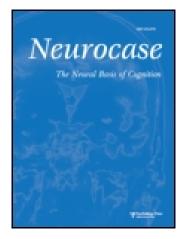
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Topographical, Autobiographical and Semantic Memory in a Patient with Bilateral Mesial Temporal and Retrosplenial Infarction

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According to Consolidation Theory (Squire, 1992, Psychological Review, 99, 195; Squire & Alvarez, 1995, Current Opinion in Neurobiology, 5, 169), the mesial temporal lobes have a time-limited role in the maintenance, storage and retrieval of retrograde declarative memories, such that they are not necessary for recalling remote memories. In contrast, proponents of the Multiple Trace Theory (Fuji, Moscovitch, & Nadel, 2000, Handbook of neuropsychology, 2nd ed., p 223, Amsterdam, New York: Elsevier; Nadel & Moscovitch, 1999, Current Opinion in Neurobiology, 7, 217) posit that the mesial temporal lobe (MTL) is necessary for remembering detailed autobiographical and topographical material from all time periods. A third theory of hippocampal function, the Cognitive Map Theory (O'Keefe & Nadel, 1978, The hippocampus as a cognitive map. Oxford: Clarendon), states that the hippocampus is involved in the processing of allocentric spatial representations. The precise role of the MTL in remote memory has been difficult to elucidate, as the majority of studies present cases with widespread brain damage that often occurred many years prior to testing. We investigated retrograde autobiographical, semantic and topographical memories in a subject (SG) who had recently sustained infarctions confined to the MTL and retrosplenial region bilaterally. Inconsistent with the predictions of Cognitive Map Theory, memory for spatial maps that were learned in the past was preserved. Additional testing indicated that SG suffered from a landmark agnosia, which affected remotely and recently acquired information equally. SG was also poor at imagining which direction he would have to turn his body to move from one landmark to another. In accordance with Consolidation Theory, SG performed similarly to control subjects for remote time periods on various measures of retrograde autobiographical memory and demonstrated intact knowledge regarding famous faces and vocabulary terms that were acquired in the past. In contrast, memory for remote public events was impaired. The current findings indicate that the mesial temporal and/or retrosplenial regions have little role to play in memory for remotely acquired spatial maps, autobiographical memories, famous faces or vocabulary terms. However, the findings for landmark naming, directional calculations between landmarks and knowledge of public events suggest that the MTL and/or retrosplenial cortices remain important for accessing these types of memories indefinitely.

Keywords: Brain lesions, retrograde memory, cerebrovascular accident, Consolidation Theory, Multiple Trace Theory, Cognitive Map Theory, stroke

Introduction

There are a number of competing theories about the way in which autobiographical, topographical and semantic memories are represented in the brain. Most emphasise some role of the hippocampus and adjacent structures, but the time course and nature of this role has been debated. There are only three cases in the published literature with bilateral hippocampal damage that have had the relationships between these three aspects of retrograde memory investigated, and they provide

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somewhat conflicting results. In this paper, we review the findings from these cases as well as their limitations and provide new findings from a fourth case.

Squire and his colleagues (Reed & Squire, 1998; Stefanacci, Buffalo, Schmolck, & Squire, 2000; Teng & Squire, 1999) reported on subject EP, a 76-year-old man, who incurred bilateral anterior MTL damage subsequent to an episode of herpes simplex encephalitis. EP demonstrated a temporal gradient in his memory for topographical information and autobiographical episodes, such that his memory for his childhood years was preserved. In contrast, he could not recall any information about his current neighbourhood or any autobiographical episodes from the past 50 years of his life. Knowledge pertaining to news events, famous faces, famous names and vocabulary that had been acquired during his late twenties and onwards was found to be markedly impaired. Unfortunately, this sort of knowledge was not sampled from the whole of his life span and so we do not know the state of EP's knowledge for information that he would have acquired prior to his late twenties and a temporal gradient similar to the one found for autobiographical memories cannot be ruled out.

Squire and his colleagues concluded that the findings from EP support the predictions of the Consolidation Theory (Squire, Cohen, & Nadel, 1984; Squire, 1992; Squire & Alvarez, 1995). This theory posits that the hippocampus and adjacent structures (dentate gyrus, subiculum and parahippocampal gyrus) direct the recall of recently acquired topographical, episodic and semantic memories, the various components of which are maintained in a distributed neocortical network and are partially stored (Alvarez & Squire, 1994) or linked (Meeter & Murre, 2005; Murre, 1996) by the hippocampal system. Over time, the remote memory becomes independent of the mesial temporal lobe (MTL) region through a process termed consolidation, and is sustained entirely by the neocortex.

Rosenbaum et al. (2000) found a different pattern of results in a second patient, KC, a 49-year-old male, who had become amnesic 18 years prior to testing as the result of a motorcycle accident. KC had sustained widespread brain lesions that virtually encompassed both MTL and also involved left mesial occipital-temporal, left frontal-parietal, right mesial frontal and right parieto-occipital regions. KC was completely unable to recall detailed autobiographical events for the whole of his life, including his early years (Rosenbaum, McKinnon, Levine, & Moscovitch, 2004a; Tulving, Schacter, McLachlan, & Moscovitch, 1988; Tulving, Hayman, & Macdonald, 1991; Westmacott, Leach, Freedman, & Moscovitch, 2001). In terms of his topographical memory, Rosenbaum et al. (2000) found that KC was impaired at distinguishing incidental landmarks in his own locality from those in nearby neighbourhoods (Tulving et al., 1988; Westmacott et al., 2001; Rosenbaum et al., 2004a), but otherwise demonstrated intact topographical knowledge. KC's retrograde memory for vocabulary terms and famous personality's names was intact except for those he should have learnt during the 5 years prior to his injury (Westmacott & Moscovitch, 2002). His memory for public events was not tested.

The findings for KC were interpreted as being in accordance with the predictions of Multiple Trace Theory (MTT, Nadel & Moscovitch, 1997; Moscovitch & Nadel, 1998; Fujii, Moscovitch, & Nadel, 2000). A central tenet of MTT is that the hippocampal complex remains involved in the storage, maintenance and retrieval of autobiographical episodes for as long as the memories are in existence. Complete damage to the MTL bilaterally is predicted to result in an equivalent impairment of remote and recent memory for autobiographical incidents. MTT postulates that the hippocampus has no long-term role in the maintenance of factual or semantic knowledge and therefore only very recently acquired information should be compromised following a lesion involving this structure. It should be noted, however, that inferences pertaining to brain-behaviour relationships drawn by the Rosenbaum et al. (2000) study are limited by the fact that KC incurred damage to several brain regions. This raises the possibility that the observed deficits in incidental landmark recognition and/or remote autobiographical event memory might be the result of damage to regions outside the MTL.

The third case in the literature where all three domains of retrograde memory were compared was TT, a 65-year-old retired London taxi driver who suffered an episode of limbic encephalitis associated with a series of complex partial and tonic-clonic seizures during the course of his recovery (Maguire, Nannery, & Spiers, 2006). Magnetic resonance imaging (MRI) revealed damage throughout the length of both hippocampi. The entorhinal, perirhinal and parahippocampal cortices appeared relatively preserved in the context of some generalised atrophy. TT's retrograde topographical memory was assessed through use of a virtual reality replication of London and his performance was compared to other taxi drivers of a similar age. Interestingly, TT was able to recall routes that primarily consisted of main artery roads ("A roads"), but performed poorly when he was required to navigate in areas that contained few or no "A roads". Knowledge of landmarks and directions was intact. Maguire et al. (2006) concluded that the hippocampus plays a vital role in the recollection of remotely learned spatial details, consistent with the predictions of MTT. Similar to KC, and in contrast to EP, TT demonstrated a complete loss of memory for autobiographical incidents across his lifespan. Consistent with findings from EP, knowledge of public events was impaired, although the authors do not provide information with regard to TT's pattern of performance across each decade. In contrast to the findings for EP, however, TT's knowledge of famous faces was found to be intact.

