

## RAPID COMMUNICATION

## Detailed Descriptions of Routes Traveled, but not Map-Like Knowledge, Correlates With Tests of Hippocampal Function in Older Adults

Marnie Hirshhorn,\* Leorra Newman, and Morris Moscovitch

**ABSTRACT:** We examined hippocampal contribution to remote spatial memory in older adults by correlating their performance on tests sensitive to hippocampal damage with their description of routes they traversed many times or only once, and with their map-like knowledge of downtown Toronto. We found that performance on table-top tests of spatial location (Smith and Milner (1981) *Neuropsychologia* 19:781–793) and on paired-associate learning, and the number of Internal Details on the Autobiographical Interview (Levine et al., (2002) *Psychol Aging* 17:677–689), all correlated significantly with the number and type of perceptual details used in describing routes one has traversed, but not with map-like knowledge of Toronto. No significant correlations were found with performance on tests of frontal function (WCST, phonemic fluency, and backward digit span). We conclude that the hippocampus is implicated in vivid re-experiencing of a familiar route, but not with map-like knowledge of a large-scale environment. These findings are interpreted as consistent with Multiple Trace Theory's prediction that it is the degree of detail of a retrieved memory that is crucially dependent on the hippocampus. © 2010 Wiley Periodicals, Inc.

**KEY WORDS:** aging; allocentric; episodic; memory; spatial

## INTRODUCTION

Multiple Trace Theory (MTT) (Nadel and Moscovitch, 1997; Moscovitch et al., 2005) distinguishes between two types of representation of allocentric spatial information in memory—a map-like representation sufficient for navigation and a rich representation for re-experiencing the environment. For navigation the information is represented schematically so that only major landmarks and the relations among them are preserved. For re-experiencing, the representation is perceptually detailed and includes sensory features of the environment, such as the color and texture of buildings, and incidental entities not needed for navigation. This latter representation is analogous to episodic memory of an environment and, as such, is likely to be dependent on the hippocampus, whereas the former, schematic representation, which is akin to semantic memory, is likely to be dependent on

extra-hippocampal structures. In this study, we test these hypotheses by examining descriptions of real-life walking routes in older adults and correlating them with performance on neuropsychological tests sensitive to hippocampal and extra-hippocampal function.

Evidence from patients supports the dissociation between semantic-like and episodic-like components of spatial memory. Several case studies of patients with hippocampal damage indicate that they have preserved ability to navigate in an old environment (Teng and Squire, 1999) but are impaired at recognizing finer details from the same environment (Rosenbaum et al., 2000; Maguire et al., 2006). For instance, patient K.C. (Rosenbaum et al., 2000) retained a schematic spatial representation of his neighborhood and navigated normally within it, but was unable to recognize individual houses and landmarks in his neighborhood that were not critical for navigation. Likewise, patient T.T. (Maguire et al., 2006), a former London taxi driver, could navigate normally along major routes, but not along side streets that may have required a more detailed representation. Patients with hippocampal damage also generated fewer details in a scene construction task and their constructions exhibited impaired spatial coherence (Hassabis et al., 2007).

Evidence for hippocampal involvement in these two types of representations from functional neuroimaging is supportive but not as clear-cut. Maguire et al. (1997) report hippocampal activation when experienced London taxi drivers had to navigate from one location to another when the familiar route was blocked. However, the region of activation is on the border of the hippocampus and parahippocampal cortex, not in the body of the hippocampus proper (Moscovitch et al., 2005). Rosenbaum et al. (2004) also report activation in a region bordering the hippocampus and the parahippocampal cortex when experienced Toronto residents performed various mental navigation tasks between Toronto landmarks. The absence of activation in the body of the hippocampus in these two studies is likely due to the fact that the mental navigation tasks could be accomplished using a schematic representation of the environment. According to MTT, such schematic representations should exist independently of the hippocampus. Still, other neuroimaging studies report activation within the body of the hippo-

Department of Psychology, University of Toronto, Rotman Research Institute, Toronto, Ontario, Canada

Grant sponsor: Canadian Institute for Health Research; Grant number: 135818.

