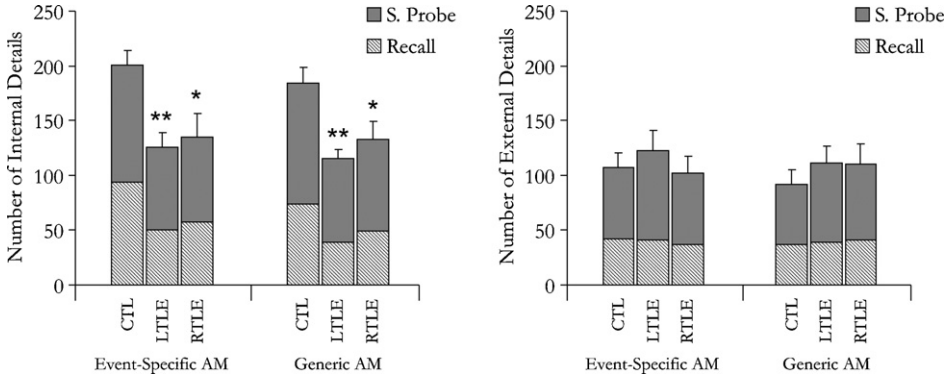

Fig. 4. The AI: details categories for each AM condition. On the left: mean number of INTERNAL details for two Event-Specific AMs, and mean number of INTERNAL GENERIC details for two Generic AMs. On the right: mean number of EXTERNAL details for two Event-Specific AMs and two Generic AMs. Data are shown for the Recall condition (striped portion of the histogram), and for the Specific Probe (S. Probe) conditions (grey portion of the histogram) for each of the groups: controls, LTLE and RTLE. The bars represent the standard error of the mean for each group, for a composite score of the Recall and Specific Probe conditions. Significant differences relative to the control group are indicated by an asterisk. *Note*: $^{*}p < .05$; $^{**}p < .01$.

Table 3
Inter-rater reliability: intraclass correlation coefficients per details subcategories.

	Internal/internal generic details					External details		
	Event	Place	Time	Percept.	Th./Emo.	Semantic	Repet.	Other
Ev-Speci AM	0.86	0.37	0.76	0.92	0.78	0.85	0.83	0.84
Generic AM	0.87	−0.04	0.80	0.85	0.80	0.75	0.85	0.31

Note: Intraclass correlation coefficients are calculated between the main scorer (MSL)'s and an external scorer's ratings. Two different scorers scored the event-specific and the generic AMs. A ceiling effect contributed to lower the coefficient for Place details. Emo. = Emotion, Ev-speci = Event-Specific; Percept. = Percetual, Repet. = Repetition, Th. = Thought.

reporting fewer details than controls. The main effect of AM condition, and the group × AM condition interaction effect were both non-significant ($F(1, 41) = 1.630$, $p = .209$ and $F(1, 41) = .116$, $p = .735$, respectively). The effect size of the difference between the controls and TLE patients was identical for the two AM conditions (Event-Specific AM: Cohen's $d = 1.20$ (d.f. = 42); Generic AM: Cohen's $d = 1.21$ (d.f. = 41)), suggesting that TLE hinders the recollection of Generic AM to the same extent that it hinders the recollection of Event-Specific AM. Importantly, the group difference remained significant when the mean number of actions produced during the script generation task was used as a covariate (($F(1, 39) = 13.131$, $p < .005$); the script generation covariate was not significant ($F(1, 39) = 3.145$, $p = .084$), suggesting that post-surgery TLE patients' script generation deficit could not account for our patient's poor performance on the AI.

2.2.5. Details subcategories: Event-Specific AMs

TLE patients were compared to controls for the mean number of details from each of the INTERNAL details subcategories generated during the Event-Specific AM condition (see Fig. 5A). A two-way ANOVA with repeated measure over details categories revealed significant main effects of group ($F(1, 42) = 15.522$, $p < .001$) and detail categories ($F(4, 168) = 117.526$, $p < .001$), and a significant group x detail category interaction effect ($F(4, 168) = 8.572$, $p < .001$). Planned t-tests revealed significant differences between the controls and the TLE patient group for INTERNAL TIME details ($t(42) = 2.727$, $p < 0.01$; Cohen's $d = .83$), INTERNAL PERCEPTUAL details ($t(42) = 6.337$, $p < 0.001$; Cohen's $d = 1.93$), and INTERNAL THOUGHT/EMOTION details ($t(42) = 3.859$, $p < 0.001$; Cohen's $d = 1.18$). As evident from Fig. 5A, patients' reduced generation of INTERNAL PERCEPTUAL details is what accounts for most of their reduced production of INTERNAL details. No significant group difference was revealed for the INTERNAL EVENT details ($t(42) = 1.422$, $p = .163$; Cohen's $d = .43$) or for the INTERNAL PLACE details ($t(42) = 1.889$, $p = .066$; Cohen's $d = .57$). All the significant group differences remained significant when performance on the script generation task (mean number of actions generated per script) was used as a covariate (TIME: $p < .05$; THOUGHT & PERCEPTUAL: $p < .001$). While the script covariate was significant for some analyses (TIME & PERCEPTUAL: $p < .05$), our results indicate that a script generation deficit could not account entirely for our patient's poor performance on the AI.