Amongst these three patients there are varying degrees of impairment in topographical, autobiographical and semantic retrograde memory and the reason for this is not clear. It is possible that etiology and/or site of lesion contribute to the different profiles of impairment. As such, the exploration of patterns of impairment in patients with different types of MTL damage should help to resolve this issue.

The neural organisation of topographical memory has been described by two main theories. One, the Cognitive Map Theory (O'Keefe & Nadel, 1978), proposes that the hippocampus is involved in the mapping of space, where the locations of objects are defined relative to the environment (allocentric spatial representation). According to this theory, observer dependent (egocentric) spatial representations are thought to be processed by the posterior parietal cortices. An alternative conceptualisation of the neural representation of large scale space has been proposed by Aguirre and D'Esposito (1999). Based on a review of the literature, they argued that the inferior temporo-occipital regions are important for the recognition of previously familiar landmarks. Way-finding, they argued, can be achieved using a variety of strategies involving allocentric and egocentric processes in conjunction with landmark recognition. As such, a preservation of way-finding in familiar environments might be expected even when the hippocampus is dysfunctional. They also concluded that the retrosplenial region calculates the observer's orientation with respect to the external environment and damage to this region is predicted to result in "heading disorientation". The preserved memory for routes and layouts of remotely learned environments observed for EP and KC, was interpreted by Teng and Squire (1999) and Rosenbaum et al. (2000) as inconsistent with Cognitive Map Theory, but the findings may well fit into Aguirre and D'Esposito's model. Unfortunately, in EP and KC, not all aspects of their model were explored. TT's intact knowledge of landmarks, main routes and directional information was also judged to be inconsistent with the Cognitive Map Theory. However, his data were not entirely consistent with Aguirre & D'Esposito's model either, as seen in his poor navigational ability on local roads in the face of seemingly focal bilateral hippocampal damage.

In order to evaluate these theories of memory representation, we investigated topographical, autobiographical and semantic memory in a patient (SG) who had recently developed bilateral lesions affecting the mesial temporal and the retrosplenial regions subsequent to sequential infarctions. Impairments in all allocentric aspects of topographical memory would be evidence for the Cognitive Map Theory (O'Keefe & Nadel, 1978). In contrast, based on Aguirre and D'Esposito's model, SG's lesion should cause deficits in heading orientation, but possibly spare knowledge of routes. Aguirre and D'Esposito's (1999) model would also predict deficits in landmark recognition, although according to Rosenbaum et al. (2000) this should only affect recognition of incidental landmarks. Furthermore, evidence of a temporal gradient in autobiographical memory would indicate support for the Consolidation Theory of long-term memory, whereas compromised recall of memories across all time periods would substantiate the claims of MTT. Due to the restricted nature of SG's temporal lobe lesions, both MTT and Consolidation Theory would predict minimal disruption to his retrograde semantic stores, with recently acquired memories more vulnerable than those learnt in the remote past.

Case description

When he first presented in May 1998, SG was a 62-year-old right handed male, with a Bachelor of Science and Engineering degree, who had retired 6 years earlier from his job as Telecommunications Engineer/General Manager of a multinational company. He had suffered an infarct in the territory of the right posterior cerebral artery, associated with left visual field difficulties, which resolved completely soon after. Prior to and after this infarction SG was on antihypertensive medication. There were no known premorbid neurological or psychiatric conditions. In July 2001, SG suffered a second infarct, in the territory of the left posterior cerebral artery. Neurological examination revealed a right upper quadrantanopia, which again proved transient. Limb functions were normal.

In October 2001, SG and his wife were interviewed at Royal Prince Alfred Hospital. The main complaint was of poor anterograde memory since the second stroke. In addition, SG's wife reported that her husband would become lost in previously familiar environments such as the streets around their home and the local shopping centre. By contrast, she described his premorbid navigational abilities as "excellent". Conversational abilities were unaltered and he retained his knowledge of Spanish and French. At reassessment in October 2002, SG's wife thought that her husband's functioning had remained relatively stable. All testing reported in the current study was conducted after the second stroke (in 2002 and 2003).

Magnetic resonance imaging (MRI) in July 2001 revealed a previously sustained infarction of the right mesial temporal cortex as well as an acute cerebral infarction involving the mesial aspect of the left temporal lobe and the occipital lobes bilaterally (Figure 1). Neuroradiological review of the MRI data indicated an old cortical infarct involving all of the hippocampus and much of the parahippocampal gyrus, entorhinal cortex and perirhinal cortex on the right. Additional signal change, consistent with more recent damage was noted in the right retrosplenial region. Within the left hemisphere, all of these same regions were affected, with more extensive changes suggested in the posterior parahippocampal/retrosplenial region. In contrast, the temporal poles and inferior cortex lateral to the parahippocampal gyri is largely spared.

For the purposes of the study, fluoro-deoxyglucose positron emission tomography (FDG-PET) was conducted in January 2003 (Figure 2). Visual inspection of the FDG-PET data by a neurologist (AM) revealed glucose hypometabolism in a number of regions. The largest of these involved the entire right mesial temporal lobe with some suggestion of dilatation of the right temporal horn and body of the lateral ventricle, particularly posteriorly. Additional areas of reduced glucose metabolism included the left entorhinal region and hippocampus as well as the retrosplenial region bilaterally. Glucose metabolism was relatively spared in the prefrontal cortex and in both thalami.

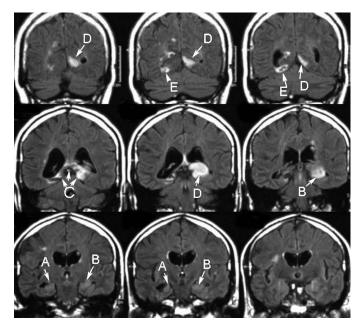


Fig. 1. MR FLAIR images taken soon after the second stroke showing left/right reversed coronal slices moving more anteriorly from the top left to the bottom right of the figure. There is increased signal and atrophy due to infarction in the right hippocampus (A); as well as signal change in the head and body of the left hippocampus (B); retrosplenial regions bilaterally (C); left parahippocampal gyrus and mesial occipital cortex (D); and right inferior occipital cortex (E).

For quantitative analysis, the FDG-PET data were transformed to Talairach and Tournoux (1988) space and measurements of cerebral glucose metabolism (CMRGlu) in four brain regions (left and right retrosplenial regions, left and right parahippocampal gyri) were taken. The CMRGlu measurements were then compared with data procured in a similar fashion from 25 male normal control (NC) subjects, aged 65-75. In order to control for inter-individual variations in total brain volume, the CMRGlu for each of the four brain regions was divided by the CMRGlu obtained for the pons for each individual brain. Subsequent to this, modified t-tests were performed according to a formula proposed by Crawford and his colleagues (Crawford & Howell, 1998; Crawford & Garthwaite, 2002) for each of the four brain regions. Significant differences in glucose metabolism were found between SG's brain and NCs for the right (p < .01) and left (p < .0167) retrosplenial cortices and right parahippocampal region (p < .012). The left parahippocampal region did not differ significantly from those of controls.

