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# The Perceptual Richness of Complex Memory Episodes is Compromised by Medial Temporal Lobe Damage

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**ABSTRACT: Perceptual richness, a defining feature of episodic memory, emerges from the reliving of multimodal sensory experiences. Although the importance of the medial temporal lobe (MTL) to episodic memory retrieval is well documented, the features that determine its engagement are not well characterized. The current study assessed the relationship between MTL function and episodic memory's perceptual richness. We designed a laboratory memory task meant to capture the complexity of memory for life episodes, while manipulating memory's perceptual content. Participants encoded laboratory episodes with rich (film clips) and impoverished (written narratives) perceptual content that were matched for other characteristics such as personal significance, emotionality and story content. At retrieval, participants were probed to describe the stories' perceptual features and storyline. Participants also recalled autobiographical memories (AMs) in a comparison condition. We compared the performance of patients with unilateral medial temporal lobe epilepsy (mTLE) and healthy controls to assess how damage to the MTL affects retrieval in these conditions. We observed an overall decrease in detail count in the mTLE group, along with a disproportionate deficit in perceptual details that was most acute in the AM and the perceptually enriched film clip conditions. Our results suggest that the impaired sense of reliving the past that accompanies MTL insult is mediated by a paucity of perceptual episodic memory details. We also introduce a new protocol that successfully mimics naturalistic memories while benefiting from the experimental control provided by using laboratory stimuli. © 2014 Wiley Periodicals, Inc.**

**KEY WORDS: autobiographical memory; hippocampus; recollection; episodic memory; medial temporal lobe epilepsy**

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## INTRODUCTION

Although the importance of the medial temporal lobe (MTL) to episodic memory is well established, much ongoing research is focused on refining our understanding of the types of memory processes and representations supported by the MTL during retrieval. It has been shown that recollection, the sense of travelling mentally back in time to relive past events, depends crucially on the MTL (e.g. Nadel and Moscovitch, 1997; Moscovitch and McAndrews, 2002; Moscovitch et al., 2005; Piolino, Desgranges, and Eustache, 2009; Ranganath, 2010). Recollection, however, can be broken down into several components that include self-projection and awareness of the self in time, sense of "pastness," the binding of memory details into a subjective mental construct, and the vivid evocation of past sensory and mental experiences. The current study tested the hypothesis that perceptual richness, the retrieval of rich sensory-based memory details, is among the key determinants of MTL engagement at retrieval. Specifically, we tested whether medial temporal lobe epilepsy (mTLE), a condition that compromises the integrity of the MTL, affects the perceptual richness of complex episodic memories acquired both in the real world and in the laboratory.

Perceptual imagery reflects the combination of impressions from different sensory modalities experienced in one's mind's eye. It is a core feature of episodic memory, as the retrieval of context-specific perceptual details contributes to how vividly one can recollect past events (Brewer, 1986, 1995; Rubin et al., 2003; Conway, 2009). A consideration of neuroanatomy provides some evidence consistent with our suggestion that retrieving imagery-based episodic details depends on the MTL. Patterns of hippocampal connectivity provide an anatomical template for the hippocampus to play a central role in the integration of perceptual details into rich memory constructs. Input from the posterior neocortex, via the parahippocampal gyrus which supports spatial and scene representation (Epstein and Kanwisher, 1998; Epstein, 2008), reaches the hippocampus through the entorhinal cortex, and converges into the cornu ammonis (CA) subfields with input from the apex of the ventral visual stream which reaches the hippocampus via the

perirhinal and entorhinal cortex (Eichenbaum and Lipton, 2008; Litman et al., 2009; Derdikman and Moser, 2010; Ranganath, 2010; Suzuki, 2010). A convergence of indirect inputs from olfactory and polysensory cortical regions (Insausti et al., 1987; Amaral and Lavenex, 2007) are also funneled through the entorhinal cortex, and likely contribute to add richness and complexity to memory for past events.

The cognitive neuroscience literature also suggests a link between MTL function and the perceptual richness of episodic memory. For example, reports of autobiographical memories by patients with mTLE have a paucity of perceptual features (St-Laurent et al., 2009). In healthy individuals, hippocampal activation has been shown to correlate with ratings of vividness (Gilboa et al., 2004; Rabin et al., 2010), imagery use (Andrews-Hanna et al., 2010) and intensity of reliving (St Jacques et al., 2012; but see Daselaar et al., 2008) during the retrieval of autobiographical events. Furthermore, evidence from functional neuroimaging indicates that connectivity between the hippocampus and posterior visual association regions supports retrieval and elaboration of episodic details during autobiographical recall (McCormick et al., in press). Tellingly, patient Jon, a young amnesic who has grown up with extensive bilateral hippocampal lesions, describes himself as "the complete opposite of a visual person." He adds: "I find it difficult to visualize things in my mind's eye. When I do try, I can do it. It doesn't come automatically, though. I know it probably does with most people. It's not something I used to be able to do, but I've worked on it a lot over the years" (Maguire et al., 2010). The hippocampus has also been shown to be essential to scene construction and for imagining the future, which require the assemblage and retrieval of object and spatial details into complex scenes and events (Hassabis and Maguire, 2007; Hassabis et al., 2007; Hassabis and Maguire, 2009; Schacter and Addis, 2009; Addis et al., 2011). Like episodic memory retrieval, these processes require binding of disparate multimodal elements such as sounds, smells, visual inputs, people and objects (Hassabis and Maguire, 2009).

Although some evidence of the impact of MTL damage on the retrieval of perceptual memory content emerges from self-reports of extended events such as past autobiographical episodes or future scenarios, there is no empirical work demonstrating a specific loss of multi-modal perceptual episodic details in well controlled situations such as AM-like laboratory events. Our study was intended to fill this gap by using a novel episodic memory task (see below) that dissociated perceptual content from knowledge about what happened during an event, two forms of episodic memory content that are intertwined in naturalistic memories. Our task manipulated the perceptual richness of laboratory memory episodes at encoding, and quantified the richness of memory representations at retrieval. We then compared performance between healthy individuals and patients with unilateral mTLE to determine whether compromised MTL integrity affects perceptually rich memory content.

Some of our patients suffered from seizures of unilateral hippocampal origin, a condition linked to MTL damage and to poor autobiographical memory (AM; Viskontas et al., 2000; Addis et al., 2007; Noulhiane et al., 2008; St-Laurent et al., 2011). The remainder of our patient group had received a unilateral resection of temporal lobe structures, which included at least the anterior half of the hippocampus, in order to control seizures of unilateral hippocampal origin. Although postsurgery patient's MTL lesions are more extensive than those of presurgery candidates, evidence indicates that both groups suffer from a comparable autobiographical memory impairment (Viskontas et al., 2000; St-Laurent et al., 2009; Herfurth et al., 2010; McAndrews, 2012). Here, we refer to both pre- and postsurgery patients' conditions as mTLE. Assessing memory in patients with mTLE enables us to address fine-grained questions about the impact of MTL damage on memory content because, unlike patients with hippocampal amnesia who have very few memories for personal events (e.g., Steinvorth et al., 2005), their memory performance is not at floor. Also, the unilateral aspect of their disease provides an opportunity to assess the respective contribution of the left and right MTL to AM and episodic memory.

One definitive advantage of using laboratory events to investigate perceptual richness is the ability to control for other dimensions such as complexity (e.g., how much happened), emotionality, and personal relevance, that are typically correlated in studies of naturalistic AMs (Levine et al., 2002; Rubin et al., 2003; Daselaar et al., 2008), parameters which are known also to modulate hippocampal engagement (Addis et al., 2004). Our task required participants to study short laboratory events with an unfolding story line, presented in one of two formats: as perceptually enriched audio-visual film clips or as perceptually impoverished written narratives (see also Furman et al., 2007; Kurby and Zacks, 2008; Wechsler, 2009; Ben-Yakov and Dudai, 2011 for examples of other paradigms using film clips or narratives). Crucially, *story content* ("what happened in the story?") was matched between these two conditions, allowing us to determine how MTL damage affects the retrieval of perceptually rich and of impoverished material regardless of its event detail content, which cannot be achieved with naturalistic events such as AM, constructed scenes or future events. Both types of laboratory events were designed to resemble autobiographical episodes: they had a narrative structure that unfolded over time, with one or more characters interacting in a given situation, performing sequences of actions which could be re-told and rehearsed (Radvansky et al., 2005). Using laboratory episodes also allowed us to minimize the influence of other characteristics of no interest to our hypothesis, such as emotionality and personal relevance.

