

Recollection and familiarity for public events in neurologically intact older adults and two brain-damaged patients

Raluca Petrican^{a,*}, Nigel Gopie^{a,b}, Larry Leach^b, Tiffany W. Chow^b, Brian Richards^b, Morris Moscovitch^{a,b}

^a Department of Psychology, University of Toronto, 100 St. George Street, Toronto, Ontario M5S 3G3, Canada

^b Rotman Research Institute, Toronto, Ontario, Canada

ARTICLE INFO

Article history:

Received 2 October 2008

Received in revised form 28 October 2009

Accepted 23 November 2009

Available online 26 November 2009

Keywords:

Remote memory

Older adults

Recollection

Familiarity

Remember

Know

ABSTRACT

Despite extensive investigations of the role of recollection and familiarity on laboratory-acquired memories, there is a dearth of such research on memories formed in real life settings. We used the *Remember/Know* paradigm to investigate the relative contribution of recollection and familiarity processes to memory of public historical events reported in the media across the life span of two groups of neurologically intact older adults (old-old: 74–85, young-old: 58–69) and on two patients with brain damage. First, in neurologically intact participants, recollection rates decreased as a function of time elapsed since the event occurred, at a significantly higher rate than the corresponding decrease in familiarity or global memory. Second, consistent with the hypothesis that memories become increasingly semantic as they age, and that recollection is selectively impaired in older adults, across decades, old-old participants exhibited lower recollection, but not familiarity, relative to young-old participants. Finally, as a demonstration of how this procedure may be applied to studies of clinical populations, we tested two patients, one with medial temporal lesions and another with relative sparing of the medial temporal lobes, but with anterior temporal damage. We found that recollection was disproportionately impaired relative to familiarity across most of the life span in the patient with medial temporal lesions severely while recollection was relatively intact in the patient with anterior lateral temporal damage. We discuss the present results in the context of neuroanatomical and process-oriented theories of how memories age.

© 2009 Elsevier Ltd. All rights reserved.

1. Recollection and familiarity for public events in neurologically intact older adults and two brain-damaged patients

The processes through which a momentary experience becomes imprinted in the mind of an individual, remaining available for later perusal and re-interpretation, changing and being changed by the individual's previous body of knowledge, have been the subject of investigation and debate for more than a century (Moscovitch et al., 2006). The long-standing consensus in the literature is that memory formation entails two distinct sets of processes: (a) a relatively rapid cascade of biochemical processes taking place at the cellular level, which encode the newly formed memory trace (Moscovitch, 1995; Moscovitch et al., 2005; Dudai, 2004); (b) a more prolonged psychological and neural process occurring at the systems level through which the new memory is integrated with an individ-

ual's already existing store of knowledge (Burnham, 1904, cited in Moscovitch et al., 2005; Dudai, 2004; Squire, Cohen, & Nadel, 1984).

The present paper focuses on the psychological or system level to examine the structure of the memories associated with public events in two groups of neurologically intact older adults. Specifically, our current studies investigate the differential contribution of two dissociable conscious memory systems, semantic and episodic (Tulving, 1985), to older adults' memory of public events spanning over five decades. The aforementioned memory sub-components are assumed to store distinct types of knowledge (Tulving, 2002) and be characterized by distinct states of awareness (Tulving, 1985, 2002; Wheeler, Stuss, & Tulving, 1997). More specifically, the semantic (or fact) memory system stores context-free representations of general knowledge (Moscovitch et al., 2006; Tulving, 2002). Retrieval from the semantic memory system is accompanied by a state of noetic awareness, i.e., awareness that the information is *familiar*, although the retrieved information is devoid of any contextual details pertaining to the circumstances under which the knowledge was acquired (Tulving, 2002). In contrast, the episodic (or event) memory system stores past experiences of events (Tulving & Markowitsch, 1998), which

* Corresponding author.

E-mail addresses: raluca@psych.utoronto.ca (R. Petrican), momos@psych.utoronto.ca (M. Moscovitch).

incorporate experience-specific details, such as spatio-temporal context, perceptions, thoughts, and emotions (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002; Wheeler & Buckner, 2004). Retrieval from the episodic memory system is accompanied by a state of auto-noetic consciousness (Tulving, 2002; Wheeler et al., 1997), namely an awareness that the experience is from the rememberer's past (Wheeler & Buckner, 2004); the memory is not merely familiar, but is said to be recollected.

So far, studies of remote memory have focused either on public or autobiographical events, to study semantic or episodic memory, respectively. The problem with this approach, as many investigators have noted, is that memory for each type of event may depend on both semantic and episodic components, making it difficult to know the relative contribution of each. To address this problem in the autobiographical realm, investigators have suggested procedures for identifying the two components and dissociating them from one another at both a functional and neuroanatomical level (i.e., the Autobiographical Interview, Levine et al., 2002; Test Episodique de Memoire du Passe autobiographique [TEMPau], Piolino et al., 2006). Findings based on these dissociations have also had important implications for neuropsychological theories of remote memory and consolidation, and to debates regarding these theories (see Moscovitch, 2008; Moscovitch et al., 2005, 2006; Paller, 2009; Squire, Wixted, & Clark, 2007).

To our knowledge, comparable procedures have not been developed for examining public events. To address this gap in the literature, the present research applies the *Remember/Know* (R/K) paradigm to study the unique contribution of episodic and semantic components to older adults' memory for public events. This paradigm, initially proposed by Tulving (1985) to examine recollection-based versus familiarity-based memories associated with retrieval of laboratory-experienced events, has been used extensively in behavioural (Gardiner, 1988; Gardiner & Parkin, 1990; Gardiner & Java, 1991; Knowlton & Squire, 1995) and functional neuroimaging studies (Viskontas, Carr, Engel, & Knowlton, 2009; Wheeler & Buckner, 2004; see reviews by Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, Yonelinas, & Ranganath, 2007; Yonelinas, 2002), but not to study remote memory for public events. Westmacott and Moscovitch (2003) applied the R/K paradigm to good advantage to study names of famous people. They found that high-R names, (i.e., names for which participants had a high number of recollective experiences associated with them) were recalled and recognized better than low-R names (i.e., names for which participants had a low number of recollective experiences associated with them), and they were even read faster and identified more quickly as famous. Moreover, they found that the advantage that high-R names have over low-R names was eliminated in people with medial temporal lobe lesions or degeneration, but was preserved in people with semantic dementia characterized by anterior and lateral temporal degeneration. By applying the R/K paradigm to memory for public events, we hope that it will prove to be as methodologically useful, and theoretically valuable, in studying remote memory for public events, as it has been in studying other types of memory.

In the first study, we used the *Remember/Know* paradigm to examine changes in recollection and familiarity of public events ranging across the life span of two groups of neurologically intact older adults, 58–69 and 74–85 years old. Studies on memories acquired in the laboratory typically show that aging affects recollection more than familiarity (Grady, 1998; Grady & Craik, 2000; Verhaeghen, Marcoen, & Goossens, 1993). We wished to determine whether such differences would also be observed for memories acquired long before participants entered the laboratory.

Greater deficits in recollection than in familiarity with aging have been attributed to deterioration of the prefrontal cortex (Bugajska et al., 2007) and hippocampus and related medial

temporal-diencephalic structures (Ivy, MacLeod, Petit, & Markus, 1992; Van Petten, 2004; Van Petten et al., 2004). It is not known, however, whether deterioration of such structures would affect memories acquired long before extensive age-related deterioration began. If we find that it does, it would suggest that these structures are implicated in the retention and retrieval of remote memories, as much as in the formation, retention and retrieval of recent ones. Based on previous findings that recollection of remote autobiographical memories is affected by aging (Levine et al., 2002; Piolino et al., 2006) and by mild cognitive impairment (MCI; Murphy, Troyer, Levine, & Moscovitch, 2008), we predicted selective loss of recollection compared to familiarity with age in our tests of memory for public events.

Study 2 is meant primarily as a demonstration that the procedure developed in Study 1 can be used to study remote memory for public events in a clinical population. To this end, we tested two patients with verified damage, one primarily to the medial temporal lobes (Mr. D.), and the other to anterior and lateral temporal structures, with relative sparing of the medial temporal lobes (Mr. R.). These patients, like the ones studied by Westmacott, Black, Freedman, and Moscovitch (2005), therefore, may provide a more direct way than does testing older adults for assessing the involvement of medial temporal and neocortical regions in mediating recollection and familiarity. Because the hippocampus and its projections were affected in the first patient (Mr. D.), recollection was expected to be affected more than familiarity. By contrast, recollection should be relatively spared in the second patient (Mr. R.), though familiarity may be affected, as structures in the anterior temporal cortex, particularly the peri-rhinal cortex, are known to be implicated in familiarity for memories acquired in the laboratory.

2. Study 1

In the first study, we investigated whether episodic and semantic aspects of memories for public events show distinct decay trajectories across five decades in two groups of neurologically intact older adults (58–69 years and 74–85 years, respectively). We included two different groups of older adults for two reasons: first, because we wanted to test memory for public events across extended time periods, and second, based on the hypothesis that the hippocampal complex and prefrontal cortex degenerate with age, we predicted that such degeneration would affect recollection more than familiarity, hence the difference between recollection and familiarity rates would be more pronounced in the older group (Jennings & Jacoby, 1993).

3. Method

3.1. Participants

Twenty neurologically-intact “older old” adults between the ages of 74 and 85 years ($M = 78.6$ years, $SD = 2.98$ years) and twenty neurologically-intact “younger old” adults between the ages of 58 and 69 years ($M = 65.35$ years, $SD = 3.17$ years). All participants were native English speakers and had not traveled outside North America for more than two months at a time. Both groups of older adults had been living in North America for the past 50 years. The “older old” adults completed, on average, 15.65 years of education ($SD = 3.53$ years) and the “younger old” adults completed, on average, 14.33 years of education ($SD = 3.25$ years). Independent samples *t*-test analyses revealed that the two groups did not differ with respect to their educational level.

The older adults were recruited via an older adult volunteer pool at the University of Toronto and participated in the present study for financial compensation at the rate of \$10/h. Prior to joining the pool, all volunteers were screened for neurological damage and

cognitive impairments by the pool coordinator. Part of the consent form process for the present study, participants were asked whether they had any neurological problems. Only participants who reported no known neurological or cognitive impairments were admitted to the study. Informed consent was obtained from all participants in accordance with the guidelines of the Social Sciences and Humanities Research Ethics Board at the University of Toronto.

3.2. Materials

Our stimulus set consisted of 150 real public events (e.g., “Hurricane hazel strikes southern Ontario.”) and 14 imaginary public events (e.g., “Dalai Lama announces his support for the Chinese Communists.”). We included the imaginary events in order to assess the participants’ response biases, i.e., giving a *Know* response to a public event that was not familiar to them, merely because the respective event appeared on the test list.

The real events ranged from 1952 until 2001. We selected 3 events per year with the restrictions that two of them would have occurred in North America (i.e., Canada or United States) and one of them would not have occurred in North America. Canadian events were included in the test set if they appeared in all of the following sources for the year in which they occurred: *Chronicle of Canada* (1990), *Facts on File* (1952–2001), and CBC Digital Archives (only for the most recent decade; <http://archives.cbc.ca>). Non-North American events, as well as events occurring in the United States were included in the test set if they appeared in all of the following sources for the year in which they occurred: *American Chronicle of the Twentieth Century: Year by Year Through the Twentieth Century* (Gordon & Gordon, 1999), *The World Almanac and Book of Facts* (Joyce, Lazzarra, & Janssen, 1950–1999) and *Britannica, Calendar of Events* (1952–2001). By selecting events that appeared in all the publications, we ensured that they were very well-known, and likely to have been noted by our participants at the time they occurred.