Standard neuropsychological assessment of SG

Three and 15 months after his second stroke, SG underwent neuropsychological assessment (Table 1). His estimated premorbid Full Scale IQ was 122, in the superior range (National Adult Reading Test – NART, Nelson, 1982). Scores on tests of general knowledge, word definitions, mental arithmetic,

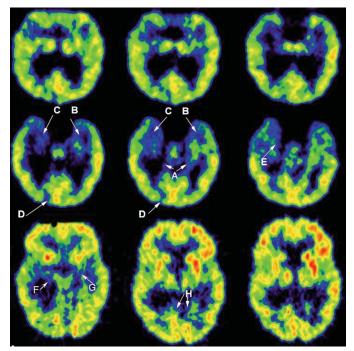


Fig. 2. FDG PET scan showing (from top to bottom of the figure, inferior to more superior- and left/right reversed) slices parallel to the main axis of the hippocampus. These reveal glucose hypometabolism in: the posterior parahippocampal gyri (A); left entorhinal cortex (B); right entorhinal cortex (C); right occipital pole (D); the right hippocampus from the head (E) to the tail (F); the body of the left hippocampus (G); and retrosplenial regions (H) (L>R). This figure is available to subscribers in color: Please visit the Journal's website at http://www.psypress.com/neurocase.

verbal abstract reasoning, visuoconstruction and immediate attention span were consistent with this expectation. Visuoperceptual and visuospatial skills along with mental flexibility and conceptual problem solving were found to be intact. SG was also proficient in producing rote learned sequences, as assessed by the Mental Control subtest of the Wechsler Memory Scale – Revised (WMS-R, Wechsler, 1987).

As can be seen in Table 1, SG's anterograde memory for both visual and verbal material was severely impaired. He sometimes denied having heard or seen material that had been presented 30 min earlier.

Normal Control subjects

On the experimental measures, SG's performance was compared with that of 11 NC subjects (six males and five females) who were chosen as approximate matches for age, intellectual ability and level of education. Table 2 presents the demographics for these subjects.

This study was approved by the ethics committees of the Central Sydney Area Health Service and Macquarie University. All subjects gave their informed consent to participate.

Table 1. Summary of SG's	performance on clinical	l measures of c	cognitive ability	y

	3 months post second stroke		15 months post second stroke	
Measure	Raw Score	Percentile	Raw Score	Percentile
WAIS-R Information	28	99	_	_
WAIS-R Vocabulary	69	>99	_	_
WAIS-R Arithmetic	15	72-81	-	_
WAIS-R Similarities	25	99	-	_
WAIS-R Block Design	40	90–94	-	_
WAIS-R Digit Span Forwards	10	92	12	99
WAIS-R Digit Span Backwards	10	96	10	96
WMS-R Visual Memory Span Forwards	_	_	9	92
WMS-R Visual Memory Span Backwards	_	_	7	80
VOSP Incomplete Letters	_	_	20	Pass
VOSP Cube Analysis	_	_	10	Pass
WCST Categories	_	_	6	>16
WCST Failure To Maintain Set	_	_	0	>16
WCST Perseverative Errors	_	_	3	98
WCST Total Trials	_	_	70	_
WMS-R Mental Control	6/6	72-81	6/6	72-81
WMS-R Information & Orientation	11/14	_	9/14	_
WMS-R Logical Memory I	19	11-18	19	11-18
WMS-R Logical Memory II	0	<1	2	1
WMS-R Visual Reproduction I	16	<1	28	11-18
WMS-R Visual Reproduction II	0	<1	9	3–5
RAVLT Learning Over Time	7	6–10	-	_
RAVLT Immediate Recall List A	3	1	_	_
RAVLT 20 min Delayed Recall List A	0	<1	-	_
Rey Complex Figure Copy	34	>16	36	>16
Rey Complex Figure 30 min delay	0	<1	5	1
Boston Naming Test	_	_	59	98
Semantic Battery Category Fluency	_	_	62	31
Semantic Battery Picture Naming	_	_	48/48	
Semantic Battery Word Definitions	-	_	12/12	
Semantic Battery Word Picture Matching	_	_	48/48	

WAIS-R, Wechsler Adult Intelligence Scale – Revised [Wechsler, 1981; Minnesota Older Adult Normative Study (MOANS) normative data (Ivnik, Malec, Smith, Tangalos, & et al., 1992b)]; VOSP, Visual Object Space Perception Battery (Warrington & James, 1991); WCST, Wisconsin Card Sorting Test (Heaton, Chelune, Talley, Kay, & Curtis, 1993); WMS-R, Wechsler Memory Scale – Revised, [Wechsler, 1987; MOANS normative data (Ivnik, Malec, Smith, Tangalos, & et al., 1992c)]; RAVLT, Rey Auditory Verbal Learning Test [Rey, 1958; MOANS normative data (Ivnik, Malec, Smith, Tangalos, & et al., 1992c)]; RAVLT, Rey Auditory Verbal Learning Test [Rey, 1958; MOANS normative data (Ivnik, Malec, Smith, Tangalos, & et al., 1992c)]; Rey Complex Figure, (Rey, 1941; Meyers & Meyers, 1995); Boston Naming Test (Kaplan, Goodglass & Weintraub, 1983); Semantic Battery (Hodges & Patterson, 1995)

Table 2. Demographics for SG and the NC subjects

		Control C	Control Group	
	SG	mean	sd	
Age	65	63.7	5.0	
Age Years of Education	16	16.5	2.1	
Estimated FSIQ ¹	122	120.1	4.5	

¹National Adult Reading Test (NART; Nelson, 1982); sd = standard deviation.

Statistical analyses

For each of the experimental measures, modified *t*-test analyses (Crawford & Howell, 1988) were conducted using a

programme developed by Crawford and Garthwaite (2002) called "singlims". Multiple comparisons were controlled for using a sequentially rejective Bonferroni procedure proposed by Holm (1979). Tasks were grouped according to cognitive domain and this technique was applied multiple times.

Topographical memory

It has recently been proposed that various aspects of topographical memory can be differentially affected by damage to specific brain areas (Aguirre & D'Esposito, 1999). Topographical skills such as an individual's ability to recognise landmarks (Hecaen, Tzortzis, & Rondot, 1980; Whiteley & Warrington, 1978), obtain directional information from them (Hirayama, Taguchi, Sato, & Tsukamoto, 2003; Suzuki, Yamadori, Hayakawa, &

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Fujii, 1998; Takahashi, Kawamura, Shiota, Kasahata, & Hirayama, 1997) and recall routes (Bottini, Cappa, Geminiani, & Sterzi, 1990; della Rocchetta, Cipolotti, & Warrington, 1996; Paterson & Zangwill, 1945) have been considered in various studies. However, few of these investigations have obtained detailed neuroimaging data of their subjects, limiting the conclusions that can be drawn with regard to the neural underpinnings of retrograde topographical memory. In light of this, we tested SG on a battery of retrograde topographical memory tasks measuring landmark naming, heading orientation, landmark map localisation and route recall to investigate the effect of mesial temporal and retrosplenial lesions on these various abilities.

Performance on the tests of topographical memory was thought possibly to be contingent upon a number of more basic abilities including visual perception, visual imagery and visuospatial skills. In order to establish whether any difficulties SG had on tests of topographical memory might be due to an underlying deficiency in any of these domains, a number of control tests were administered.

Subjects

All 11 NC subjects, as described in Table 2 had either grown up in the Sydney metropolitan region or had moved to Sydney three or more decades earlier. Their performance was compared to SG, who had lived and worked in Sydney all of his life.

Tasks

Sydney City Test of topographical memory

All subjects were administered the Sydney City Test of Topographical Memory (the "Sydney City Test"). Briefly, this test is comprised of 50 photographs (21×15 cm) of landmarks (buildings, bridges and scenes) in Sydney. First, subjects were required to recall the name of each landmark. Second, for incorrect items, the correct landmark name along with the names of three other Sydney landmarks were presented to the subject, who was then asked to choose the appropriate name from amongst the distracters.