In addition, our paradigm included an AM condition during which participants retrieved memories of personal life episodes. The purpose of including this condition was to compare the magnitude of the anticipated deficit in retrieval of AM perceptual details (St-Laurent et al., 2009) to performance on the two laboratory conditions in participants with mTLE. Showing that the type of deficits found in our laboratory conditions corresponded to those in AM, over which we have little control and whose content we cannot verify, would lend validity to findings on AM.

For our task, laboratory events (narratives and film clips) were encoded, and then AMs and laboratory events were retrieved using a cued recall paradigm. Participants were given a few seconds to recall each AM, clip or narrative, after which they were probed to provide a verbal description of their retrieval experience. Participants reported both the *story* elements they had time to retrieve ("what happened": who did what, what was the situation, etc.), as well as the *perceptual* features they re-experienced at recall (what they "saw in their mind's eye": visual, auditory and other sensory details). Story and perceptual elements were identified from participants' transcripts and tallied according to a scoring procedure adapted from Levine and colleagues (Levine et al., 2002). Transcripts were also fed to the Linguistic Inquiry and Word Count software, or LIWC, to perform an automated count for words falling under 80 different categories defined by an integrated dictionary (LIWC2007; Pennebaker et al., 2007). Word counts from categories that reflected perceptual memory content were included in the current analysis to corroborate our manual detail scoring.

Based on our hypothesis that the MTL is necessary for representing perceptually rich information in memory, we made the following predictions:

–Controls should recall more perceptual details in the perceptually enriched film clip than in the perceptually impoverished narrative condition.

–Patients with mTLE should retrieve fewer perceptual details than controls across all three memory conditions, indicating that the paucity of perceptual autobiographical memory details observed in mTLE (St-Laurent et al., 2009) can also be observed for laboratory memories.

–The enhancement of perceptual details in the clip relative to narrative condition for controls should be significantly reduced in the mTLE group, indicating that MTL damage is particularly disruptive to the ability to benefit from perceptual enrichment of memoranda.

–Similar patterns of impairments should be observed between the AM and the perceptually rich clip condition.

–As story content was designed to be matched between the film clip and the narrative conditions, all participants should recall similar numbers of story details in both conditions. However, participants with mTLE could recall fewer story details than controls, based on evidence that the MTL plays a supportive role in memory for episodic event details.

## MATERIALS AND METHODS

### Participants

Thirty-one participants with mTLE (17 with right- and 14 with left-lateralized pathology) and 15 neurologically intact controls were tested on this paradigm. Participants with mTLE were recruited through the Epilepsy Clinic of the Toronto Western Hospital following a protocol approved by the University Health Network's Research Ethics Board. Controls were recruited through advertisement in the community, among staff from the Toronto Western Hospital, and among friends and colleagues.

All 12 presurgery participants with mTLE were candidates for a unilateral temporal lobe resection. Six presurgery participants had seizures originating in the right hippocampus, and the remaining six participants had seizures originating in the left hippocampus. Five of these presurgery participants (three right, two left) were diagnosed with mesial temporal sclerosis (MTS) by a radiologist according to clinical criteria of atrophy on T1-weighted MRI scans and high intensity indicative of gliosis on T2-weighted MRI scans. One pre-surgery participant (left) had an arteriovenous malformation in the left medial temporal lobe, three (two right, one left) had indications of neuroepithelial tumors in their epileptic medial temporal lobe, and the other four (two right, two left) had normal-looking brains based on MRI scans. Among the postsurgery mTLE participants, 14 had received a traditional unilateral resection of the anterior temporal lobe that included the temporal pole, the amygdala, the anterior portion of the hippocampus, the rhinal and lateral temporal cortex, and portions of the parahippocampal cortex (six were left and eight were right lateralized). The remaining five postsurgery participants (two left, three right) had received a selective amygdalo-hippocampectomy that included the amygdala, the anterior two-thirds of the hippocampus, the rhinal cortex and portions of the parahippocampal cortex. One participant with a left selective resection had an arachnoid cyst in the contralateral temporal lobe that displaced the tissue, which was described as otherwise healthy by a radiologist. In all the other participants, no structural brain damage was observed outside the epileptogenic/resected temporal lobe. All postsurgery participants were seizure free at the time of testing which occurred at least 6 months following surgery.

In order to quantify potential language-dependent effects, participants with mTLE were classified according to whether their pathology was ipsilateral or contralateral to their language dominant hemisphere. Two postsurgery participants with left-lateralized mTLE whose language was atypically localized in the right hemisphere were merged with pre- and postsurgery participants with right mTLE whose language was left-lateralized. This group is referred to as nonlanguage-dominant. Participants with left mTLE whose language was left-lateralized are referred to as language-dominant. All participants were fluent English speakers, and only two controls were not native English speakers. Table 1 presents the mTLE participants' performance on neuropsychological tests, as well as additional demographic information about the mTLE participants and the control group.

### Paradigm

All testing was performed on a Lenovo T500 computer using E-Prime 2.0 (Psychology Software Tools Inc. Release candidate version 2.0.8.22).

*TABLE 1.*

*Mean Demographic and Neuropsychological Characteristics of the Control and mTLE Groups*

| | Controls ($n = 15$) | N-Domin mTLE ($n = 19$) | Domin mTLE ($n = 12$) | Norms |
|---|---|---|---|---|
| Gender (M/F) | 3M/12F | 8M/11F | 5M/7F | n/a |
| Surgical status (pre/postsurgery) | n/a | 13 Post/6 pre | 6 Post/6 pre | n/a |
| Age (yr) | 40.9 (10.0) | 38.9 (10.1) | 46.8 (10.4) | n/a |
| Years of education | 15.7 (2.3) | 14.1 (2.1) | 14.6 (2.2) | n/a |
| WASI full scale IQ | n/a | 101.4 (7.7) | 104.6 (13.8) | 100 (15)[a] |
| Performance IQ | n/a | 98.7 (9.0) | 105.3 (14.2) | 100 (15)[a] |
| Verbal IQ | n/a | 103.8 (8.7) | 104.8 (14.2) | 100 (15)[a] |
| WASI matrix reasoning subtest (standard score) | 11.7 (3.0) | 10.5 (2.7) | 11.2 (3.1) | 10 (3)[a] |
| RAVLT total recall score | n/a | 48.4 (7.3) | 45.0 (9.7) | 51.1 (8.6)[a] |
| RVDLT total recall score | n/a | 31.3 (10.2) | 37.4 (10.9) | 44.4 (12.4)[b] |
| Warrington words | n/a | 46.9 (3.0) | 42.2 (4.2) | 45.5 (3.2)[c] |
| Warrington faces | n/a | 38.4 (5.0) | 40.2 (4.3) | 44.8 (3.3)[c] |
| Verbal phonemic fluency (FAS) | n/a | 36.4(7.7) | 41.1 (10.0) | 34.2 (12.5)[a] |
| Boston naming test | n/a | 52.8 (7.0) | 48.4 (9.8) | 55.5 (3.9)[b] |

Standard deviation is between parentheses. Norms were obtained from 40 to 49 years old.
[a]Strauss, Sherman and Spreen (2006).
[b]Spreen and Strauss (1991).
[c]Warrington (1984).
Domin = language-dominant; N-Domin = nonlanguage-dominant; F = female; M = male; IQ = Intellectual Quotient; n/a = not applicable; RAVLT = Rey auditory verbal learning test, RVDLT = Rey visual design learning test; WASI = Wechsler Abbreviated Scale of Intelligence.

## Encoding

Eleven memories from the participants' personal life were selected from a list of suggestions (e.g. "New Year's Eve celebration," "Learning about someone's condition," "Walking through a new city for the first time"). One memory was reserved for practice. Participants selected personal events (AMs) that took place over a year ago, and lasted from a few minutes to a few hours. Each AM was given a title that would serve as retrieval cue. Memories were typically selected in the laboratory on testing day. The few participants whose memories were collected a few days in advance (e.g., over the phone) were read their AMs' titles at the beginning of the testing session to ensure the cues were still effective.