A two-way ANOVA with repeated measure over detail categories was also performed on the EXTERNAL details subcategories. The main effect of detail categories was significant ($F(2, 84) = 4.848$, $p < .05$), with post hoc paired-sample t-tests indicating that participants reported significantly fewer REPETITION details than SEMANTIC or OTHER details ($t(43) = 3.113$, $p < .01$; $t(43) = 2.663$, $p < .05$, respectively). However, the main group effect ($F(1, 42) = .036$, $p = .851$) and the group x detail category interaction effect ($F(2, 84) = 1.516$, $p = .226$) were not significant, indicating that patients did not differ from controls for EXTERNAL details categories (see Fig. 5B).

2.2.6. Details subcategories: Generic AMs

Patients and controls were compared for the mean number of details for each of the INTERNAL GENERIC details subcategories generated during the Generic AM condition (see Fig. 6A). A two-way ANOVA with repeated measure over INTERNAL GENERIC details categories revealed significant main effects of group ($F(1, 41) = 15.407$, $p < .001$) and details categories ($F(4, 164) = 136.653$, $p < .001$), and a significant group x detail category interaction effect ($F(4, 164) = 11.110$, $p < .001$). Planned t-tests revealed significant differences between the controls and the TLE patient group for INTERNAL GENERIC PLACE details ($t(41) = 2.449$, p, 0.05; Cohen's $d = .76$), INTERNAL GENERIC TIME details ($t(41) = 2.105$, $p < 0.05$; Cohen's $d = .65$), and INTERNAL GENERIC PERCEPTUAL details ($t(41) = 6.162$, $p < 0.001$; Cohen's $d = 1.90$). Here again, a patients' reduced generation of INTERNAL GENERIC PERCEPTUAL details is what accounts for the largest part of their reduced overall generation of INTERNAL GENERIC details (see Fig. 6A). No significant group difference was revealed for the INTERNAL GENERIC EVENT details ($t(41) = 1.403$, $p = .168$; Cohen's $d = .43$) or for the INTERNAL GENERIC THOUGHT/EMOTION details ($t(41) = 1.985$, $p = 0.054$; Cohen's $d = .61$). With the exception of INTERNAL GENERIC TIME details ($F(1, 39) = 2.616$, $p = .114$), group differences were still significant when performance on the script generation task was introduced as a covariate (PERCEPTUAL: $p = .000$; PLACE: $p = .017$), even though the script covariate was significant for the PERCEPTUAL details analysis ($p < .05$).

A two-way ANOVA with repeated measure over detail categories was performed on the EXTERNAL details subcategories. The main effect of detail categories was significant ($F(2, 82) = 27.239$, $p < .001$), with post hoc paired-sample t-tests indicating that participants reported significantly more SEMANTIC details than REPETITION or OTHER details ($t(42) = 6.653$, $p < .001$; $t(42) = 4.133$, $p < .001$, respectively), and significantly more OTHER details than REPETITION details ($t(42) = 4.273$, $p < .001$). However, the main group effect ($F(1, 41) = .724$, $p = .400$) and the group × detail category interaction effect ($F(2, 82) = .755$, $p = .473$) were not significant, indicating that patients did not differ from controls for EXTERNAL details categories (see Fig. 6B).

2.2.7. Description of Generic AMs

Participants specified whether they remembered a repeated AM as a collection of distinct, separate episodes, or as a blended, generic memory for all the times the event took place. Most Generic AMs were described as blended memory constructs (controls: 34 out of 38 AMs; RTLE: 16 out of 20 AMs for RTLE, 2 ratings N/A; LTLE: 24 our of 28 AMs), suggesting that they were perceived as truly generic by our participants.

3. Discussion

Patients with left and right unilateral TLE recalled significantly fewer internal details compared to controls on a modified version of Levine et al. (2002) Autobiographical Interview, regardless of whether the personal event they described was event-specific or

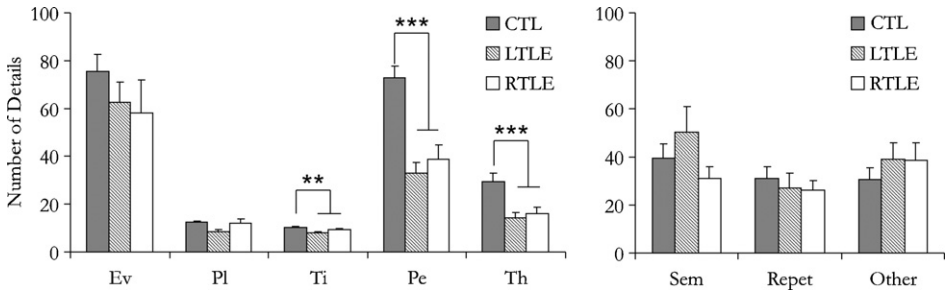

Fig. 5. Event-Specific AMs – INTERNAL and EXTERNAL details subcategories. On the right: mean number of INTERNAL details per subcategory (Ev, Pl, Ti, Pe, and Th) for the controls and the two patient groups. On the left: mean number of EXTERNAL details per subcategory (Sem, Repet, and Other). Details are summed for two Event-Specific AMs. The bars indicate the standard error of the mean for each group. Significant differences from the control group are indicated by an asterisk. *Note*: Ev = event details; Pe = perceptual details; Pl = place details; Repet = repetition; Sem = semantic; Th = thought/emotion details; Ti = time details; $^{**}p < 0.01$; $^{***}p < 0.001$.