A subset of these items (n = 15) was used to test heading orientation. Subjects were asked to look at the photograph, given the name of the landmark where necessary and asked to imagine that they were standing in the same position as the photographer. They were then asked (1) the direction of the Queen Victoria Building (a very well known Sydney landmark) (i.e., "directly in front of me, behind me, to my right, to my left, to the front and right, to the front and left, behind and right or behind and left") and (2) the cardinal direction they were facing (i.e., north, south, east or west).

Eight pairs of relatively well-known landmarks were chosen to serve as start and end points of the route recall subtest. The landmarks that were chosen represented a good cross section of the city of Sydney, and most routes were comprised of a combination of main and local roads. Responses were scored according to the provision of correct street names or landmarks (e.g., keep walking until you reach the supermarket), and correct number of turns. If the response from a subject was too brief (eg. "walk down the main street and you'll get there eventually"), the experimenter guided the subject through each stage of the route by providing specific prompts ("so you're at landmark X/on street Y, what would be the first step you'd take ... then what would you do next?" and so on). The score for each item was converted to the percentage correct and the final route recall score was the average of these.

On the map localisation subtest, subjects were asked to label a map of the city of Sydney, which had been edited using Adobe[®] Photoshop[®] 7 to remove identifying information. Subjects were asked to label the map with the locations of 16 landmarks (in response to being shown the picture and given the name). The error score was a measure of distance on the map (in cm) between the placement by the subject and the true location. The total score was the sum of these error measurements.

Control tasks

Building/scene matching. To evaluate a subject's ability to process architectural and scenic details, a building/scene matching test was created. In each of 15 items, a target photograph $(21 \times 15 \text{ cm})$ of a non-famous building or scene was presented to the subject along with 4 other photos (Figure 3). One of those four photographs was the same building or scene as the one depicted in the target photograph, but taken from a slightly different angle. The other three photographs were of closely matched distracters. Each subject was asked to indicate which of the four photographs was the same as the target photo.

Mental imagery. Two tests of mental imagery were administered, which required the subject to visualise either 26 common objects (Taller/Wider test: Kosslyn, Reiser, Farah, & Fliegel, 1983) or 20 animals (Animal Tails Test: Martha Farah, personal communication) and make judgements about their physical properties. In the Taller/Wider Test, the subject was asked to decide whether objects (e.g., a bow-tie or garbage bin) were taller than they were wide or wider than they were tall. In the Animal Tails Test, subjects were asked to think of different animals (e.g., a lion, deer etc) and determine whether they had a long or a short tail.

Mental rotation. The Space Thinking [Flags] Test (Thurstone & Jeffrey, 1984) was used to assess mental rotation. In this test, subjects are shown a target drawing of a flag along with six other drawings of the same flag that were rotated at different angles, with some inverted on their axis. Subjects then had to compare each of the six drawings with the target drawing and indicate whether they represented the same side as the target flag or whether they were a mirror image. There were 21 target items in total and each subject was given 5 min to complete as many items as possible.





Fig. 3. An item from the Building/Scene Matching test. This figure is available to subscribers in color: Please visit the Journal's website at http://www.psypress.com/neurocase.

Results

Table 3 provides a summary of SG's scores compared to mean of the NC group on each of the six Sydney City subtests, using the sequential rejective Bonferroni procedure. His ability to recall or recognise the names of landmarks was found to be impaired relative to NCs (p < .008, p < .01, respectively). SG also encountered difficulty on the test of heading orientation when asked to give the direction of a specific Sydney landmark when he imagined that he was standing in front of another (p < .013). In contrast, SG's performance did not differ from the NCs when he was asked which cardinal direction he would be facing as the

 Table 3. Results for the Sydney City Test of Topographical Memory and visual control tasks

Task	SG's Score	NC mean (sd)	t	р
Sudnay City Tast		()		1
Sydney City Test Landmark Name	23*	41.0 (4.3)	-4.04	0.001
Recall (/50)	23	11.0 (1.5)	1.01	0.001
Landmark Name	36*	48.3 (1.7)	-6.76	0.000
Recognition (/50)				
Direction of Second	7*	11.8 (1.0)	-4.70	0.000
Landmark (/15)				
Cardinal	9	11.4 (2.7)	-0.83	0.213
Direction (/15)				
Landmark Map	22.8	12.1 (9.6)	1.07	0.155
Localisation				
(Sum of Error				
Measurements)				
Spoken Route Recall (percentage correct)	64.1	77.2 (8.5)	-1.48	0.084
Visual Control Tasks				
Building/Scene	13	12.9 (1.2)	0.1	0.472
Matching (/15)				
Taller/Wider (/20)	19	19.2 (1.0)	-0.18	0.431
Animal Tails (/26)	22	23.6 (1.2)	-1.30	0.112
Mental Rotation	44	37.2 (12.7)	0.52	0.309

sd = standard deviation;

* = significantly different from the control group, based on calculations performed using Crawford & Garthwaite's (2001) programme 'singlims' and sequentially rejective Bonferroni corrections (Holm, 1979) (applied separately for Sydney City subtests and set of visual control tasks).

photographer for the same items. Similarly, SG was able to place landmarks on a map of Sydney as well as recall routes between various landmarks within the Sydney metropolitan region at a level comparable to NCs. On all control measures, SG's performance fell within normal limits (Table 3).

Comment

In summary, SG had difficulty remembering the names of famous landmarks and their location with respect to other landmarks when he had to imagine himself facing a particular direction. His impaired ability to recall or recognise the names of well known landmarks from his home city was unlikely to be due to underlying visual processing impairments, a general object agnosia or a naming problem, as he performed normally on standardised neuropsychological tests and experimental control tasks of these underlying abilities. Similarly, his inability to make spatial judgements regarding the position of one landmark in relation to his position in front of another landmark was unlikely to be due to a lack of knowledge about the 15 landmarks used in this subtest, since he was able to place 13 of these relatively accurately on the map and recall or recognise the names of 12 of them. Once the identities of the three items that he was unable to name were disclosed to him, he stated that he was indeed familiar with these places and correctly determined the position of the second landmark for two of these items.

Remote versus recent topographical memory

Teng and Squire (1999) and Rosenbaum et al. (2000) hold disparate views regarding the role of the hippocampus and related mesial temporal structures in the processing of topographical memories, advocating the Consolidation Theory (Squire, 1992; Squire & Alvarez, 1995) and MTT (Fujii et al., 2000; Nadel & Moscovitch, 1997), respectively. Following damage to these regions, Teng and Squire (1999) argue that there will be a temporal gradient, with sparing of the most remote topographical memories. In contrast, Rosenbaum et al. (2000) maintain that the hippocampus plays a role in memory for incidental landmarks acquired at any point in one's lifetime. Accordingly, we set out to look for a temporal gradient in topographical memories and also to determine whether SG would be able to recognise incidental landmarks from his remote and recent past.

Subjects

For the test of remote incidental topographical memory, SG's knowledge of the University of Sydney campus was compared with that of five male and two female NC subjects, matched for age, education and estimated FSIQ (Table 4). SG had attended the University of Sydney from the mid 1950s to the early 1960s (aged 18–26) and had returned only to attend his sons' graduation ceremonies in 1992 and 1994. During these visits he stated that he had not reacquainted himself with the campus, but remained in the graduation hall. All seven control subjects had attended the University of Sydney during the same time period as SG, and had only returned sporadically for conferences or reunions (none within the past 5 years). Like SG, they all stated that they had not reacquainted themselves with the University grounds during these visits.

For the test of recent incidental topographical memory, SG's performance was compared with that of his wife and

Table 4. Demographics for	r the University	of Sydney Test
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		Control	Group
	SG	mean	sd
Age	65	61.9	1.6
Age Years of Education	16	17.3	1.6
Estimated FSIQ ¹	122	119.7	5.2

¹National Adult Reading Test (NART; Nelson, 1982); sd = standard deviation.

adult son. Both SG and his wife had lived in their current neighbourhood for the past 40 years. Their son, aged 33 at the time of testing, reported that although he had left the family home 9 years earlier he had maintained regular contact with his former neighbourhood.