3.3. Procedure

Participants were presented with a self-paced computer-administered survey, where they were asked to make a *Remember/Know/Don't Know* judgment for each of the 150 real events and the 14 imaginary events, presented in randomized order for each participant. Participants were not provided with the date at which the events occurred. The participants were instructed to give a *Remember* response to a public event if they could recollect a particular image from the TV, radio or newspaper coverage of the respective event or a personal experience associated with it, such as their thoughts, emotions or the specific circumstances under which they first found out about the event. In contrast, participants were instructed to give a *Know* response to a public event that was only familiar to them but for which they could not recollect any personal experience or any specific details related to the TV, radio or newspaper coverage of the respective event. Finally, for events that elicited neither a recollection nor a familiarity response, participants were instructed to give a *Don't Know* response. For example, a participant would give a *Remember* response to the event “Bobby Kennedy is assassinated” if he or she recollected the TV image of the Ambassador Hotel’s kitchen where Bobby Kennedy was shot. In contrast, a participant would give a *Know* response to the same event if he or she knew that the assassination did take place and, perhaps, also knew some additional factual information about Bobby Kennedy, such as the fact that he served as an attorney general, had 11 children and so on; however, he or she could not recollect no specific details or personal experiences associated with the episode of the assassination itself. For the first 5 events to which the participants gave

either a *Know* or a *Remember* response and for the first 5 *Remember* responses (or until the participants demonstrated that they understood the distinction between *Remember* and *Know* responses) and then, sporadically throughout the study session, the experimenter prompted the participants to justify their response by providing an oral account of the memories on which they based their decision. All participants “passed” the practice phase, meaning that, after the first 5 *Remember* responses, when prompted by the experimenter, they justified their responses (i.e., *Know* or *Remember*) appropriately.

4. Results and discussion

For all groups, the false alarm rates (i.e., *Remember* or *Know* responses to the imaginary events) were very low, such that “older old” adults had false alarms rates of .004 for *Remember* responses and .05 for *Know* responses and the “younger old” adults had false alarms rates of .004 for *Remember* responses and .04 for *Know* responses.

In order to test our hypotheses regarding memory changes across the five decades included in our study, we first computed a *Recognition* score for each decade, which reflects the proportion of events that the participants recognized as being *old* (i.e., recognize as having occurred) out of the total of 30 events corresponding to each decade. For those items recognized as *old*, we next analyzed separately *Remember* and *Know* responses for the two older adult groups. For each decade, we computed a *Remember* and a *Know* score, reflecting the proportion of public events *remembered* and *known*, respectively, for that decade out of the total of 30 events corresponding to each decade. Additionally, we also computed *Familiarity* based on previous suggestions that recollection and familiarity are two independent processes (Yonelinas & Jacoby, 1995) and that the *Remember/Know* paradigm underestimates familiarity rates because it allows for either a recollection-based *Remember* response or a familiarity-based *Know* response. Consequently, in the *Remember/Know* paradigm, an event, which is both *recollected* and *familiar*, counts only towards the *Remember*, but not to the *Know* score. The composite *Familiarity* score was computed according to the formula $F = K / (1 - R)$, as recommended by Yonelinas and Jacoby (1995), where *F* represents the corrected *Familiarity* score, *K* represents the *Know* score for the respective decade and *R* represents the *Remember* score for the respective decade. As such, the corrected *Familiarity* score represents the proportion of *Know* responses out of the total number of memory responses, after having eliminated the number of *Remember* responses.

For the *Recognition*, *Remember*, *Know*, and *Familiarity* scores, an arcsine transformation was used to ensure the normality and homogeneity of variance of the memory scores across the five decades. We used these transformed scores to test our hypotheses regarding memory aging through hierarchical linear modeling analyses.

4.1. Preliminary analyses

Figs. 1–4 present the means of the four memory scores corresponding to each of the five decades examined, computed separately for each of the two age groups. Table 1 presents the 95% confidence intervals for the four memory response types across the five decades.

4.2. Hierarchical linear modeling analyses

In order to provide a more integrated description of the changes in memory responses across the five decades, as well as of the age-related differences in recollection and familiarity, we turned

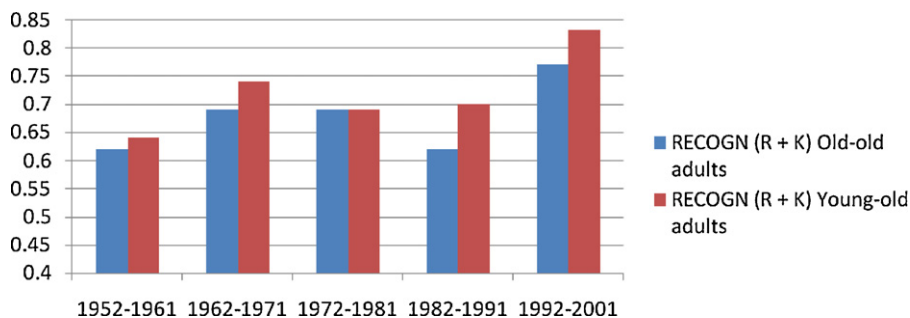


Fig. 1. Mean percent values of the *Recognition* scores for the two old adult groups.

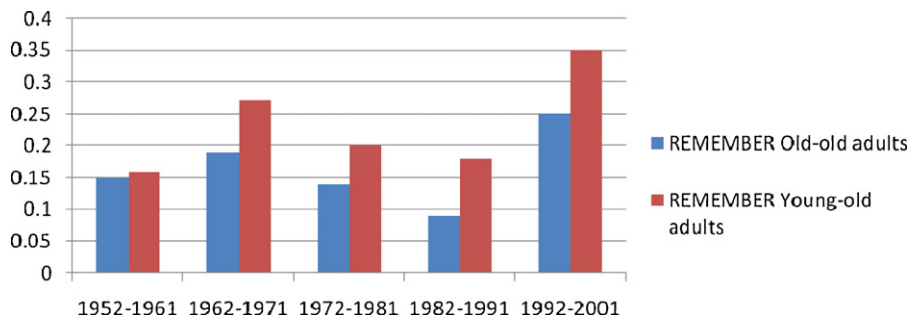


Fig. 2. Mean percent values of the *Remember* scores for the two old adult groups.

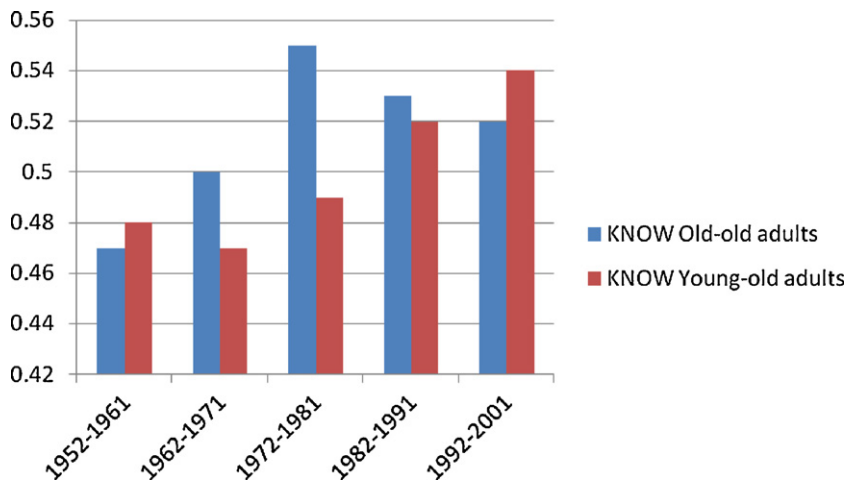


Fig. 3. Mean percent values of the *Know* scores for the two old adult groups.

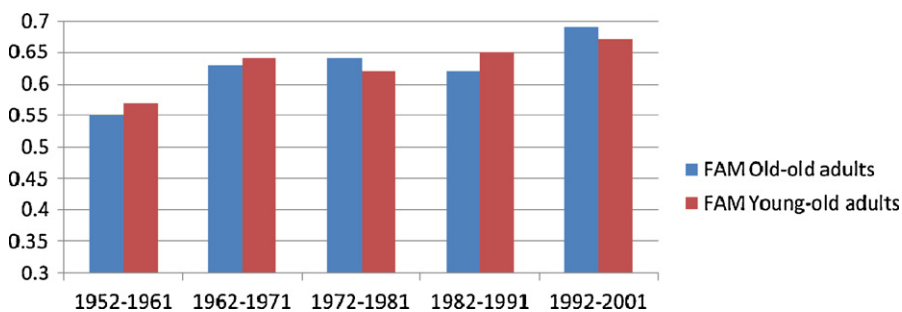


Fig. 4. Mean percent values of the *Familiarity* scores for the two old adult groups.

to multilevel or hierarchical linear modeling software (HLM 6.03, Raudenbush, Bryk, & Congdon, 2005). Our repeated measures, i.e., multiple memory response data set is very well-suited for multilevel modeling analyses, because of its hierarchical struc-

ture where memory responses for each decade (level 1 data) are nested within participants (level 2 data) (Nezlek, 2001; Schwartz & Stone, 1998). We ran four separate sets of hierarchical linear modeling analyses, for each memory response type, i.e., *Recognition*,

Table 1

95% Confidence intervals (CI) for the mean values of remember, know, recognition, and familiarity scores.

Age group	Decade	1952–1961		1962–1971		1972–1981		1982–1991		1992–2001	
1. “Very Old” Adults	Remember	0.12	0.19	0.14	0.25	0.09	0.19	0.1	0.18	0.18	0.33
	Know	0.4	0.54	0.44	0.57	0.48	0.62	0.47	0.6	0.44	0.61
	Familiarity	0.48	0.63	0.56	0.7	0.57	0.72	0.55	0.69	0.62	0.76
	Recognition	0.52	0.73	0.58	0.82	0.57	0.81	0.57	0.78	0.62	0.94
Mr. R.	Remember	.50 [*]		.47 [*]		.37 [*]		.47 [*]		.64 [*]	
	Know	.27 [*]		.37 [*]		.5		.37 [*]		.25 [*]	
	Familiarity	0.53		0.69		0.79 [*]		0.69		0.69	
	Recognition	.77 [*]		.84 [*]		.87 [*]		.84 [*]		0.89	
2. “Younger Old” Adults	Remember	0.09	0.23	0.18	0.34	0.13	0.28	0.11	0.24	0.25	0.42
	Know	0.38	0.53	0.37	0.54	0.41	0.56	0.43	0.58	0.38	0.57
	Familiarity	0.47	0.62	0.53	0.68	0.53	0.69	0.53	0.72	0.62	0.72
	Recognition	0.47	0.76	0.55	0.88	0.54	0.84	0.54	0.82	0.63	0.99
Mr. D.	Remember			.03 [*]		.03 [*]		0 [*]		.10 [*]	
	Know			0.6		0.63		.27 [*]		0.67	
	Familiarity			0.62		0.65		.27 [*]		.61 [*]	
	Recognition			0.63		0.66		.27 [*]		0.77	

Note: $N_1 = 40$ individuals.^{*} $p < .05$.

Remember, Know, and Familiarity. For each set of analyses, the memory response, *Recognition, Remember, Know, or Familiarity*, was the outcome variable, the decade was the level 1 predictor variable and the participants' age was the level 2 predictor variable. Our hypotheses concerned both the relationship between the level-1 variable, i.e., decade, and the outcome variables, i.e., memory response types, as well as the effect of the level-2 variable, i.e., participants' age, on the relationship between decade and memory response types. First, we investigated whether *Recognition, Remember, Know, or Familiarity* response rates increased from the most remote to the most recent decade and whether *Recognition, Remember, Know, or Familiarity* response rates follow distinct patterns of change across the five decades. Second, we examined whether participants' age exerts a distinctive modulating effect on changes in *Recognition, Remember, Know, or Familiarity* response rates as a function of decade.