generic. Additional probing did not reduce the difference in performance between patients and controls. Our findings extend previous evidence that TLE patients are impaired at recollecting event-specific AM (Addis et al., 2007a; Noulhiane et al., 2007; Steinvorth et al., 2005; Viskontas et al., 2000; Voltzenlogel et al., 2006), by showing that our patients' AM deficit is specific to the retention and/or recovery of event-bound contextual details and is not affected by temporal specificity. These results are consistent with functional neuroimaging evidence that the hippocampus is equally activated during the recollection of event-specific and generic AM in healthy adults (Addis et al., 2004a,b; Nadel, Campbell, & Ryan, 2007).

In absolute terms, the TLE patients' memory impairment for both event-specific and generic AMs primarily involved retrieving perceptual details about these events in all modalities. This is consistent with electrophysiological evidence that human hippocampal cells can be activated by the visualization of both common and unique visual features from memory (Kreiman, Kock, & Fried, 2000), and with neuroimaging findings that hippocampal activation correlates positively with the self-rated vividness of retrieved autobiographical events in healthy participants (Addis et al., 2004b; Gilboa et al., 2004). Perhaps because perceptual details were among the most numerous internal details, they contributed inordinately to the deficit. However, a deficit was also observed for details concerning time, place and emotion/thoughts. The only category for which a deficit was not observed was event details, which essentially provide the story elements to the episode. Together, these findings support the idea that the hippocampus is needed to allow for a rich perceptual re-experiencing of a familiar episode, whether event-specific or generic, but less so, or not at all, for the retention and retrieval of its story elements.

Our lack of a deficit for event details is a unique finding given previous evidence of a loss of event details in amnesic patients with medial temporal damage. Rosenbaum et al. (2004) have shown how KC, an amnesic patient with extensive bilateral hippocampal damage, shows a dramatic loss of internal details across all AI categories, including event and perceptual details. However, the presence of lesions to KC's frontal, parietal and occipital lobes prevents us from ruling out that his loss of event details reflects extra-hippocampal damage. Other reports of impaired performance on the AI in hippocampal amnesics typically do not distinguish between perceptual or event details, but present a reduced composite score for all internal detail categories (e.g. Moscovitch, Yaschyshyn, Ziegler, & Nadel, 2000; Rosenbaum et al., 2008; Steinvorth et al., 2005; see also Bayley, Hopkins, & Squire, 2003 for a lack of effect). Nonetheless, well-known patient HM, who became amnesic following a bilateral medial temporal lobe resection (Scoville & Milner, 1957), scored so low on the internal composite score that performance across all internal details categories, including event details, must have been impaired (Steinvorth et al., 2005). While HM's medial temporal resection extends beyond the hippocampus to include adjacent cortical structures (Corkin, Amaral, González, Johnson, & Hyman, 1997), patient SJ, who suffers from damage mostly restricted to the hippocampus bilaterally, also obtained a reduced internal composite score on the AI (Rosenbaum et al., 2008). Further analyses suggest that SJ reported fewer event details than controls, although his performance was not at floor, suggesting that at least some event details were preserved (Levine, unpublished results).

While the current results clearly indicate that event details are more resilient to TLE-related hippocampal damage than perceptual and spatio-temporal details, two things must be considered about our TLE patients. Firstly, their medial temporal lobe damage is unilateral. Secondly, they are not amnesic: their performance on the AI is not at floor, but reflects a more subtle memory deficit (see also Addis et al., 2007a). Further work will be needed to determine whether the recollection of detailed story elements, which is preserved in our patients, is impaired following more extensive bilateral hippocampal damage (as suggested by SJ's performance on the AI), and whether

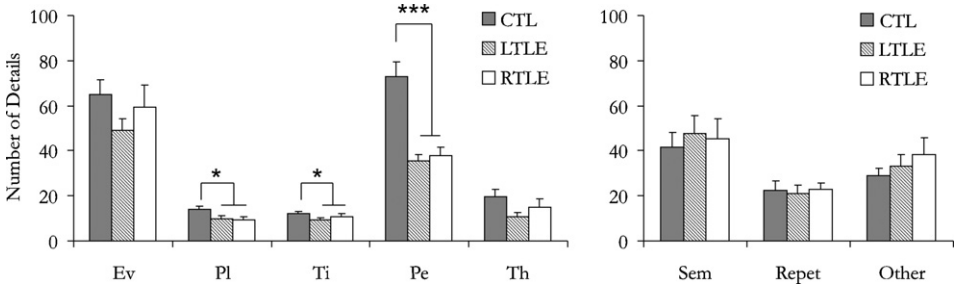

Fig. 6. Generic AMs – INTERNAL GENERIC and EXTERNAL details subcategories. On the right: mean number of INTERNAL GENERIC details per subcategory (Ev, Pl, Ti, Pe, and Th) for the controls and the two patient groups. On the left: mean number of EXTERNAL details per subcategory (Sem, Repet, and Other). Details are summed for two Generic AMs. The bars indicate the standard error of the mean for each group. Significant differences from the control group are indicated by an asterisk. *Note*: Ev = event details; Pe = perceptual details; Pl = place details; Th = thought/emotion details; Ti = time details; $^{*}p < 0.05$; $^{***}p < 0.001$.

this component of the AM narrative can become at least partially supported by extra-hippocampal structures under some conditions.