During the story encoding phase (see Fig. 1) participants were shown 20 short laboratory events (LEs) on a computer screen, and sound was delivered through headsets. For each participant, events were randomly assigned to one of two conditions, so that 10 LEs were presented as verbal narratives, and 10 LEs were presented as film clips. The film clips were 23s in duration, and contained minimal or no English dialogue, so that the story was carried by the actions of the actors on screen. Out of 20 clips, only 3 contained minimal English dialogue (e.g., "goodbye" while waving), 10 contained no dialogue, and 7 contained dialogue in a foreign language. The clips were presented at the center of a 15" screen, within a window that occupied 45% and 42% of the screen's width and height, respectively.

The narratives were verbal descriptions of what took place in the film clip (see Supporting Information). Five written sentences were presented in the middle of a white screen (Courier New, Black, Font 18), one sentence at a time, for 6 s each. A male voice-over was played simultaneously, so that sentences were read to the participant. An LEs title was displayed on screen for 2 s immediately before and after the LE was presented. Participants were instructed to pay attention to the titles, and to try their best to remember what took place in the story. LEs were presented in alternating blocks of three or four from the same condition, narrative or clip. The block to which clips and narratives were assigned, and their order within that block, was randomized for each participant. The material used was developed through pilot testing in healthy adult participants. Our final pilot data indicated that the retained story content was equivalent between the narrative and the clip condition, but that the two conditions differed considerably in the amount of perceptual content experienced at recall (as determined through detail count; see Scoring and data analysis section).

## Retrieval

Immediately after the encoding phase, participants received instructions and underwent a practice session during which they encoded two additional LEs (one narrative and one clip), which they then retrieved along with the AM reserved for practice. Retrieval took place immediately after practice, 15 to 20 min following encoding. At retrieval, the condition, "Laboratory Memory" or "Autobiographical Memory," was indicated on screen for 1 s, followed by a block of three or four trials from that condition. Stories originally seen as narratives and clips were intermixed randomly within the Laboratory Memory condition. For each trial, a title was displayed for 16

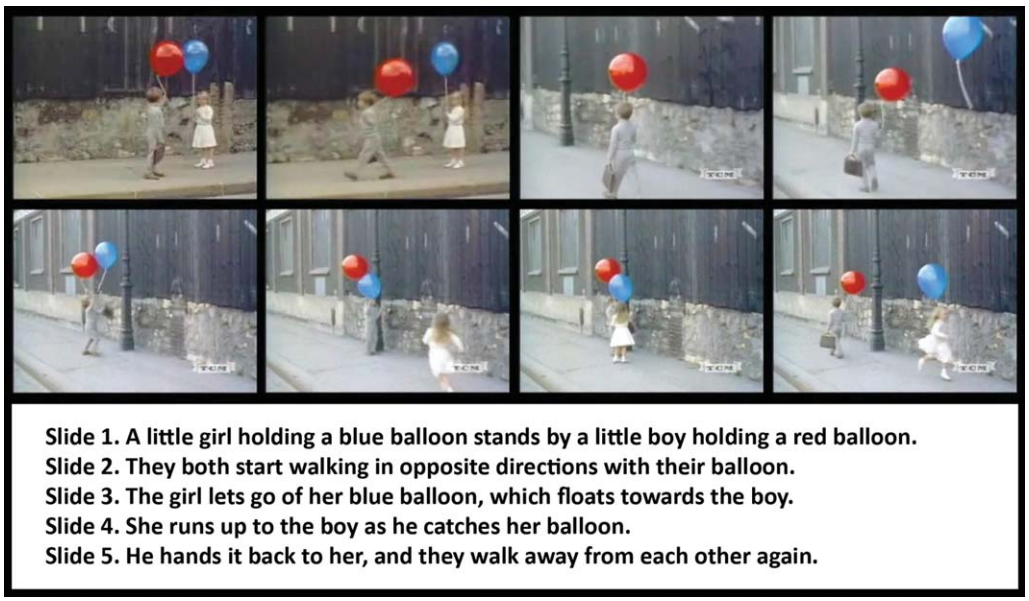


**FIGURE 1. Example of the video and narrative versions of a laboratory event. Top: frames from the video, which was a 23 s extract from the movie The Red Balloon (Lamorisse, 1956). Bottom: segments 1 to 5 from the narrative version that were shown on five consecutive on-screen slides (with recorded voice-over).**

s. For AM trials, participants were instructed to re-experience their personal memory in as much details as possible over those 16 s. For LE trials, they were told to recount silently what took place in the story, from beginning to end. The 16 s retrieval time limit was used to constrain the amount of AM details retrieved. Pilot testing indicated that most healthy adults reported taking under 13 s to recall an entire LE, and so 16 s was a sufficient time window for participants to complete their recall.

After the 16 s elapsed, participants used a keypad to rate their memory's *Story Content* on a 1 to 5 Likert scale, for which 1 = "no LE/AM details," and 5 = "all the LE details/my most detailed AM (in the context of this task)." Then, they rated the *Vividness* of their memory on a 1 to 5 scale, for which 1 = "no visual/perceptual details," and 5 = "my most vivid LE/AM (in the context of this task)." Vividness was defined to participants as the totality of sensory details (visual, auditory, olfactory, gustatory, tactile, proprioceptive, etc.) they experienced while recalling the memory. Then, participants were recorded with a microphone while they narrated everything they had time to recall within the 16 s time limit. First, they were given up to 100 s to describe what they recalled about the memory's story content: what happened either during their personal event or in the LE (who did what, what was the situation, etc.). Then, they were given up to 100 s to report any perceptual details they experienced in their mind during the 16 s time limit, including images of characters or people, scene elements, scents, tastes, physical sensations, sounds, etc. Participants were instructed to describe perceptual memory details experienced through all senses, including visual, auditory, olfactory, gustatory, tactile, and proprioceptive details.

It is important to note that participants were instructed to report any sensory elements they experienced in their mind at retrieval, regardless of whether such details were originally present at encoding. This is especially relevant to the narrative condition, for which, unlike in the clip and AM conditions, participants were *told* rather than *shown* what happened, and for which stories were practically devoid of perceptual content (see Fig. 1 and Supporting Information). Thus, if participants visualized elements associated with the narrative at retrieval which they were not shown at encoding but could have imagined as they remembered the story (e.g., a person's shape or face, his or her voice, elements from the scenery, etc.), they were instructed to report these perceptual details just as they did for those they saw in the clip condition. Typically, unless instructed otherwise, we find that participants tend to report only what they encoded, and imagery experienced in the narrative condition may thus be underestimated. Rather than assuming that perceptual imagery differed during narrative and clip retrieval based on what was shown at encoding, we decided to validate this assumption by quantifying all perceptual details experienced by participants when they recalled stories from each condition. In doing so, we hoped to characterize more appropriately the perceptual richness of these conditions irrespective of its provenance (on the screen, on the "page," or in the mind). Growing evidence indicates that damage to the MTL disrupts non-recall tasks that require imagining new scenes and visualizing future or alternative events (Hassabis et al., 2007; Addis et al., 2008; Rosenbaum et al., 2009; Race et al., 2011), and so we considered it plausible that participants with mTLE may experience less imagery than controls even when encoding and retrieving perceptually impoverished

**NARRATIVE (Control Participant #20)**

**1st Recording (Story Content) - What happened?**

A boy is walking down the street (***Sto***) and two boys run up to him (***Sto***) and push him down to the ground (***Sto***) and run off (***Sto***). As the boy is getting up (***Sto***) and grabbing his glasses (***Sto***), obviously they're knocked off, he looks across the street, and he sees two mimes (***Sto, Pe***), miming a sad face and then putting the hand over the face to change the sad into a happy face (***Sto, Pe***). The boy puts on his glasses to see this (***Sto***) and the boy smiles (***Sto, Pe***) and then turns and runs away (***Sto***).

**2nd Recording (Perceptual Content) - What did you perceive in your mind's eye?**

Visually, even thought this was a written story I can kind of visualize the mimes, I see the boy with the glasses (***Pe***), I don't really visualize the bullies. I don't have any other sensory thing other than visual.