\*Correspondence to: Marnie Hirshhorn, Department of Psychology, 100 St. George Street, Toronto, Ontario, Canada M5S 3G3.

E-mail: marnie.hirshhorn@utoronto.ca

Accepted for publication 6 July 2010

DOI 10.1002/hipo.20871

Published online 20 September 2010 in Wiley Online Library (wileyonlinelibrary.com).

TABLE 1.  
Mean Performance on Battery of Neuropsychological Tests

Test	Mean
Hippocampal tests	
Table top spatial test	
Items recalled (maximum = 10)	6.85 (1.42)
Mean displacement (cm)	5.52 (1.52)
VPAI (recall total score; maximum = 32)	19.40 (9.33)
Autobiographical interview	
Total internal details	45.61 (21.34)
Total external details	22.28 (16.39)
Frontal/executive function tests	
WCST (perseverative errors)	8.37 (5.75)
Phonemic fluency (FAS total score)	45.25 (12.56)
Digit span backwards (total score)	8.10 (2.10)
Schematic spatial memory test	
Accuracy (easy questions)	90.27 (18.14)
Accuracy (difficult questions)	77.78 (19.61)

Standard deviations are given in parentheses. Scores on all of the standardized tests were within two standard deviations of the age-corrected scaled scores for each participant. For age-corrected scaled scores please refer to Wechsler (1987) for VPA I, Tombaugh et al. (1999) for FAS fluency, and Kong et al. (2000) for WCST.

campus during mental navigation tasks (Niki and Luo, 2002; Mayes et al., 2004). However, these activations are related to the recency of the memory or the vividness of the mental representation, suggesting that re-experiencing may have contributed to the tasks. These findings are consistent, therefore, with MTT's prediction that it is the degree of detail of the remembered environment that determines hippocampal activation.

If these hypotheses are correct, then the number of details provided in a description of walking routes should be correlated with performance on tests known to be sensitive to hippocampal function, but not on tests of functions mediated by other regions, such as prefrontal cortex. By contrast, correlations with hippocampal function should not be evident on tests of schematic spatial knowledge related to map-like, allocentric representations of landmarks in large-scale environments.

We chose to test our predictions in a population of twenty healthy older adults [six males; aged 66–92 years,  $M = 77.25$ , standard deviation (SD) = 7.07] because previous studies have shown that older adults have greater variability in hippocampal structure (Van Petten, 2004) and related memory function (Levine et al., 2002). Normal aging is associated with volume decline in the hippocampus and its related structures which is hypothesized to lead to a decline in the ability to retrieve contextually-specific episodic details of autobiographical events (Levine et al., 2002). Previous research has documented a decline in the number of episodic details given in autobiographical memories in older adults, using the Autobiographical Interview (AI) (Levine et al., 2002). Further, Addis et al. (2008) found a correlation between performance on a relational memory task presumed to be mediated by the hippocampus and the number of episodic details in descriptions of past, and imagined future autobiographical events.

Following Levine et al. (2002) and Addis et al. (2008), we used an interview technique to assess participants' ability to re-experience real-life walking routes. As is the case with methods such as the AI, that ask participants to recall real-life memories, we were unable to assess the accuracy of the details provided. However, findings that hippocampal patients provide impoverished descriptions of novel scenes and events (Hassabis et al., 2007; Addis et al., 2008) suggest that the recollective quality of the memory is hippocampally-dependent regardless of the veracity of the individual details.

We asked participants to describe two routes, a familiar route that they habitually used at least three times a week in the past year (or longer), and a unique route that they had used only once. Recent evidence from lesion and functional neuroimaging studies on autobiographical memory indicates that it is the detailed representation of the remembered event, rather than its temporal specificity, that is crucially-dependent on the hippocampus (Addis et al., 2004; St-Laurent et al., 2009). We wished to know whether the same applies to spatial memories.