While we expected medial temporal structures to play a role in the AI, evidence also lead us to expect lateral temporal cortical structures to support some of the cognitive processes at play during script generation, for example semantic memory retrieval, narrative skills or semantic verbal fluency (Cosentino et al., 2006; Henry & Crawford, 2004; Patterson et al., 2007). Consistent with the literature, post-surgery TLE patients, in whom extrahippocampal temporal cortical structures are resected, were impaired on the script generation task. Meanwhile, pre-surgery patients, in whom these structures are spared, performed as controls on the script task. Importantly, there was no difference in performance between controls and the LTLE and RTLE patient groups, both composed of pre- and post-surgery patients. Nevertheless, we controlled for the potential interaction between performance on the script task and performance on the AI: we used performance on the script task as a covariate while comparing patients to controls on the AI. While the script covariate was significant for some detail categories, with the exception of generic time details, all group differences were significant when script performance was accounted for. Also, pre- and post-surgery patients performed similarly poorly on the AI, while only post-surgery patients were impaired on the script task. Together, these results indicate that patients' performance on the AI cannot be explained by a deficit in the cognitive functions at play during script generation, but reflects a true deficit for retrieving highly contextualized personal memories.

3.1. Implication for MTT

Our results on the modified AI and on the script generation task are broadly consistent with Multiple Trace Theory. As discussed earlier, MTT stipulates that the hippocampus is involved in the encoding and subsequent retrieval of event-specific AM, while more semantic forms of declarative memories, such as memory for scripts, can become supported by other neural structures (Moscovitch et al., 2005; Nadel & Moscovitch, 1997). We found that this pattern of sensitivity to MTL damage extends to memory for repeated events. TLE patients' performance on the script generation task, which captures the schema or gist of a prototypical familiar event, was normal. Similarly, patients showed no deficit in retrieval of event details, the story elements regarding unique and repeated events. By contrast, the retrieval of spatio-temporal and multi-sensorial re-experiential information was severely impaired, whether it was for an event-specific or a generic episode, suggesting that these aspects of the memory remain dependent on the hippocampus with repeated subsequent encoding. Importantly, the majority of the generic AMs reported here were described by the participants as blended, and not as a collection of separate, distinct episodes. These results give us confidence that our generic AMs were indeed experienced as generic, and were not abstracted on-line from many instances of separate episodes, at least at the conscious level. The current results have implications for the formulation of MTT: the key determinants of a memory's vulnerability to hippocampal damage are the perceptual qualities and spatial and temporal contextual information associated with an episode, not the detailed story elements of the episode, its semantic gist, or its temporal specificity.

As a side note, while the hippocampus was clearly implicated in the retrieval of both event-specific and generic episodes, our data do not address whether these two types of AM are also supported by the same neural structures in the rest of the brain. Neuroimaging work has identified subtle activation differences between the two AM types in areas such as the cingulate cortex, the left precuneus and fusiform gyrus, and the left superior temporal gyrus; overall though, the similarities in activation patterns and in functional connectivity with the hippocampus greatly outweighed the differences (Addis et al., 2004a,b), suggesting that the two AM types are supported by similar networks of brain structures.

3.2. Implications for other theories of hippocampal function

The paucity of perceptual details observed in our patients' memory narratives is also consistent with a model of AM retrieval according to which the MTL integrates visual details stored in higher order cortical areas (Greenberg, Eacott, Brechin, & Rubin, 2005). This model predicts that damage to the MTL should disrupt visual detail integration. It has been established that visual imagery strongly contributes to the self-rated vividness of event-specific AM (Rubin, Schrauf, & Greenberg, 2003), and that damaging the above-mentioned circuit leads to a decrease in the subjective, self-rated vividness and imageability of AM (Greenberg et al., 2005). Here, we demonstrate that damaging this circuit can also lead to a deficit on an objective measure of AM vividness: the number of perceptual details recalled from an episode, the majority of which were in the visual modality. While our analysis did not address this issue, it would be worth extending Greenberg et al. (2005)'s model by investigating how MTL damage affects vividness across sensory modalities.