**Story Details: 11, Perceptual Details: 4**

**FILM CLIP (Control Participant #24)**

**1st Recording (Story Content) - What happened?**

There's a boy in the middle of the street (***Sto, Pe***), two kids on each end of his left side and right side come (***Sto, Pe***) and basically knock him down, onto the floor (***Sto, Pe***), he has a backpack, a brown backpack on his back (***Pe***). He gets up (***Sto***) and he looks in front of him and he sees two mimes looking at him (***Sto, Pe***) and basically putting on a happy face (***Sto***). The kid smiles (***Sto, Pe***), he puts his glasses on (***Sto***), and he runs down the street (***Sto***).

**2nd Recording (Perceptual Content) - What did you perceive in your mind's eye?**

I remember it was a street, I believe it was the Eiffel tower (***Pe***). I remember he had a brown bag, he had black glasses (***Pe***), eventually when he put them on (***Pe***). I remember the mimes, they were behind a little gate or a fence, a black fence (***Pe***). And that's about it.

**Story Details: 9, Perceptual Details: 10**

**FIGURE 2. Recall of a laboratory event seen as a narrative or a film clip by two different control participants. Recall is scored according to the procedure employed in the current study. Pe = Perceptual Detail; Sto = Story Detail.**

narratives. Note, however, that no additional imagining was encouraged in the narrative condition, and that visualization was not *required* to retrieve narratives: participants were told explicitly not to make a special effort to conjure up vivid images of the memories. They were simply encouraged to report any incidental perceptual imagery they may have experienced in their mind when recalling the material.

There were three blocks of retrieval trials, interspaced by two breaks of at least 30 s. Two blocks contained three AMs and six LEs, and one block contained four AM and eight LE trials. Each AM or LE was attributed to a block randomly, and the order of first, second, and third block was randomized for each participant. On average, participants took about 45 min to complete the retrieval portion of the study. Note that retention intervals were on a different time scale for AMs than for the laboratory episodes, which were between 20 and 100 min old, rather than going back weeks, months, or years. However, retention intervals were equated between the two laboratory memory conditions, ruling out a concern that this factor mediated differences in performance between the narrative and the clip condition.

## *Scoring and data analysis*

Recordings from the retrieval trials were transcribed by MSL and RJ. Each retrieval trial produced two recordings: first, the recall of "story content," and second, the recall of "perceptual content." Transcripts from both recordings were broken down into *meaningful units of information*, or details, according to a scoring system adapted from Levine et al. (2002; see Fig. 2 for examples of scored protocols). Details were tallied across the two recordings, so that a single score was available per trial for each detail category. Only information that was specific to what took place within the LE or AM was scored. Less specific information, such as general opinions or facts, and details that pertained to a different event, were not scored (i.e., they were ignored). Also, no additional points were given for repetitions. In both recordings, memory-specific details were categorized into one, or both, of two detail categories: *Story Details*, and *Perceptual Details*. Story Details corresponded to information about "what happened," such as the type of event described (e.g., a lab meeting), the people who were present, their actions and conversations, and other happenings. Thoughts or emotions experienced by the person at the time a personal event took place were considered mental events, and were counted as Story Details (e.g., "I was shocked when she told me"). Opinions about an event that were not experienced at the time the event took place were not counted (e.g., "this is such sad story").

Perceptual details corresponded to information experienced through the senses, that was either visual (light intensity, elements from a scene, pieces of clothing, objects in the room), auditory (laughter, street sounds), olfactory or gustatory (smell of rain, coffee taste), tactile or proprioceptive (feeling tired or sick, being cold, dizzy, feeling your skin burning). While most details were categorized exclusively as Story details or as Perceptual details, some text segments that contributed to advance the story by describing what people or story characters were doing, while also reflecting sensory imagery, were counted in both detail categories (e.g., "a boy was leaning back against a wall (*Story and Perceptual*). He was waiting for a girl (*Story*).

His blazer was blue (*Perceptual*)"). Note that, unlike the current analysis, Levine et al.'s (2002) original scoring system classified details into exclusive categories. Our modification reflects the fact that we were specifically interested in capturing perceptual elements in all conditions, as well as fully accounting for story elements, and we did not want to "sacrifice" either in our detail counts when such details were inextricably bound together. We did not score information about time (e.g., "it happened two years ago"; "that was in January") or place (e.g., "this was in Toronto"), unless it provided perceptual information (e.g., "it was a hot summer day," "we were at the back of the bar"), or information about the type of event described (e.g., Christmas dinner, baseball game).

In the narrative and clip conditions, Story Details that differed from what was presented at encoding (e.g., made up or distorted Story Details) were counted as *Story Errors*. In the clip condition, perceptual elements that were not part of the original film clip (e.g., recalling a hat when the person did not wear one) were considered *Perceptual Errors*. For the narrative condition, imagined percepts that were not shown at encoding were counted as Perceptual Details unless they were unrelated to or in conflict with the studied narrative (e.g., visualizing a young boy running down the street when the narrative's main character was a girl; imagining additional characters not mentioned in the story). Note that very few errors were committed in the two story conditions by either the control or the patient group (see Fig. 5). In the AM condition, participants were given the benefit of the doubt regarding the accuracy of their recall unless (1) a participant corrected him/herself, or (2) two memory elements contradicted each other, in which case the "correct" detail was determined arbitrarily, and the conflicting detail was counted as a *Story Error* or a *Perceptual Error*, depending. Additional examples of scored protocols from patients and controls, and a scoring manual detailing this scoring system, are available as Supporting Information.

We conducted two different analyses on mean numbers of details, one of which excluded non-successful trials (Story Content rating of 1 = "no story details"), and one of which included all trials (Story Content rating = 1 to 5). There was little difference between the two sets of results (see Supporting Information Fig. S1), and so we are reporting analyses performed on successful trials only (Story Content rating > 1). Trials with recording errors were also excluded from the detail analysis. We elected to exclude unsuccessful trials from the final analysis because we wanted to characterize qualitative memory content between conditions, and because such content could not be characterized on trials for which no memory was accessed. In fact, having poorer retrieval success in some conditions could create the false impression of differences between conditions in recall of perceptual elements, even though no such differences exist when only successful trials are compared. Just as failed trials are typically excluded from brain imaging studies comparing the neural correlates of two cognitive states so that brain activity reflects what happens when one performs a task, failed trials for which participants recalled no content were excluded from the current analysis to properly characterize potential differences in the types of memory content across our conditions.

*TABLE 2.*

***Inter-Rater Reliability: Intraclass Correlation Coefficients per Detail Category***

| | Score per memory condition | | | |
|---|---|---|---|---|
| | Global score ($n = 120$) | AM ($n = 40$) | Narrative ($n = 40$) | Film clip ($n = 40$) |
| Story Details | 0.859 | 0.869 | 0.889 | 0.850 |
| Perceptual Details | 0.811 | 0.707 | 0.910 | 0.828 |

Intraclass correlations were calculated following the guidelines of McGraw and Wong (1996). The global score was calculated based on trials from all three memory conditions.
AM = autobiographical memory.

## Scoring reliability: Intraclass correlations

Intraclass correlations (McGraw and Wong, 1996) were calculated using SPSS 18.0 (Statistical Package for the Social Sciences, IBM) for the tallied number of Story Details and of Perceptual Details, respectively. M.S.L. and R.J. (who was blinded to the identify of participants) both scored the same 120 memory transcripts (40 AM, 40 narratives, and 40 clips) obtained from four different participants. Intraclass correlation coefficients (two-way mixed model, absolute agreement, single measures) are reported in Table 2 and were deemed acceptable.

## Linguistic inquiry and word count (LIWC)

Memory transcripts were processed with the LIWC2007 computer software (Linguistic Inquiry and Word Count) for an automated word count analysis. Transcripts of a participant's first (Story Content) and second (Perceptual Content) recordings from all successful trials (Story Content rating >1, excluding trials with missing recordings) were saved into a single Microsoft Word document for each memory condition. For each document, LIWC2007 calculated the number of words falling into each of the 80 different categories defined by its 2007 English dictionary (Pennebaker, et al., 2007). For each category, the average number of words per memory was calculated per condition. Here we report results from the *Perceptual Processes* word category, which included words referring to the process of perceiving ("observing," "seen," "heard," "feeling," "listen," "touch"). Importantly, while Perceptual Details scored manually reflected the content of what was perceived (e.g., "I heard a ***loud scream***"), the LIWC Perceptual Processes category counted words reflecting a perceptual experience in the narrator (e.g., "I ***heard*** a loud scream"). Because both the percept and the narrator's experience are related in the memory narrative, we used the LIWC analysis as a user-independent measure of perceptual memory content to corroborate results from the manual scoring.

