Spatial memory and the human hippocampus

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The hippocampus and adjacent medial temporal lobe structures are known to support declarative memory, but there is not consensus about what memory functions the hippocampus might support that are distinct from the functions of the adjacent cortex. One idea is that the hippocampus is specifically important for allocentric spatial memory, e.g., the hippocampus is especially needed to remember object locations when there is a shift in viewpoint between study and test. We tested this proposal in two experiments. Patients with damage limited to the hippocampus were given memory tests for object locations in a virtual environment. In the first experiment, participants studied locations of a variable number of images (one to five) and tried to remember the image locations from either the same viewpoint as during study (shift of 0°) or a different viewpoint (shift of 55°, 85°, or 140°). In each viewpoint condition (shifts of 0°, 55°, 85°, and 140°), patients performed normally when remembering one or two image locations. Further, performance declined to a similar degree in each viewpoint condition as patients tried to remember increasing numbers of image locations. In the second experiment, participants tried to remember four images after viewpoint shifts of 0°, 55°, 85°, or 140°. Patients were mildly impaired at all conditions (shifts of 0°, 55°, 85°, and 140°), and the impairment was no greater when viewpoint shifted. We conclude that damage to the hippocampus does not selectively impair viewpoint-independent spatial memory. Rather, hippocampal damage impairs memory as the memory load increases.

amnesia | medial temporal lobe | virtual reality | space

The medial temporal lobe has long been known to be essential for the formation of long-term memory (1). Animal models of human memory impairment identified the critical structures within the medial temporal lobe: the hippocampal region (hippocampus proper, dentate gyrus, and subicular complex) and the adjacent cortex (perirhinal, entorhinal, and parahippocampal cortices) (2, 3). Although it is widely agreed that these structures are important for memory, specifically declarative memory (4), there is no consensus about what memory functions the hippocampal region might support that are distinct from the functions of the adjacent medial temporal lobe cortex.

According to one view, the hippocampal region stores information about allocentric (viewpoint-independent) space (5). Many findings in humans are consistent with this idea. The noted patient H.M., who has damage to the hippocampus (and adjacent medial-temporal lobe structures) was impaired in recalling object locations (6). Similarly, patients who had undergone unilateral temporal lobectomy were impaired on spatial memory tests requiring topographical knowledge or the ability to navigate through novel environments (7–9). The patient Jon, who has perinatal damage thought to be limited to the hippocampus, was impaired at navigating through a novel environment (10), and patient Y.R. exhibited a modest impairment on a task of allocentric memory (11). Moreover, a study of five patients, including Jon, revealed impaired topographical memory (12). Lastly, studies with functional MRI and positron emission tomography have revealed hippocampal activation in tasks requiring either spatial memory or navigation (13–17).

Although damage to the human hippocampus unequivocally results in spatial memory impairment, the same damage also causes memory deficits that have no obvious spatial component. Thus, patients with damage to the hippocampal region are impaired on memory tests involving words, facts, nonsense sounds, odors, and faces (18–23). In addition, the patient Jon was impaired on nonspatial tests about events that had occurred within a virtual environment (10).

Although the hippocampal region does not exclusively support spatial memory, one can ask whether the region has a special or disproportionately large role in allocentric memory compared with other kinds of memory. In two recent studies, the patient Jon was tested for object location memory in a virtual environment in two conditions, one that involved a shift in spatial viewpoint between study and test and was considered to require allocentric memory, and another that did not involve a shift in viewpoint and therefore did not require allocentric memory. Jon was reported to be disproportionately impaired on the test that required allocentric memory (24, 25).

Inasmuch as these findings were based on the performance of a single patient with developmental memory impairment, it is prudent to ask how a group of patients with adult-onset memory impairment and selective hippocampal damage would perform on a similar task that tests memory for object locations from different viewpoints. We have therefore developed a task similar to the one used by King *et al.* (24, 25) (Fig. 1) and have examined the nature of memory impairment in a group of six memory-impaired patients with adult-onset damage thought to be limited to the hippocampal region.