Our finding that the MTL is not sensitive to the temporal specificity of AM is also consistent with recent understandings of hippocampal function, according to which the role of the hippocampus extends to a realm of cognitive functions beyond memory-related processes. Following Tulving's initial speculation, growing evidence suggests that the hippocampus plays a key role in complex mental simulation, whether imagined, prospective or remembered (Addis et al., 2007b; Addis & Schacter, 2008; Hassabis, Kumaran, Vann, & Maguire, 2007; Hassabis, Kumaran, & Maguire, 2007). Buckner and Carroll (2007) have proposed that the hippocampus is implicated in processes that involve shifting perspective from the immediate present to alternative perspectives. Other groups have similarly theorized that the hippocampus is crucial for imagining complex, spatially coherent scenes. Examples of processes requiring mental simulation include AM retrieval, imagining future or fictious events, spatial navigation, vivid dreaming (Buckner & Caroll, 2007; Hassabis & Maguire, 2007; Moscovitch et al., 2005; Schacter & Addis, 2007) and theory of mind (but see Rosenbaum et al. (2008) who cast doubt on this last possibility). According to this view, the hippocampus contributes to integrate details into experiential constructs which may or may not be temporally specific (e.g. event-specific AM versus imagined fictitious event). Our results fit within this theoretical framework by showing that memory for personal episodes can be vulnerable to hippocampal damage regardless of its temporal specificity. We identified the integration of multiple perceptual details as a defining characteristic of hippocampo-dependant mental simulation, and demonstrated the resilience of the detailed story elements of the memory construct to hippocampal damage. What is still unresolved is whether the hippocampus is crucial for all these tasks because it provides the detailed memories which serve as the building blocks for these other functions, but which are integrated by structures such as the prefrontal cortex, or whether the hippocampus is necessary also for binding these details together at retrieval as it does at encoding (Eichenbaum, Cohen, & Otto, 1992; Eichenbaum, 2004).

3.3. Implications for models of autobiographical memory

By demonstrating that both single and repeated personal events can be rich in re-experiential qualities, our results have implica-

tions for theoretical models of autobiographical memory. Conway (1996, 2001) and Conway and Pleydell-Pearce (2000) classifies AM according to three different levels of temporal specificity: event-specific AM, generic AM (repeated or extended events), and memory for life-time periods (general autobiographical facts). Our findings are inconsistent with Conway's (2001) claim that only event-specific AM have experience-near sensory-perceptual characteristics. We show that event-specific and generic AM can contain an equal amount of perceptual information, which demonstrates that temporal specificity and re-experiential qualities are in fact dissociable. Instead, our results support Brewer (1986, 1996) classification of AMs into four categories according to two distinct, dissociable factors: temporal specificity and re-experiential qualities. Additionally, the large number of perceptual details produced by our participants is consistent with the claim that imagery is one of the core characteristics of re-experiential memory for personal episodes (see Brewer, 1996, for a review).

The striking similarity in results between our two AM conditions also supports views according to which the line is blurred between unique and generic AM features. Neisser (1981) documented memories for singular events that contained elements from multiple repeated episodes, which he termed 'repisodic memories'. Similarly, Eichenbaum (2004) proposed a computational model in which the hippocampus is involved in representing both unique and generic features, building on the idea that common event features share a representation to promote efficient storage (e.g. McClelland, McNaughton, & O'Reilly, 1995). Of interest, our participants experienced most generic AMs in this study as blended constructs. By contrast, we found in pilot testing of this paradigm that memory for repeated events that took place in at least three different spatial locations were experienced as collections of distinct events and participants needed to abstract commonalities at retrieval actively and consciously (unpublished data). Thus, shared location and other contextual similarities between repeated episodes appear to favour the blending of representations of these events.

3.4. Laterality of the lesion

Our study did not reveal a significant difference in AI performance between RTL and LTL patients. Although some evidence from functional neuroimaging suggests that the left hippocampus plays a more prominent role in episodic AM than the right hippocampus (Gilboa et al., 2004; Maguire & Frith, 2003; Maguire et al., 2001; Maguire & Mummery, 1999; Nadel et al., 2007), other studies have reported that the right hippocampus can contribute just as actively to retrieval (Addis et al., 2004b; Denkova et al., 2006; Fink et al., 1996; Graham, Lee, Brett, & Patterson, 2003; Piefke, Weiss, Zilles, Markowitsch, & Fink, 2003; Piolino et al., 2004; Rekkas & Constable, 2005; Ryan et al., 2001; Steinvorth et al., 2006; Vandekerckhove et al., 2005). Behavioural evidence from TL patients also seems to indicate that damage to either hemisphere leads to comparable deficits in AM (Addis, 2005; Noulhiane et al., 2007; Viskontas et al., 2000; but see Voltzenlogel et al., 2006), corroborating the current findings. It is likely that each hemisphere contributes in a special way to AM (e.g. Addis et al., 2004b), though the nature of those contributions have yet to be determined. A finer discrimination of perceptual details into more specific categories (e.g. sensory modalities, spatial versus non-spatial information, etc.) may highlight functional differences between the two hemispheres in AM. That AM appears more lateralized on functional neuroimaging studies than on lesion studies suggests that the left hemisphere may assume a dominant role in retrieving or organizing of memories into a narrative, but that it draws on information supplied by both hemispheres (Addis et al., 2007a).