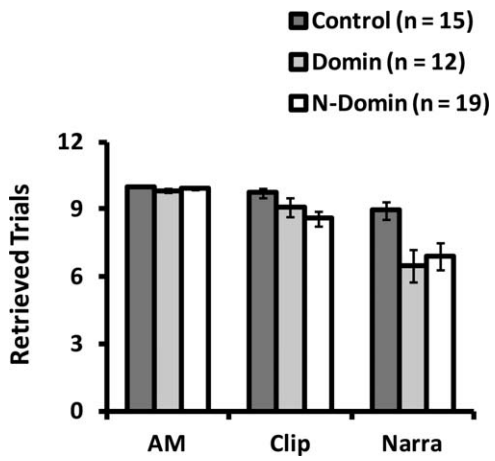


**FIGURE 3. Mean number of successful trials (Story Content rating > 1; maximum 10 trials per condition) plotted per condition for the language dominant (Domin) and nondominant (N-Domin) mTLE groups and the control group, respectively. Error bars represent SEM. Note: AM = autobiographical memory; Narra = narrative condition; Clip = film clip condition.**

## RESULTS

We conducted direct comparisons between the narrative and the film clip conditions, as they were well matched in terms of overall story content. Because the AM condition contained more information than the two laboratory conditions, it made direct comparisons difficult to interpret, and so we analyzed those data separately. Nevertheless, observing similar patterns of group differences in both the laboratory tasks and the AM task in the same cohort of participants would indicate that the AM deficit typically observed in mTLE extends to new memories acquired in the laboratory. We also observed high positive correlations between the number of details per category recalled across the three memory conditions, indicating that similar processes supported the AM and the laboratory conditions (see Supporting Information Table S1).

The proportion of pre- and postsurgery participants with mTLE was not perfectly balanced between the language dominant and the language nondominant mTLE groups. The lack of orthogonality between surgical status and laterality prevented us from conducting two-way ANOVAs assessing the independent contribution of these two factors to task performance. Instead, we conducted series of nonparametric Mann-Whitney *U* tests comparing presurgery ($n = 12$) and postsurgery patients ($n = 19$), regardless of laterality, on all the measures reported below. We also conducted a series of Mann-Whitney *U* tests comparing language dominant ($n = 12$) and language nondominant ($n = 19$) mTLE groups on the same measures. None of these tests reached significance ($P = 0.101$–$0.952$), providing no indication that surgery status and laterality influenced mTLE participants' preformance on the current task. For simplicity, we are reporting results from statistical tests for which all mTLE patients were merged into a single mTLE group.

### Successful Trials

Following the 16 s allowed for retrieval, participants rated the story content ("how much do you remember about what happened?") and the vividness ("how much sensory information did you visualize at retrieval?") of their memory, on 1 to 5 Likert scales. Based on the Story Content self-ratings, we identified trials for which participants failed to retrieve an AM or a LE (Story Content rating = 1, "no story/AM details"). We calculated the number of trials for which a memory was retrieved successfully for each condition (Story Content rating = 2 to 5), which we compared between controls and participants with mTLE (see Fig. 3). A 2 × 2 repeated measures ANOVA with condition (narrative and clip) as within-subject factor revealed that controls retrieved significantly more memories than participants with mTLE ($F_{(1,44)} = 10.242$, $P = 0.003$). A significant main effect of condition ($F_{(1,44)} = 20.820$, $P < 0.001$) revealed that fewer memories were retrieved successfully in the narrative condition in comparison to the clip condition, indicating that narratives were either less memorable, less distinguishable, or less easily accessed through cuing than the film clips. A trend for a group × condition interaction effect ($F_{(1,44)} = 3.941$, $P = 0.053$) indicated that this effect was driven mostly by the mTLE group, who had higher ratings for clips than for narratives.

### Detail Scoring

#### *Story and perceptual details*

Immediately after the self-ratings, participants were recorded while describing the story content and perceptual features of the memory they retrieved within the 16 s retrieval phase. From the transcripts of these recordings, we tallied Story and Perceptual Details. In Figure 4, the mean number of these details is plotted per group, per condition. The means were

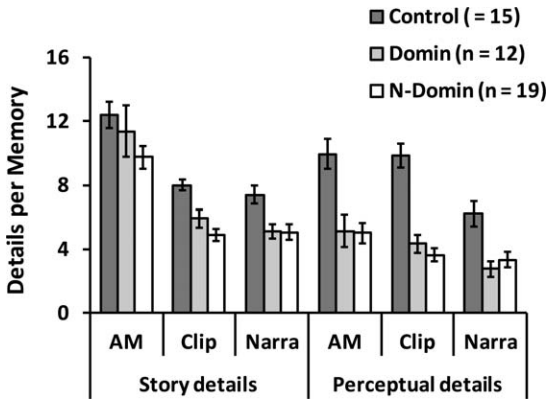


**FIGURE 4. Mean tallied number of Story Details and Perceptual Details per memory condition for successful trials only (Story Content rating > 1). Trials with recording errors, and Error details, were excluded from these counts. Details are plotted for language dominant (Domin) and nondominant (N-Domin) mTLE participants, and for controls. Error bars represent SEM. Note: AM = autobiographical memory; Narra = narrative condition; Clip = film clip condition.**

calculated for successful trials only (Story Content ratings >1). Including unsuccessful trials, which were given a score of 0 details, into the means calculation did not change the overall pattern of results (see Supporting Information Fig. S1 for means calculated across successful and unsuccessful trials; Story Content ratings 1–5).

We compared the number of Story and Perceptual Details between the mTLE group and the controls in the AM condition. A two-way repeated measures ANOVA with details (Story and Perceptual) as within-subject factor revealed significant main effects of group ($F_{(1,44)} = 11.553$, $P = 0.001$) and type of details ($F_{(1,44)} = 59.451$, $P < 0.001$), with the mTLE group recalling fewer details than the control group, and with participants recalling fewer Perceptual Details than Story Details. A significant group × detail interaction effect ($F_{(1,44)} = 7.949$, $P = 0.007$) was also observed, indicating that the mTLE group had a larger memory deficit for Perceptual Details than for Story Details.

We then compared the number of Story and Perceptual Details recalled by the control and the mTLE group in the narrative and clip conditions. A three-way ANOVA with repeated measure over detail type and memory condition revealed significant main effects of group ($F_{(1,44)} = 39.397$, $P < 0.001$), detail type ($F_{(1,44)} = 7.226$, $P = 0.010$), and condition ($F_{(1,44)} = 46.872$, $P < 0.001$). We also observed significant group × details ($F_{(1,44)} = 16.153$, $P < 0.001$), group × condition ($F_{(1,44)} = 18.112$, $P < 0.001$), details × condition ($F_{(1,44)} = 39.857$, $P < 0.001$) and group × details × condition ($F_{(1,44)} = 18.079$, $P < 0.001$) interaction effects. These results indicated a general decrease in all detail categories in the mTLE group. More importantly, the analysis revealed that the difference in Perceptual Details between conditions was more salient in the control group than in the mTLE group, but that this interaction between group and condition was either significantly reduced or absent for Story Details.

