

# Human Hippocampus and Viewpoint Dependence in Spatial Memory

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**ABSTRACT:** Virtual reality was used to sequentially present objects within a town square and to test recognition of object locations from the same viewpoint as presentation, or from a shifted viewpoint. A developmental amnesic case with focal bilateral hippocampal pathology showed a massive additional impairment when tested from the shifted viewpoint compared with a mild, list length-dependent, impairment when tested from the same viewpoint. While the same-view condition could be solved by visual pattern matching, the shifted-view condition requires a viewpoint independent representation or an equivalent mechanism for translating or rotating viewpoints in memory. The latter mechanism was indicated by control subjects' response latencies in the shifted-view condition, although the amnesic case is not impaired in tests of mental rotation of single objects. These results show that the human hippocampus supports viewpoint independence in spatial memory, and suggest that it does so by providing a mechanism for viewpoint manipulation in memory. In addition, they suggest an extremely sensitive test for human hippocampal damage, and hint at the nature of the hippocampal role in episodic recollection. *Hippocampus* 2002;12:811–820.

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**KEY WORDS:** developmental amnesia; hippocampal lesion; virtual reality; cognitive map; recognition memory; allocentric; mental rotation

## INTRODUCTION

Developmental amnesics with focal bilateral hippocampal damage tend to have spared performance in recognition memory paradigms but strongly impaired performance in the recollection of episodic information (Vargha-Khadem et al., 1997; Baddeley et al., 2001). The profound deficit in the recollection of episodic memory also invariably results in cases of similar damage acquired in adults, while recognition memory appears to be spared in some cases (e.g., Holdstock et al., 2000a), but not in others (e.g., Manns

and Squire, 1999; see Spiers et al., 2001b, for a comprehensive review). What does the human hippocampus do that is so crucial to episodic recollection, but not to recognition?

One line of attack is to examine the restricted deficit of the developmental amnesics (Vargha-Khadem et al., 1997) in more detail. Interestingly, these cases were impaired on two types of recognition memory: memory of object locations and memory for voice–face associations. In this study, we attempt to characterize the basic functional deficit of one of these patients, “Jon,” within the recognition paradigm and the spatial modality. Jon has focal bilateral hippocampal pathology with apparent sparing of other mesial temporal lobe structures (Gadian et al., 2000) (Fig. 1). We hope that isolating specific functional impairments in the spatial domain will provide a link to the general deficit in episodic recollection.

The cognitive map theory relates episodic memory to the human hippocampus by suggesting that it stores the spatiotemporal context of personally experienced events (O'Keefe and Nadel, 1978). This supported the then tentative suggestion that episodic memory (Tulving, 1983) relies on the hippocampus (Kinsbourne and Wood, 1975) and was proposed as an extension of the hippocampal role in the rat, of enabling locations in the environment to be remembered. A cognitive map can be defined in terms of the spatial behaviors it allows. Principally, these concern memory for locations defined relative to the environment as opposed to locations that can be approached by sensory guidance or as a series of body movements from a given starting point. Thus, a cognitive map enables behaviors such as finding an unmarked goal location from a novel starting position and taking a novel short cut. In addition, the human Cognitive Map provides the framework within which a person's subjective viewpoint can be moved to different locations in an environment (O'Keefe, 1993).

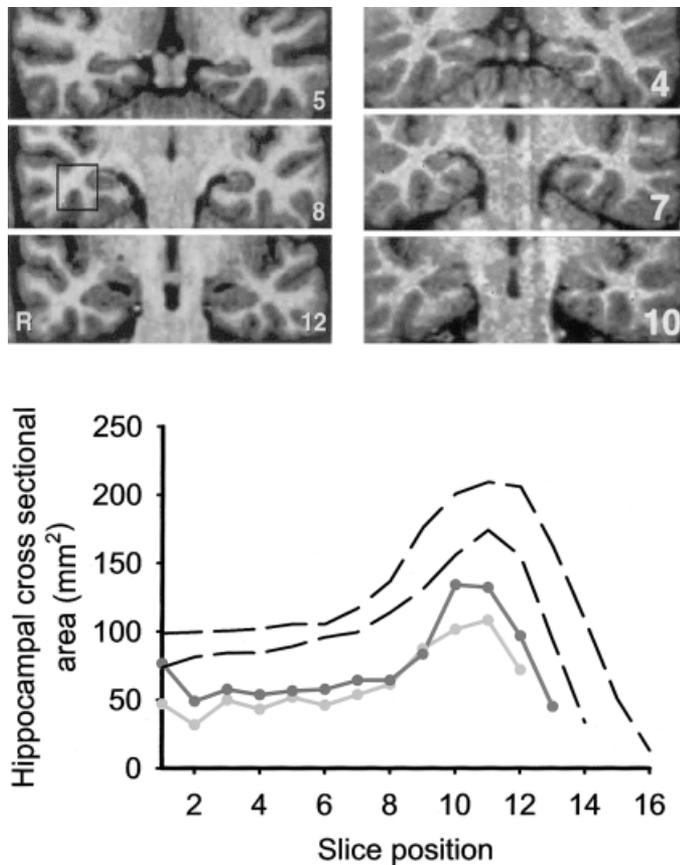
A strong prediction of the cognitive map theory therefore is that patients with selective damage to the hippocampus, either bilaterally or unilaterally on the right,

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**FIGURE 1.** Hippocampal cross-sectional area as a function of slice position, sectioned posterior to anterior. Upper: slices from a control subject (left) and Jon (right). Lower: solid lines show Jon's data (right hippocampus dark-shaded), the broken lines are  $\pm 2$  SD the mean hippocampal cross-sectional area of a group of 22 normal healthy subjects (Van Paesschen et al., 1997). Volumes are uncorrected for intracranial volume. Adapted from Spiers et al. (2001a).