4. Conclusion

We have shown that the ability to retrieve experiential qualities of AM relies on the integrity of medial temporal structures which include the hippocampus. Our results show that with unilateral hippocampal damage, the story elements of the episode are preserved, but the perceptual details are lost. These data indicate that hippocampal function determines qualitative aspects of the re-experience, such as complexity and vividness in accordance with MTT (Moscovitch et al., 2005; Nadel & Moscovitch, 1997) and with Tulving's (1985) hypothesis regarding the nature of recollection. Future studies should look into how this re-experiential deficit affects different sensory modalities. Future work should also address whether MTL damage, which has been shown to reduce the number of re-experiential details and which impairs functions such as binding, also disrupts the organization of these details during AM retrieval.

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References

Addis, D. R. (2005). *Investigating the engagement of the hippocampus and related structures during autobiographical memory retrieval in healthy individuals and temporal lobe epilepsy patients*. Unpublished PhD thesis. Toronto, Canada: University of Toronto.

Addis, D. R., & Schacter, D. L. (2008). Constructive episodic simulation: Temporal distance and detail of past and future events modulate hippocampal engagement. *Hippocampus*, *18*, 227–237.

Addis, D. R., McIntosh, A. R., Moscovitch, M., Crawley, A. P., & McAndrews, M. P. (2004). Characterizing spatial and temporal features of autobiographical memory retrieval networks: A partial least squares approach. *NeuroImage*, *23*, 1460–1471.

Addis, D. R., Moscovitch, M., Crawley, A. P., & McAndrews, M. P. (2004). Recollective qualities modulate hippocampal activation during autobiographical memory retrieval. *Hippocampus*, *14*, 752–762.

Addis, D. R., Moscovitch, M., & McAndrews, M. P. (2007). Consequences of hippocampal damage across the autobiographical memory network in left temporal lobe epilepsy. *Brain*, *130*, 2327–2342.

Addis, D. R., Wong, A. T., & Schacter, D. L. (2007). Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia*, *45*, 1363–1377.

Bayley, P. J., Hopkins, R. O., & Squire, L. R. (2003). Successful recollection of remote autobiographical memories by amnesic patients with medial temporal lobe lesions. *Neuron*, *38*, 135–144.

Brewer, W. F. (1986). What is autobiographical memory? In D. C. Rubin (Ed.), *Autobiographical memory* (pp. 25–49). Cambrige, England: Cambridge University Press.

Brewer, W. F. (1996). What is recollective memory? In D. C. Rubin (Ed.), *Remembering our past: Studies in autobiographical memory* (pp. 19–66). Cambridge, England: Cambridge University Press.

Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *TRENDS in Cognitive Sciences*, *11*, 49–57.

Cipolotti, L., Shallice, T., Chan, D., Fox, N., Scahill, R., Harrison, G., et al. (2001). Long-term retrograde amnesia. . . the crucial role of the hippocampus. *Neuropsychologia*, *39*, 151–172.

Conway, M. A. (1996). Autobiographical memory. In E. L. Bjork & R. A. Bjork (Eds.), *Memory. Handbook of perception and cognition* (2nd ed., pp. 165–194). San Diego, CA: Academic Press, Inc.

Conway, M. A. (2001). Sensory-perceptual episodic memory and its context: Autobiographical memory. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *356*, 1375–1384.

Conway, M. A., & Pleydell-Pearce, C. W. (2000). The construction of autobiographical memories in the self-memory system. *Psychological Review*, *107*, 261–288.

Corkin, S., Amaral, D. G., González, R. G., Johnson, K. A., & Hyman, B. T. (1997). H M.'s medial temporal lobe lesion: Findings from magnetic resonance imaging. *The Journal of Neuroscience*, *17*, 3964–3979.

Cosentino, M., Chute, D., Libon, D., Moore, P., & Grossman, M. (2006). How does the brain support script comprehension? A study of executive processes and semantic knowledge in dementia. *Neuropsychology*, *20*, 307–318.

Denkova, E., Botzung, A. C., & Manning, L. (2006). Neural correlates of remembering/knowing famous people: An event-related fMRI study. *Neuropsychologia*, *44*, 2783–2791.

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

Eichenbaum, H., Otto, T., & Cohen, N. J. (1992). The hippocampus—what does it do? *Behavioral and Neural Biology*, *57*, 2–36.

Fink, G. R., Markowitsch, H. J., Reinkemeier, M., Bruckbauer, T., Kessler, J., & Heiss, W. D. (1996). Cerebral representation of one's own past: Neural networks involved in autobiographical memory. *The Journal of Neuroscience*, *16*, 4275–4282.

Gao, F. Q., Black, S. E., Leibovitch, F. S., Callen, D. J., Lobaugh, N. J., & Szalai, J. P. (2003). A reliable MR measurement of medial temporal lobe width from the Sunnybrook Dementia Study. *Neurobiology of Aging*, *24*, 49–56.

Gilboa, A., Winocur, G., Grady, C. L., Hevenor, S. J., & Moscovitch, M. (2004). Remembering our past: Functional neuroanatomy of recollection of recent and very remote personal events. *Cerebral Cortex*, *14*, 1214–1225.

Gilboa, A., Ramirez, J., Kohler, J., Westmacott, R., Black, S. E., & Moscovitch, M. (2005). Retrieval of autobiographical memory in Alzheimer's disease: Relation to volumes of medial temporal lobe and other structures. *Hippocampus*, *15*, 535–550.