In all the analyses reported next, the level 1 predictor, i.e., decade, was entered uncentered, since it is a fixed factor across all participants (Hofmann & Gavin, 1998). Following the most recent recommendations in the literature, we grand-mean centered our level 2 individual differences predictor, the participants' age (Nezlek, 2001; Paccagnella, 2006). As in simple regression, the outcome variables, memory response rates, were uncentered. Given that memory responses to the events of the most recent decade were significantly higher relative to the remaining events, we also report results of the relevant analyses when events of the most recent decade have been excluded.

4.3. HLM analyses of memory responses across five decades

4.3.1. Hierarchical linear modeling analyses predicting Recognition responses

Recognition response rates decreased linearly from the most recent to the most remote decade, $b = .03$, $SE = .003$, $t(198) = 8.19$, $p < .0001$. This effect remained significant after we eliminated the events of the most recent decade, $b = .03$, $SE = .003$, $t(198) = 8.19$, $p < .0001$. In order to test the hypothesis that increased aging results in lower recognition rates in the “older old” group relative to the “younger old” group, we evaluated cross-level interactions between the level 1 variables, *Recognition* response rates and decade, and the level 2 variable, participants' age. Results of this analysis revealed no evidence that participants' age modulated the effect of decade on their *Recognition* response rates (Fig. 1).

4.3.2. Hierarchical linear modeling analyses predicting Remember responses

As predicted, for all our participants, *Remember* response rates decreased linearly from the most recent to the most remote decade, $b = .05$, $SE = .01$, $t(198) = 4.99$, $p < .0001$ (Fig. 2). However, after we eliminated the events of the most recent decade, we detected a curvilinear relationship between decade and *Remember* response rates, with *Remember* responses peaking for the events of the second most remote decade, $b = -.05$, $SE = .01$, $t(157) = -3.61$, $p < .001$ (Fig. 2). Given that during the 1962–1971 decade our participants were in their late twenties, our finding is consistent with previous research on autobiographical memory, which documents a “reminiscence bump” peaking around that time, and is associated with identity formation processes in young adulthood (e.g., Rathbone, Moulin, & Conway, 2008).

Subsequently, we tested the hypothesis that increased aging results in lower recollection rates in the “older old” group relative to the “younger old” group (Ivy, MacLeod, Petit, & Markus, 2002; Jennings & Jacoby, 1993). Results of this analysis revealed that the relationship between *Remember* response rates and decade was moderated by the participants' age, such that the linear increase in *Remember* response rates for the recent decades relative to remote decades was attenuated for the “older old” adult group relative to the “younger old” adult group, $b = -.004$, $SE = .001$, $t(196) = -2.47$, $p < .05$ (Fig. 2). For the events of the four most remote decades, where we had detected a curvilinear relationship between decade and *Remember* response rates, the old-old adults' *Remember* response rates peaked earlier relative to young-old adults' responses, $b = .01$, $SE = .002$, $t(154) = 2.49$, $p < .05$. Given that the old-old adults in our sample reached their critical identity formation age earlier relative to young-old adults, the aforementioned finding is consistent with our interpretation that the *Remember* response peak, occurring around the events of the 1962–1971 decade, as a reflection of the previously documented “reminiscence bump”, which would support the creation of a stable sense of self (Rathbone et al., 2008).

4.3.3. Hierarchical linear modeling analyses predicting Know responses

Similarly to the *Remember* response rates, the *Know* response rates decreased linearly from the most recent to the most remote decade, $b = .02$, $SE = .01$, $t(198) = 2.49$, $p < .0001$ and this effect remained significant after the events of the most recent decade were eliminated, $b = .04$, $SE = .01$, $t(158) = 3.35$, $p < .001$ (Fig. 3).

Next, we examined whether age had an effect on participants' *Know* response rates across decades. Results of this analysis revealed that the effect of participants' age on the relationship between decade and the corresponding *Know* response rates was non-significant (Fig. 3).

4.3.4. Hierarchical linear modeling analyses predicting Familiarity responses

Similarly to the *Remember* and *Know* response rates, the *Familiarity* response rates decreased linearly from the most recent to the most remote decade, $b = .07$, $SE = .01$, $t(198) = 6.27$, $p < .0001$ (Fig. 4). Again, the effect remained significant after we eliminated the events of the most recent decade, $b = .05$, $SE = .02$, $t(158) = 3.21$, $p < .01$.

Similarly to the analysis examining *Know* response rates and in contrast to the analysis examining *Remember* response rates, the effect of participants' age on the relationship between decade and the corresponding *Familiarity* response rates was non-significant (Fig. 4).

To summarize, we found that overall *Recognition* memory did not differ significantly between the two old groups, but showed a steady decline from the most recent decade to the most remote. When examining subcomponents of recognition, however, the predicted group difference for *Remember* responses based on *Recollection* did emerge. Because recollective response rates to the most recent events were more impaired in the older group, the decline in recollection from recent to remote events was not as steep as in the younger-old group. Unlike *Remember* responses, the decline for *Know* and *Familiar* responses was comparable in the two groups.

To control for the possibility that group differences between the different types of memory responses emerged because people in the old-old group were always older when each event occurred than the younger-old group, we next analyzed the data by equating the age of the participants at encoding. In this way, we could test whether it was the age of acquisition that accounted for the difference between the two groups, and by comparing the results with the previous analysis, we would know whether the age of retrieval also contributed.

4.3.5. HLM analyses of memory responses equating participants' age at encoding

We examined the decay trajectories of episodic and semantic memories for events from decades in which the average age of the participants in the two groups was equivalent. Since all participants' memory for the events of the most recent decade was disproportionately higher relative to the events of the remaining decades, and since we could not equate the ages of the two groups for the most recent decade, this decade was eliminated from the analyses reported next. Thus, old-old participants' memory for events occurring during the 1952–1981 interval was compared to young-old participants' memory for events occurring during the 1962–1991 interval. For all the analyses reported next, decade of acquisition was introduced as the level 1 predictor. As such, decade 1, where the participants' average age was 33 years, corresponded to the 1952–1961 decade for old-old adults and to the 1962–1971 to the young-old adults. Decade 2, where the participants' average age was 43 years, corresponded to the 1962–1971 decade for old-old adults and to the 1972–1981 to the young-old adults. Decade 3, where the participants' average age was 53 years, corresponded to the 1972–1981 decade for old-old adults and to the 1982–1991 to the young-old adults.

4.3.6. Hierarchical linear modeling analyses predicting Recognition responses

We found no evidence that participants' age at acquisition, $b = .003$, $SE = .002$, $t(118) = 1.21$, $p > .20$ or their age at retrieval (i.e.,

current age) exerted any effect on their *Recognition* response rates, $b = .01$, $SE = .002$, $t(116) = 1.63$, $p > .10$.

4.3.7. Hierarchical linear modeling analyses predicting Remember responses

Results of these analyses revealed that age at retrieval and age at acquisition exerted independent effects on memory performance. As such, old-old adults exhibited significantly lower *Remember* response rates across all decades relative to young-old adults, $b = -.02$, $SE = .01$, $t(38) = -2.54$, $p < .05$. Additionally, the participants' age at encoding had a significant effect on overall *Remember* response rates, such that the older the participants were at the time that the event occurred, the less likely they were to form an episodic representation of that event, $b = -.07$, $SE = .02$, $t(116) = -3.43$, $p < .01$.

4.3.8. Hierarchical linear modeling analyses predicting Know responses

In contrast with the results for the *Remember* response rates, we found that the older the participants were at the time they encoded a specific event, the more likely they were to give a *Know* response to the respective event, $b = .07$, $SE = .02$, $t(116) = 3.17$, $p < .01$. However, we found no evidence that participants' age at retrieval (i.e., their current age) exerted any effect on their *Know* response rates.

4.3.9. Hierarchical linear modeling analyses predicting Familiarity responses

Similar to the results for the *Know* response rates, the older the participants were at the time they encoded a specific event, the more likely they were to give a *Familiarity* response to the respective event, $b = .06$, $SE = .03$, $t(116) = 2.60$, $p < .01$. Finally, we found no evidence that participants' age at retrieval exerted any effect on their *Familiarity* response rates.

Taken together, the results of Study 1 suggest that overall *Recognition*, as well as its components, episodic (*Remember/Recollection*) and semantic (*Know/Familiarity*) event memory, decrease as a function of time elapsed since the event occurred. These decreases are similar to previous findings on memory changes across decades (Bahrick, 1965; Bahrick, Bahrick, & Wittlinger, 1974; Rubin, Hinton, & Wenzel, 1999) that did not distinguish between recollection and familiarity. Importantly, by fractionating overall recognition into recollection and familiarity, we were able to show that the two follow different decay trajectories across time. Specifically, recollection response rates peaked for the events of the most recent decade, and then they exhibited a significant drop. For the four most remote decades, recollection response rates were relatively stable, exhibiting a peak for the events of the second most remote decade, which corresponds roughly to the "reminiscence bump" period, previously identified in autobiographical memory research and linked to identity formation processes (e.g., Rathbone et al., 2008). In contrast, *Know* and *Familiarity* responses exhibited a linear decay function from the more recent to the most remote decade. Thus, application of the R/K procedure to memory for remote public events helps dissociate between the contribution of familiarity and recollection processes to those memories. Our findings show that even memories for public events, which ostensibly are semantic, contain episodic components, in many instances.

We also found that the decay trajectories for recollection and familiarity are different in the two age groups. Specifically, with increasing age, individuals exhibited lower recollection response rates for the more recent events relative to the more remote ones. Even when we equated participants' age at encoding, the poorer recollection in the older group suggests that it results from age-related deficits in both encoding and retrieving episodic memories—the older the person was at encoding and at retrieval, the lower the recollection rates. In contrast, *Know* and *Familiarity*

responses followed a generally linear decay from the more recent to the more remote events, and were unaffected by participants' age at retrieval (i.e., their current age). When we equated participants' age at encoding, we found that semantic memory as assessed by *Know and Familiarity*, was better at older ages; the older the participants were at the time they encoded a specific event, the more likely they were to give a *Familiarity* or *Know* response to the respective event.

These findings are consistent with the hypothesis that as medial temporal lobe (MTL) structures, particularly the hippocampus, and the prefrontal cortex (PFC) deteriorate with age, they affect primarily recollection-related processes, leading to impairments either in creating resilient episodic memory traces, retrieving those episodic memories, or both. This interpretation would account for our finding that the older group exhibits lower *Remember* responses for the more recent events relative to the more remote ones. Though familiarity also decays with time since acquisition, it is not affected significantly by the age of the participants. We acknowledge, however, that it is possible that familiarity may be affected by age more than it appears to be since some of the initial familiarity-based memories may have been forgotten or lost, and been replaced by others that were initially recollection-based, but converted to familiarity-based representations. Future studies with a longitudinal design are needed to an in-depth investigation of the role of age in semantic memory decay (see *Paller, 2009*; and *Winocur, Moscovitch, & Sekeres, 2007*, for a discussion of this *transformation hypothesis*).

Broadly, our findings suggest that at initial encoding, and for a while thereafter, many events retain contextual information about the circumstances under which they were encoded, behaving as episodic traces that support recollection. However, after some time, many of these memories lose the contextual information and fade to the point of no longer being recollected. At that point, they can be considered either to have become transformed into familiarity-based, semantic memories or to have been lost entirely, giving way to the underlying, co-occurring memory which was familiarity-based from the very beginning. Either interpretation, accounting as it does for the steep decrease in recollection rates from the events of the most recent decade to the events of the remaining decades, is consistent with previous laboratory findings that as the retention interval increases, episodic memories based on recollection are replaced by familiarity-based memories (e.g., *Knowlton & Squire, 1995*) and lose their hippocampal signature (*Viskontas et al., 2009*). Our study suggests that even the latter memories fade as indicated by the decay over decades in *Know* and *Familiarity* response rates, and may do so even more than they appear because of replacement by transformed recollection-based memories. In contrast, the relatively stable recollection rates for events of the four most remote decades suggest that episodic memories, which had been strong enough to survive an initial pruning phase during the first decade, remain available throughout the individual's lifetime.