Tasks

To examine remote topographical memory, the Sydney University Test was constructed. It consisted of 15 sets of four colour photographs of landmarks $(21 \times 15 \text{ cm})$ (Figure 4). One of the four photos in each set depicted a landmark from the University of Sydney that was present in the late 1950s. The other three photographs were of closely matched distracters from outside of Sydney. A number of these were obtained from the internet.

To assess more recent topographical memory, 20 sets of four photographs $(21 \times 15 \text{ cm})$ were used in the Neighbourhood Test (Figure 5). Only one of the four photographs in each set depicted an incidental landmark (house, intersection or shop front) from SG's current neighbourhood. Again, the other three photographs were of closely matched distracters. All photographs were taken by I.H. using a digital camera and identifying information was removed. For each item on the Sydney University and Neighbourhood Tests, subjects were asked to indicate which of the four landmarks was part of the University of Sydney or part of their home neighbourhood, respectively.

Results

SG's ability to recognise both recent and remote landmarks as familiar was impaired. Compared to NCs on the Sydney University Test, who averaged 13.7 correct, SG made only nine correct choices (t = -4.63, p < .05). On the Neighbourhood Test, SG's wife and son both chose 18/20 items correctly. SG performed much more poorly, making only 13/20 correct choices.

Comment

SG demonstrated a deficiency in recognising photographs of incidental landmarks from both the remote and recent time periods. These findings, combined with the results from the previous section that demonstrated difficulties with naming prominent landmarks yet intact perception of buildings and scenes provide further evidence that SG's symptomatology is



Fig. 4. An item from the Sydney University test. This figure is available to subscribers in color: Please visit the Journal's website at http://www.psypress.com/neurocase.



Fig. 5. An item from the Neighbourhood test. This figure is available to subscribers in color: Please visit the Journal's website at http://www.psypress.com/neurocase.

consistent with the features of a landmark agnosia, as predicted by Aguirre and D'Esposito (1999). The results are somewhat consistent with the proposal of Rosenbaum et al. (2000), that deficient memory for topographical details, such as incidental landmarks is a likely consequence of MTL damage.

Autobiographical memory

We examined SG's recall of personal semantic details and autobiographical incidents, with the intent to test the predictions of two theories of long-term memory (Consolidation theory and MTT). Proponents of Consolidation Theory (Squire, 1992; Squire & Alvarez, 1995) would argue that SG should show a time-limited loss of memory for personal semantic details and autobiographical events, with remotely acquired memories being intact. On the other hand, MTT (Fujii et al., 2000; Nadel & Moscovitch, 1997) would predict poor recollection of remotely and recently acquired autobiographical events in the context of a restricted loss of memory for personal semantic details.

Because Moscovitch and colleagues (Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002; Moscovitch, Yaschyshyn, Ziegler, & Nadel, 2000) have argued that the hippocampal complex is important in the recollection of detailed autobiographical incidents (rather than the gist of an autobiographical experience) for the whole of a person's lifetime, two measures of autobiographical memory were administered to SG. The first yielded data pertaining to personal semantic details and autobiographical incidents in moderate detail and the second required the recall of highly detailed autobiographical incidents.

Subjects

All 11 NC subjects described in Table 1 performed the modified Crovitz Cue Technique (mCCT). Both tests of autobiographical memory were administered to SG in mid 2002.

Tasks

Autobiographical Memory Interview

The Autobiographical Memory Interview (AMI; Kopelman, Wilson, & Baddeley, 1989) was used to assess SG's memory for personal semantic details and autobiographical incidents. The personal-semantic scale of the AMI requires the subject to provide personal semantic details, such as the name of the primary school they attended. Questions from the autobiographical-incident scale require the subject to recall specific and detailed autobiographical incidents. These two domains are assessed across three different life periods: Childhood, Early Adult Life (until the age of 35 for SG) and Recent Life. Normative data obtained from the manual were used to gauge SG's performance on this test.

mCCT

In a modified version of the Crovitz Cue Technique (Crovitz & Schiffman, 1974; Cimino, Verfaellie, Bowers, & Heilman, 1991) subjects were presented with each of four cue words (happy, afraid, angry and surprised) and were asked to recall a specific and detailed autobiographical incident that the word brought to mind. They were first instructed that the incident was to have occurred between the ages of 0 and 12 years of age ("Childhood"). This procedure was then repeated, using three other time periods: 13-21 years of age ("Teenage/Young Adult"); 1993–1997 (the 5 years preceding SG's first stroke); and the most recent 5 years (post first stroke). If the subject provided only scant detail, prompts such as "Can you tell me more about that?", or "Who was there?" etc., were used. Responses were taped and then transcribed. Scoring was conducted by an independent rater who was blind to subject group. Responses were scored out of a possible seven points with respect to whether they included details about who was involved (1 point), where the event took place (1 point), when the event took place (1 point) and what had occurred (2 points). One point was also awarded if the memory described a specific episode and another if it was clearly within the specified time period. Responses were also scored according to the number of prompts required. The questions ranged from general probing ("can you think of a specific incident?") to more specific prompts (e.g., "who else was there?", "where were you at the time?" and "what happened next").

Results

SG's autobiographical memories were all verified by his wife. SG's performance on the personal semantic scale on the AMI fell within normal limits, as stated in the manual, for all three time periods. (Childhood = 16.5/21; Early Adult Life = 21/21; Recent Life = 19/21). His scores on the autobiographical incident scale for childhood and early adult time periods were also well within the normal range (Childhood = 7/9; Early Adult Life = 8/9). His score (6/9) on the recall of autobiographical incidents from the recent time period was rated in the borderline range (between 1 and 2 standard deviations from the control mean). This period covered the year since his second stroke.

Similarly, on the mCCT, SG was able to recall detailed autobiographical incidents from the two remote time periods (Childhood: t = 0.39, ns; Teenage/Young Adult: t = 0.49, ns) (see Figure 6). SG's recall of events that occurred within the most recent 5 years in response to cue words, however, was significantly impaired relative to NCs (t = -4.70, p < .006).

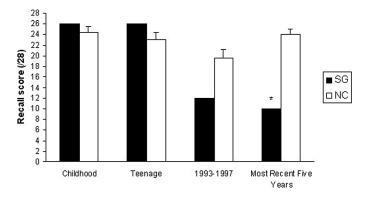


Fig. 6. SG's performance on the Modified Crovitz Technique across four time periods, compared with NCs. *p < .007. Error bars indicate the standard error of the mean.

Recall of autobiographical events from the 5 years prior to his first stroke (1993–1997) although lower than the NC mean, was not significantly impaired (t = -1.61, ns). It may be important to note, however, that compared with NCs, SG required significantly more prompting to generate complete memories of incidents for the 5 years prior to his first stroke only (t = 3.55, p < .006) (Figure 7).

Comment

As assessed by the AMI, SG was able to recall personal semantic details from his own past across all time periods. Neither MTT nor Consolidation Theory would have predicted complete preservation of personal semantic memory. Two possibilities may explain SG's intact performance on this measure. First, it may be that a remnant of preserved entorhinal or other anterior mesial temporal tissue was capable of sustaining the retrieval of personal semantic details. In support of this, Kapur and Brooks (1999) reported preserved memory for personal semantic details in two patients with restricted bilateral hippocampal damage

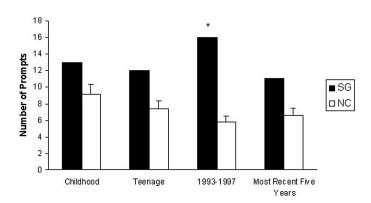


Fig. 7. Number of prompts required by SG and NCs, for each time period on the Modified Crovitz Cue Technique. *p < .006. Error bars indicate the standard error of the mean.

that was incurred subsequent to an episode of limbic encephalitis. Second, a more sensitive test of personalsemantic memory might have detected some subtle deficits, since other authors have commented on the reduced sensitivity of the AMI for both personal semantic details and events (Eslinger, 1998; Kapur & Brooks, 1999; Manes, Hodges, Graham, & Zeman, 2001).