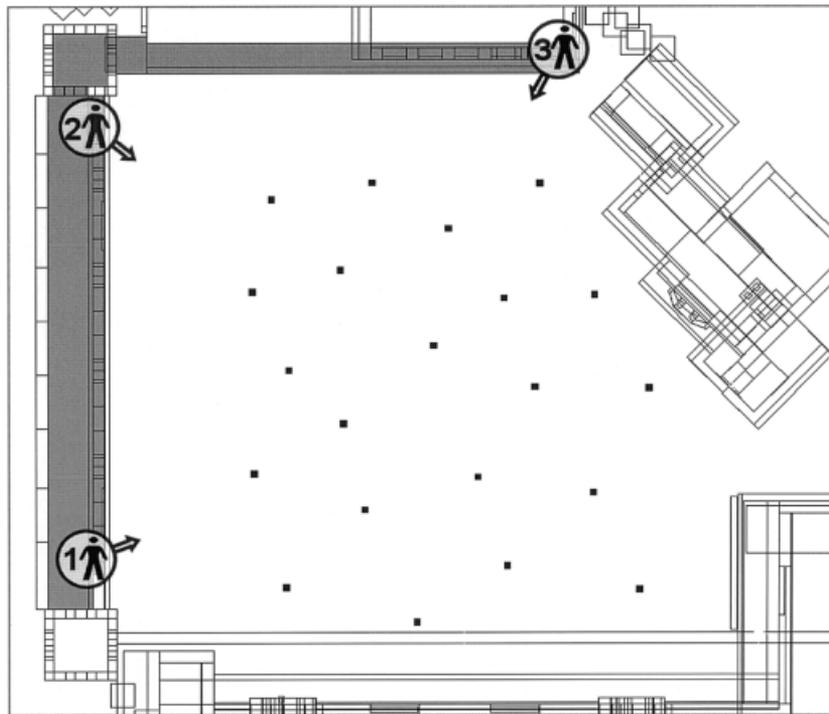
will have a specific deficit in memory for locations defined relative to the environment as opposed to locations defined by their sensory characteristics or by their location relative to the body. We refer to this former type of memory as "allocentric" memory and to the latter types of memory as forms of "egocentric" or "sensory" memory. To distinguish between "allocentric" behavior, directed toward a location in the environment, and "egocentric" or "sensory" behavior, directed toward locations defined by their appearance or position relative to the body at encoding, it is necessary for the subject to move with respect to the environment between encoding and retrieval.

Experiments involving movement of the subject or manipulation of their viewpoint have played an important role in understanding the mechanisms supporting human spatial memory. First, automatic processes may support the accommodation of a change of viewpoint within one's mental representation of object locations. Wang and Simons (1999) showed that subject's recognition memory for an array of objects on a circular table top was better after the subject had moved around the table to a new viewpoint than after an equivalent rotation of the tabletop. This was

interpreted as evidence for an automatic updating process driven by the active motion of the subject. A replication of this result using purely visual virtual reality (Christou and Bulthoff, 1999) indicates that the important variable is movement of view-point relative to the subject's cognitive model of the world rather than actual movement and the attendant vestibular/proprioceptive feedback or movement of the objects relative to the subject. Second, when subjects are shown a scene of scattered objects from one viewpoint and given a recognition memory test using scenes from a second viewpoint, their response latencies vary linearly with the angular difference between the views (Diwadkar and McNamara, 1997).

The above results in which subjects or their viewpoints are moved between presentation and retrieval are also found in studies on the effects of imagined movement. Testing memory for spatial locations following imagined movement shows a good chronometric relationship between reorientation distance (either translation or rotation; Easton and Sholl, 1995) and reaction times. Increased response accuracies have also been reported in memory for locations from new imagined points of view that are aligned with environmental landmarks (Shelton and McNamara, 2001; McNamara et al., 2002; Mou and McNamara, 2002). Note that none of these results is simply analogous to the type of mental rotation found in recognition of single objects (Shepherd and Metzler, 1971). Indeed, paralleling the results of Wang and Simons for actual movement, memory for the locations of objects in an array is superior following imagined movement of the viewer than following an equivalent imagined movement of the array (Wraga et al., 2000). Only when a single location from the array needed to be rotated did performance or latencies for imagined array-rotation approach that for imagined movement of the viewer. Thus we see again that movement of viewpoint relative to the subject's cognitive model of the world is privileged relative to movement of the objects within it. Note that these results hold whether or not the actual world is visible: subjects performing imagined movements are typically blindfolded, and Simons and Wang (1998) found the same advantage for view-point movement when subjects were tested in a dark room, using phosphorescent objects.

In the present study, we use a virtual environment (Figs. 2, 3) to test memory for object location in two conditions, one involving movement of the subject between encoding and retrieval and the other not. On each trial a number of objects were presented sequentially in different locations within an enclosed courtyard while the subject watched from a given vantage point. Subsequently, the subject was required to recognize the objects' locations when viewed either from the same viewpoint or from a different, shifted, viewpoint (Fig. 3). The two retrieval conditions were interleaved across trials in random order. In the same-view condition the object location could be remembered relative to the virtual environment (allocentric memory), or relative to the subject, the frame of the video display unit, or the perceptual features of the display as seen from that view (all forms of egocentric or iconic memory). In the shifted-view condition, using any of the latter forms of memory would leave the subject severely disadvantaged compared with using allocentric memory.



**FIGURE 2.** Plan view of the virtual town square. Shaded areas represent places the subject was able to traverse. The three viewpoints are marked (1, 2, and 3; with 2 used only during testing, not at presentation), with arrows showing the direction of view. Small squares mark the positions of placeholders on which objects were presented.

We reasoned that Jon should have preserved egocentric or iconic memory performance but impaired allocentric memory. The preserved egocentric memory should support some ability to recognize object locations in the same-view condition, but not in the shifted-view (allocentric) condition. In addition, the use of virtual reality makes recording response latencies straightforward, to allow some insight into the processes supporting these behaviors.