We were encouraged by these findings to use the same R/K procedure to examine possible differential memory deficits for public events in patients with memory disorders. In particular, we wished to see whether recollection associated with public events would be disproportionately affected in a person with medial temporal lobe damage, but not in a person with relatively preserved MTL, but with degeneration in lateral and anterior temporal cortex. The following study served as a demonstration that such dissociations are possible.

5. Study 2

In the second study, we examined the time course of recollection and familiarity of public events in two patients, one with damage to the medial temporal lobe, primarily the hippocampus

and fornix, and a secondary lesion to the left occipital-temporal region, and the other, with damage to the anterior and lateral temporal structures. The putative damaged sites in the two patients affect primarily episodic and semantic memory, respectively. Previous findings have shown that patients with large lesions to the hippocampal complex are expected to exhibit severe and temporally-extensive *episodic* memory loss (*Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004*; *Maguire, Vargha-Khadem, & Mishkin, 2001*; *Moscovitch et al., 2006*; *Nadel & Moscovitch, 1997*; *Rosenbaum et al., 2008*; but see *Squire et al., 2007*) and temporally graded *semantic* memory loss for events that occurred ten years prior to the damage (for reviews see *Moscovitch, 2008*; *Moscovitch et al., 2006*; *Squire et al., 2007*). The aforementioned findings are consistent with previous evidence that the most recently acquired semantic knowledge is likely to be contextually bound and partially dependent upon the hippocampal complex (*Rosenbaum, Winocur, & Moscovitch, 2001*; *Westmacott, Freedman, Black, Stokes, & Moscovitch, 2004*; *Westmacott & Moscovitch, 2002*). Additionally, patients with neurodegenerative disorders affecting their anterior and lateral temporal lobe structures, but with relative sparing of the MTL (*Westmacott & Moscovitch, 2002*; *Westmacott, Leach, Freedman, & Moscovitch, 2001*), are expected to exhibit relatively preserved episodic memory functions and a disproportionate sparing of recent, relative to remote, semantic memories (*Graham & Hodges, 1997*; *Graham, Kropelnicki, Goldman, & Hodges, 2003*; *Matuszewski et al., 2009*; *McKinnon et al., 2008*; *Moss, Kopelman, Cappalletti, De Mornay Davies, & Jaldow, 2003*; *Murre, Graham, & Hodges, 2001*; *Piolino, Belliard, Desgranges, Perron, & Eustache, 2003*; *Piolino et al., 2003*). This finding would be consistent with the claim that even recent semantic memories are contextually bound, hence they can be supported by MTL/hippocampal structures (*Moscovitch, 2008*; *Rosenbaum et al., 2001*).

Based on the findings from Study 1 and the conjecture that age-related MTL/hippocampal or prefrontal degeneration, or both, led to decreased episodic memory (*Remember*) response rates, but intact semantic memory (*Know/Familiarity*) response rates, we predicted that recollection would be much more severely affected in the patient with lesions to the MTL/hippocampus, with familiarity and overall recognition being relatively preserved. In contrast, we predicted that the patient with lesions to the anterior and lateral temporal cortex, with relative sparing the hippocampal complex and prefrontal cortex, will exhibit intact episodic memory response rates in comparison to his age-matched controls.

6. Method

6.1. Participants

6.1.1. Case 1: Medial temporal lesion

Mr D., born in 1962 (age 42 at the time of testing), had an undergraduate degree in engineering and an M.A. in economics and finance, which enabled him to work as a securities analyst up to the time of his illness.

He presented at a local hospital in December 2001 with severe headache, unsteady gait, increased confusion and lethargy. A CT scan revealed a third ventricle cyst causing hydrocephalus. He underwent a ventriculostomy and then surgery for removal of the cyst, complicated, two days later, by a right posterior cerebral infarct. With rehabilitation, he made a good recovery, his only major deficit being a residual left visual field impairment and an anterograde memory loss related to his lesion. At the time of testing, he was living independently, though he needed some monitoring concerning his memory, and had a good appreciation of the extent of his deficits. He arrived at the appointment by himself.

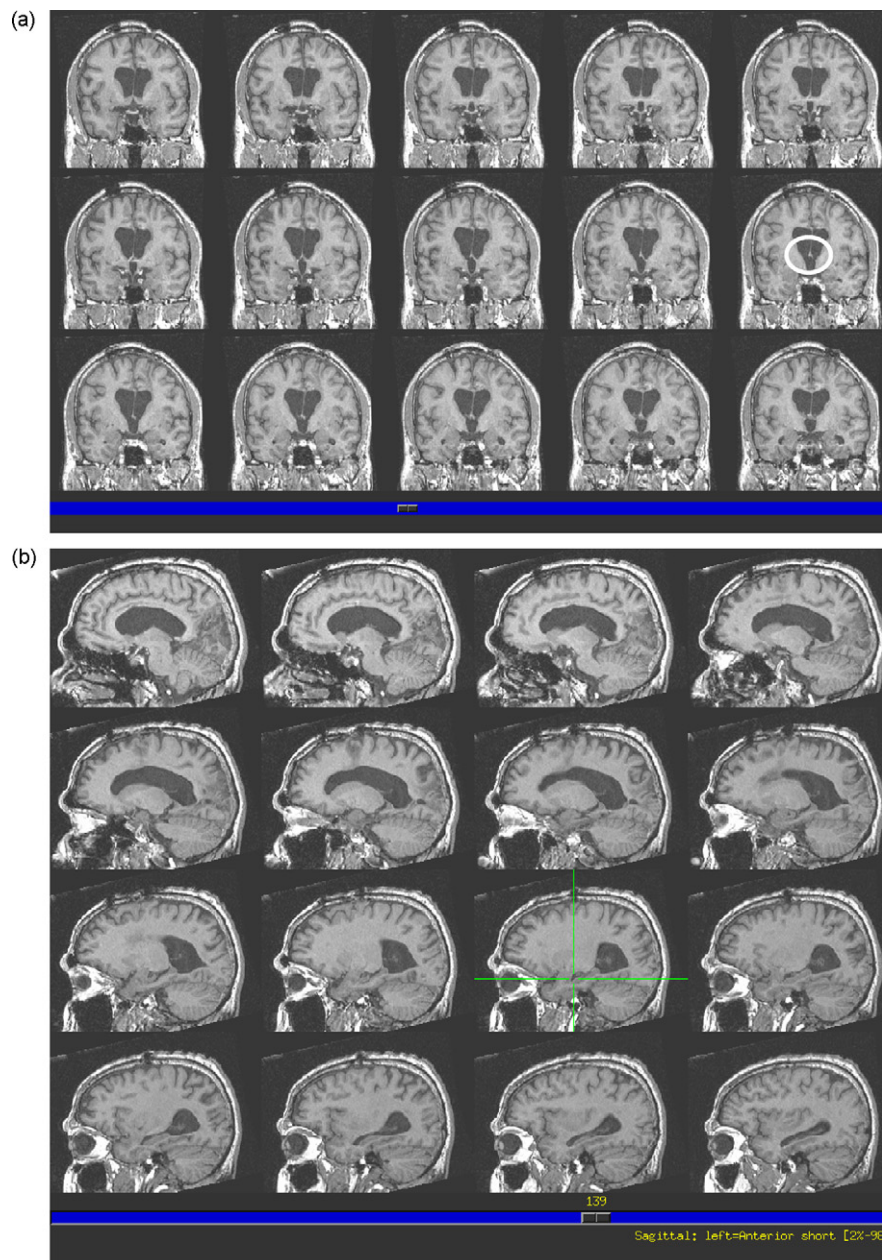


Fig. 5. (a and b) T1-weighted MRI images of the MTL lesions incurred by Mr. D. Subpart a shows that the fornices are severed bilaterally, and b shows enlarged ventricles caused by his third ventricle cyst, along with possible atrophy of the hippocampus.

MRI scans show that his lesion affected the inferior temporal lobes on the right and both fornices, which had been severed, it is believed, during removal of the cyst (see Fig. 5a). The posterior aspect of the hippocampus bilaterally may have been atrophied or may simply be distorted because of the enlargement of the ventricles associated with the hydrocephalus MR. D. experienced (see Fig. 5b).

Neuropsychological testing conducted at the time of the study showed a high average full scale IQ (113), average verbal IQ (107), and high average performance IQ (118) as determined by Wechsler Abbreviated Scale of Intelligence (WASI). We also administered the Kaplan Baycrest Neurocognitive Assessment (KBNA) which showed high average attention (75th percentile), average digit span forward and high average backward (63rd percentile), superior visual construction and praxis (95th percentile). On tests sensitive to executive function, he was superior on conceptual shifting and practical reasoning (95th percentile) normal on the Wisconsin Card

Sorting Test (WCST, 5 categories) but borderline on Trails B (1st percentile), and on phonemic (2nd percentile) and semantic verbal fluency (2nd percentile). He thus has, at most, a modest deficit in cognitive flexibility.

His major impairment, consistent with his lesion, is a residual deficit in processing visual information on the left side, and a severe and lasting anterograde memory loss. On the California Verbal Learning Test (CVLT), he was severely impaired on all tests (27 total on first five trials, 1st percentile), especially if the memory test was delayed, scoring 0 on short and long delayed recall, and only 2 on cued recall in both cases. Immediate story recall on Wechsler Memory Scale III (WMS-III) was low average (16th percentile), but delayed recall was severely impaired (9th percentile). Visual location memory (KBNA) was low average (16th percentile), but visual reproduction (Brief Visuospatial Memory Test, BVMT), immediate and delayed, was severely impaired (below 1st percentile). Interestingly, his memory for faces (WMS III) was average, with scores

of 30 (37th percentile) and 43 (50th percentile) for parts I and II, respectively.

6.2. Case 2: Semantic dementia or atypical Alzheimer's Disease (AD)

Mr. R. is a 75-year-old, right-handed man who presented with a history of progressive speech and language changes over the year prior to the study. He received a university education in engineering and worked as an engineer and in management positions until he retired in 1996.

He presented as a very affable person, aware of many of his deficits, and quite independent. He arrived at this appointment on his own. He was alert, appropriate and co-operative. He reported having difficulty in finding names and remembering addresses and phone numbers but remembered faces well. He had an overall good appreciation of his deficits. He seemed to be unduly tired during testing. His responses tended to be delayed, because he was deliberate and careful, and did not wish to make mistakes.

Because of his obvious word-finding deficits, neuropsychological testing focused on his non-verbal abilities. His performance IQ on WASI was slightly above average (63rd percentile), with good compatibility across test scores. His patterns of preserved and impaired functions across this and other tests (see below), except for face recognition, were indicative of semantic dementia, though performance at a year later suggested atypical AD. Attention/Concentration (KBNA, 18th percentile) was impaired, though he was normal on sequences. Conceptual reasoning and cognitive flexibility was normal on KBNA (76th percentile), but impaired on WCST. His vocabulary (WASI: 2nd percentile) and naming (Boston Naming Test: 40/60) were impaired.

With respect to memory, he was impaired on immediate verbal recall (5th percentile), but this deficit may be related to his word-finding difficulties. Delayed recall was low normal (25th percentile), but what he learned he retained perfectly. Delayed recognition was normal (63rd percentile). Immediate and delayed visual reproduction (KBNA) was normal (63rd percentile).

Given the pattern of his deficits, a single photon emission computed tomography (SPECT) scan was deemed more useful for diagnosis than an MRI scan. On SPECT, he showed hypoperfusion in the temporo-parietal region, more on the left than on the right, but was normal in the medial-temporal region, consistent with his relatively preserved memory and poor language and semantic abilities.