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Results

Experiment 1: Increasing Image Number and Increasing Viewpoint Shift. Fig. 2*a* shows scores for controls (CON) and patients with hippocampal lesions (H) on the memory test for different numbers of images (one, two, three, four, or five) and for different viewpoint-shift conditions (0°, 55°, 85°, or 140°). An ANOVA (number of images × size of viewpoint shift × group) revealed an effect of number of images [$F_{(4, 64)} = 18.5$; $P < 0.001$] and of viewpoint shift [$F_{(3, 48)} = 14.3$; $P < 0.001$] and an interaction of number of images × group [$F_{(4, 64)} = 4.4$; $P = 0.003$]. There was no number of images × viewpoint shift × group interaction [$F_{(12, 192)} = 4.4$; $P > 0.2$], and the main effect of group fell short of significance [$F_{(1, 16)} = 3.7$; $P = 0.07$], because the patients performed quite well when they needed to remember only one or two images. However, in each viewpoint condition, patients performed more poorly than CONs when they had to remember five images ($t > 2.9$; $P < 0.02$).

To appreciate the effect of increasing image number, scores for each group were collapsed across the four viewpoint-shift condi-

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Abbreviations: CONs, controls; H, patient(s) with hippocampal lesions.

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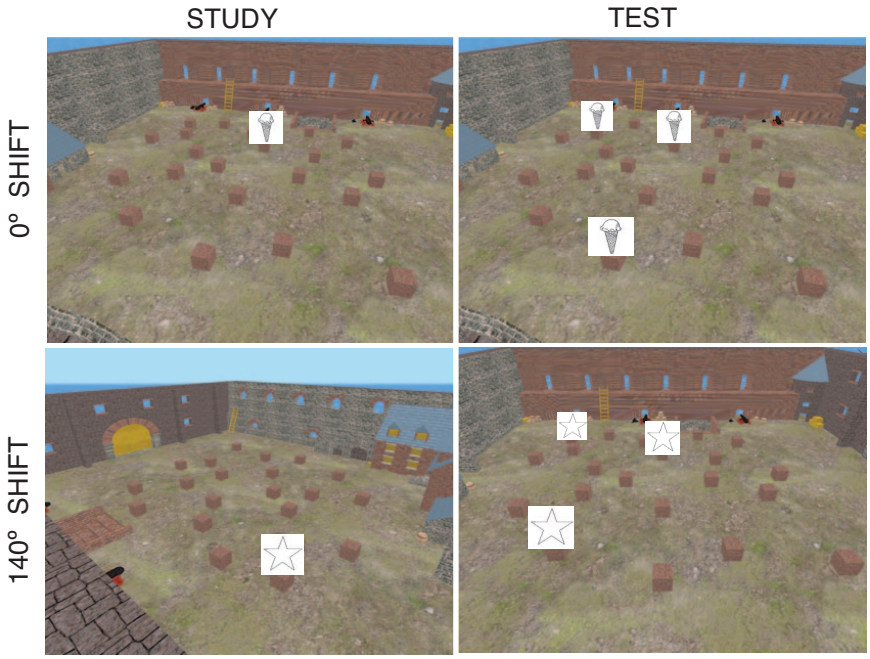

Fig. 1. Sample trials from the image-location memory task. Each trial consisted of a study phase, a delay (≈8 sec), and a test phase. At study, different numbers of images (one, two, three, four, or five) were presented, one at a time. (*Left*) Each image appeared in one of 21 locations in a virtual environment (*Left*). During the delay, the virtual environment rotated 0° (*Upper*), 55°, 85°, or 140° (*Lower*). (*Right*) At test, each image appeared in three locations. Participants chose the image that was in the same location as during study. The upper right cone and the upper left star are the correct choices.

tions (Fig. 2*b*). Patients performed as well as CONs when they needed to remember only one image, but their performance declined as the number of images increased. Specifically, patients were impaired when they needed to remember five images [$t_{(16)}$ = 4.9; $P < 0.001$] and marginally impaired when they needed to remember four images [$t_{(16)}$ = 2.1; P = 0.056] [interaction of number of images × group, $F_{(4,\ 64)}$ = 4.4; P = 0.003]. For an appreciation of the effect of increasing viewpoint shift, scores for each group were collapsed across the number of images that needed to be remembered (Fig. 2*c*). In each viewpoint condition, patients performed numerically more poorly with respect to CONs [for 0° shift, $t_{(16)}$ = 3.4; $P < 0.01$, for 55°, 85°, and 140° shifts, $t_{(16)} < 1.8$, $P > 0.10$]. Importantly, the two groups declined at a similar rate, and there was no viewpoint shift × group interaction [$F_{(3,\ 48)} = 0.25$; $P > 0.80$]. A linear trend analysis revealed that performance of both groups declined with increasing viewpoint shift [$F_{(1,\ 3)}$ = 22.3; $P < 0.05$].