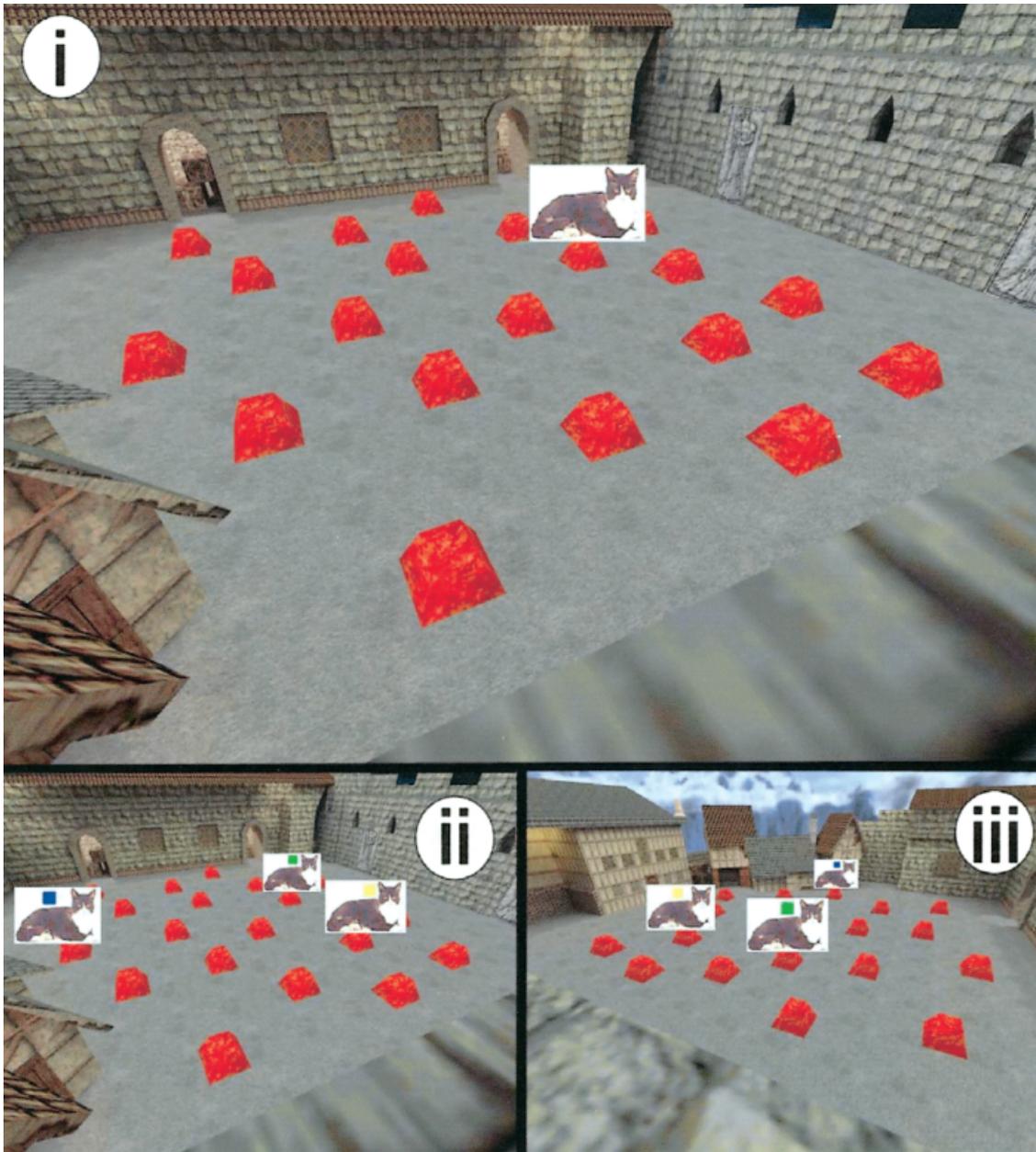
## MATERIALS AND METHODS

### Subjects

Jon shows bilateral hippocampal pathology due to perinatal anoxia (Gadian et al., 2000; Vargha-Khadem et al., 1997). Neuropathological assessment of Jon was done using MRI volumetric measurement (Van Paesschen et al., 1997), T2 relaxometry and proton magnetic resonance spectroscopy ( $^1\text{H}$  MRS) (Vargha-Khadem et al., 1997; Gadian et al., 2000). Volumetric assessment found the hippocampi to be reduced in volume by 50% along the length of both (Fig. 1). Relaxometry showed elevated hippocampal water volumes bilaterally, suggesting disruption of remaining tissue. However, there are also indications from functional MRI that this tissue may be functional (Maguire et al., 2001).  $^1\text{H}$  MRS examined a  $2 \times 2 \times 2$  cm area including hippocampal and surrounding tissue, and found neural cell to other cell intensity signals

were normal on the left and near normal on the right, suggesting that tissues around the hippocampi are uncompromised. A more recent analysis of MRI data using voxel-based morphometry of Jon and four other patients who had suffered perinatal or infantile hypoxic-ischemic incidents (Gadian et al., 2000) confirmed that, within the temporal lobes, the damage is confined to the hippocampi. Outside the mediotemporal lobes in this group there was also reduced gray matter density in the putamen and ventral thalamus bilaterally.