6.3. Materials and procedure

We used the same materials and procedure as in Study 1.

7. Results

As in Study 1, we computed a *Remember* and a *Know* score for each decade, reflecting the proportion of public events *remembered* and *known*, respectively, for that decade out of the total of 30 events corresponding to each decade. We also computed a *Familiarity* score, reflecting the total proportion of events that are only familiar, together with the events that are both familiar and recollected. The composite *Familiarity* score was computed according to the same formula used in Study 1, $F = K / (1 - R)$, where F represents the corrected *Familiarity* score, K represents the *Know* score for the respective decade and R represents the *Remember* score for the respective decade. Finally, we also computed a *Recognition* score as a sum between the patients' *Remember* and *Know* responses.

Table 1, as well as Figs. 6–13 present the patients' *Recognition*, *Remember*, *Know*, and *Familiarity* rates for each decade in comparison with the control memory response rates. In order to evaluate

statistically the memory performance of our two patients, we examined whether their *Recognition*, *Remember*, *Know*, and *Familiarity* rates for each decade fell within the 95% confidence interval of the mean *Recognition*, *Remember*, *Know*, and *Familiarity* response rates, provided by the neurologically intact older adults in Study 1, for the respective decade. Mr. R.'s performance was compared with that of the "older old" adult group in Study 1. Mr. D.'s memory response rates were compared with those of the "younger old" adult group in Study 1. However, given that he was younger than the younger old adult group in Study 1, we eliminated his responses to the most remote decade (when he was not yet born) from all the analyses reported next. By doing so, the results reported next underestimate the extent of his memory deficits, since he was not only younger, but also better educated than the younger old adult group in Study 1.

In Table 1, patients' response rates that fall outside the 95% confidence interval of the mean response rates for their comparison group in Study 1 are marked with an asterisk. As both patients sustained their brain damage after 2001, the memory scores reported next provide an estimate of the severity of their retrograde amnesia.

7.1. False alarm rates

Mr. D. made *Don't Know* responses to all 14 false events, while Mr. R. made a *Know* response to one false event.

7.2. Episodic and semantic memory response rates

As presented in Table 1 and Fig. 3, Mr. R., the patient with semantic dementia or atypical AD, exhibited superior *Remember* response rates, outperforming the controls across all decades, consistent with previous proposals that anterior and lateral temporal damage does not impair episodic memory performance (Moscovitch et al., 2006; Nadel & Moscovitch, 1997). Despite his impaired naming, sufficient language was preserved to convey information about his memories (see Moss et al., 2003). Across all decades, Mr. R. exhibited intact *Familiarity* and *Recognition* response rates (see Table 1 and Figs. 6 and 9). Although unexpected, these results can be readily understood within the context of Mr. R.'s superior recollective abilities. Specifically, our formula for computing *Recognition* scores explicitly allows for high *Remember* rates to compensate for low *Know* response rates in the overall score. While less salient, the formula for computing familiarity rates allows for a similar compensation. Specifically, *Familiarity* scores are computed as a proportion of the items that are known (but not recollected) and items that are unknown to the participants. Consequently, given the formula for computing *Familiarity*, a deficit in *Familiarity* responses would be very difficult to detect in participants who give very few *Don't Know* responses. This is exactly the case for Mr. R. who, due to his exceptional recollective abilities, had significantly higher *Recognition* scores (i.e., significantly fewer *Don't Know* responses) for all but the most recent decade, where he performed similarly to controls (see Fig. 6). However, although Mr. R. exhibited intact *Familiarity* response rates for the aforementioned reasons, his uncorrected *Know* response rates remained consistently below that of his control group both in absolute terms and as a proportion of the sum of R and K responses (see Table 1 and Fig. 3). Given these considerations, we conclude that although he exhibited overall normal memory performance, the underlying mechanisms are considerably distinct from those supporting memory performance in neurologically intact older adults. Specifically, Mr. R.'s performance on a putative semantic memory task seems to be supported (almost exclusively) by his episodic memory system, to a strikingly higher degree than in neurologically intact older adults.

Mr. D., the patient with medial temporal lobe lesions and some impaired frontal functions (but no frontal lesions), exhibited

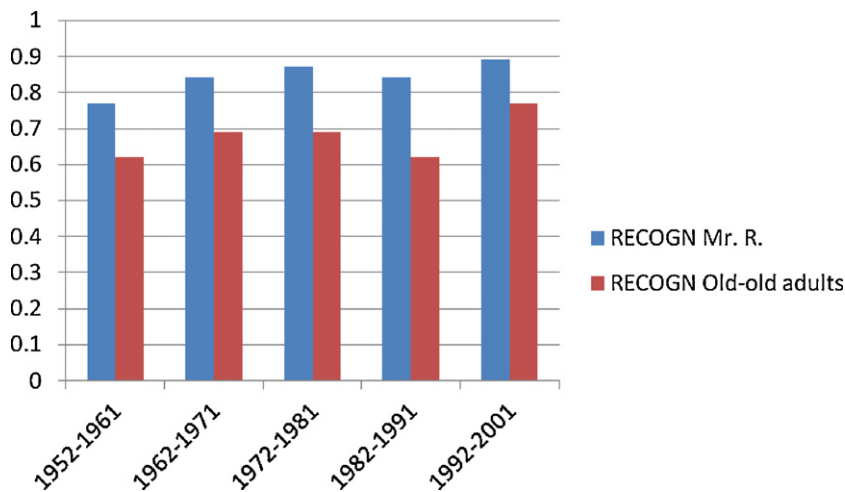


Fig. 6. Mean percent values of the *Recognition* scores for the semantic dementia patient (Mr. R.) relative to the old-adult group.

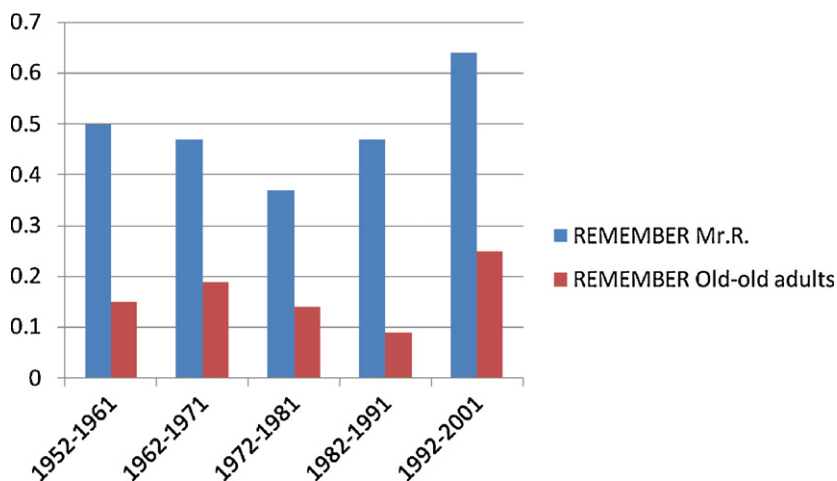


Fig. 7. Mean percent values of the *Remember* scores for the semantic dementia patient (Mr. R.) relative to the old-adult group.

almost complete episodic memory loss across all decades, with *Remember* response rates ranging from 0 to 0.10 (for the most recent decade, see Table 1 and Fig. 11). In contrast, Mr. D. exhibited a pattern of impaired *Familiarity* response rates only for

the most recent two decades, but with good retention for the most remote two decades (i.e., 1962–1971 and 1972–1981) (see Table 1 and Fig. 13). Additionally, he presented a pattern of impaired *Know* and *Recognition* response rates for only one of

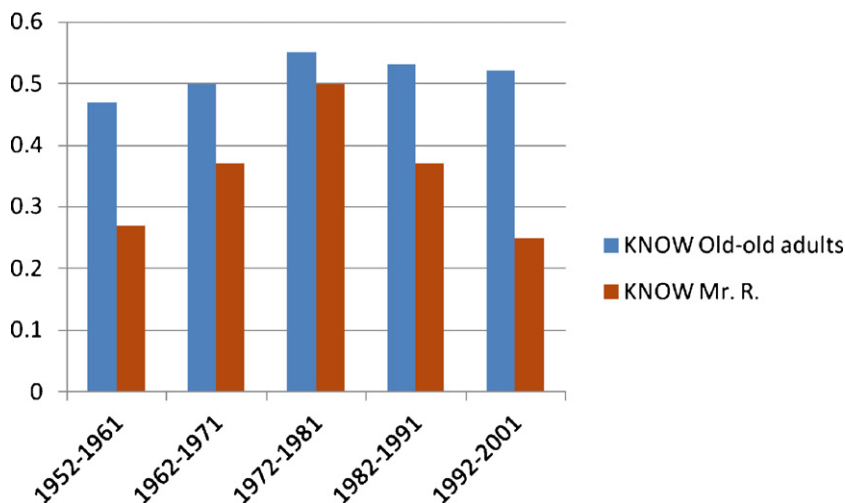


Fig. 8. Mean percent values of the *Know* scores for the semantic dementia patient (Mr. R.) relative to the old-adult group.

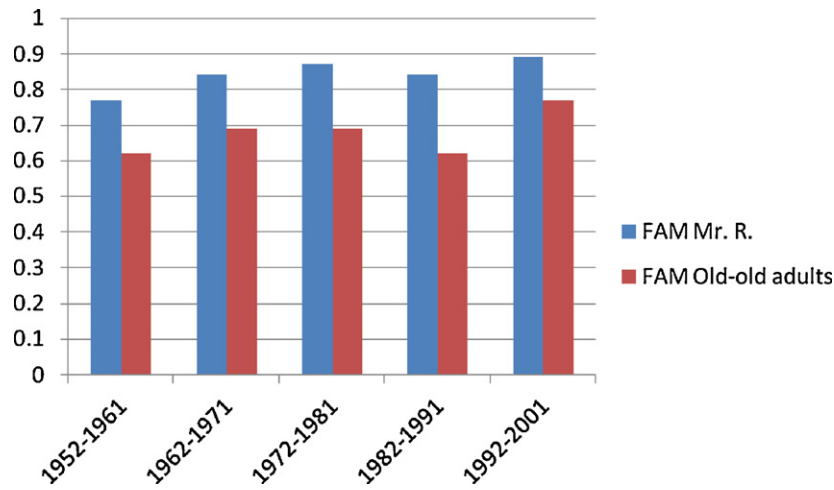


Fig. 9. Mean percent values of the *Familiarity* scores for the semantic dementia patient (Mr. R.) relative to the old-adult group.

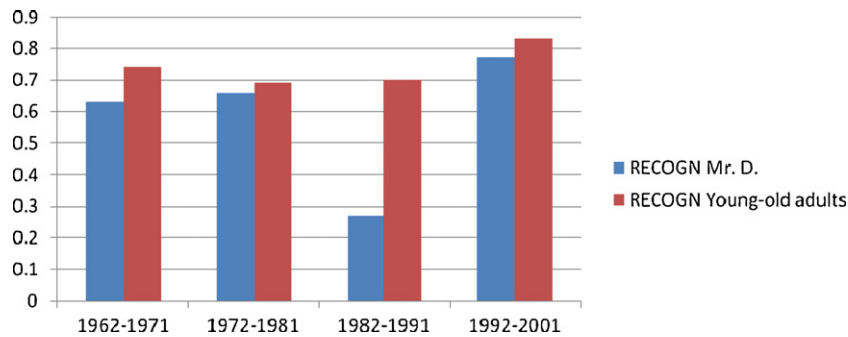


Fig. 10. Mean percent values of the *Recognition* scores for the medial temporal lobe patient (Mr. D.) relative to the young-adult group.

the four decades examined (i.e., 1982–1991) (see Table 1 and Figs. 10 and 12).