Experiment 2: Increasing Viewpoint Shift. Fig. 3 shows scores for the CON and H groups on the memory test for four images and four viewpoint-shift conditions. An ANOVA (size of viewpoint shift × group) revealed an effect of viewpoint shift [$F_{(3,\ 48)}$ = 10.4; $P < 0.001$] and an effect of group [$F_{(1,\ 16)}$ = 9.8; P = 0.006] but no interaction [$F_{(3,\ 48)}$ = 0.54; $P > 0.60$]. Post hoc t tests indicated that the patients performed more poorly than the CONs in the 0°-shift condition (t = 4.4; P = 0.006) and marginally more poorly in the 55° and 85°-shift conditions ($P < 0.08$). The difference between groups in the 140°-shift condition did not reach significance (t = 1.7; P = 0.11). There was no special difficulty with viewpoint shifts, compared to the no-shift (0°) condition.

Discussion

In two experiments, patients with damage thought to be limited to the hippocampal region were given memory tests for images and their locations. Memory was tested from the same viewpoint as during presentation (0° shift) or from a different viewpoint (55°, 85°, or 140° shift). In each of the four shift-in-viewpoint conditions in Experiment 1, patients performed as well as CONs when asked to remember only one or two image locations. Performance declined as the number of images increased, and patients were impaired in every condition (from viewpoint shifts of 0° to shifts of 140°) when they needed to remember five images. In Experiment 2, patients needed to remember four images and performed poorly overall across the four viewpoint conditions (shifts of 0°, 55°, 85°, or 140°). Neither experiment revealed any special difficulty with the trials that involved shifts in viewpoint (55°, 85°, and 140°) compared with trials with no shift in viewpoint. Thus, damage to the hippocampus did not disproportionately impair memory when there was a shift in spatial viewpoint between study and test. Rather, hippocampal damage impaired memory as the memory load increased (i.e., as more image locations needed to be remembered).

The present findings agree with previous reports that hippocampal patients performed similarly on memory tests involving spatial and nonspatial material. In one study, patients with damage to the hippocampus studied an array of objects, and their memory was then tested for recall and recognition of the objects, as well as locations of the objects (26). Patients were impaired on all three tests. Critically, when performance of patients was matched to that of CONs on the object recall and object recognition tests, their performance also matched that of CONs on the object location test. In another study, patients with damage to the hippocampus performed as well as CONs on tasks involving short-term retention of both spatial and nonspatial material (27). There was no special difficulty with maintaining the material in mind across delays up to at least 12 sec. Nevertheless, these previous studies did not test allocentric memory specifically (i.e., memory for the location of objects relative to the environment and independent of one's viewpoint).

Our study extends these previous findings by showing that patients with damage limited to the hippocampus were no more impaired on tests that required viewpoint-independent memory than on tests that did not. Thus, patients were intact when only one or two image locations had to be remembered, regardless of