Participants gave a detailed description of each route followed by three probe questions encouraging further description of specific entities mentioned in the initial description. Transcripts of these descriptions were scored for the total number of details according to the protocol developed by Hassabis et al. (2007). Inter-rater reliability was established on the basis of 10 familiar and 10 unique routes and was high for both ( $r = 0.98$  and  $r = 0.89$ , respectively). To assess map-like schematic representations, we administered a computerized test of allocentric Toronto landmark locations. This test asked participants to make comparisons about the absolute (allocentric) locations of pairs of Toronto landmarks (e.g., "Which building is farther North?"). (Note: we define an allocentric representation as one that represents the relative locations of landmarks independently of the viewpoint of the individual (see King et al., 2002).) All landmark pairs were presented with both an easy and a difficult question. The difficult questions required participants to compare the landmarks along the dimension with less distance between them. All participants had greater than ten years experience living and navigating within Toronto, except three participants who lived outside the city and did not complete this particular task.

We then correlated performance on the above tests with a variety of tests sensitive to hippocampal and frontal functions (mean performance is reported in Table 1. Correlations between these tests are reported in Table 2). We chose to examine frontal functions because they, too, deteriorate with age, and would serve as a control for a nonspecific aging effect on performance in our spatial tasks.

For the frontal tests, we relied on a traditional neuropsychological battery that included phonemic fluency, WCST, and backwards digit span. For hippocampal tests we chose the AI because the number of internal details has been shown to be affected by hippocampal lesions (Rosenbaum et al., 2008), and a tabletop spatial memory test (Smith and Milner, 1984), performance on which varies with the extent of right hippocampal removal. Briefly, this test involves incidental encoding of object

TABLE 2.

Correlations Between Neuropsychological Tests

Test	Table top	VPAI	AI	WCST	FAS	Digit span
Hippocampal tests						
Table top spatial test (mean displacement)	1.00	-0.54*	-0.26	-0.24	-0.31	0.36
VPAI	-0.54*	1.00	0.35	-0.14	-0.12	-0.01
AI (internal details)	-0.26	0.35	1.00	-0.21	-0.20	0.16
Frontal/executive function tests						
WCST (perseverative errors)	-0.24	-0.14	-0.21	1.00	-0.37	-0.44
Phonemic fluency (FAS total score)	-0.31	-0.12	-0.20	-0.37	1.00	0.13
Digit span backwards (total score)	0.36	-0.01	0.16	-0.44	0.13	1.00

\* $P < 0.05$ .

locations with mean displacement of the objects at recall being the measure of interest (with higher mean displacement reflecting poorer performance). Finally, we also administered the verbal paired associates test (VPA I) from the Wechsler Memory Scale—Revised (Lezak, 1995). Though it is a test of relational memory, and as such is affected by hippocampal lesions, there may be components that are affected by damage to other regions of MTL and lateral temporal cortex (for discussion see Lowndes and Savage, 2007). We predict the strongest correlation to be between the number of details provided in descriptions of walking routes and the tabletop spatial memory test, because this test is particularly sensitive to right hippocampal function.

Participants reported a significantly greater number of details for familiar than unique routes (mean diff = 47.3,  $t_{(19)} = 4.67$ ,  $P < 0.001$ , two-tailed). It is important to note that the number of details provided for familiar routes did not correlate with the number of years of experience with the route ( $r = 0.29$ ,  $P = 0.24$ ), suggesting that familiarity alone cannot account for the variability in details recalled. However, the pattern of correlations between the number of details provided for familiar and unique routes and performance on the neuropsychological tests did not differ. As such, we will discuss the correlations with reference to the total details generated across both types of routes. Importantly, the total number of details provided was significantly correlated with all of our tests that were sensitive to hippocampal function (mean displacement on the table top task:  $r = -0.51$ ,  $P = 0.01$  (see Fig. 1.); internal details on the AI:  $r = 0.63$ ,  $P = 0.001$ ; VPA I total score:  $r = 0.38$ ;  $P = 0.04$ , one-tailed) (see Table 3 for summary of correlation values). The smaller correlation between total details and performance on the VPA I may be due to the fact that the VPA I is more sensitive to left sided lesions, or because it is not as specific to hippocampal function as the other tests. In contrast, the number of details provided was not significantly correlated with any of our measures of frontal function (FAS:

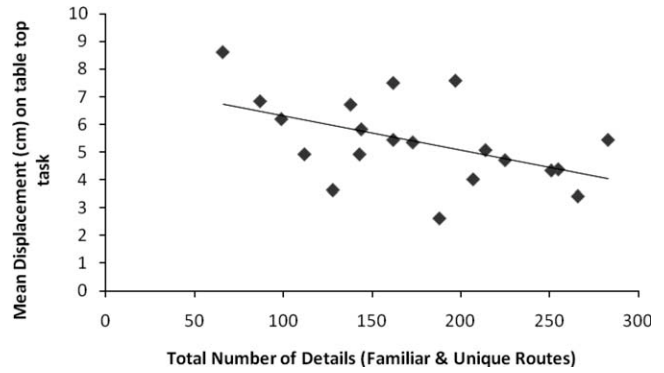


FIGURE 1. The correlation between the total number of details given for familiar and unique routes and mean displacement (cm) on the table top test of spatial location.

$r = -0.32$ ,  $P = 0.18$ ; backwards digit span:  $r = 0.03$ ,  $P = 0.91$ ; WCST:  $r = -0.09$ ,  $P = 0.73$ , two-tailed) or with our test of schematic spatial memory ( $r = 0.11$ ,  $P = 0.70$ , two-tailed).

Accuracy on the test of schematic spatial memory was high for both easy (94.03%) and difficult (80.76%) questions. One participant had performance below chance and greater than two standard deviations below the mean. This participant was excluded from the subsequent analyses ( $N = 16$  for this task).

Performance on the easy questions from the test of schematic spatial memory was not significantly correlated with any of the measures sensitive to hippocampal function (mean displacement:  $r = -0.16$ ,  $P = 0.57$ ; internal details:  $r = -0.12$ ,  $P = 0.65$ ; VPA:  $r = -0.30$ ,  $P = 0.26$ , two-tailed). The absence of a correlation between performance on the easy questions and tests sensitive to hippocampal function may be due to lack of variability in performance on the easy questions ( $SD = 9.67$ ). Although performance on the difficult questions showed greater variability ( $SD = 15.76$ ), there still was no correlation between accuracy and any of the tests sensitive to hippocampal function

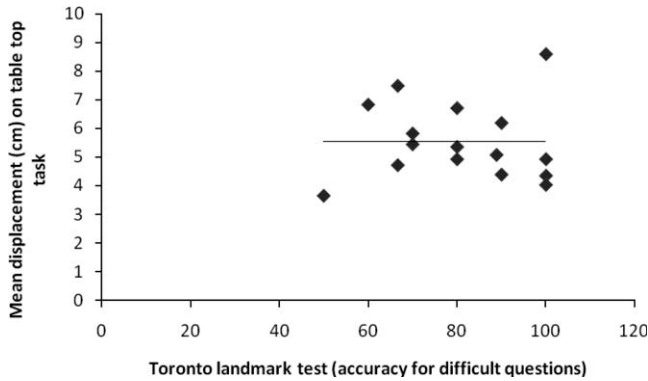
TABLE 3.

Correlations Between Neuropsychological Tests and Total Details From Spatial Interview and Accuracy on Landmark Test (Difficult Questions)

Test	Total details	Landmark test
Hippocampal tests		
Table top spatial test (mean displacement)	-0.51*	0.01
VPAI	0.38**	-0.04
Autobiographical interview (internal details)	0.63*	-0.14
Frontal/executive function tests		
WCST (perseverative errors)	-0.07	-0.07
Phonemic fluency (FAS total score)	-0.32	0.25
Digit span backwards (total score)	0.03	-0.10

\* $P < 0.01$ , one-tailed.

\*\* $P < 0.05$ .



**FIGURE 2.** The correlation between accuracy on the test of Toronto landmark knowledge and mean displacement (cm) on the table top test of spatial location.

[mean displacement:  $r = 0.00$ ,  $P = 0.99$  (see Fig. 2); internal details:  $r = -0.23$ ,  $P = 0.40$ ; VPA:  $r = 0.19$ ,  $P = 0.48$ ]. In addition, performance on the difficult questions also was not correlated with any measures sensitive to frontal function (FAS:  $r = 0.25$ ,  $P = 0.34$ ; backwards digit span:  $r = -0.14$ ,  $P = 0.59$ ; WCST:  $r = 0.25$ ,  $P = 0.34$ ). In addition, reaction times for both question types were not correlated with any of the tests sensitive to hippocampal and frontal function.