Godbout, L., & Doyon, J. (1995). Mental representation of knowledge following frontal-lobe or postrolandic lesions. *Neuropsychologia*, *33*, 1671–1796.

Graham, K. S., & Hodges, J. R. (1997). Differentiating the roles of the hippocampal complex and the neocortex in long-term memory storage: Evidence from the study of semantic dementia and Alzheimer's disease. *Neuropsychology*, *11*, 77–89.

Graham, K. S., Lee, A. C. H., Brett, M., & Patterson, K. (2003). The neural basis of autobiographical and semantic memory: New evidence from three PET studies. *Cognitive, Affective & Behavioral Neuroscience*, *3*, 234–254.

Greenberg, D. L., Eacott, M. J., Brechin, D., & Rubin, D. C. (2005). Visual memory loss and autobiographical amnesia: A case study. *Neuropsychologia*, *43*, 1493–1502.

Hassabis, D., & Maguire, E. A. (2007). Deconstructing episodic memory with construction. *Trends in Cognitive Sciences*, *11*, 299–306.

Hassabis, D., Kumaran, D., & Maguire, E. A. (2007). Using imagination to understand the neural basis of episodic memory. *The Journal of neuroscience*, *27*, 14365–14374.

Hassabis, D., Kumaran, D., Vann, S. D., & Maguire, E. A. (2007). Patients with hippocampal amnesia cannot experience new experiences. *Proceedings of the National Academy of Sciences of the United States of America*, *104*, 1726–1731.

Henry, J. D., & Crawford, J. R. (2004). A meta-analytic review of verbal fluency performance following focal cortical lesions. *Neuropsychology*, *18*, 284–295.

Kallai, J., Csathó, A., Kövér, F., Makány, T., Nemes, J., Horváth, K., et al. (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 Research*, *140*, 199–210.

Kreiman, K., Kock, C., & Fried, I. (2000). Imagery neurons in the human brain. *Nature*, *408*, 357–361.

Levine, B., Svoboda, E., Hay, J. F., Winocur, G., & Moscovitch, M. (2002). Aging and autobiographical memory: Dissociating episodic from semantic retrieval. *Psychology and Aging*, *17*, 677–689.

Levine, B., Turner, G. R., Tisserand, D., Henevor, S. J., Graham, S. J., & McIntosh, A. R. (2004). The functional neuroanatomy of episodic and semantic autobiographical remembering: A prospective functional MRI study. *The Journal of Cognitive Neuroscience*, *16*, 1633–1646.

Maguire, E. A. (2001). Neuroimaging studies of autobiographical event memory. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *356*, 1441–1451.

Maguire, E. A., & Frith, C. D. (2003). Lateral asymetry in the hippocampal response to the remotness of autobiographical memories. *The Journal of Neuroscience*, *23*, 5302–5307.

Maguire, E. A., & Mummery, C. J. (1999). Differential modulation of a common memory retrieval network revealed by positron emission tomography. *Hippocampus*, *9*, 54–61.

Maguire, E. A., Henson, R. N. A., Mummery, C. J., & Frith, C. D. (2001). Activity in prefrontal cortex, not hippocampus, varies parametrically with the increasing remoteness of memories. *NeuroReport*, *12*, 441–444.

McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insight from the successes and failures of connectionist models of learning and memory. *Psychological Review*, *102*, 419–457.

McGraw, K. O., & Wong, S. P. (1996). Forming inferences about some intraclass correlation coefficients. *Psychological Methods*, *1*, 30–46.

McKinnon, M. C., Nica, E. I., Sengdy, P., Kovacevic, N., Moscovitch, M., Freedman, M., et al. (2008). Autobiographical memory and patterns of brain atrophy in frontotemporal lobar degeneration. *Journal of Cognitive Neuroscience*, *20*, 1839–1853.

Moscovitch, M., Yaschyshyn, L., Ziegler, M., & Nadel, L. (2000). Remote episodic memory and retrograde amnesia: Was Endel Tulving right all along? In Ed. Tulving (Ed.), *Memory, consciousness and the brain: The Tallinn conference* (pp. 331–345). Philadelphia, PA: Psychology Press/Taylor & Francis.

Moscovitch, M., Rosenbaum, R. S., Gilboa, A., Addis, D. R., Westmascott, R., Grady, C., et al. (2005). Functional neuroanatomy of remote episodic, semantic and spatial memory: A unified account based on multiple trace theory. *The Journal of Neuroanatomy*, *207*, 35–66.

Nadel, L., & Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current Opinion in Neurobiology*, *7*, 217–227.

Nadel, L., Campbell, J., & Ryan, L. (2007). Autobiographical memory retrieval and hippocampal activation as a function of repetition and the passage of time. *Neural Plasticity*, 14. Article ID 90472.

Neisser, U. (1981). John Dean's memory: a case study. *Cognition*, *9*, 1–22.

Noulhiane, M., Piolino, P., Hasboun, D., Clemenceau, S., Baulac, M., & Samson, S. (2007). Autobiographical memory after temporal lobe resection: Neuropsychological and MRI volumetric findings. *Brain*, *130*, 3184–3199.

Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, *8*, 976–987.