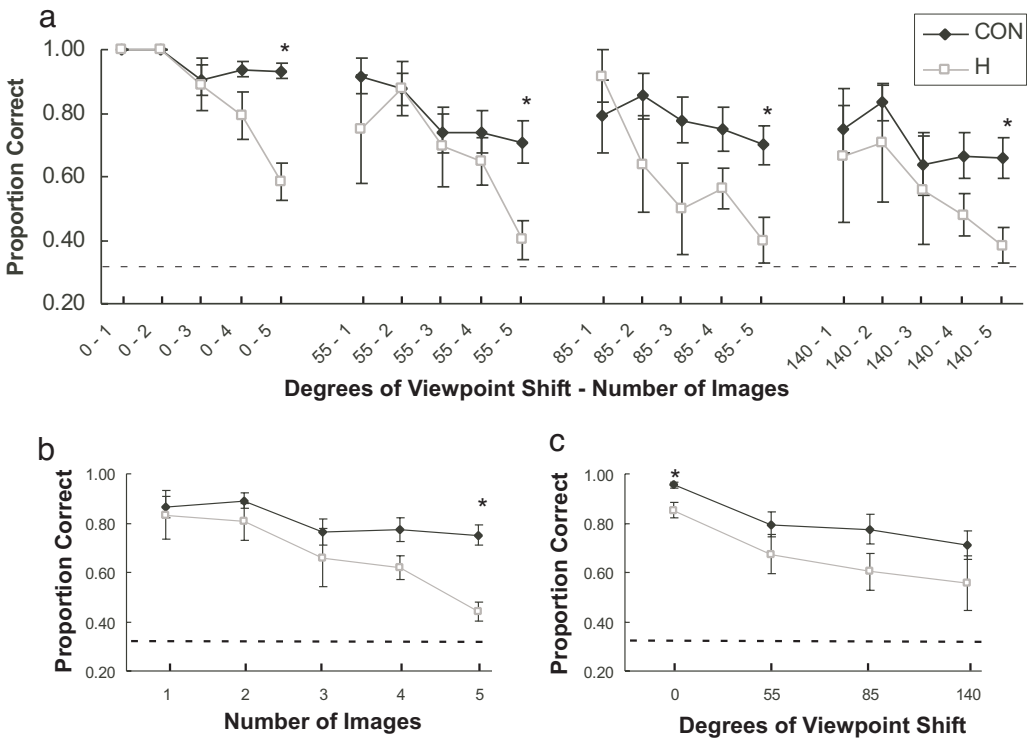

Fig. 2. Effect of image number and viewpoint shift in Experiment 1. (*a*) Proportion correct scores for the CON ($n = 12$) and H ($n = 6$) groups on a memory test for images (one, two, three, four, or five) and four shift-of-viewpoint conditions (0°, 55°, 85°, or 140°). (*b* and *c*) Proportion correct scores for the CON and H groups collapsed across shift-of-viewpoint conditions to show the effect of increasing image number (*b*) and collapsed across image number to show the effect of increasing viewpoint shift (*c*). Asterisks indicate difference between groups, $P < 0.02$. Error bars indicate SEM, and the dashed lines indicate chance performance.

whether the viewpoint shifted from study to test. Further, as the memory load increased (i.e., as the number of images to be remembered increased), performance declined in every condition, i.e., when there was no shift in viewpoint as well as when the viewpoint shifted from study to test.

In two earlier studies, the developmental amnesic patient Jon was reported to be disproportionately impaired on tests of object location memory when there was a shift in viewpoint between study and test, relative to when there was no shift (24, 25).[‡‡] The format of these tests was quite similar to the one in the present study. It is worth mentioning, though, that the shift in viewpoint was instantaneous in the tests used by King *et al.* (24, 25), whereas in our study, the environment rotated gradually and in full view. Also, our experiments tested patients with adult-onset rather than developmental amnesia.

In the first of the two studies (24), participants had to remember the locations of 4, 7, 10, or 13 images in a virtual environment when there was no shift (0° shift) between study and test and also the locations of one, two, three, four, five, or seven images after a shift in viewpoint of 140° between study and test. Jon's performance was matched to that of CONs in the easiest conditions (four and seven images in the no-shift condition), and his performance was then compared with CON performance in the more difficult conditions (10 and 13 images in the no-shift condition and all six tests in the 140°-shift condition). The matched performance on the four- and seven-image tests in the no-shift condition was achieved by presenting CONs with a six-alternative forced-choice test, whereas Jon was presented with an easier three-alternative forced-choice test. When the number of images to be remembered in the no-shift condition exceeded seven (i.e., 10 and 13 images), Jon was impaired. In the shift condition, Jon performed as well as CONs