The data presented here provide evidence that spatial memory can be behaviorally dissociated into an episodic-like and a semantic-like (schematic) component. The episodic-like component, as assessed by the number of details provided in descriptions of walking routes, is strongly correlated with hippocampal function. In contrast, the semantic-like component, as assessed by a test of memory for allocentric landmark locations, is not correlated with hippocampal function. These results support MTT's prediction that it is the richly detailed aspects of a memory which are crucially dependent on the hippocampus, and not those schematic aspects that are sufficient for navigation. The fact that the same pattern of correlations was observed for both familiar and unique routes (in spite of more details being provided for familiar routes) supports the idea that it is the degree of detail of a retrieved memory, rather than its age or degree of rehearsal, that determines hippocampal involvement.

It is important to note that the details provided were not only spatial in nature, but also included a large proportion of sensory details (sensory descriptions accounted for 31% of the total details for familiar routes, and 37% of the total details provided for unique routes). This suggests that the correlations between the details provided and tests sensitive to hippocampal function cannot be explained simply in terms of spatial function. It appears that the role of the hippocampus is not limited to the encoding and maintenance of spatial context, but may include the encoding and maintenance of more general perceptual details that contribute to the overall vividness of the memory. It is possible, however, that the spatial context provides a framework for representing these nonspatial details, as suggested by proponents of Cognitive Map Theory (Nadel, 2008) and implied in Hassabis et al.'s (2007) proposal that the hippocampus is necessary for scene construction.

The finding that the number of details correlated with performance on the VPA I, a test of relational memory ability, is consistent with the notion that the hippocampus is important for integrating details into a cohesive representation of an environment or scene. Such an explanation is consistent with the findings of Hassabis et al. (2007) who report impaired spatial coherence in the description of imagined scenes in patients with hippocampal lesions. Although these patients were able to imagine some details, the scenes that they described were found to be incoherent and fragmented in nature.

Throughout our analyses we have made the assumption that the number of details provided in descriptions of walking routes is a valid measure of the episodic component of spatial memory in which we are interested. The fact that the total number of details shows a positive correlation with the number of internal, but not external, details on the AI validates our assumption. Internal details on the AI are considered a measure of episodic memory, whereas external details reflect semantic memory. In addition, the number of internal, but not external, details has been shown to be affected by hippocampal lesions (Rosenbaum et al., 2008). Therefore, the correlation between details on walking routes and internal details on the AI is consistent with the other reported correlations with tests of hippocampal function.

Importantly, the number of details provided in the descriptions of both familiar and unique routes did not correlate with any of the neuropsychological tests of prefrontal function (WCST, backwards digit span, FAS). These findings allow us to reject the interpretation that the correlations we have reported are due to variability in frontal lobe function, or to a more general (nonspecific) variability in cognitive function with age. In addition, the absence of a correlation between the number of details provided and performance on the FAS suggests that the results we report cannot be explained by variability in verbal output.

This study has been successful in dissociating an episodic-like and semantic-like component of spatial memory in older adults. The results presented here provide support for MTT's prediction that even for spatial memory, it is the degree to which a memory is vividly recalled as reflected by its coherence and the number of details provided that is crucially dependent on the hippocampus.

## REFERENCES

- Addis DR, McIntosh AR, Moscovitch M, Crawley AP, McAndrews MP. 2004. Characterizing spatial and temporal features of autobiographical memory retrieval networks: A partial least squares approach. *Neuroimage* 23:1460–1471.
- Addis DR, Wong AT, Schacter DL. 2008. Age-related changes in the episodic simulation of future events. *Psychol Sci* 19:33–41.
- Hassabis D, Kumaran D, Vann SD, Maguire EA. 2007. Patients with hippocampal amnesia cannot imagine new experiences. *Proc Natl Acad Sci USA* 104:1726–1731.
- King JA, Burgess N, Hartley T, Vargha-Khadem F, O'Keefe J. 2002. Human hippocampus and viewpoint dependence in spatial memory. *Hippocampus* 12:811–820.