8. Discussion

The two patients presented with different patterns of preserved and spared memory loss. Following fornix resection and possible hippocampal atrophy, Mr. D. had a severe deficit in recollection across all decades, whereas he had preserved recognition and familiarity, except for a single decade. On the other hand, Mr. R., whose medial temporal lobes were relatively preserved, but whose dementia was associated primarily with lateral and anterior temporal lobe dysfunction, demonstrated better than normal recollective abilities, which seemed to compensate for any potential semantic memory impairments.

Mr. D.’s performance resembles that of patient A.D. who also had bilateral fornix lesions (Gilboa et al., 2006; Poreh, Winocur, Moscovitch, Backon, & Goshen, 2006). A.D. had preserved recognition for public events, personalities and personal semantics, extending from the most recent, post-operative memories, to the most remote, accompanied by severe episodic (recollection) memory loss across the lifespan. The pattern of deficits exhibited by the two fornix patients differs primarily with regard to Mr. D.’s *Familiarity* score in the next to the most recent decade tested, with *Familiarity* for the most recent decade being only slightly impaired. We have no ready explanation to account for Mr. D.’s poor *Familiarity* scores for the next to the most recent decade. Perhaps growth of his cyst began interfering with acquisition of even semantic memories during that decade and improved for the most recent decade once the cyst was removed.

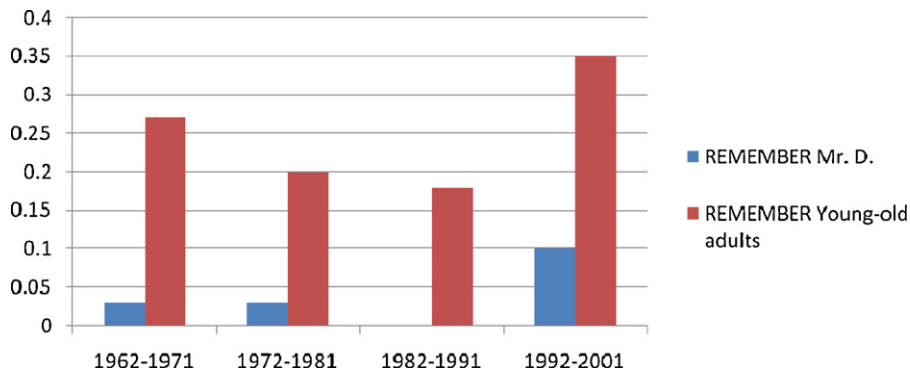


Fig. 11. Mean percent values of the *Remember* scores for the medial temporal lobe patient (Mr. D.) relative to the young-adult group.

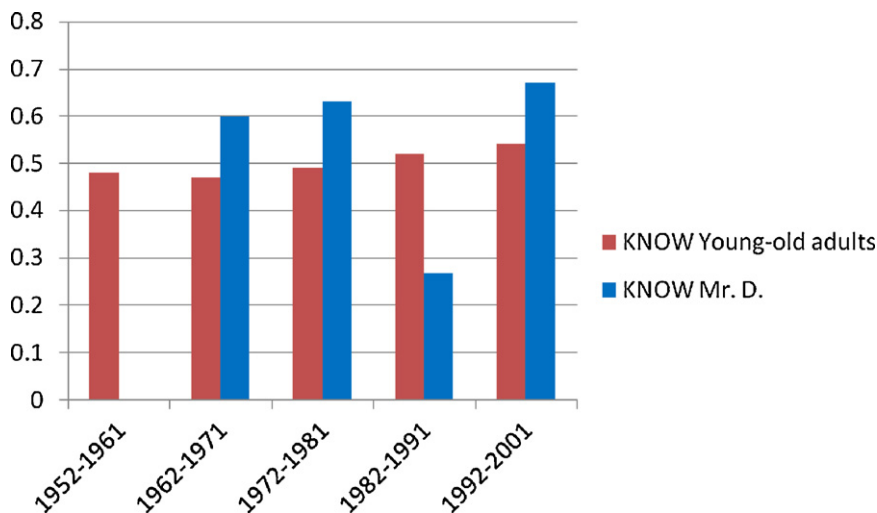


Fig. 12. Mean percent values of the *Know* scores for the medial temporal lobe patient (Mr. D.) relative to the young-adult group.

Because overall recognition is preserved even for the most recent, post-operative decade in Mr. D., as it was in patient A.D., it suggests that his pattern of deficits most likely is caused by his fornix lesions rather than by hippocampal atrophy, as hippocampal damage produces a severe anterograde amnesia and a retrograde amnesia for about 10 years, even for public events and personal semantics (Manns, Hopkins, Reed, Kitchener, & Squire, 2003; Rosenbaum et al., 2001; Steinvorth, Levine, & Corkin, 2005; Westmacott & Moscovitch, 2002). The different pattern of deficits in the two cases suggests that there are non-fornical routes that allow the hippocampus to support the formation and temporary maintenance of familiarity-based (semantic) memories.

Though it was predicted that Mr. R.'s recollection would be preserved, it was unexpected that it would be better than normal. It suggests either that Mr. R. always had exceptional recollective abilities or that the structures mediating recollection and familiarity typically compete with one another, so that when one set of structures is damaged, responses reflect the output of the other set. Effects indicative of spared (or even superior) recollection combined with poor familiarity have been reported by Bowles et al. (2007) for recently acquired memories in a patient with anterior temporal (peri-rhinal) damage, and by Davidson, Anaki, Saint-Cyr, Chow, and Moscovitch (2006) in patients with Parkinson's Disease under some testing conditions (Davidson et al., 2006). The results of the present study, however, resemble most those reported by Westmacott et al. (2004) in other patients with suspected seman-

tic dementia (SD) on tests of episodic and semantic memory for names of famous people. They, too, showed a recollection advantage that in absolute terms exceeded that shown by controls. Our study indicates that comparable effects can also be obtained for remote memory for public events.

It may seem surprising at first that Mr. R. exhibited intact recognition and familiarity rates; however, as discussed earlier, these findings can be readily accounted by the fact the *Recognition* and *Familiarity* formulas allowed his superior recollective abilities to compensate for a potential familiarity-based (semantic) memory deficit in the overall scores.

In sum, the performance of the two patients demonstrates that the R/K procedure as adapted for remote public events can be put to good use in studying clinical populations. The findings of Study 2 show clearly that recollection and familiarity are dissociable one from the other, as predicted based on our findings from Study 1. The pattern of spared and impaired memory favours the view that damage to MTL, together with possible prefrontal dysfunction, lead to deficits in recollection without a temporal gradient across the lifespan, with deficits in familiarity being restricted to the more recent time period. By contrast, when the MTL is relatively preserved, but the anterior and lateral temporal cortex is affected, then recollection is spared and may even be superior. We are mindful, however, that given the patients' lesion profile these assertions are not conclusive. With this proviso in mind, in the General Discussion that follows, we consider the implication of these findings for theories of memory consolidation.

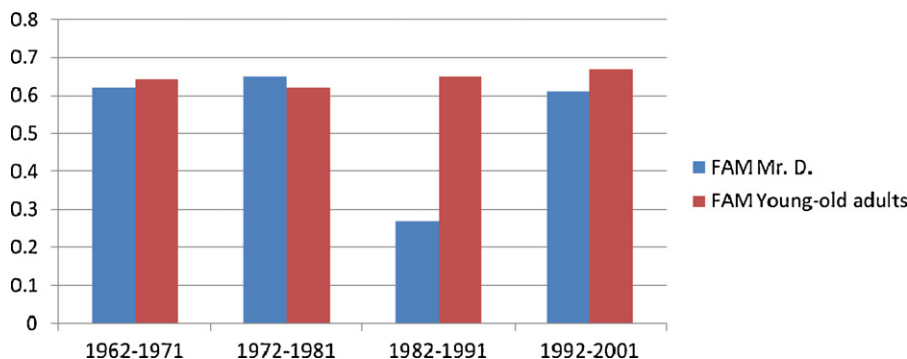


Fig. 13. Mean percent values of the *Familiarity* scores for the medial temporal lobe patient (Mr. D.) relative to the young-adult group.

9. General discussion

The aim of our two studies was to examine the relative contribution of semantic and episodic systems over the lifetime of memories associated with public events. In Study 1, we found, in both young-old (58–69) and old-old adults (74–85), that recollections associated with public events exhibited a marked decrease from the most recent decade to the four more remote ones, the latter remaining relatively stable across the years. By comparison, semantic memory responses (*Know/Familiarity*) exhibited a generally linear decrease from the most recent to the most remote decade. Furthermore, after excluding the events of the most recent decade and equating the two participant groups' age at encoding, we found that age at encoding and age at retrieval exhibit independent effects on recollective response rates. Specifically, *Remember* response rates are relatively constant across the four more remote decades, with the exception of the second most remote decade, finding that replicated previous reports on the “reminiscence bump” in the autobiographical memory literature (e.g., Rathbone et al., 2008). However, across all decades examined, we found that old-old participants exhibited significantly lower *Remember* response rates relative to their younger counterparts. Furthermore, we found that the older the participants were at the time that the event occurred, the less likely they were to encode a recollection-based, episodic memory trace of the respective event. Consistent with the hypothesis that the hippocampus or prefrontal cortex, or both, are necessary for proper encoding and retrieval of episodic memories, our results suggest that age-related hippocampal and prefrontal degeneration may affect both the capacity to form and store resilient episodic traces, as well as the ability to retrieve episodic memories. This conclusion was reinforced by findings from Study 2 which showed though that bilateral damage to the fornix, possibly accompanied by hippocampal atrophy, impairs the ability to retrieve recollection-based, episodic memories across the life-span, but affected familiarity and overall recognition only for the most recent decades. By contrast, recollection was not only preserved, but was superior, in a patient with damage to lateral and anterior temporal cortex with relative sparing of the medial temporal lobes.

Broadly, our present research achieved its main goals of showing that recollection and familiarity both contribute to memory for public events across the lifespan, and that adaptation of the R/K procedure can reveal the contribution of each. Moreover, our study also showed that when applied to a patient population, dissociations between recollection and familiarity are even more starkly evident than they are in normal aging. Our findings complement those on the contribution of semantic information to performance on tests of autobiographical, episodic memory (see Levine et al., 2002; Piolino et al., 2006) by adding to the growing body of literature showing that episodic memory contributes to performance on tests of memory that typically are considered to be semantic. Westmacott and Moscovitch (2003) and Westmacott et al. (2004) showed that recollection-based episodic memory facilitates even classification and reading names of famous people. This benefit is lost after damage to the MTL consistent with the hypothesis that recollection is dependent on the MTL. Likewise, identification and memory for faces is affected by familiarity, and especially so by personal-relevance (Douville et al., 2005), which is associated with activation of the MTL, and the hippocampus in particular, during encoding and retrieval (Douville et al., 2005; Gilboa et al., 2006). Even performance on tests of semantic fluency draws on information from episodic memory (Pihlajamaki et al., 2000; Ryan, Cox, Hayes, & Nadel, 2008; Vallee-Tourangeau, Anthony, & Austin, 1998), and, predictably, deficits are associated with temporal lobe damage (Martin, Loring, Meador, & Lee, 1990; Newcombe, 1969;

Troyer, Moscovitch, Winocur, Alexander, & Stuss, 1998), particularly to the hippocampus (Gleissner & Elger, 2001).