To clarify these results, we conducted two-way ANOVAs with repeated measure over condition separately for Perceptual and Story Details. The analysis conducted on Story Details revealed that controls retrieved more story information than patients ($F_{(1,44)} = 21.762$, $P < 0.001$). The magnitude of this deficit was similar in the narrative and the clip conditions, as neither the condition ($F_{(1,44)} = 3.843$, $P = 0.056$) nor the group × condition interaction ($F_{(1,44)} = .976$, $P = 0.329$) effects were significant. Follow-up comparisons confirmed that neither the mTLE ($t_{(30)} = 0.895$, $P = 0.378$) nor the control group ($t_{(14)} = 1.637$, $P = 0.124$) showed differences in the number of Story Details recalled between the narrative and the clip condition, indicating that story content was equated between these conditions in both groups. The two-way ANOVA conducted on Perceptual Details revealed that fewer details were recalled by the mTLE group than by controls ($F_{(1,44)} = 44.422$, $P < 0.001$), and that more details were recalled in the clip than in the narrative condition ($F_{(1,44)} = 67.519$, $P < 0.001$). In addition, the large increase in Perceptual Details in the clip in comparison to the narrative condition observed in the controls was significantly reduced in the mTLE group ($F_{(1,44)} = 27.905$, $P < 0.001$). In other words, the gain in Perceptual Details that controls reported when recalling perceptually enriched clips was reduced in participants with mTLE, whose recall of Perceptual Details in the enriched clip condition was almost as impoverished as when they recalled narratives. Of interest, the deficit in Perceptual Details observed in the mTLE group in the clip condition was of the same magnitude as that which we observed in the AM condition.

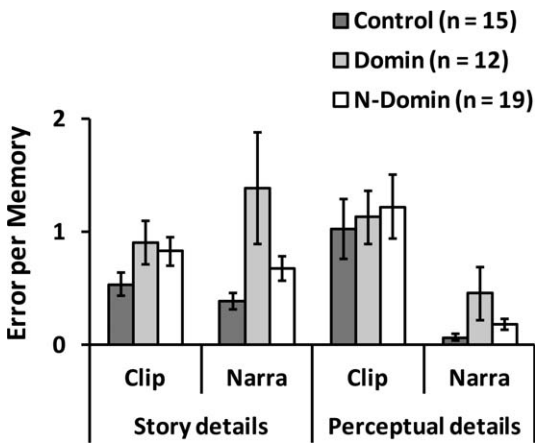


**FIGURE 5. Mean number of incorrect Story and Perceptual Details per memory for the narrative and clip conditions (excluding trials with recording errors). Details are plotted for participants with language dominant (Domin) and nondominant (N-Domin) mTLE, and for controls. Error bars represent SEM. Note: Narra = narrative condition; Clip = film clip condition.**

### *Errors*

Participants were given the benefit of doubt as to the veracity of AM details because their accuracy could not be verified. However, in the narrative and clip conditions, Story and Perceptual Details that did not correspond to what was presented at encoding were counted as errors. On average, very few errors were committed by participants, and the total number of errors made by individuals with mTLE was generally within the same range as that of controls (see Fig. 5).

## LIWC

The LIWC software, which counted the number of words falling under categories identified based on its 2007 English dictionary (Pennebaker et al., 2007) was used for automated scoring of memory transcripts. Unlike the manual scoring, LIWC could not discriminate between what was correctly and incorrectly recalled, but the small number of errors identified in the manual scoring indicates that most of the information recalled was correct (see Fig. 5). Figure 6 illustrates the mean number of words per memory from the Perceptual Processes category.

We compared the number of Perceptual Processes words between the mTLE and the control group for the narrative and the clip condition. A two-way ANOVA with repeated measure

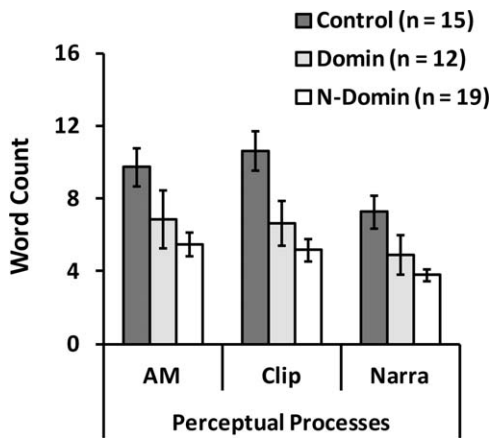


**FIGURE 6. Mean number of words per successful trial (Story Content rating > 1, complete recording) from LIWC2007's Perceptual Processes category. Numbers of words are plotted per memory condition for each group. Error bars represent SEM. Note: AM = autobiographical memory; Domin = language dominant; Narra = narrative condition; N-Domin = nonlanguage-dominant, Clip = film clip condition.**

over condition (narrative and clip) revealed significant main effects of group ($F_{(1,44)} = 17.484$, $P < 0.001$) and condition ($F_{(1,44)} = 27.696$, $P < 0.001$), indicating that controls produced significantly more Perceptual Processes words than individuals with mTLE, and that more words were produced during the clip than the narrative condition. We also observed a group × condition interaction effect ($F_{(1,44)} = 3.970$, $P = 0.053$) indicating that the difference in Perceptual Processes words between the narrative and clip conditions was greater in controls than in participants with mTLE. This pattern is identical to what we observed with Perceptual Details scored manually: memory for enriched clips was almost as perceptually impoverished as memory for narratives in the mTLE group. In the AM condition, controls produced significantly more Perceptual Processes words than participants with mTLE ($t_{(44)} = 2.875$, $P = 0.008$), which is also consistent with the group differences observed with the manual scoring. Manually scored Perceptual Details correlated highly with the number of Perceptual Processes words recalled across participants ($r = 0.749$, 0.708, and 0.755 for the AM, narratives and clips conditions, respectively; $P < 0.001$). These results establish that the automated count of Perceptual Processes words from memory transcripts could serve as a reasonable substitute for the manual scoring of Perceptual Details.

## DISCUSSION

We designed a paradigm that differentiated successfully between two dimensions of complex episodic memory: *storyline*, which corresponds to what happens over the course of an event, and *perceptual richness*, which results from percepts retained or evoked in the recollector's mind. Contrasting performance on this task between patients with mTLE and healthy controls confirmed our hypothesis that damage to the MTL leads to a disproportionate reduction in perceptual richness as compared to storyline.

In controls, a considerable number of story and perceptual details were retrieved in the AM condition, which is consistent with evidence that memory for event-specific personal episodes is characterized by a rich narrative structure (Neisser et al., 1996; Radvansky et al., 2005; Conway, 2009), and by experience-near sensory content (Brewer, 1986, 1995; Moscovitch et al., 2005; Conway, 2009; Conway and Loveday, 2010; Moscovitch, 2012b). In the mTLE group, a significant interaction effect revealed a greater paucity for perceptual details than for story details. This result replicates findings from our previous study comparing mTLE participants to healthy controls on a different AM task (St-Laurent et al., 2009) and together the results highlight the importance of perceptual information to the characterization of the memory deficit caused by MTL dysfunction. In the perceptually enriched clip condition, the perceptual details deficit we observed in the TLE group was as pronounced as in the AM condition. As expected based on our experimental manipulation of stimulus content, controls retrieved more perceptual details in the clip than in the narrative condition, an advantage that was virtually eliminated in patients with mTLE. The comparable number of perceptual details recalled by patients in the clip and the narrative conditions indicates that their memory for clips was almost as perceptually impoverished as their memory for narratives. This pattern of results was observed both with manual scoring and with the LIWC count of Perceptual Processes words. Thus, our findings indicate that the lack of vivid and detailed AM recollection found in patients with MTL damage is not peculiar to the retrieval of distant episodes from remote memory, but rather reflects a general condition that also applies to recently acquired memories of extended well-controlled laboratory events.

We must clarify that while perceptual details were retrieved from memory in the film clip condition, they were mainly elicited by story retrieval in the narrative condition. In order to portray the imagery experienced by the participants in each recall condition accurately, and avoid potential self-censoring of mnemonic details, we instructed them to report all imagery regardless of its origin (stimulus or imagination). This feature of our paradigm allowed us to validate that retrieval of sensory details was truly superior in the clip compared to the narrative condition in healthy individuals, and to fully estimate the magnitude of the mTLE group's perceptual memory deficit by a direct comparison between the clip and the narrative conditions. In addition, it allowed us to determine that narrative retrieval evoked some sensory imagery in both groups. Interestingly, the mTLE group experienced significantly less imagery than controls when recalling narratives, which is consistent with a literature linking MTL function to one's capacity to imagine new visuospatial scenes, future events and other detailed mental constructs (Addis et al., 2007b; Hassabis et al., 2007; Rosenbaum et al., 2009; Rabin et al., 2010; Viard et al., 2012).