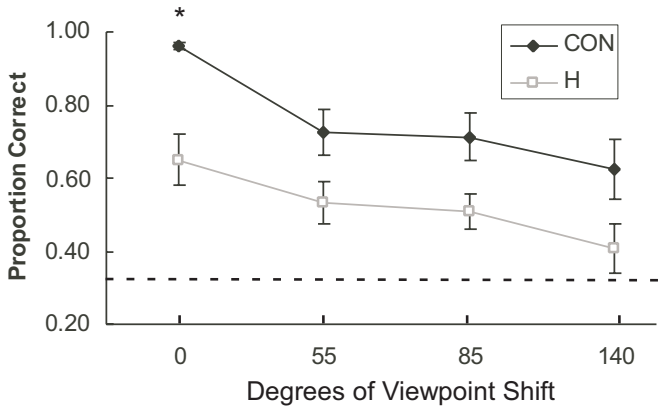

Fig. 3. Effect of viewpoint shift in Experiment 2. Proportion correct scores for the CON and H groups on a memory test for four images and four shift-of-viewpoint conditions (0°, 55°, 85°, or 140°). Asterisk indicates difference between groups, $P < 0.01$. Error bars indicate SEM, and the dashed line indicates chance performance.

[‡‡]Another study from the same group (28) found that a different memory-impaired patient, thought to have very early Alzheimer's disease, was also impaired in the shift but not the no-shift condition. However, that patient had no detectable brain damage, as measured in MR images, and it is thus difficult to relate the findings to brain structure. Further, the condition with a shift in viewpoint between study and test was more difficult for CONs than the condition with no shift in viewpoint, making it possible that difficulty was one factor that could have worsened the patient's performance in the shift-in-viewpoint condition.

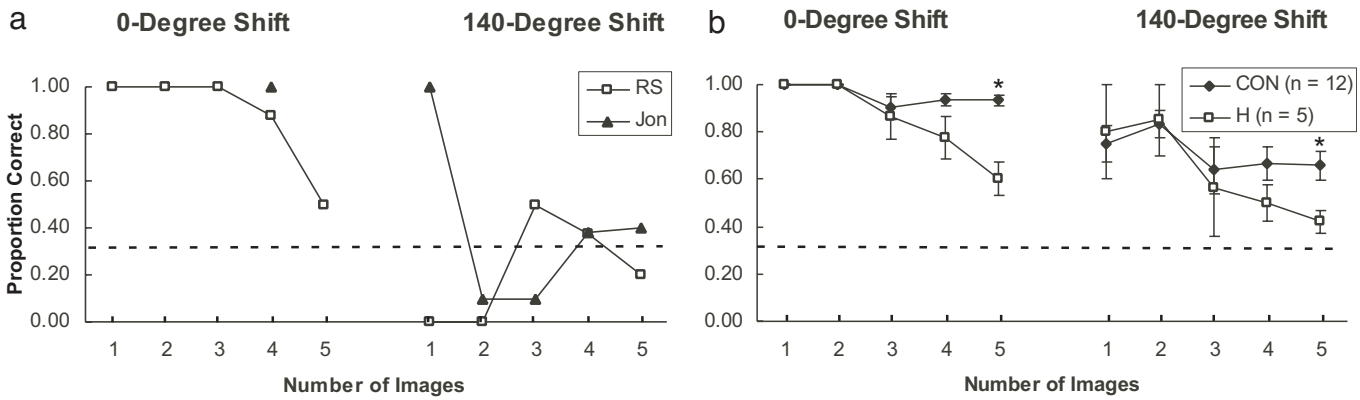

Fig. 4. Comparison of patient Jon (24) with patient R.S. and our other patients. (*a*) Proportion correct scores for patient R.S. in the present study and patient Jon (scores for Jon were estimated from figure 5*a* of ref. 24). The performance of these two patients was qualitatively similar (relatively good performance in the no-shift condition and poor performance in the 140°-shift condition). (*b*) Proportion correct scores for the H group in the present study (excluding R.S.) and CONs, showing that the H group did not have a special difficulty with the 140°-shift condition. Asterisks indicate difference between groups, $P < 0.05$. Error bars indicate SEM, and the dashed line indicates chance performance.

when he had to remember only one image location, but his performance dropped to chance levels when he had to remember more than one image location.

The second study (25) matched the performance of the CON group in the viewpoint-shift (140°) and no-shift (0°) conditions by strategic assignment of target and foil locations. Specifically, in the no-shift condition, targets were presented in locations far from the viewer (which made the test more difficult), and foils were located close to the target (which also made the test more difficult). In each condition, a list of three images had to be remembered on each trial. Again, Jon performed as well as CONs in the no-shift condition (Jon, 90%; CON, 80%, as estimated from figure 6 of ref. 25) but worse than CONs in the shift condition (Jon, 50%; CON, 75%, also estimated from figure 6 of ref. 25).