Jon was aged 22 at time of testing. His IQ was assessed with the WAIS-R test at age 19 (full-scale IQ 114; performance IQ 120; verbal IQ 108) and performance IQ tested at age 22 using Ravens Advanced Matrices Set I (90th percentile). He regularly plays video games using first-person perspective virtual reality. Two groups of 12 male control subjects were recruited for each of the two behavioral experiments, and a group of 24 male control subjects were recruited for the response latency study (Fig. 6b). All groups were matched for age and performance IQ (PIQ, estimated using the NART and the short form of Ravens Advanced Matrices Set I). For the behavioral data shown in Figure 6a, the values were as follows: mean age: 21.8, range 19–26 years; NART-PIQ: mean 113.8, SD 7.1; Ravens PIQ: mean: 76.7th percentile, SD 18.3%. For the behavioral data shown in Figures 4, 5a, and 5b, the values were as follows: mean age: 20.9, range 20–22 years; NART-PIQ mean 109.6, SD. 12.6 Ravens PIQ: 86th percentile, SD 8.0%. For the response latency data in Figure 6b, the values were as follows: NART-PIQ mean 110.8, SD 5.7 Ravens PIQ: 78th percentile, SD



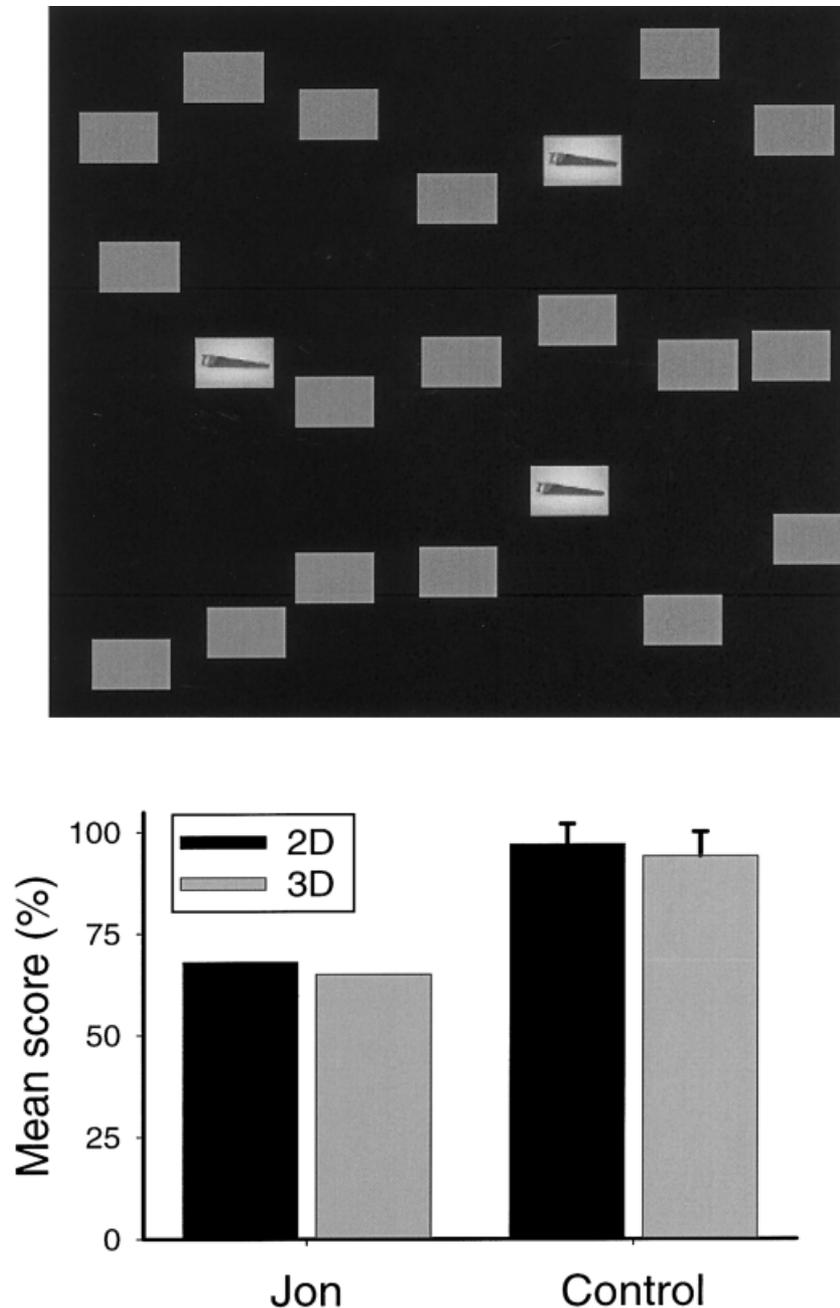
**FIGURE 3.** Views of the virtual environment during presentation of a typical item from location 3 (i) and testing from the same view (ii, location 3) and an alternative view (iii, location 1). Note the red and white marker in panel (iii) showing the original viewing location during the testing phase.

22.1%. Informed consent for Jon's participation was obtained in accordance with guidelines set by the Great Ormond Street Hospital for Children and the Institute of Child Health Ethics Committee. All control subjects gave their informed consent in accordance with the UCL/UCLH Ethics Committee.

### Computerized Tests

The virtual environment (VE) in this study was implemented using a modified version of the computer game *Quake2* (© Id Software). The modifications allowed timed presentation of ob-

jects and repositioning of the subject's viewpoint. The VE was presented in first-person perspective using an Intel P3 600-MHz computer on a standard 19 inch monitor at a resolution of  $800 \times 600$  pixels and a frame rate of 40 Hz. The environment consisted of a courtyard surrounded on all sides by visually distinct buildings and can be moved smoothly through using the cursor keys on keyboard. Subjects were able to move around the edge of the courtyard at rooftop level, providing a clear view into it and the objects it contained. Inside the courtyard were 21 randomly distributed placeholders, upon which the test stimuli appeared. Subjects were