In both controls and patients, the number of story details recalled did not differ between the clip and the narrative condition, indicating that story content was well matched between the two laboratory conditions, and that perceptual cues did not bolster recall of story details. We also observed a general loss of story content across conditions in the mTLE group that was unrelated to the perceptual richness of the memory, as it affected the clip and the narrative conditions equally. This loss of story content is consistent with evidence that damage to the MTL impairs the detailed recollection of episodic memory, and renders memory more schematic or gist-like (Nadel and Moscovitch, 1997; Moscovitch et al., 2005; Piolino et al., 2009; Rosenbaum et al., 2009; St-Laurent et al., 2011; Winocur and Moscovitch, 2011). Although we hypothesized that perceptual richness is an important determinant of MTL engagement at retrieval, our results indicate that highly context-specific information that is not perceptual, such as specific thoughts or rapid sequences of actions, can also be affected by damage to the MTL (St-Laurent et al., 2011). Nevertheless, the interaction effect between detail category, group and condition indicates that, while patients with mTLE recalled fewer details across most categories and conditions, the magnitude of their deficit for perceptual details was disproportionate, especially in the perceptually enriched conditions which had "more to lose."

## Laterality and Temporal Lobe Pathology

Performance on our task was indistinguishable between participants with left and right mTLE, indicating that both hemispheres contribute to the retrieval of complex episodic memories. This is consistent with other AM studies that did not observe significant differences in memory performance based on laterality of mTLE (Viskontas et al., 2000; Lah et al., 2004, 2006; Noulhiane et al., 2007, 2008; Herfurth et al., 2010; St-Laurent et al., 2009, 2011; but see Voltzenlogel et al., 2006 for a greater deficit in patients with left-lateralized mTLE, and see McAndrews, 2012, for a review), and with functional brain imaging data indicating bilateral hippocampal activation during AM retrieval (see Svoboda et al., 2006, and McDermott et al., 2009, for meta-analyses). For the current laboratory tasks, we anticipated that pathology localized in the language-dominant hemisphere might have affected the language-based narrative condition disproportionally, but here again no laterality effects were observed. Typically, damage to the left MTL disrupts memory for verbal material (Frisk and Milner, 1990; Rausch and Babb, 1993; Sass et al., 1995; Helmstaedter et al., 1997; Djordjevic et al., 2010), while damage to the right MTL interferes with memory for visual and spatial material (Jones-Gotman and Milner, 1978; Smith and Milner, 1989; Morris et al., 1995, 1996; Bohbot et al., 1998; Spiers et al., 2001). However, tasks that assess memory for associative material tend to be less lateralized based on material-specificity than tasks relying on familiarity with single test items (Glosser et al., 1998; Cohn et al., 2009; Saling, 2009; McAndrews and Cohn, 2012). Thus, the complexity of the current laboratory events may account for the absence of laterality effect in our results.

That being said, the scoring system we used awarded points for story details regardless of how they were worded, and it is possible that language-dominant TLE participants' memories were less literal than those of nonlanguage-dominant participants, as suggested based on findings from Djordjevic et al. (2010), and Frisk and Milner (1990). A more stringent scoring system that is sensitive to wording, or a task of autobiographical fluency that is more sensitive to word-retrieval processes (Barr et al., 1990; Barnett et al., 2000; Lah et al., 2004), may have revealed subtle modality-specific differences between the mTLE groups. Nevertheless, the current data suggest that both hemispheres contributed importantly to performance on the current task, and that the episodic memory deficit observed in participants with mTLE was not mediated by impaired language processes, which is consistent with work from Lah et al. (2006; see also Race et al., 2011).

Importantly, our results do not rule out that the left and the right MTL might contribute differently to episodic memory retrieval. Both hippocampi are known to share extensive connectivity during AM retrieval (Addis et al., 2007a; St Jacques et al., 2011; McCormick et al., in press). Furthermore, relatively focal damage can lead to brain-wide changes in patterns of activation (Maguire et al., 2001; Addis et al., 2007a; McAndrews, 2012). In addition, structural brain imaging has identified extra-hippocampal atrophy in people with mTLE, within (e.g., Moran et al., 2001) and outside (Keller and Roberts, 2008; e.g., Bernhardt et al., 2009) the temporal lobe, although the greatest and most consistent atrophy by far is found within the epileptogenic hippocampus proper (Mathern et al., 1996; Moran et al., 2001; Keller and Roberts, 2008). While our selection of participants was quite rigorous (e.g., only individuals with clearly documented unilateral seizures, IQ within normal range, a cognitive profile showing disproportionate material-specific memory impairment, no seizures postsurgery), which minimizes the potential influence of other factors that can affect cognitive performance in mTLE patients (Bell et al., 2011), it is possible that there is a blurring of the potentially distinct contributions of each hippocampus in this population.

Our results also indicate that surgical status did not influence performance significantly in our mTLE group. Performance on verbal memory tasks has been shown to decline postsurgically in a number of individuals with left-lateralized mTLE, although the effect of a right temporal lobectomy on memory for non-verbal material is less clear-cut (Rabin et al., 2004; Richardson et al., 2004; Baxendale et al., 2006; Binder et al., 2008; Harvey et al., 2008; St-Laurent, et al., 2014). The laboratory tasks we designed were intended to mimic the processes involved in AM retrieval, where there is a robust literature on the minimal impact of surgical status in mTLE. Specifically, we and others have reported similar memory performance in pre- and postsurgery mTLE groups (Viskontas et al., 2000; Addis, 2005; Voltzenlogel et al., 2007; St-Laurent et al., 2009; Herfurth et al., 2010). Interestingly, a longitudinal fMRI study assessing AM pre and postsurgically in a cohort of individuals

with mTLE reveals very little change in their whole-brain pattern of activation during AM retrieval following the surgery (McAndrews, 2012). This growing evidence suggests that retrieval of memories such as laboratory and autobiographical events may be so sensitive to disruption of normal MTL function that seizure-related damage is sufficient to disrupt activity within the entire retrieval network, and that further removal of MTL tissue has little additional impact on performance. It also indicates that damage restricted mainly to the hippocampus is sufficient to induce episodic memory deficit in the current patient group (see also Moscovitch and McAndrews, 2002; Gilboa et al., 2006; Rosenbaum, et al., 2008). Current theory of MTL function suggests that memory for single items can be supported by the cortex, but that memory that requires the formation of associations between items and context always involves the hippocampus proper (Eichenbaum et al., 1992; Eichenbaum, 2004; Ranganath, 2010; McAndrews and Cohn, 2012). Clearly, for the laboratory and autobiographical events used here, MTL damage was sufficient to disrupt task performance.

## Encoding Versus Retrieval

The results show that perceptual richness depends on the integrity of the MTL, but the current clip and narrative tasks could not be used to determine with certainty whether mTLE interfered with memory encoding, with retention, with retrieval, or with all processes. The crucial role played by the MTL in memory acquisition is well documented (Scoville and Milner, 1957; Eichenbaum et al., 1992; Squire, 1992), and one must be mindful that participants with mTLE encoded laboratory events with a defective MTL. With the exception of remote events such as childhood memories retrieved by individuals with late onset mTLE, AM encoding was also performed with an epileptogenic MTL in the current mTLE group. Importantly, the literature indicates that memory for personal events that precede the onset of seizures is just as impaired as memory for postonset events, and that age of onset is a poor predictor of AM performance in general (Bergin et al., 2000; Viskontas et al., 2000; Lah et al., 2004; Voltzenlogel et al., 2006; Noulhiane et al., 2007). Although perceptual memory content was not measured in these studies, qualitative losses of AM details were reported whether or not patients suffered from seizures at the time of encoding.

Evidence of retrograde AM deficits observed in individuals with adult-onset damage to the MTL due to trauma, dementia or infections (Kapur, 1999; Cipolotti et al., 2001; Steinvorth et al., 2005; Gilboa et al., 2006; Rosenbaum et al., 2005, 2008; Piolino et al., 2009; Seidl et al., 2011) clearly indicates that MTL damage interferes with the retrieval of episodic memory features (see reviews in Moscovitch et al., 2005, 2006; Winocur and Moscovitch, 2011; but see Squire and Wixted, 2011). Together, these findings suggest that the presence of MTL damage at retrieval is sufficient to induce the kind of memory deficit reported here. Thus, although it is likely that mTLE interfered to some extent with the encoding phase of our task, the literature suggests that mTLE also disrupts the retention and/or retrieval of perceptual memory details.