Piefke, M., Weiss, P. H., Zilles, K., Markowitsch, H. J., & Fink, G. R. (2003). Differential remotness and emotional tone modulate the neural correlates of autobiographical memory. *Brain*, *126*, 650–668.

Piolino, P., Giffard-Quillon, G., Desgranges, B., Chetelat, G., Baron, J.-C., & Eustache, F. (2004). Re-experiencing old memories via hippocampus: A PET study of autobiographical memory. *NeuroImage*, *22*, 1371–1383.

Pruessner, J. C., Collins, D. L., Pruessner, M., & Evans, A. C. (2001). Age and gender predict volume decline in the anterior and posterior hippocampus in early adulthood. *Journal of Neuroscience*, *21*, 194–200.

Rekkas, P. V., & Constable, R. T. (2005). Evidence that autobiographical memory retrieval does not become independent of the hippocampus: An fMRI study contrasting very recent with remote events. *The Journal of Cognitive Neuroscience*, *17*, 1950–1962.

Rosenbaum, R. S., McKinnon, M. C., Levine, B., & Moscovitch, M. (2004). Visual imagery deficits, impaired strategic retrieval, or memory loss: Disentangling the nature of an amnesic person's autobiographical deficit. *Neuropsychologia*, *42*, 1619–1635.

Rosenbaum, R. S., Kohler, S., Schacter, D. L., Moscovitch, M., Westmacott, R., Black, S. E., et al. (2005). The case of KC.: Contributions of a memory-impaired person to memory theory. *Neuropsychologia*, *43*, 989–1021.

Rosenbaum, R. S., Moscovitch, M., Foster, J. K., Verfaellie, M., Gao, F. Q., Black, S. E., et al. (2008). Patterns of autobiographical memory loss in medial temporal lobe amnesic patients. *Journal of Cognitive Neuroscience*, *20*, 1490–1506.

Rubin, D. C., Schrauf, R. W., & Greenberg, D. L. (2003). Belief and recollection of autobiographical memories. *Memory and Cognition*, *31*, 887–901.

Ryan, L., Nadel, L., Keil, K., Putnam, K., Schnyer, D., Trouard, T., et al. (2001). Hippocampal complex and retrieval of recent and very remote autobiographical memories: Evidence from functional magnetic resonance imaging in neurologically intact people. *Hippocampus*, *11*, 707–714.

Schacter, D. L., & Addis, D. R. (2007). The cognitive neuroscience of constructive memory: Remembering the past and imagining the future. *Philosophical Transactions of the Royal Society B*, *362*, 773–786.

Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology Neurosyrgery and Psychiatry*, *20*, 11–12.

Selnes, O. A., Jacobson, L., Machado, A. M., Becker, J. T., Wesch, J., Miller, E. N., et al. (1991). Normative data for a brief neuropsychological screening battery. *Perceptual and Motor Skills*, *73*, 539–550.

Steinvorth, S., Levine, B., & Corkin, S. (2005). Medial temporal lobe structures are needed to re-experience remote autobiographical memories: Evidence from H.M. and W.R. *Neuropsychologia*, *43*, 479–496.

Steinvorth, S., Corkin, S., & Halgren, E. (2006). Ecphory of autobiographical memories: An fMRI study on recent and remote memory retrieval. *Neuroimage*, *30*, 285–298.

Strauss, E. & Spreen, O. (Eds.). (1991). Rey Visual Design Learning Test (RVDLT). In *A compendium of neuropsychological tests* (pp. 168–176). New York, NY: Oxford University Press.

Svoboda, E., McKinnon, M. C., & Levine, B. (2006). The functional neuroanatomy of autobiographical memory: A meta-analysis. *Neuropsychologia*, *44*, 2189–2208.

Tanskanen, P., Veijola, J. M., Piipo, U. K., Haapea, M., Miettunen, J. A., Pyhtinen, J., et al. (2005). Hippocampus and amygdala volumes in schizophrenia and other psychoses in the Northern Finland 1996 birth cohort. *Schizophrenia Research*, *75*, 283–294.

Tulving, E. (1985). Memory and consciousness. *Canadian Psychologist*, *25*, 1–12.

Vandekerckhove, M. M. P., Markowitsh, H. J., Mertens, M., & Woermann, F. G. (2005). Bi-hemispheric engagement in the retrieval of autobiographical episodes. *Behavioural Neurology*, *16*, 203–210.

Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Conneley, A., Van Paesschen, W., & Mishkin, M. (1997). Differential effects of early hippocampal pathology on episodic and semantic memory. *Science*, *277*, 376–380.

Viskontas, I. V., McAndrews, M. P., & Moscovitch, M. (2000). Remoted episodic memory deficits in patient with unilateral temporal lobe epilepsy and excisions. *The Journal of Neuroscience*, *20*, 5853–5857.

Voltzenlogel, V., Després, O., Vignal, J. P., Steinhoff, B. J., Kehrli, P., & Manning, L. (2006). Remote memory in temporal lobe epilepsy. *Epilepsia*, *47*, 1329–1336.

Wechsler Abbreviated Scale of Intelligence (1999). San Antonio, TX: The Psychological Corporation (Harcourt Assessment, Inc.).