SG's recall of autobiographical events for remote time periods (childhood and teenage/young adult years) was within normal limits, as measured by the AMI and mCCT. Furthermore, his recollections were as detailed as those provided by NCs and he did not require significantly more prompts to elicit these memories. It is unlikely that these memories were semanticised or over-rehearsed, as SG's wife confirmed that the episodes that SG had recalled were not a recurring topic of discussion within their family.

Although the quality of SG's responses on the mCCT for the years 1993–1997 (the 5 years prior to his first stroke) was rated within normal limits, he required a significantly greater number of prompts than NCs to recall details of events from this period, suggesting a subtle deficit in the ability to retrieve these memories. Not surprisingly, given his very impaired anterograde memory, SG had even more difficulty recalling events from his more recent life (largely since his second stroke). His performance on the recent epoch of the AMI was rated in the Borderline range. Similarly, when his ability to recall more detailed autobiographical incidents from the most recent 5 years was assessed using the mCCT, his performance was significantly impaired. SG's wife informed us that on this measure, all of her husband's recollections from the last 5 years referred to events that had occurred since his second stroke (i.e., from the past year). Examination of his responses from the most recent time period indicated that they were predominately factual with little indication of episodic re-experiencing. For two of the cue words for this time period he simply responded with "I can't recall anything", which in turn limited the total number of prompts that could be asked

Anecdotally, compared with his wife's memory of two trips in 1999 and 2000 (years between his first and second strokes), SG's recollection was quite poor and he had a tendency to confuse events between these two holidays. SG's wife stated that he had been able to recollect the events of these holidays prior to having suffered his second stroke and reiterated that the first stroke had not resulted in any memory difficulties that she could detect. Taken together, these findings are indicative of a clear loss of memory for autobiographical incidents from the three (i.e., 1999–2001) years prior to SG's second stroke, with more minor difficulties dating back as far as 8 years. More remote autobiographical events, however, were remembered well.

Semantic memory

Squire and colleagues (Manns, Hopkins, & Squire, 2003; Reed & Squire, 1998; Squire, 1992; Zola-Morgan, Squire, & Amaral, 1986) maintain that all types of declarative memories from the time period just prior to lesion onset will be affected by damage to the hippocampus and adjacent structures. However, there is a growing body of evidence to suggest that retrograde episodic and semantic memories can be differentially affected (Miller et al., 2001; de Renzi, Liotti, & Nichelli, 1987; Schacter, Wang, Tulving, & Freedman, 1982; Tulving et al., 1988; Viskontas, McAndrews, & Moscovitch, 2000, 2002; Warrington & McCarthy, 1988; Yasuda, Watanabe, & Ono, 1997). Furthermore, differential impairments in semantic knowledge may be evident; Maguire et al. (2006) reported deficits in knowledge of public events, but intact recognition of famous faces in a patient with relatively circumscribed hippocampal damage. As such, we assessed aspects of SG's retrograde semantic memory to further investigate the nature of retrograde semantic knowledge subsequent to relatively circumscribed bilateral MTL retrosplenial lesions.

Subjects

For all the measures of semantic knowledge, SG's performance was compared with all 11 NCs as described in Table 1.

Tasks

The Australian-adapted version of the New Vocabulary test (Verfaellie, Reiss, & Roth, 1995) was used to assess knowledge of vocabulary that entered the Australian-English language during the subject's lifetime. There were ten words per decade spanning the period 1940-1999. Subjects were first asked to define each word and where necessary, a threechoice recognition procedure involving possible definitions was administered. Each item was spoken aloud by the tester and presented visually. Two scores were recorded for each decade: the number of definitions correctly recalled and the number correctly recalled and/or recognised. For both the recall and recognition conditions, three scores were calculated for each subject. Performance on the ten items from the subjects' first full decade of life was taken as the score for Childhood, the most recent full decade (1990s) was taken as the score for Recent Life and the Midlife score was an average of the scores achieved for decades between the first decade and 1990.

Each subject's knowledge of famous faces and public events was also assessed using Shum and O'Gorman's (2001) Australian Remote Memory Battery. The Famous Faces subtest utilized black and white photographs of famous people's faces. These were shown one at a time to the subject, who was then asked to recall the person's name. Half points were awarded for providing only the first or last name (in such cases, the subject was prompted for the full name). A three choice recognition procedure, using three famous names as possible options, followed for incorrect items. The Public

	SG's Score	NC mean (sd)	t	р
New Vocabulary	$\sqrt{1}$ Recall (/10)			
Childhood	10	9.6 (0.6)	0.63	0.271
Midlife	9.38	9.4 (0.5)	0.05	0.480
Recent Life	10	7.5 (1.9)	1.29	0.113
New Vocabulary	¹ Recognition	(/10)		
Childhood	10	10 (0.01)	0	0.5
Midlife	10	9.9 (0.2)	0.40	0.348
Recent Life	10	9.5 (0.5)	0.83	0.212
Famous Faces ² I	Recall (/9)			
Childhood	2	3.8 (1.2)	-1.45	0.089
Midlife	4.5	4.7 (2.1)	-0.08	0.469
Recent Life	5	5.5 (2.1)	-0.21	0.419
Famous Faces ² I	Recognition (/9))		
Childhood	8	6.8 (1.3)	0.85	0.207
Midlife	8.25	8.4 (0.5)	-0.24	0.408
Recent Life	8	8.9 (0.3)	-2.89	0.008
Public Events ² R	Recall (/9)			
Childhood	2.5*	7.9 (1.1)	-4.56	0.001
Midlife	6.13	7.5 (0.8)	-1.62	0.068
Recent Life	6	7.6 (1.1)	-1.40	0.096
Public Events ² R	Recognition (/9)			
Childhood	6*	8.8 (0.4)	-6.67	0.000
Midlife	7.75*	8.9 (0.2)	-7.21	0.000
Recent Life	9	8.9 (0.2)	0.56	0.317

Table 5. SG's performance on tests of semantic knowledge

*=significantly different from the control group, based on calculations performed using Crawford & Garthwaite's (2001) programme 'singlims' and sequentially rejective Bonferroni corrections (Holm, 1979).

Events subtest was used to assess memory for past news events. Questions pertaining to famous events were administered simultaneously in oral and written form and a free recall format was used initially followed by a three choice recognition procedure for any incorrect items. For both subtests, there were nine items per decade. Only decades relevant to each subject's lifetime were used in this study. Results for the Famous Faces and Public Events subtests were analysed in the same manner as outlined for the New Vocabulary test. That is, for both the recall and recognition conditions, three scores were calculated for each subject (Childhood, Midlife and 1990s).

Results

There were no differences detected between SG and the NCs on the New Vocabulary test or Famous Faces subtest, for either recall or recognition for any of the three time periods examined (Table 5). On the Public Events subtest, SG's performance on the Childhood (p < .013) epoch for recall and on the Childhood (p < .008) and Midlife (p < .008) time periods for recognition was impaired relative to NCs (see Table 5).

His scores did not differ from control subjects when asked questions about public events from the 1990s.