We do not mean to leave the impression that identical results would be obtained in patients with bilateral hippocampal lesions. As we noted earlier, such patients have great difficulty encoding, retaining, and/or retrieving novel event information, including story content, and their performance on our task would most likely be at floor. Also, it is still an open question whether both elements of an event memory, story content and perceptual details, are equally compromised if the initial memories were acquired long before the bilateral medial temporal insult.

## Theoretical Implications

We report that perceptual richness is especially prone to disruption when MTL integrity is compromised. These findings confirm results from previous studies linking MTL function to the perceptual imagery content of episodic memory and other mental constructs (e.g., imagined new scenes; Greenberg and Rubin, 2003; Hassabis and Maguire, 2009; St-Laurent et al., 2009; St Jacques et al., 2011a,b, 2012). Our study's strength lies in the additional control provided by the use of laboratory stimuli, which, unlike naturalistic memories, are matched for age, personal relevance, emotionality and degree of rehearsal. Also, we manipulated perceptual richness while controlling for narrative-driven story content, two memory dimensions that are typically intertwined in AM (Brewer, 1995). These measures allow us to conclude that although memory for both event content and perceptual details is impaired in mTLE patients, perceptual richness is particularly vulnerable. The latter finding suggests that perceptual richness is an important determinant of MTL engagement during episodic memory retrieval, whether it is of memories acquired in the laboratory or outside of it. It remains to be determined whether richness in other domains, such as emotion, would also be impaired.

Patterns of structural and functional hippocampal connectivity are concordant with our findings. The hippocampus forms indirect reciprocal connections with the apex of the ventral visual stream and with cortical regions processing multimodal spatial information, enabling it to integrate multimodal features from memory into a rich and coherent mental representation at retrieval (Eichenbaum and Lipton, 2008; Coward, 2010; Derdikman and Moser, 2010; Poppenk and Moscovitch, 2011; Poppenk et al., 2013). A recent functional imaging study from our group demonstrates that connectivity of bilateral hippocampi with posterior visual association errors is specifically enhanced when healthy participants are asked to relive mentally personal remote memories by recovering as many details as they can (McCormick et al., 2014). Maguire et al. have shown that patients with hippocampal amnesia struggle to imagine rich visuospatial scenes they have never experienced before, leading them to claim that the hippocampus plays an important role in constructing scenes from multimodal memory details (Hassabis et al., 2007; Hassabis and Maguire, 2009). While our analysis included both spatial and non-spatial

features in the Perceptual Details category, it revealed a paucity of sensory episodic memory details in patients with damage to the MTL, which is consistent with the Maguire group's views on hippocampal function.

Experiencing vivid imagery during memory retrieval contributes to one's sense of reliving the past (Brewer, 1995; Rubin et al., 2003; Park et al., 2011), a phenomenon known as recollection. Recollection is a hallmark of episodic memory (Tulving, 1985; Wheeler et al., 1997; Tulving, 2002), and it is well established that the experience of recollection is a determinant of hippocampal engagement during episodic memory retrieval, whether the episode is recent or remote (Nadel and Moscovitch, 1997; Moscovitch and Nadel, 1998; Moscovitch et al., 2005; Aggleton and Brown, 2006; Eichenbaum et al., 2007; Cohn et al., 2009; Piolino et al., 2009; Yonelinas et al., 2010). The current results indicate that perceptual episodic memory details, which are severely disrupted following damage to the MTL, could be a mediating factor in the relationship between hippocampal function and recollection (Piolino et al., 2009). Since the retrieval of perceptual details is supported by the hippocampus, and since these details provide a vivid sense of re-experiencing the past, one's inability to retrieve perceptual details due to hippocampal damage should lead to a specific deficit in recollection (see discussions in Poppenk and Moscovitch, 2011; Poppenk et al., 2013, on the neuroanatomical basis of this effect).

Our findings are also consistent with Martin Conway's theory which states that episodic memory is composed of experience-near episodic elements (EEs), which often are represented in the form of visual images (Conway, 2009; Conway and Loveday, 2010). EEs are bundled together by a conceptual frame that provides the memory with its meaning or gist. The perceptual details that were measured with our task, as well as highly specific story details (e.g., specific actions), fit under the definition of EEs. Conway suggests that the frame is supported by a frontotemporal brain network, while EEs are supported by a temporo-occipito-parietal network. Should damage to the temporo-occipito-parietal network occur, Conway predicts a dramatic loss of EEs, so that the gist or frame is accessed in the absence of experiential details (Rubin and Greenberg, 1998; Greenberg and Rubin, 2003; Greenberg et al., 2005; Conway and Loveday, 2010). Our current results are consistent with these predictions, as perceptual details and specific story elements were drastically reduced in individuals with mTLE. Of importance, it is likely that EEs are not stored in the MTL per se, but rather are indexed, accessed and integrated into a memory through the actions of the MTL (Teyler and DiScenna, 1986; McClelland et al., 1995; Greenberg and Rubin, 2003; Moscovitch et al., 2005; Teyler and Rudy, 2007; Hassabis and Maguire, 2007, 2009; Buckner, 2010; Conway and Loveday, 2010). Storage may instead take place in posterior cortical regions, as evidenced in cases of severe retrograde amnesia from patients with extensive bilateral posterior regions that include visual cortices (Rubin and Greenberg, 1998; Greenberg and Rubin, 2003; Greenberg et al., 2005). Retrieval may also depend on the operation of various regions in the pre-frontal and parietal cortex which initiate and guide search processes, and attend, monitor and verify its outcome (Moscovitch, 1992; Cabeza et al., 2008; Ciaramelli et al., 2008; Rugg and Vilberg, 2013). Thus, though we are mindful that other regions are also implicated in episodic memory retrieval, we suggest that the hippocampus plays the distinctive functional role of linking EEs to conceptual long-term memory knowledge by supporting the assemblage of experiential details into recollective memory episodes (see also Moscovitch, 2008, 2012a,b, for a related view).

### Methodological Advances

Our demonstration that extended laboratory events can be used to isolate specific autobiographical memory features in order to determine how they are affected by circumscribed brain lesions is a valuable addition to the memory literature. Other groups have pioneered the use of complex laboratory events like narratives and film clips to identify the neural substrates of features such as event boundaries, spatiotemporal organization and remoteness of memory (Zacks et al., 2006; Hasson et al., 2008; Kurby and Zacks, 2008; Furman et al., 2012; Honey et al., 2012), and some paradigms that rely on laboratory events have been used to link event features to MTL function (Ben-Yakov and Dudai, 2011; Swallow et al., 2011; Ben-Yakov et al., 2013). However, our study is the first to demonstrate a parallel memory deficit for naturalistic AMs and for laboratory events (but see Bailey et al., 2013 for a study linking event perception to competence on a naturalistic test in a clinical population), lending validity to evidence from the AM literature where content is poorly controlled and memory veracity cannot be verified.

Our study is also the first to disentangle story content from perceptual richness, and to tackle the relationship between perceptual richness and MTL function via experimental manipulation. Laboratory events are a flexible tool that can be tailored to manipulate specific dimensions of complex memory episodes without being bound by the limits of a person's experience. As others have shown (e.g., Furman et al., 2012), laboratory events can also be used in combination with brain imaging to identify neural substrates and patterns of neural connectivity that support very specific characteristics of episodic memory. Our paradigm serves as a model for how one can identify brain regions that support perceptual richness in autobiographical and episodic memory, and to determine whether the hippocampus is among them (Steinvorth et al., 2005; Kirwan et al., 2008; Rosenbaum et al., 2009).

## CONCLUSION

Our findings support the hypothesis that perceptual richness is an important determinant of MTL function, and are in line with theories that emphasize its role in the retention, retrieval, and assemblage of multimodal memory elements into vivid

recollective experiences, regardless of whether the memories were acquired in the laboratory or in the real world. Future work using functional brain imaging should address how interactions between the MTL and other regions that form an event retrieval network are modulated by the perceptual richness of recollection.

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