The possibility is worth considering that Jon's performance in these two studies reflected a broad impairment in declarative memory rather than a specific impairment in allocentric memory. In the first experiment, Jon might have tried to rely on his working memory in the no-shift condition and was thus able to maintain up to seven image locations. As the number of images exceeded his working memory capacity (i.e., 10 and 13 images), his performance declined. Likewise, the 140°-shift condition might have been so difficult that it exceeded the capacity of Jon's working memory when more than a single-image location had to be remembered. In the second experiment, one wonders whether long-term memory was more important for the shift than for the no-shift condition, even though CON performance was matched between the two conditions. That is, perhaps CONs relied more heavily on long-term memory and less on working memory in the shift than in the no-shift condition, with the result that in the no-shift condition, Jon could have more readily maintained the image locations in memory.

It is also important to note that both these studies (24, 25) involved a single patient. Because task performance is quite variable, data are usually clearer when a group of patients, rather than one patient, is tested. Indeed, it is interesting that the performance of one of the patients in our study (R.S.) was qualitatively similar to Jon's, in that R.S.'s performance appeared especially impaired in the 140°-shift condition. Specifically, R.S. performed well when one, two, three, or four images had to be remembered in the 0°-shift condition, and his performance was poor when five images had to be remembered (Fig. 4). His score in the 0°-shift condition across all tests (one, two, three, four, or five images) was 88% correct (Jon scored 75% correct for 4, 7, 10, and 13 images in the 0°-shift condition, as estimated from figure 5*a* of ref. 24). Then, in the 140°-shift condition, R.S.'s performance dropped to chance even when only one image needed to be remembered. In contrast, the other patients in our study, as a group, performed well when they had to remember up to three images. R.S. obtained an average score of 22% across all tests (one, two, three, four, or five images) in the 140°-shift condition (Jon obtained an average score of 23% when two, three, four, five, and seven images had to be remembered in the 140°-shift condition, as estimated from figure 5*a* of ref. 24. Thus, if only R.S. had been tested, one might have concluded that hippocampal damage disproportionately impaired performance in the shift condition, which required viewpoint-independent memory for the image locations. Yet, when performance was averaged across all six patients (also see Fig. 1*a*), performance was similar across all viewpoint shifts, and there was no special difficulty when the viewpoint shifted.

One difference between the tests used in our study and the tests used by King *et al.* (24, 25) concerned how viewpoint was shifted from study to test. In our study, the environment was in full view as it gradually rotated (although the place markers were not visible). In the tests used by King *et al.* (24, 25), the shift in viewpoint was instantaneous. This difference could have rendered the test used in our study less difficult than the tests used by King *et al.* (24, 25) or might have led to the use of somewhat different strategies in the two studies. Nevertheless, both our test and those used by King *et al.* required memory for image locations to be expressed from a viewpoint that was different from that during study.

A body of work in the human literature using functional imaging has suggested that the hippocampus functions to store information about allocentric space. For example, functional imaging studies have reported that activation in the hippocampus is correlated with successful navigation in a virtual environment, as compared with following a marked path or a well learned route (14, 15). Another study also found right hippocampal activation in participants who used a spatial strategy to solve a radial arm maze task but not in participants who used a nonspatial strategy to solve the same task (16). Each of these findings was taken to mean that the hippocampus specifically supports spatial memory. Yet, for the conclusions to be compelling, the control and spatial memory tasks in these studies must differ only in the dimension of interest; that is, the only relevant difference should be that one task requires allocentric spatial memory, and the other does not. This is a difficult standard to meet. Task difficulty, for instance, could be a relevant difference, because spatial tasks (or approaching tasks

Table 1. Characteristics of memory-impaired patients

Patient	Age, yr	Education, yr	WAIS-III IQ	WMS-R Attention	Verbal	Visual	General	Delay
A.B.	67	20	107	87	62	72	54	<50
K.E.	64	13.5	108	114	64	84	72	55
L.J.	68	12	101	105	83	60	69	<50
R.S.	49	12	99	99	85	81	82	<50
G.W.	46	12	108	105	67	86	70	<50
J.R.W.	43	12	90	87	65	95	70	<50