Evidence on the joint contribution of recollection and familiarity to performance on tests of remote memory for everyday public and personal events are consistent with observations on laboratory-based tests of anterograde memory. There is now an extensive behavioural, neuropsychological and functional neuroimaging literature, dating at least as far back to observations by William James (1890), but coming into modern prominence with the work of Mandler (1980), Tulving (1985) and Yonelinas and Jacoby (1995), that recognition memory is based on two components or processes, recollection and familiarity (but see Wixted, 2007, for a dissenting opinion). These processes are presumed by many investigators to be mediated by different structures in the medial temporal lobe (for reviews, see Diana et al. 2007; Eichenbaum et al., 2007). Although not universally-accepted (see Squire et al., 2007), the fact that remote memory for everyday events seems to follow a similar pattern, lends weight to the dual-process model of recognition memory. That recollection and familiarity-based responses were affected differentially in the two patients in Study 2 is more consistent with this dual process model than its single-process competitor (Kirwan, Wixted, & Squire, 2008).

The different decay trajectories of recollection and familiarity in older adults provide further support for the dual process model. Recollection shows a decline over the first decade, followed by curvilinear performance in the remaining decades, whereas familiarity drops steadily over all decades. The hypothesis that memory aging results in loss of episodic information and concurrent increase in the proportion of semantic (relative to episodic) details (Cermak & O'Connor, 1983; Knowlton & Squire, 1995; Manns et al., 2003) seems to be true only when comparing the most recent decade to the one preceding it: the proportion of familiarity-based memories to recollection increases over those two decades, but then remains steady or even drops when we consider more remote decades. When the superior recollection abilities of Mr. R. are taken into account, a more complex transformation model emerges (Winocur, Moscovitch, Caruana, & Binns, 2005; Winocur, Moscovitch, & Sekeres, 2007). Transformation need not imply the obliteration or loss of the original episodic trace from which the semantic memory has been extracted. Insofar as episodic traces remain, these can co-exist, and maybe even compete, with semantic representations of the same events, even if the events occurred in the remote past. The loss of familiarity-based memories allows the more recollection-based memories to be revealed, a finding that also applies to recently-acquired laboratory memories (Bowles et al., 2007).

Our results also have implications for the current debate concerning the formation and long-term retention episodic and semantic memory, and the neural substrates that mediate them. As some of the controversy centers on the location and extent of the lesions producing the memory deficits, we are mindful that results from the older adults in Study 1 and the two patients in Study 2 cannot adjudicate conclusively between competing theories because the structures affected are not sufficiently circumscribed to satisfy all the conditions of the debate. However, their performance, nonetheless, can be instructive in two ways: (1) it can demonstrate that the R/K paradigm for public events is applicable to a patient population and can provide further evidence that recollection and familiarity are dissociable from one another; (2) it can provide evidence that supports one position more than the other without the evidence being conclusive.

With these provisos and limitations in mind, we can now consider how our findings can inform debates in the literature regarding the time order and redundancy of episodic and semantic memory formation, and the structures that mediate them. The standard model of consolidation (Alvarez & Squire, 1994; Squire,

1992) asserts that recent episodic and semantic memories alike are dependent upon hippocampal structures, while remote episodic and semantic memories are supported by neocortical structures, independently of the hippocampal complex (Alvarez & Squire, 1994; Squire, 1992). Thus, damage to the MTL and hippocampus, in particular, leads to a pattern of temporally graded memory loss that is similar for semantic and episodic memory (Alvarez & Squire, 1994; Squire, 1992; Squire et al., 2007; Kirwan et al., 2008). Consequently, damage or age-related deterioration of hippocampal structures (Ivy et al., 1992) should affect recent episodic and semantic memories alike, while sparing remote episodic and semantic memories (Alvarez & Squire, 1994; Squire, 1992; Squire et al., 2007). In contrast, damage to extra-hippocampal neocortical structures, such as the anterior and lateral temporal lobes, should lead to loss of both remote semantic and episodic memories, with relative sparing of recently acquired semantic and episodic memories (if those memories were formed prior to the damage; Graham & Hodges, 1997).

The alternative view, posited by Multiple Trace Theory (Nadel & Moscovitch, 1997), is that the hippocampus plays a time-independent role in the formation and retention of recollection-based, episodic memory, but a limited, time-dependent role in familiarity-based, semantic memory (Moscovitch et al., 2005, 2006; Rosenbaum et al., 2001; Winocur et al., 2005), which ultimately comes to be mediated by the neocortex.

The results of our two studies are broadly consistent with MTT. We found that relative to young-old adults, old-old adults show a decrease in recollection-based episodic memory across all decades, even when age of acquisition was equated, and not just from the most recent decades, as the standard consolidation model would predict. Moreover, performance in the two groups was comparable for familiarity-based memories, suggesting the aging deficit was attributable to age-related hippocampal degeneration (Ivy et al., 1992; Van Petten, 2004; Van Petten et al., 2004). It is possible, however, that the deleterious, age-related effects on recollection-based, episodic memory response rates may not reflect (only) hippocampal degeneration; they may (also) reflect prefrontal function deficiencies (Lustig, May, & Hasher, 2001; Raz, 2000), which would result in increased interference at retrieval, particularly in the case of episodic retrieval, which may require superior controlled processing resources (Jennings & Jacoby, 1993).

The results of Study 2, however, pose greater difficulty for the standard consolidation model, even if one makes allowances for lesion size and location. According to that model, at the very least, damage to anterior and lateral temporal cortex, as seen in Mr. R., should have left remote episodic and semantic memory impaired, because these structures are believed to mediate consolidated memories. By contrast, damage to the fornix, and possibly the hippocampus, in Mr. D. should have left his remote memories undisturbed. Neither outcome was obtained. Instead, Mr. D. had almost complete loss of recollection-based memory, extending to the most remote decades, whereas Mr. R. showed superior recollection-based, episodic memory, which compensated for any potential impairments in familiarity-based, semantic memory, across the life-span.

Taken together, our findings from Study 1 and 2 favour MTT, which posits that the MTL, and the hippocampus in particular, are needed to support recollection-based memories no matter how long ago they were acquired. This conclusion, however, is mitigated by the fact that the lesions in our patients, and the degeneration and dysfunction in our older adults, are not confined to the crucial structures. For example, though unlikely, Mr. D.'s deficits may have been exacerbated by lesions that extend to posterior occipital cortex and to his mild frontal dysfunction, which together may affect recollection much more severely than familiarity. Likewise,

the damage sustained by Mr. R. may have affected some regions of the MTL, which may have accounted for his poor *Know* responses. Thus, though the findings favour MTT, the evidence is not conclusive and awaits verification from studies of patients whose lesions are more circumscribed.

In sum, in two studies with neurologically intact older adults and brain-damaged patients, respectively, we examined the time course of episodic and semantic memory response rates for public events spanning over five decades. Broadly, our present research brought preliminary support to one view on the contribution of semantic and episodic systems to remote event memory, specifically the one promoted by MTT and its related formulations (Moscovitch, 2008; Nadel & Moscovitch, 1997; Rosenbaum et al., 2001). While our studies constitute an important step in fostering ecologically valid investigations of remote memory, future studies are needed to shed further light on the brain networks, as well as the retrieval-specific factors and individual differences variables (e.g., executive control) that may modulate episodic and semantic memory retrieval of remote events.

References

- Alvarez, P., & Squire, L. R. (1994). Memory consolidation and the medial temporal lobe: A simple network model. *Proceedings of the National Academy of Sciences*, 91(15), 7041–7045.
- Bahrick, H. P. (1965). The ebb of retention. *Psychological Review*, 72(1), 60–73.
- Bahrick, H. P., Bahrick, P. O., & Wittlinger, R. P. (1974). Long-term memory: Those unforgettable high school years. *Psychology Today*, 8(7), 50–56.
- Bowles, B., Crupi, C., Mirsattari, S. M., Pigott, S. E., Parrent, A. G., Pruessner, J. C., et al. (2007). Impaired familiarity with preserved recollection after anterior temporal-lobe resection that spares the hippocampus. *PNAS Proceedings of the National Academy of Sciences of the United States of America*, 104(41), 16382–16387.
- Bugaiska, A., Clarys, D., Jarry, C., Taconnat, L., Tapia, G., Vanneste, S., et al. (2007). The effect of aging in recollective experience: The processing speed and executive functioning hypothesis. *Consciousness and Cognition: An International Journal*, 16(4), 797–808.
- Cermak, L. S., & O'Connor, M. (1983). The anterograde and retrograde retrieval ability of a patient with amnesia due to encephalitis. *Neuropsychologia*, 21(3), 213–234.
- Davidson, P. S. R., Anaki, D., Saint-Cyr, J. A., Chow, T. W., & Moscovitch, M. (2006). Exploring the recognition memory deficit in Parkinson's disease: Estimates of recollection versus familiarity. *Brain: A Journal of Neurology*, 129(7), 1768–1779.
- Diana, R. A., Yonelinas, A. P., & Ranganath, C. (2007). Imaging recollection and familiarity in the medial temporal lobe: A three-component model. *Trends in Cognitive Sciences*, 11(9), 379–386.
- Douville, K., Woodard, J. L., Seidenberg, M., Miller, S. K., Leveroni, C. L., et al. (2005). Medial temporal lobe activity for recognition of recent and remote famous names: An event-related fMRI study. *Neuropsychologia*, 43(5), 693–703.
- Dudai, Y. (2004). The neurobiology of consolidations, or, how stable is the engram. *Annual Review of Psychology*, 55, 51–86.
- Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*, 30, 123–152.
- Gardiner, J. M. (1988). Functional aspects of recollective experience. *Memory & Cognition*, 16(4), 309–313.
- Gardiner, J. M., & Java, R. I. (1991). Forgetting in recognition memory with and without recollective experience. *Memory & Cognition*, 19(6), 617–623.
- Gardiner, J. M., & Parkin, A. J. (1990). Attention and recollective experience in recognition memory. *Memory & Cognition*, 18(6), 579–583.
- 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(11), 1214–1225.
- Gilboa, A., Winocur, G., Rosenbaum, R. S., Poreh, A., Gao, F., Black, S. E., et al. (2006). Hippocampal contributions to recollection in retrograde and anterograde amnesia. *Hippocampus*, 16(11), 966–980.
- Gleissner, U., & Elger, C. E. (2001). The hippocampal contribution to verbal fluency in patients with temporal lobe epilepsy. *Cortex*, 37(1), 55–63.
- Gordon, L., & Gordon, A. (Eds.). (1999). *American chronicle: Year by year through the twentieth century*. New Haven, CT: Yale University Press.
- Grady, C. L. (1998). Brain imaging and age-related changes in cognition. *Experimental Gerontology*, 33(7–8), 661–673.
- Grady, C. L., & Craik, F. I. (2000). Changes in memory processing with age. *Current Opinion in Neurobiology*, 10(2), 224–231.
- Graham, K. S., & Hodges, J. R. (1997). Differentiating the roles of the hippocampal system and the neocortex in long-term memory storage. *Neuropsychologia*, 11(1), 77–89.
- Graham, K. S., Kropelnicki, A., Goldman, W. P., & Hodges, J. R. (2003). Two further investigations of autobiographical memory in semantic dementia. *Cortex*, 39(4–5), 729–750.