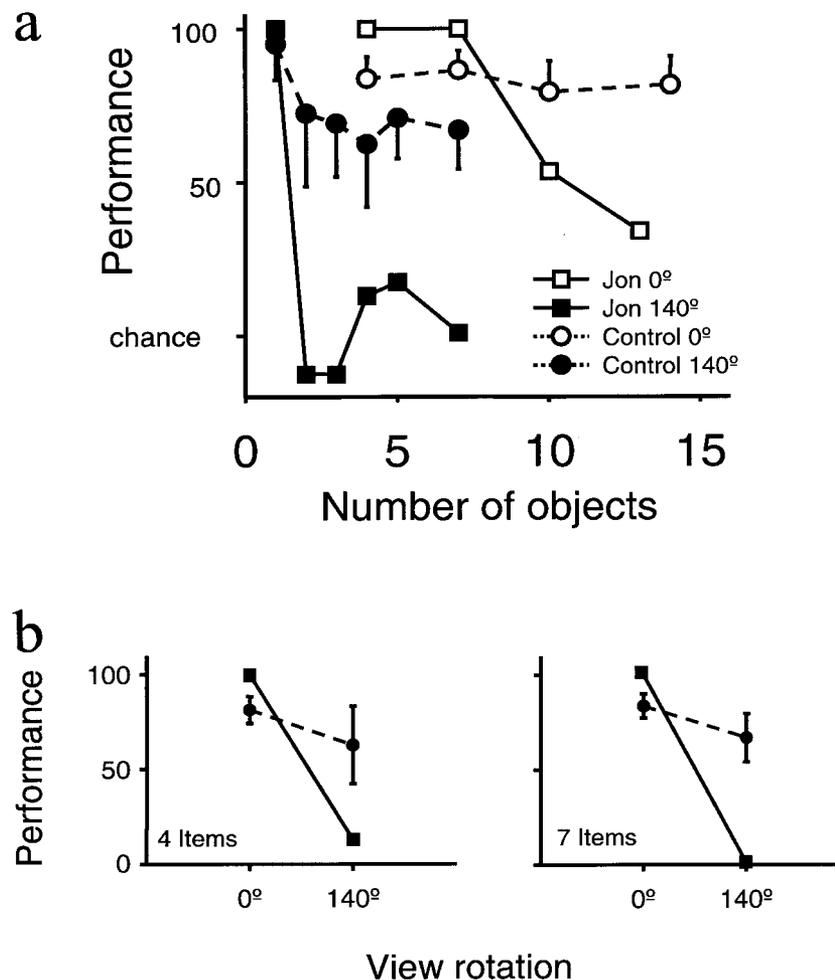
**FIGURE 4.** Performance in the same view condition is equivalent to performance in two-dimensional object location tasks. Upper: The two-dimensional object location task, shown in the testing phase. One of the pictures (of a saw) is in the same location as originally presented, the other two pictures (foils) are in randomly chosen locations. The shaded rectangles are placeholders, three of which are obscured by the objects. Lower: Performance in 2D and 3D. In both

2D and 3D test, ten objects were presented and testing involved forced-choice recognition with 2 foils. In the 3D test, the same view was used for presentation and testing. Control subjects perform near ceiling on both conditions (2-D: mean score = 97%,  $sd = 5\%$ ; 3-D: 94%,  $sd = 6\%$ ), while Jon is equally impaired on both (2-D: mean score = 68%,  $z = 5.7$ ; 3-D: 65%,  $z = 4.8$ ).

initially given a familiarization task in the VE, in which they moved around all of the available viewing areas. Three particular locations were used for presentation and testing purposes, chosen such that moving from one to the other involved a rotation of either 140°, 85°, or 55° in viewing orientation. The corresponding changes in angular position of viewing location about the centroid of the placeholders were 151°, 85° and 66° (the slightly different

sets of angles occur because views were not centered on the centroid of the placeholders due to the necessity of ensuring that all placeholders were visible). See Figures 2 and 3 for further details.

Testing took the following form. Subjects always appeared in the same spot in the VE. One of the presentation positions was marked, and the subject moved to that marker. On contact with the marker, their view was adjusted to a standard orientation from



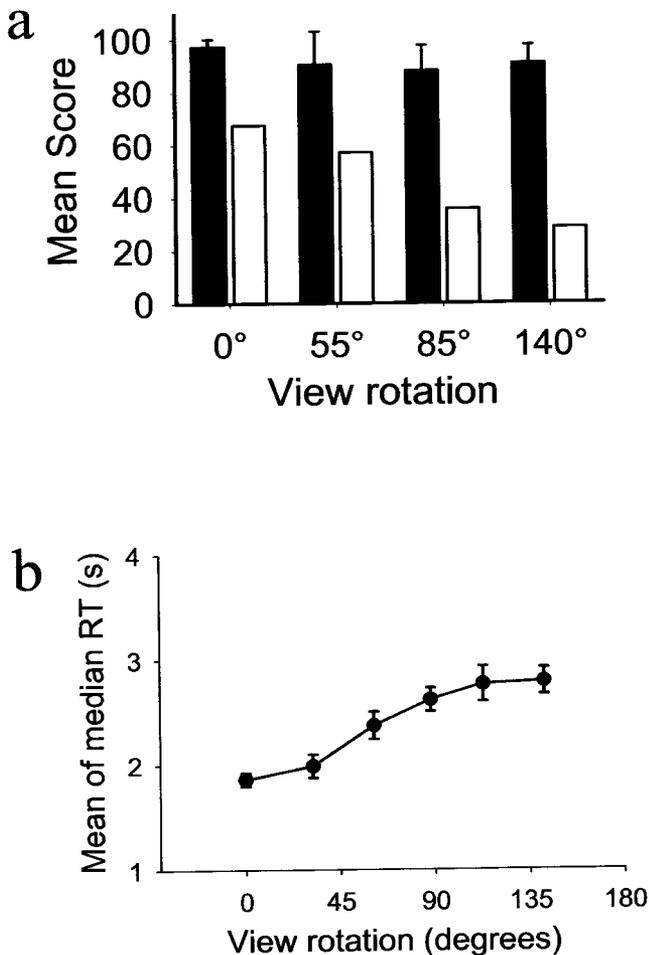
**FIGURE 5.** a: Performance as a function of list length for Jon and controls, testing controls with five foils and Jon with two foils, expressed as a percentage of the range between chance (0) and perfect (100), i.e., percentage correct ( $x$ ) scaled by the level of chance ( $c$ ) using the formula:  $\text{performance} = 100(x - c)/(1 - c)$ . This allows a clearer comparison between Jon and controls, for whom the level of chance is