Comment

SG's performance was comparable to NCs on both the recall and recognition conditions of the New Vocabulary test (Miller & Batchelor, 2004; Verfaellie et al., 1995) and there was no evidence of a temporal gradient. However, it was noted that the NC group and SG performed at ceiling on this test, which raised the possibility that any subtle impairments in knowledge of vocabulary terms may have been obscured. On the Famous Faces test, where there was sufficient variation in the NC data, SG's performance was well within normal limits across all time periods tested. Other aspects of semantic knowledge (as shown earlier in Table 1) also indicated intact abilities; semantic fluency, picture naming, word definition and word-picture matching scores as well as his scores on the WAIS-R Information and Vocabulary subtests all fell at or above the average range.

In contrast, SG's memory for public events from most periods of his life was deficient. Although the current study did not control for the effects of possible differences in media exposure, which has been shown to influence performance on tests of retrograde semantic knowledge (Kapur et al., 1999), this explanation is unlikely to account for SG's poor memory for remote public events for three reasons (1) the control group was matched to SG in terms of level of education and intellectual function, (2) premorbidly, SG was a high functioning and well travelled individual who (according to his wife) regularly listened to the news and read newspapers, and (3) SG's performance was comparable to the NC group on all aspects of the Famous Faces test. Surprisingly, he did not show a significant deficit in memory for public events from the 1990s. Unfortunately, inspection of the public events data from this decade again revealed a possible ceiling effect, particularly for the recognition component.

Discussion

Detailed investigations into SG's memory for the past indicate that some, but not all aspects of retrograde memory are dependent on mesial temporal and/or retrosplenial brain regions. SG's impaired ability to identify photographs of landmarks from both the remote and recent time periods indicated that the mesial temporal lobes and/or retrosplenial cortices are involved in the processing of this type of information indefinitely. He was also unable to determine the direction of one landmark in relation to his position in front of another landmark. A temporal gradient was seen for autobiographical event memory; SG's recall of autobiographical event memories from the few years prior to his strokes was deficient, whereas his recall of autobiographical incidents from the more remote past was intact. In contrast, his memory for public events seemed to be impaired for much of his lifetime. Knowledge of routes, cardinal direction, landmark locations, personal semantic details, vocabulary and famous faces were all preserved.

Topographical memory

With regard to his retrograde topographical memory deficits, SG encountered difficulty when he was required to identify major or incidental landmarks across all time periods tested Aguirre and D'Esposito (1999) and others (e.g., Epstein & Kanwisher, 1998; Habib & Sirigu, 1987; Rosenbaum, Gao, Richards, Black, & Moscovitch, 2005) would attribute such landmark agnosia to a loss of posterior parahippocampal/ anterior lingual gyrus function. These findings only offer partial support to the notion proposed by Rosenbaum et al. (2000), who argue that bilateral mesial temporal lobe damage results in a loss of detailed topographical information. Given the findings from SG, it is perhaps more appropriate to conclude that damage to the posterior parahippocampal/anterior lingual gyri (as sustained by both SG and KC) results in a temporally extensive recognition deficit for landmarks per se. This notion complements the findings of Maguire et al. (2006) who documented intact landmark recognition in their patient TT, with relatively preserved parahippocampal gyri in the context of focal hippocampal damage. A role for the right posterior parahippocampal gyrus in the identification of familiar landmarks has been documented in two functional neuroimaging studies (Rosenbaum et al., 2004b; Rosenbaum, Ziegler, Winocur, Grady, & Moscovitch, 2004c). Both these studies examined their subjects' topographical memories for their current home town only. To our knowledge, there have not been any functional neuroimaging studies to date that have investigated recognition or identification of landmarks that were encountered in the remote past. Findings from the current study indicate that the posterior parahippocampal/ anterior lingual gyri may be the permanent repository for knowledge pertaining to landmark identity, and as such, we predict that there would be posterior parahippocampal/anterior lingual involvement in landmark identification, regardless of the age of the memory.

A second topographical memory deficit that we detected in SG was his heading disorientation. That is, he was poor at imagining which direction he would have to turn his body to move from one landmark to another. Through his intact performance on the cardinal direction subtest, SG demonstrated that he was able to imagine himself standing in a particular position relative to a given landmark. Neither he nor his wife described any classic signs of egocentric disorientation (as outlined by Aguirre and D'Esposito, 1999) and he performed normally on table top tests of visuospatial ability This would suggest that SG's difficulties in judging the spatial relationships between landmarks based on his imagined position were either the result of problems with allocentric processes or with transforming spatial information from an egocentric to allocentric frame of reference. His intact performance on the landmark map localisation and route recall subtests, which both require some form of allocentric processing, make this first explanation less likely. A number of researchers have theorised that the retrosplenial cortex may be instrumental in performing spatial transformations because of its connections with the posterior parietal lobe and parahippocampal gyrus (Maguire, Frith, Burgess, Donnett, & O'Keefe, 1998; Vogt, Finch, & Olson, 1992). This notion is particularly significant since neither EP, KC or TT (who were unimpaired on similar tasks) sustained bilateral retrosplenial damage, whereas FDG-PET and MRI data indicated that SG had. Patients with damage to the retrosplenial cortices have been described by Aguirre and D'Esposito (1999) as suffering from heading disorientation: an inability to derive directional information from landmarks that they are able to recognise. It is therefore quite plausible that SG was unable to derive directional information even from landmarks, because he had difficulty transforming spatial information from an egocentric to an allocentric representation (and vice versa).

Interestingly, our findings indicate that damage to the retrosplenial regions does not necessarily affect one's appreciation for cardinal direction. Compared to making spatial relationships judgements, identifying cardinal direction relied on the application of well established knowledge regarding Sydney, which subjects were heard to verbalise as they performed the test. For example, knowing that the "North Shore" lies at the far end of the Sydney Harbour Bridge allowed subjects to deduce the north–south axis of the city. Future studies, using healthy subjects and patients with circumscribed retrosplenial damage are warranted to further investigate the neural mechanisms underlying the appreciation of cardinal direction and the cognitive processes used by normal subjects to determine cardinal direction.

Despite his virtually complete bilateral hippocampal damage, SG retained some form of spatial map that allowed him to access information regarding routes and positions of landmarks within a familiar environment. Both Teng and Squire (1999) and Rosenbaum et al. (2000) also reported that their subjects (both with almost complete damage to both hippocampi) were able to recall such information. These findings contrast somewhat with those of Maguire et al. (2006), who documented poor navigational ability in areas that did not contain many (or any) major roads. Methodological differences may account for this discrepancy, as Maguire et al.'s patient TT was asked to navigate in a virtual reality environment, whereas SG, EP and KC were asked to recall routes from memory. Furthermore, none of the three latter subjects were required to navigate in areas that did not contain any major roads. Thus, more subtle deficits in route knowledge may have been missed.

Taken together, it would appear that the hippocampi are not necessary to support memory for most aspects of remotely learned topographical information, contrary to the predictions of Cognitive Map Theory (O'Keefe & Nadel, 1978). More recently, it has been proposed that the hippocampus might only be necessary for the initial acquisition and navigation within novel environments and that the right caudate nucleus, lateral temporal or posterior parietal cortices are essential for the maintenance of these long-term topographical memories (Aguirre & D'Esposito, 1999; Hartley, Maguire, Spiers, & Burgess, 2003; Rosenbaum et al., 2004b,c). In support of this, in another study (manuscript in preparation), we have documented poor route recall in patients with combined temporal and parietal atrophy. In combination with these and previous results, findings from SG suggest that the posterior parietal cortices alone are sufficient for storing this sort of material. Nonetheless, the fact that TT had difficulty with memory for lesser routes (and that KC had difficulty recognising less obvious landmarks in his neighbourhood) continue to raise the possibility that the hippocampi do play a role in the very long-term storage of the fine details of topographical knowledge.