The Wechsler Adult Intelligence Scale-III (WAIS-III) and the Wechsler Memory Scale-Revised (WMS-R) yield mean scores of 100 in the normal population with a standard deviation of 15. The WMS-R does not provide numerical scores for individuals who score below 50. IQ scores for J.R.W. and R.S. are from the WAIS-Revised.

with a spatial strategy) have often proved more difficult than nonspatial tasks (or approaching tasks with a nonspatial strategy) (e.g., see performance on tasks of wayfinding vs. route following in ref. 15 and performance using spatial vs. nonspatial strategy in ref. 16; Experiment 1). Furthermore, because neuroimaging techniques provide data that are correlative, these techniques do not provide evidence for the necessity or importance of a particular structure for a particular function. Specifically, these studies do not provide evidence that the hippocampus is necessary for allocentric spatial memory but not for nonspatial memory.

Other experiments with Jon tested spatial and nonspatial components of tasks and found that he was impaired at remembering both kinds of information (refs. 10 and 25; Experiment 1). In these experiments, Jon explored a virtual environment and collected objects from different characters in different locations within the environment. He was then tested for his memory of the spatial layout as well as for episodes that took place during the exploration (including an old/new recognition memory test for which objects had been collected). Jon was impaired on tests of the spatial layout. He was also impaired on several tests of (nonspatial) episodic memory (i.e., which object was received from a given character, which object was received in a given location, and which of two objects was received first). He performed normally on the recognition memory test for which objects had been collected. Thus, these studies all found that damage to the hippocampus impaired memory for nonspatial as well as spatial information.

In conclusion, patients with damage to the hippocampus were similarly impaired relative to CONs on tests of object location memory that involved a shift in viewpoint between study and test and on tests that did not involve a shift in viewpoint. The performance of all participants declined with increasing viewpoint shift, but the patients had no additional difficulty when the viewpoint shifted. In contrast, patients did have more difficulty than CONs as the memory load (number of images) increased. The results suggest that the hippocampus is not dedicated to or especially important for viewpoint-independent (or allocentric) memory. Rather, the hippocampus is generally important for declarative memory, and viewpoint-independent memory is one example of that broad category.

Methods

Participants. The six memory-impaired patients (one female; Table 1) have bilateral lesions thought to be limited to the hippocampal region (dentate gyrus, CA fields, and subiculum). A.B. and J.R.W. became amnesic after episodes of cardiac arrest in 1976 and 1990, respectively. G.W. and R.S. became amnesic after drug overdoses and associated respiratory failure in 2001 and 1998, respectively. K.E. became amnesic in 2004 after an episode of ischemia associated with kidney failure and toxic shock syndrome. L.J. became amnesic in 1988 during a 6-mo period with no known precipitating event. Her memory impairment has remained stable since that time.

Scores for copy and delayed (12-min) reproduction of the Rey-Osterrieth figure (29) (maximum score, 36) were 28.7 and 2.5, respectively (CONs from ref. 30, scored 30.3 and 20.6). Recall of a short prose passage after a 12-min delay was 0.3 segments for the patients and 6.4 segments for CONs (21 segments maximum). Paired-associate learning of 10 noun–noun pairs across three trials was 0.7, 0.8, and 1.5 pairs for patients and 6.0, 7.6, and 8.9 for CONs.

For five of the six patients (all but A.B.), estimates of medial temporal lobe damage were based on quantitative analysis of MRI, compared with data for 19 CONs (K.E., R.S., G.W., and J.R.W.) or 11 CONs (L.J.) (31). Nine coronal MR images for the five patients are available as supplemental material to ref. 32. The volume of the full anterior-posterior length of the hippocampus and the parahippocampal gyrus were measured by using criteria based on histological analysis of healthy brains (33–35). For each patient, the volumes of the hippocampus and parahippocampal gyrus were divided by the intracranial volume to correct for brain size (31). K.E., L.J., R.S., G.W., and J.R.W. have an average bilateral reduction in hippocampal volume of 49%, 46%, 33%, 48%, and 44%, respectively (all values >3.0 SDs below the control mean). The volume of the parahippocampal gyrus (temporopolar, perirhinal, entorhinal, and parahippocampal cortices) is reduced by 17%, −8%, 1%, 12%, and 6%, respectively (all values within two SDs of the control mean). On the basis of two patients (L.M. and W.H.) with similar bilateral volume loss in the hippocampus for whom detailed postmortem neurohistological information was obtained (36), this degree of volume loss likely reflects nearly complete loss of hippocampal neurons (also see ref. 31).