different (33% and 16.7%, respectively). Note that Jon's performance falls to chance for two objects in the shifted-view condition, but remains above chance for at least 13 objects in the same-view condition. b: When compared directly with controls at list length 4 and 7 (dashed lines), Jon's performance on (solid lines) same and shifted views is clearly dissociated. Scores are percentage correct scaled as in (a)

which all placeholders were visible, and presentation began. A number of images of everyday objects were presented in turn for 3s each, with an inter stimulus interval of 1s. Each object appeared over a particular randomly chosen placeholder, each of which was used only once per presentation. The subjects were instructed to name the objects aloud as they appeared, and to remember their locations (Fig. 3). After the presentation phase, memory could be probed from the same viewpoint or from a shifted viewpoint. In shifted-view trials, the subject's viewpoint was changed instantaneously to the new location immediately after the last object had been displayed. After a 5-s pause, during which the place markers were visible in the square, testing began. Memory for the locations of the objects was tested in random order:  $N$  copies (where  $N = 3-6$ ) of the object to be tested were presented, one at its original location and  $N-1$  at foil locations (Fig. 3,  $N = 3$ ). Each object had a different colored square superimposed on it, and responses were made by pressing a colored key on the keyboard corresponding to

the color on the chosen object. Choices and response latencies were logged. Both list length, as well as the number of foils, could be varied to control the difficulty of the task. Subjects were given training, prior to testing, during which they practiced both same-view and shifted-view trials with list-length 5.

The 2-D task was implemented using Microsoft Visual Basic on the same hardware as the VR task. Subjects were presented with 10 pictures of objects one at a time, for 3s each with an ISI of 1s. These could appear on any of 21 randomly scattered placeholders, which were not reused as a target location during that trial. After 10 objects had been presented there was a 5s pause, then the testing phase began. Objects were presented individually in a random order in their original location, along with two identical foils on randomly chosen placeholders. Subjects indicated their choice, and the experimenter triggered presentation of the next object. The procedure was repeated four times, for a total of 40 object-locations probed.



**FIGURE 6.** a: The effect of varying angle of rotation. Jon (white bars) shows greater impairment on the shifted-view conditions of the 3-D object location task than on the same-view. Ten objects were presented in the same-view condition and seven in the shifted view conditions. Testing involved forced-choice recognition with two foils for controls and for Jon. Control subjects (black bars) show slightly greater variation in performance in the shifted-view conditions, but are otherwise unaffected by the view manipulation, possibly due to a ceiling effect. Scores are mean percentage correct, error bars are 1 SD. b: Comparison of response latencies as a function of the change in view orientation between presentation and testing, showing the mean and standard error of the median of control subject's raw response latencies. Angles refer to the bearing of the subjects view in the environment (angles of rotation of bearing of view location about the centroid of the placeholders were 0°, 32°, 62°, 90°, 120°, and 152°). Subjects performed six trials of each rotation, three clockwise and three anticlockwise, and made three responses per trial. There is a monotonic dependence on angle of rotation (Pearson's correlation = 0.444,  $P < 0.001$ ), which is also found individually for the first, second and third responses in each trial (1st response,  $r = 0.437$ ,  $P < 0.001$ ; 2nd response,  $r = 0.316$ ,  $P < 0.001$ ; 3rd response,  $r = 0.389$ ,  $P < 0.001$ ).

## RESULTS AND DISCUSSION

We first attempted to replicate the previously reported 2-D object-location deficit (Vargha-Khadem et al., 1997), and determine how this relates to the same-view condition of our 3-D VR test. Our rep-

lication used 10 objects sequentially presented at locations selected from 21 different possible locations on the screen. Testing involved choosing the object in the same location as at presentation in the presence of two foils (copies of the object in other locations) (Fig. 4). In line with (Vargha-Khadem et al., 1997), we found a mild impairment in this task, and found identical performance of both Jon and control subjects in the same-view condition of our virtual town square test run with the same number of objects, locations, foils, and timing.

We next compared the same-view and shifted-view conditions. Because pilot studies indicated that the same-view condition was easier, we attempted to match difficulty across conditions by using 10 items in same-view trials, versus 7 items for shifted-view trials. In the testing phase, two foils were used for all subjects. To keep within a reasonable duration, two viewer locations were used for presentation and three for testing (Fig. 2). Each combination of presentation and testing location was used twice, for a total of 12 trials: 4 same-view trials randomly interleaved with 8 shifted-view trials. Jon was impaired relative to controls in both conditions. However, he performed well above chance on same-view trials (0° shift), worse after viewpoint shifts of 55°, and at chance after viewpoint shifts of 85° and 140° (Fig. 6a). A ceiling effect in the controls' performance prevents us from quantifying the relative difference in performance between the two conditions. This is addressed in the next experiment.

Does Jon have a specific deficit in the shifted-view spatial recognition task over and above his deficit in the same-view task? To test this we needed to reduce controls' performance so that their performance in the same-view condition was equal to or inferior to Jon's, and then compare performance in the shifted-view condition. Pilot studies indicated that performance did not depend strongly on the delay between presentation and recall, leaving list-length and number of foils to be varied. We repeated the experiment, with Jon tested with two foils and control subjects with 5. List-lengths were also varied, with longer lists being used in the easier same-view condition (trials of 4, 7, 10, and 13 objects), and shorter lists in the shifted-view condition (trials of 1, 2, 3, 4, 5, and 7). Note that list lengths 4 and 7 were used in both conditions to permit direct comparison. To maximize sensitivity only one viewpoint shift was used (140°; between locations 1 and 3 in Fig. 2).