- Hofmann, D. A., & Gavin, M. A. (1998). Centering decisions in hierarchical linear models: Implications for research in organizations. *Journal of Management*, 24(5), 623–641.
- Ivy, G. O., MacLeod, C. M., Petit, T. L., & Markus, E. J. (1992). A physiological framework for perceptual and cognitive changes in aging. In F. I. M. Craik, & T. A. Salthouse (Eds.), *The handbook of aging and cognition* (pp. 273–314). Hillsdale, NJ, England: Lawrence Erlbaum Associates.
- Jennings, J. M., & Jacoby, L. L. (1993). Automatic versus intentional uses of memory: Aging, attention, and control. *Psychology and Aging*, 8(2), 283–293.
- Joyce, C. A., Lazzarra, E. J., & Janssen, S. (Eds.). (1950–1999). *The world almanac and book of facts*. New York: World Almanac Books.
- Kirwan, C. B., Wixted, J. T., & Squire, L. R. (2008). Activity in the medial temporal lobe predicts memory strength, whereas activity in the prefrontal cortex predicts recollection. *Journal of Neuroscience*, 28(42), 10541–10548.
- Knowlton, B. J., & Squire, L. R. (1995). Remembering and knowing: Two different expressions of declarative memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 21(3), 699–710.
- 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(4), 677–689.
- Lustig, C., May, C. P., & Hasher, L. (2001). Working memory span and the role of proactive interference. *Journal of Experimental Psychology: General*, 130(2), 199–207.
- Maguire, E. A., Vargha-Khadem, F., & Mishkin, M. (2001). The effects of bilateral hippocampal damage on fMRI regional activations and interactions during memory retrieval. *Brain*, 124(6), 1156–1170.
- Mandler, G. (1980). Recognizing: The judgment of previous occurrence. *Psychological Review*, 87(3), 252–271.
- Manns, J. R., Hopkins, R. O., Reed, J. M., Kitchener, E. G., & Squire, L. R. (2003). Recognition memory and the human hippocampus. *Neuron*, 37(1), 171–180.
- Martin, R. C., Loring, D. W., Meador, K. J., & Lee, G. P. (1990). The effects of lateralized temporal lobe dysfunction on formal and semantic word fluency. *Neuropsychologia*, 28(8), 823–829.
- Matuszewski, V., Piolino, P., Belliard, S., de la Sayette, V., Laisney, M., Lalevae, C., et al. (2009). Patterns of autobiographical memory impairment according to disease severity in semantic dementia. *Cortex*, 45(4), 456–472.
- 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(10), 1839–1853.
- Moscovitch, M. (1995). Models of consciousness and memory. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1341–1356). Cambridge, MA, US: The MIT Press.
- Moscovitch, M. (2008). The hippocampus as a “stupid”, domain-specific module: Implications for theories of recent and remote memory, and of imagination. *Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale*, 62(1), 62–79.
- Moscovitch, M., Rosenbaum, R. S., Gilboa, A., Addis, D. R., Westmacott, R., Grady, C., et al. (2005). Functional neuroanatomy of remote episodic, semantic and spatial memory: A unified account based on multiple trace theory. *Journal of Anatomy*, 207(1), 35–66.
- Moscovitch, M., Westmacott, R., Gilboa, A., Addis, D. A., Rosenbaum, R. S., & Viskontas, I., et al. (2006). Hippocampal complex contribution to retention and retrieval of recent and remote episodic and semantic memories: Evidence from behavioral and neuroimaging studies of healthy and brain-damaged people. *Proceedings of Tsukuba International Conference on Memory*. MIT Press.
- Moss, H. E., Kopelman, M. D., Cappelletti, M., De Mornay Davies, P., & Jaldow, E. (2003). Lost for words or loss of memories? Autobiographical memory in semantic dementia. *Cognitive Neuropsychology*, 20(8), 703–732.
- Murphy, K. J., Troyer, A. K., Levine, B., & Moscovitch, M. (2008). Episodic, but not semantic, autobiographical memory is reduced in amnesic mild cognitive impairment. *Neuropsychologia*, 46(13), 3116–3123.
- Murre, J. M. J., Graham, K. S., & Hodges, J. R. (2001). Semantic dementia: Relevance to connectionist models of long-term memory. *Brain*, 124(4), 647–675.
- Nadel, L., & Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current Opinion in Neurobiology*, 7(2), 217–227.
- Newcombe, F. (1969). *Missile wounds of the brain: A study of psychological deficits*. Oxford, England: Oxford University Press.
- Nezlek, J. B. (2001). Multilevel random coefficient analyses of event- and interval-contingent data in social and personality psychology research. *Personality and Social Psychology Bulletin*, 27(7), 771–785.
- Paccagnella, O. (2006). Centering or not centering in multilevel models? The role of group mean and the assessment of group effects. *Evaluation Review*, 30(1), 66–85.
- Paller, K. A. (2009). Memory consolidation: Systems. In *The Encyclopedia of Neuroscience* (pp. 741–749).
- Pihlajamaki, M., Tanila, H., Hanninen, T., Kononen, M., Laakso, M., Partanen, K., et al. (2000). Verbal fluency activates the left medial temporal lobe: A functional magnetic resonance imaging study. *Annals of Neurology*, 47(4), 470–476.
- Piolino, P., Desgranges, B., Belliard, S., Matuszewski, V., Lalevae, C., De la Sayette, V., et al. (2003). Autobiographical memory and auto-noetic consciousness: Triple dissociation in neurodegenerative diseases. *Brain*, 126(10), 2203–2219.
- Piolino, P., Belliard, S., Desgranges, B., Perron, M., & Eustache, F. (2003). Autobiographical memory and auto-noetic consciousness in a case of semantic dementia. *Cognitive Neuropsychology*, 20(7), 619–639.
- Piolino, P., Desgranges, B., Clarys, D., Guillery-Girard, B., Taconnat, L., Isingrini, M., et al. (2006). Autobiographical memory, auto-noetic consciousness, and self-perception in aging. *Psychology and Aging*, 21(3), 510–525.
- Poreh, M., Winocur, G., Moscovitch, M., Backon, M., Goshen, E., Ram, Z., et al. (2006). Anterograde and retrograde amnesia in a person with bilateral fornix lesions following removal of a colloid cyst. *Neuropsychologia*, 44(12), 2241–2248.
- Rathbone, C. J., Moulin, C. J. A., & Conway, M. A. (2008). Self-centered memories: The *remembrance bump* and the self. *Memory & Cognition*, 36(8), 1403–1414.
- Raudenbush, S., Bryk, A., & Congdon, R. (2005). HLM 6.03 for Windows [Hierarchical linear and nonlinear modeling software]. Multivariate Software, Inc.
- Raz, N. (2000). Aging of the brain and its impact on cognitive performance: Integration of structural and functional findings. In F. M. Craik, & T. A. Salthouse (Eds.), *The handbook of aging and cognition* (2nd ed., pp. 1–90). Mahwah, NJ, US: Lawrence Erlbaum Associates Publishers.
- Rosenbaum, R. S., Winocur, G., & Moscovitch, M. (2001). New views on old memories: Re-evaluating the role of the hippocampal complex. *Behavioural Brain Research. Special Issue: Challenging the focal role of the hippocampus in memory*, 127(1–2), 183–197.
- Rosenbaum, R. S., Moscovitch, M., Foster, J. K., Schnyer, D. M., Gao, F., Kovacevic, N., et al. (2008). Patterns of autobiographical memory loss in medial-temporal lobe amnesic patients. *Journal of Cognitive Neuroscience*, 20(8), 1490–1506.
- Rubin, D. C., Hinton, S., & Wenzel, A. (1999). The precise time course of retention. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 25(5), 1161–1176.
- Ryan, L., Cox, C., Hayes, S. M., & Nadel, L. (2008). Hippocampal activation during episodic and semantic memory retrieval: Comparing category production and category cued recall. *Neuropsychologia*, 46(8), 2109–2121.
- Schwartz, J. E., & Stone, A. A. (1998). Strategies for analyzing ecological momentary assessment data. *Health Psychology*, 17(1), 6–16.
- Squire, L. R. (1992). Declarative and non-declarative memory: Multiple brain systems supporting learning and memory. *Journal of Cognitive Neuroscience. Special Issue: Memory systems*, 4(3), 232–243.
- Squire, L. R., Cohen, N. J., & Nadel, L. (1984). The medial temporal region and memory consolidation: A new hypothesis. In H. Weingartner, & E. Parker (Eds.), *Memory consolidation* (pp. 185–210). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Squire, L. R., Wixted, J. T., & Clark, R. E. (2007). Recognition memory and the medial temporal lobe: A new perspective. *Nature Reviews Neuroscience*, 8(11), 872–883.
- Steinworth, 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*, 42(4), 479–496.
- Troyer, A. K., Moscovitch, M., Winocur, G., Alexander, M. P., & Stuss, D. (1998). Clustering and switching on verbal fluency: The effects of focal frontal and temporal lobe lesions. *Neuropsychologia*, 36(6), 499–504.
- Tulving, E. (1985). Memory and consciousness. *Canadian Psychology*, 26(1), 1–12.
- Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology*, 53(1), 1–25.
- Tulving, E., & Markowitsch, H. J. (1998). Episodic and declarative memory: Role of the hippocampus. *Hippocampus*, 8(3), 198–204.
- Vallee-Tourangeau, F., Anthony, S. H., & Austin, N. G. (1998). Strategies for generating multiple instances of common and ad-hoc categories. *Memory*, 6(5), 555–592.
- Van Petten, C. (2004). Relationships between hippocampal volume and memory ability in healthy individuals across the lifespan: Review and meta-analysis. *Neuropsychologia*, 42(10), 1394–1413.
- Van Petten, C., Plante, E., Davidson, P. S. R., Kuo, T. Y., Bajuscak, L., & Glisky, E. L. (2004). Memory and executive function in older adults: Relationships with temporal and prefrontal gray matter volumes and white matter hyperintensities. *Neuropsychologia*, 42(10), 1313–1335.
- Verhaeghen, P., Marcoen, A., & Goossens, L. (1993). Facts and fiction about memory aging: A quantitative integration of research findings. *Journal of Gerontology*, 48(4), 157–171.
- Viskontas, I. V., Carr, V. A., Engel, S. A., & Knowlton, B. J. (2009). The neural correlates of recollection: Hippocampal activation declines as episodic memory fades. *Hippocampus*, 19(3), 265–272.
- Westmacott, R., & Moscovitch, M. (2002). Temporally graded semantic memory loss in amnesia and semantic dementia: Further evidence for opposite gradients. *Cognitive Neuropsychology*, 19(2), 135–163.
- Westmacott, R., & Moscovitch, M. (2003). The contribution of autobiographical significance to semantic memory. *Memory and Cognition*, 31(5), 761–774.
- Westmacott, R., Leach, L., Freedman, M., & Moscovitch, M. (2001). Different patterns of autobiographical memory loss in semantic dementia and medial temporal lobe amnesia: A challenge to consolidation theory. *Neurocase*, 7(1), 37–55.
- Westmacott, R., Freedman, M., Black, S. E., Stokes, K. A., & Moscovitch, M. (2004). Temporally graded semantic memory loss in Alzheimer's disease: Cross-sectional and longitudinal studies. *Cognitive Neuropsychology*, 21(2–4), 353–378.
- Westmacott, R., Black, S. E., Freedman, M., & Moscovitch, M. (2005). The contribution of autobiographical significance to semantic memory: Evidence from Alzheimer's disease, semantic dementia, and amnesia. *Neuropsychologia*, 42(1), 25–48.
- Wheeler, M. E., & Buckner, R. L. (2004). Functional-anatomic correlates of remembering and knowing. *NeuroImage*, 21(4), 1337–1349.
- Wheeler, M., Stuss, D. T., & Tulving, E. (1997). Toward a theory of episodic memory: The frontal lobes and auto-noetic consciousness. *Psychological Bulletin*, 121(3), 331–354.

- Winocur, G., Moscovitch, M., Caruana, D. A., & Binns, M. A. (2005). Retrograde amnesia in rats with lesions to the hippocampus on a test of spatial memory. *Neuropsychologia*, 43(11), 1580–1590.
- Winocur, G., Moscovitch, M., & Sekeres, M. (2007). Memory consolidation or transformation: Context manipulation and hippocampal representations of memory. *Nature Neuroscience*, 10(5), 555–557.
- Wixted, J. T. (2007). Dual-process theory and signal-detection theory of recognition memory. *Psychological Review*, 114(1), 152–176.
- Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, 46(3), 441–517.
- Yonelinas, A. P., & Jacoby, L. L. (1995). Response bias and the process-dissociation procedure. *Journal of Experimental Psychology: General*, 125(4), 422–434.