Autobiographical memory

The results of autobiographical event memory testing in SG were more consistent with Consolidation Theory than MTT, as SG had a deficit for recent autobiographical events, but was able to recall detailed autobiographical events from the more distant past. Our findings do not support the notion that remote autobiographical memories are less vivid or recalled in less detail after mesial temporal lesions (Fujii et al., 2000; Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004). It seems possible that KC's inability to recall any detailed autobiographical incidents may be attributable to the widespread nature of his brain lesions, which has resulted in additional deficits (such as adynamia and reduced verbal generativity) that have compromised his capacity for complex and effortful retrieval. For example, KC has been described as someone who "does not initiate any optional activity on his own, has difficulty planning complex actions and ... when asked to describe the state of his mind when he is trying to think about any part of his past or future, he says that it is blank" (Tulving et al., 1988, pp. 7–8).

However, subject TT, with a more circumscribed temporal lobe lesion was also unable to recall any autobiographical incidents from any point in his life (Maguire et al., 2006). Cipolotti and colleagues (Cipolotti et al., 2001) reported similar findings in a patient with markedly shrunken hippocampi. Interestingly, both these patients suffered from several seizures during the course of their recovery, which may have served to disrupt or interfere with processes vital to the long-term storage of autobiographical incidents (Lah, Grayson, Lee, & Miller, 2004). Of note, neither SG, EP nor any of the patients with MTL lesions studied by Bayley, Hopkins, and Squire (2003), who all had good recollection of remote autobiographical events, were reported to have experienced seizures. Hence, in addition to demonstrable neuroanatomical variables (i.e., lesion locus), factors such as whether or not the subject experienced seizures may play an important role in determining the pattern of autobiographical memory loss.

Of note, the degree of autobiographical memory loss observed in SG was not as extensive as that documented in EP (Reed & Squire, 1998). Differences in locus of lesion probably explain this discrepancy. SG's lesion involved primarily the mesial temporal lobes and retrosplenial cortices, with sparing of the anterior lateral inferotemporal cortex. EP's damage primarily affected anterior mesial temporal structures and extended to include the lateral inferotemporal gyri (Hamann & Squire, 1997), which are thought to be particularly important with regard to the processing of remote autobiographical event memories (Calabrese et al., 1996; Fink et al., 1996; Markowitsch et al., 1993).

In patients with posterior brain lesions, a number of researchers have proposed an association between an ability to generate mental imagery and the successful recollection of autobiographical incidents (Hunkin et al., 1995; O'Connor, Butters, Miliotis, Eslinger, & Cermak, 1992; Ogden, 1993; Rubin & Greenberg, 1998). Furthermore, a loss of memory for autobiographical incidents across the entire lifespan has been documented in a patient with retrosplenial tumour (Gainotti, Almonti, Di Betta, & Silveri, 1998). Surprisingly, in spite of his bilateral retrosplenial lesions, SG demonstrated a limited loss of memory for autobiographical episodes. However, his lesions were more restricted in nature than the patients described by Gainotti et al. (1998) and the cases reviewed by Rubin and Greenberg (1998). Furthermore, he showed no loss of visual imagery (as demonstrated by normal performance on mental imagery control tasks). Taken together, it appears that mesial parietal and occipital regions outside the retrosplenial cortex have an important role in the processing of autobiographical memories, most likely through the formation of mental images.

Semantic memory

SG demonstrated relatively preserved performance on tests of memory of personal semantic details, vocabulary, object naming, famous people naming and semantic fluency. This contrasts somewhat with KC's pattern of performance on tests of famous names and vocabulary knowledge, where he showed a dense loss of information that had been acquired during the 5 years prior to his injury, but preserved ability on all other time periods examined (Westmacott & Moscovitch, 2002). Although SG did not show a similar loss of recently acquired information, it is possible that this difference might be accounted for in terms of methodology. Specifically, KC's knowledge was tested for information encoded in 5-year intervals, while SG's memory was examined for information that had been prominent during each full decade from 1940 to 2000. If SG does indeed have a subtle and very temporally limited deficit for this sort of information, our tests may not have been able to detect it. As such, it is not possible to rule out that SG may have a very restricted retrograde amnesia for famous faces or vocabulary terms, as might have been predicted by both Consolidation Theory and MTT. TT may also show a very restricted retrograde amnesia for famous faces, as Maguire et al. (2006) comment that his only errors on famous face recognition were for faces that had come to prominence 3 years prior to testing (i.e., his impairment may extend to include the year prior to his illness).

Nevertheless, neither SG, KC nor TT showed an extensive loss of knowledge for vocabulary and famous people, as documented for subject EP. This discrepancy is again considered attributable to differences in the locus of the subjects' lesions. The inferior and anterolateral temporal cortices have been implicated in the long-term processing of knowledge regarding objects and vocabulary (e.g., Hodges, Patterson, Oxbury, & Funnell, 1992; Kitchener, Hodges, & McCarthy, 1998; Verfaellie et al., 1995) and a role for fusiform gyrus in the identification of famous faces has been proposed (Gorno-Tempini & Price, 2001; Haxby et al., 1994). These areas are largely spared in SG, KC and TT but damaged in EP. Hence, memory for remotely learned vocabulary and famous faces may not be dependent on mesial temporal lobe function at all but rather would seem to be processed by anterior temporal and fusiform cortices, respectively.

Given temporally limited deficits or intact performance found on other aspects of semantic memory, SG's subtle but temporally extensive deficit on a test of public event memory was somewhat surprising. However, both TT and EP also demonstrated poor knowledge of public events (and KC's knowledge for this material was not tested). Previous studies of patients with bilateral damage limited to the hippocampal formation have demonstrated a time-limited loss of knowledge regarding public events (e.g., Hirano & Noguchi, 1998; Kapur & Brooks, 1999), while studies of patients with more extensive temporal lobe cortical damage (e.g., Cermak & O'Conner, 1983; Damasio, Eslinger, Damasio, VanHoesen, & Cornell, 1985; Kapur et al., 1996) and patients with temporal lobe epilepsy (Lah, Lee, Grayson, & Miller, 2006) have revealed more pervasive losses of memory for public events. A more complete understanding of the neural representation of public event memory would seem to depend on the accumulation of more cases with temporal lobe lesions who are tested and compared to appropriate control subjects.

In conclusion, the current findings indicate that retrograde topographical, autobiographical and semantic memories can be differentially affected subsequent to bilateral mesial temporal and/or retrosplenial damage caused by infarction. It seems clear that the site and extent of a temporal lobe lesion influences the pattern of retrograde memory deficits. None of the existing theories (Cognitive Map, Consolidation or Multiple Trace) accounted for all the findings adequately, although many of the predictions of Aguirre and D'Esposito (1999) regarding topographical memory were corroborated. Considering our findings in the context of the existing literature, we concur that posterior parahippocampal damage affects landmark recognition and identification and that retrosplenial lesions interfere with spatial transformations (egocentric to allocentric representations). Hence, a lesion to one of these two areas would be expected to affect one's memories for these particular types of information, irrespective of how long ago they were first acquired. On the other hand, these two brain regions have little role to play in other aspects of retrograde topographical memory such as memory for spatial maps and knowledge of cardinal direction. It is possible that these functions rely on posterior parietal or temporal cortices. SG's results also indicate that the mesial temporal lobes and retrosplenial region have a time-limited role in the processing of retrograde autobiographical events and no role in the retention of personal semantic details. The temporally extensive deficit for public events seen in SG and in some other patients with relatively selective MTL lesions fits with neither MTT or Consolidation Theory and merits further investigation. Knowledge pertaining to famous faces, vocabulary and objects may depend temporarily on the MTL, but SG's results in the context of the literature suggest that these sorts of semantic memories depend more on inferior temporal cortex lateral or anterior to the parahippocampal gyrus and rhinal cortices.

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