The second experiment revealed a massive deficit in Jon's allocentric spatial memory. The controls no longer performed at ceiling on the same-view task but continued to perform slightly worse in the shifted-view condition at comparable list lengths (Fig. 5a). By contrast, Jon's performance is strikingly different between conditions. Tested from the same view, his performance is at ceiling and equal to or better than controls up to 7 items, begins to fall off for longer lists, and is still above 50% at 13 items (i.e., he has a memory span of at least 13). From the shifted view, however, he only performs above chance when there is a single object to remember (i.e., a memory span of 1). Direct comparison between Jon's performance and that of the controls at list lengths of 4 and 7 shows a clear dissociation, with Jon performing better than the controls in the same view condition but markedly worse in the shifted-view condition (Fig. 5b).

The results indicate that Jon has a selective deficit in shifted-view spatial recognition memory over and above his deficit in same-view spatial recognition memory. This is strong evidence for a deficit in allocentric but not egocentric spatial memory, given

that performance in the shifted-view condition necessarily reflects allocentric memory while that in the same-view condition could reflect either egocentric or allocentric memory.

Does John also have a deficient egocentric spatial memory? In both experiments, Jon performed significantly worse than controls on the same-view condition at list lengths 10 and above. Our interpretation is that controls can use both egocentric and allocentric systems, whereas John has only the egocentric one. This suggests that the allocentric system can act in parallel to the egocentric one, but can store more locations or store locations for longer. This may reflect its ability to store a single, amalgamated, representation of the environment and the locations of all the objects presented in a single trial, rather than relying on sensory snapshots of the presentation of each object (Burgess et al., 1999; see also Milner et al., 1999; Wang and Spelke, 2000). This would explain Jon's increasing impairment with increasing list length, and implication of the hippocampus in spatial tasks that are not necessarily allocentric but involve delays or long lists. This interpretation makes the interesting prediction that there would be no difference in performance between Jon and controls on a pure egocentric task in which allocentric information was of no use.

What processes are involved in solving the shifted-view spatial memory condition? To investigate this, we looked for evidence of a chronometric relationship between the angle or distance between presentation and retrieval positions and the latencies of correct responses. We first examined the response latencies of the twelve control subjects in experiment 4c. These data did not show a linear relationship between response latencies and view rotation (Pearson's correlation = 0.08,  $P = 0.64$ ). However, this experiment included only changes in view orientation of 0°, 55°, 85°, and 140°, (corresponding to changes of location of 0, 66, 85, 151 in the bearing of the view location about environmental centroid, or changes of 0, 36.4, 39.1, and 55.1 virtual meters), and the 55° and 85° rotations occurred on different sides of the environment (between locations 1 and 2, and between locations 2 and 3, respectively), and so are confounded by perceptual differences. Accordingly, we performed a further experiment, designed to be more sensitive to trends in response latencies. This experiment involved twenty four control subjects, list length 4 (to maximize the numbers of correct responses), two presentation locations (locations 1 and 3; Fig. 2) and six testing locations: locations 1 and 3 in Figure 2 and four more locations spread evenly between them. The results show a clear correlation between response latency and the size of the change in view orientation, both overall and individually for the first, second and third responses per trial (Fig. 6b).

The response latency data imply that controls' performance of the (allocentric) shifted viewpoint recognition memory task involved an imagined movement between the subject's viewpoint relative to the array of locations. This could be either (1) a movement of viewpoint around the array of locations-to-choose-from at retrieval to bring it into correspondence with a stored representation of the object's location at presentation, (2) a movement of viewpoint within a stored representation of the object's location at presentation to bring this into correspondence with the locations-to-choose-from at retrieval, or (3) a rotation of the array as seen from a fixed viewpoint. The first two possibilities would view Jon as having an impaired ability to update locations to reflect an imagined movement of viewpoint. In case (1), this deficit would

apply to locations in the perceived world, while in case (2) it would apply to remembered locations. The last possibility (3) would view Jon as being incapable of rotating arrays of objects. We note that all of these processes can also be seen in terms of the allocentric and egocentric systems interacting to help reorient the subject to the new perspective (e.g., Hermer and Spelke, 1994) although this would only predict chronometric response times for the first response in each trial. Interestingly Jon was able to perform shifted viewpoint recognition of a single object location successfully. This preserved ability is compatible with his normal performance on tasks of mental rotation (e.g., 27/32 in the Little Man Test (Ratcliff, 1979), which is shared by other bilateral hippocampal (Holdstock et al., 2000b) and unilateral temporal lobectomy (Abrahams et al., 1997) patients. It may also relate to the fact that, when only a single location is tested, imagined rotation of an array can be almost as accurate as an equivalent imagined movement of viewpoint (Wraga et al., 2000). We conclude that Jon has a preserved ability to rotate single objects from a fixed viewpoint, but not to perform imagined movements of viewpoint.

In addition to the processes of viewpoint movement, discussed above, comparison between a stored viewpoint-dependent (i.e., egocentric or iconic) representation of presentation and the array of locations presented at retrieval is required, under conditions in which one or other has been subjected to a movement of viewpoint. Impairment to the processes of storage and comparison themselves cannot explain the difference in performance between same-view and shifted-view conditions. However, it could be that Jon's deficit arises from the nature of the stored representation being unable to support the 3-D change in viewpoint which requires knowledge of the objects' locations. For example this would be true of iconic sensory-bound "snapshot" like representations, which we think Jon can store successfully (Spiers et al., 2001a). An additional consideration is that, since the objects in a trial are presented sequentially, representations of their egocentric locations would each have to be stored and manipulated individually, imposing a high memory load for long lists. Thus another process likely to aid performance would be the amalgamation of egocentric representations into a single enduring representation that is orientated along the viewpoint at presentation. Again, Jon's deficit might arise from an impaired ability to form such a representation insofar as such a representation was required to support movements of viewpoint.