- Kongs SK, Thompson LL, Iverson GL, Heaton RK. 2000. Wisconsin Card Sorting Test—64 Card Version Professional Manual. Odessa, FL: Psychological Assessment Resources, Inc.
- Levine B, Svoboda E, Hay JE, Winocur G, Moscovitch M. 2002. Aging and autobiographical memory: Dissociating episodic from semantic retrieval. *Psychol Aging* 17:677–689.
- Lezak MD. 1995. *Neuropsychological Assessment*, 3rd ed. New York: Oxford University Press.
- Lowndes G, Savage G. 2007. Early detection of memory impairment in Alzheimer's Disease: A neurocognitive perspective on assessment. *Neuropsychol Rev* 17:193–202.
- Maguire EA, Frackowiak RSJ, Frith CD. 1997. Recalling routes around London: Activation of the right hippocampus in taxi drivers. *J Neurosci* 17:7103–7110.
- Maguire EA, Nannery R, Spiers HJ. 2006. Navigation around London by a taxi driver with bilateral hippocampal lesions. *Brain* 129:2894–2907.
- Mayes AR, Montaldi D, Spencer TJ, Roberts N. 2004. Recalling spatial information as a component of recently and remotely acquired episodic or semantic memories: An fMRI study. *Neuropsychology* 18:426–441.
- Moscovitch M, Rosenbaum RS, Gilboa A, Addis DR, Westmacott R, Grady C, McAndrews MP, Levine B, Black S, Winocur G, Nadel L. 2005. Functional neuroanatomy of remote episodic, semantic and spatial memory: A unified account based on multiple trace theory. *J Anat* 207:35–66.
- Nadel L, Moscovitch M. 1997. Memory consolidation, retrograde amnesia and the hippocampal complex. *Curr Opin Neurobiol* 7:217–227.
- Niki K, Luo J. 2002. An fMRI study on the time-limited role of the medial temporal lobe in long-term topographical autobiographical memory. *J Cogn Neurosci* 14:500–507.
- Rosenbaum RS, Moscovitch M, Foster JK, Schnyer DM, Gao F, Kovacevic N, Verfaellie M, Black SE, Levine B. 2008. Patterns of autobiographical memory loss in medial-temporal lobe amnesic patients. *J Cogn Neurosci* 20:1490–1506.
- Rosenbaum RS, Priselac S, Kohler S, Black SE, Gao F, Nadel L, Moscovitch M. 2000. Remote spatial memory in an amnesic person with extensive bilateral hippocampal lesions. *Nat Neurosci* 3:1044–1048.
- Rosenbaum RS, Ziegler M, Winocur G, Grady CL, Moscovitch M. 2004. I have often walked down this street before: fMRI studies on the hippocampus and other structures during mental navigation of an old environment. *Hippocampus* 14:826–835.
- Smith ML, Milner B. 1981. The role of the right hippocampus in the recall of spatial location. *Neuropsychologia* 19:781–793.
- Smith ML, Milner B. 1984. Differential effects of frontal-lobe lesions on cognitive estimation and spatial memory. *Neuropsychologia* 22:697–705.
- St-Laurent M, Moscovitch M, Levine B, McAndrews MP. 2009. Determinants of autobiographical memory in patients with unilateral temporal lobe epilepsy. *Neuropsychologia* 47:2211–2221.
- Teng E, Squire LR. 1999. Memory for places learned long ago in intact after hippocampal damage. *Nature* 400:675–677.
- Tombaugh TN, Kozak J, Rees L. 1999. Normative data stratified by age and education for two measures of verbal fluency: FAS and animal naming. *Arch Clin Neuropsychol* 14:167–177.
- Van Petten C. 2004. Relationship between hippocampal volume and memory ability in healthy individuals across the lifespan: Review and meta-analysis. *Neuropsychologia* 42:1394–1413.
- Weschler D. 1987. *Weschler Memory Scale—Revised Manual*. New York: Psychological Corporation.