Additional measurements, based on four CONs for each patient, were carried out for the insular cortex, fusiform gyrus, frontal, lateral temporal, parietal, and occipital lobes. The only volume reduction in these regions >1.3 SDs of the control mean is the parietal lobe of R.S. (37).

A.B. was unable to participate in MR imaging but is thought to have hippocampal damage on the basis of etiology and a neurological examination indicating well circumscribed amnesia. In addition, high-resolution computed tomography images obtained in 2001 were consistent with damage restricted to the hippocampal region (38).

Twelve healthy CONs (three female; mean age, 59.8 years; range, 42–72 years; mean education, 14.3 years) participated in the behavioral experiments.

Stimuli. The stimuli were black-and-white line drawings of objects and animals (39) presented in a virtual environment developed by NeuraTest software (NeuraTest software) meant to resemble

the virtual environment used in earlier work (24) (Fig. 1). The virtual environment, which was a medieval town square with various landmarks and 21 place markers for stimulus presentation, was administered by using a laptop computer equipped with a 15-inch color monitor. The environment was viewed from atop a stone wall that surrounded the town square.

Experiment 1: Increasing Image Number and Increasing Viewpoint Shift. Each trial consisted of a study phase, a delay (≈8 sec), and a test phase. To indicate the starting location for each trial, a red arrow appeared above the stone wall. This starting location varied from trial to trial. When participants reached the starting location using a joystick, the program automatically set the viewpoint from that location so that participants had the town square in full view. During each trial of the study phase, images (one, two, three, four, or five) were presented one at a time for 5 sec each (1-sec interstimulus interval). Participants named each image aloud and were instructed to remember its location. Each image appeared in one of 21 possible locations (Fig. 1 *Left*), such that the same location was used only once within a trial. Then, during the delay (≈8 sec), the place markers and the most recently presented image disappeared, and the environment gradually rotated 0° (Fig. 1 *Upper*), 55°, 85°, or 140° (Fig. 1 *Lower*) (i.e., there was a shift in viewpoint of 0°, 55°, 85°, or 140°). The environment was in full view during the rotation.

Memory was tested for each image that had been presented during study. One image at a time appeared simultaneously in three different locations (Fig. 1 *Right*). Using the joystick, participants chose the image that was in the same location as during the study. In the case of trials in which more than one image was presented at study, the images were presented at test in a pseudorandom order.

There were 40 trials in all, plus eight practice trials presented at the onset. Trials 1–5 involved a 0° shift in viewpoint. Each trial involved one image more than the previous trial (i.e., on trials 1, 2, 3, 4, and 5, the study and test phases consisted of one, two, three, four, and five images, respectively). Similarly, trials 6–10 involved a 55° shift in viewpoint, trials 11–15 involved an 85° shift in viewpoint, and trials 16–20 involved a 140° shift in viewpoint. As in trials 1–5, one image was presented in the first trial of each five-trial set, and the number of images that were presented increased by one across the five trials. This 20-trial sequence was repeated in trials 21–40 with new stimuli.

Experiment 2: Increasing Viewpoint Shift. Each trial was identical in structure to the trials in Experiment 1. On each trial, a red arrow appeared above the stone wall to indicate the starting location. Participants moved to the arrow, and the study phase began. Four images were presented one at a time for 5 sec each (1-sec interstimulus interval). Participants named each image aloud and were instructed to remember its location. Each image appeared in one of the 21 locations, such that the same location was used only once within a trial. During the delay (≈8 sec), the place markers disappeared along with the most recently presented image, and the environment rotated 0°, 55°, 85°, or 140° while in full view. At test, one image at a time appeared simultaneously in three locations, and participants chose the image that was in the same location as during study. There were 20 trials in all. The shift in viewpoint changed across trials, such that trials 1–4 involved a shift of 0°, 55°, 85°, and 140°, respectively. This four-trial sequence repeated four more times with new stimuli (trials 5–8, 9–12, 13–16, and 17–20).

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