Thus, the hippocampus appears to support the creation or storage of representations of location within which 3-D movements of viewpoint are possible, or supports the processes of performing those movements of viewpoint themselves. As such, it provides a mechanism that supports allocentric memory: enabling viewpoint independent behavior, despite relying on viewpoint-dependent (i.e., egocentric) representations. Interestingly, Jon may have some insight into his inability to deal with shifted-viewpoints. In a pilot experiment in which subjects moved freely between the presentation and retrieval locations, Jon, but not control subjects, stopped frequently to look back at how the array altered as he moved (this strategy proved unsuccessful for the 7-item lists tested).

Previous studies have implicated the medial temporal lobes (particularly in the right hemisphere) in various tasks requiring memory for object locations (Smith and Milner, 1981; Smith et al., 1995; Abrahams et al., 1997; Bohbot et al., 1998; Abrahams et al.,

1999 Holdstock et al., 2000b), landmarks (Habib and Sirigu, 1987), spatial scenes (Pigott and Milner, 1993) and spatial navigation (Maguire et al., 1998). Many of these impairments likely reflect damage outside the hippocampus, e.g., recognition of scenes or landmarks (Habib and Sirigu, 1987; Aguirre and D'Esposito, 1997; Epstein and Kanwisher, 1998) and navigation in very simple environments (Bohbot et al., 1998), consistent with Jon's unimpaired recognition of visual scenes (Spiers et al., 2001a). The impairments in the studies involving long delays, large numbers of locations and movement of the subject likely reflect hippocampal damage, consistent with the impairments and interpretation presented here. Of these studies, only (Holdstock et al., 2000b) explicitly compared memory for a single location from a shifted viewpoint with that from a fixed viewpoint. In their study, a patient with hippocampal damage was found to have a greater impairment in the shifted viewpoint condition. Again, this is consistent with our interpretation. However, in the study conducted by Holdstock et al., the difference in performance between the conditions was delay dependent (only approaching significance after 20- or 60-s delays) and depended in part on the performance of control subjects showing greater variance in the fixed viewpoint condition (performed in the dark) than in the shifted viewpoint condition (performed in the light).

Our results are consistent with the proposed role of the hippocampus in supporting a cognitive map (O'Keefe and Nadel, 1978). In addition, our results indicate that the allocentric behavior supported by the hippocampus in this experiment is achieved by mental movements of viewpoint within 3-D space applied to viewpoint-dependent (i.e., egocentric or iconic) representations (as suggested by O'Keefe, 1993). We note that the idea of a "flexible relational" memory system (Cohen and Eichenbaum, 1993) encompasses all of the spatial characteristics of a cognitive map, and many other nonspatial behaviors (transitive inference, Bunsey and Eichenbaum, 1996; social transmission of food preferences, Bunsey and Eichenbaum, 1995). This theory is thus equally compatible with our results, and cannot be distinguished from the cognitive map theory on the basis of tests using spatial paradigms. However, perhaps because of its generality, the "flexible relational" idea does not help to provide a mechanistic understanding of the cognitive processes underlying our result. By contrast, the consideration of viewpoints within spatial reference frames suggested by the cognitive map provides the basis for our current interpretation of these processes. In terms of Jon's nonspatial behavior the flexible-relational hypothesis can also be argued to be consistent with Jon's spared recognition and impaired recall (Baddeley et al., 2001), although this goes against the initially close link between relational memory and "declarative" memory (e.g., Eichenbaum et al., 1996; Squire, 1992) and is less consistent with Jon's relatively preserved and fluently expressed semantic knowledge. It is worth noting also that our results are not simply predicted as a consequence of Jon's acknowledged episodic memory deficit. Retrieving the event of an object's presentation corresponds at least as well to the fixed view condition as to the shifted-view condition. Conversely, it may be profitable to investigate the deficit in episodic recollection in terms of the spatial constraints that might apply to the retrieval of information relating to personally experienced events. One possibility is that the hippocampal system constrains

the set of information retrieved or reconstructed from memory to be consistent with perception from a single position. In this case, where multimodal information is retrieved, the information from each modality must be constrained to be consistent with perception from the same single position as applies to the other modalities. A second, related, possibility is that the hippocampal system allows the search through sets of retrieved information consistent with perception from positions defined by bodily movements from other, well-remembered, positions (Burgess et al., 2001; Burgess, 2002). In this case, the time taken to perform the movement may be reflected in response times. By focusing on the spatial domain we have attempted to provide specific mechanistic constraints on a subset of Jon's impairment. We hope this will provide a step toward understanding the processes underlying the more general relational, declarative, or episodic characterizations of his impairment that are not addressed in the present report.

In summary, we have demonstrated a massive impairment in recognition of object locations when viewpoint is shifted between presentation and testing compared with when it is not (e.g., memory span falls from at least 13 to 1) in a patient with focal hippocampal pathology. Our findings have at least two more general implications. First, they provide a well-controlled test that is extremely sensitive to hippocampal pathology. Given Jon's 50% reduction in hippocampal volume and much milder mnemonic impairment than patients of other etiology (Rempel-Clower et al., 1996; Zola-Morgan et al., 1986) the size of his impairment in our task implies that it might detect much milder hippocampal pathology, such as that shown early in Alzheimer's disease (e.g., Fox et al., 1996) or preterm children (Isaacs et al., 2000). Second, the very selective impairments in recognition memory in these patients may hold important clues for their debilitatingly severe impairments across all tests of recollection of episodic memory. This study presents the most severe impairment yet reported in a recognition memory paradigm for these patients. The results hint that episodic recollection might be related to the movement of viewpoint within a stored representation (see Burgess et al., 2001). This in turn might explain why the same anatomical systems (mammillary bodies, anterior thalamus, subicular/hippocampal complex) are involved in both the representation of head-direction (Taube, 1998) and episodic recollection (Aggleton and Brown, 1999).

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