

The Hippocampal Role in Spatial Memory and the Familiarity–Recollection Distinction: A Case Study

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Memory for object locations and for events (comprising the receipt of an object) was tested in a case of developmental amnesia with focal hippocampal damage (“Jon”; F. Vargha-Khadem et al., 1997). Tests used virtual reality environments and forced-choice recognition with foils chosen to equalize the performance of control participants across conditions. Memory for the objects received was unimpaired, but the context of their receipt was forgotten. Memory for short lists of object locations was unimpaired when tested from the same viewpoint as presentation but impaired when tested from a shifted viewpoint. Same-view performance was disrupted by changing the background scene. These results are consistent with Jon having preserved matching to fixed sensory-bound representations but impaired reconstructed or manipulable representations underlying shifted-viewpoint recognition and episodic recollection.

The hippocampus plays a crucial role in memory, and damage to it and related systems is central to the amnesic syndrome (Scoville & Milner, 1957). However, the precise form of its contribution to memory remains controversial. Perhaps the most reliable impairments associated with hippocampal damage concern delayed recall of test stimuli (see, e.g., Spiers, Maguire, & Burgess, 2001, and below). Deficits have also been noted in spatial navigation, paralleling the effects of hippocampal lesions in other mammals (see, e.g., Burgess, Maguire, & O’Keefe, 2002). Here we review and extend results in a patient with focal, but not necessarily complete, hippocampal damage in whom these deficits contrast with preserved functioning across many recognition memory paradigms. We investigate his tightly circumscribed deficits in recognizing spatial information, in the hope that they will illuminate the basic processes whose impairment might lie at the root of the more general deficiency in episodic recollection and navigation.

Episodic Memory

The ability to recollect personally experienced events has been termed *episodic memory* (Tulving, 1972, 1983). It has often been operationally defined as *context-dependent* memory (i.e., memory of an event in which the context of the event can also be recalled), and some authors also stress the vividness and detail of reexperiencing the event as a defining feature (Tulving, 2001). An *event* may be defined as a discontinuous change in some aspect of the world and the *context* as the remaining unchanged aspects of it. Episodic recollection can be contrasted with (at least) three other forms of memory: semantic memory, or noncontextual knowledge for facts; procedural memory, or the knowledge of how to do

things; and the ability to recognize the familiarity of a stimulus. Of these distinctions, we focus here on the distinction between context-dependent event memory and familiarity-based recognition. When tested within the recognition memory paradigm, this distinction is related to that made between associative recognition and item recognition (Yonelinas, 2002).

We assume, on one hand, that episodic recollection, in which detailed contextual information can be reconstructed from an impoverished cue, includes processes tested by context-dependent or associative recognition. On the other hand, we assume that familiarity-based recognition simply requires the detection of the strength of the match between a test stimulus and some stored representation of it (Bogacz & Brown, 2003; O’Reilly & Norman, 2002; Tulving, 2001; Yonelinas, 2002). Thus, familiarity-based recognition would be sufficient to enable a person to say which of two items was familiar but would not be sufficient for that person to say which of two equally familiar items had been received in a particular context. By contrast, episodic recollection would be sufficient for either task. The presence of these two separate processes has also been identified in behavioral responses in terms of the typical pattern of errors created when using each process (Yonelinas, 2002) and the subjective reports of confidence or of remembering versus knowing (Gardiner & Java, 1993; Knowlton & Squire, 1995; Tulving, 1993). Neuropsychological evidence from amnesic patients is mixed, but in a recent review, Rugg and Yonelinas (2003) concluded that clinical data support the dual process model, suggesting that although familiarity is commonly impaired in amnesic patients, recollection is disrupted to a greater degree.

A role for the hippocampus specific to episodic recollection, as opposed to familiarity-based recognition or semantic memory, has been proposed by many authors (Aggleton & Brown, 1999; Baddeley, Vargha-Khadem, & Mishkin, 2001; Fortin, Agster, & Eichenbaum, 2002; Kinsbourne & Wood, 1975; Mayes et al., 2001; O’Keefe & Nadel, 1978; Vargha-Khadem et al., 1997; Yonelinas et al., 2002). One specific hypothesis along these lines posits that a system including the medial thalamus and perirhinal cortex, but not the hippocampus, supports familiarity-based recognition, whereas a complimentary system including the mammillary bodies, anterior thalamus, and hippocampus supports episodic recollection (Aggleton & Brown, 1999; Delay & Brion, 1969;

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Gaffan & Parker, 1996). There are several alternatives to this position that suggest a more general memory function, many of which are closely related and none of which are entirely mutually exclusive (see, e.g., Burgess, Becker, King, & O'Keefe, 2001; Mayes & Roberts, 2001, for reviews). Among the most prominent are the ideas that the hippocampus is involved in all forms of explicit or declarative memory, including familiarity-based recognition and semantic memory (Squire & Zola-Morgan, 1991); that the hippocampus is involved in supporting flexible relational associations, including tasks such as transitive inference (Eichenbaum & Cohen, 2001); and that the hippocampus supports the cross-modal association of stimuli represented in different brain areas (Alvarez & Squire, 1994; Marr, 1971; Mayes et al., 2001; McClelland, McNaughton, & O'Reilly, 1995; McNaughton & Nadel, 1990; Rolls, 1996).

The precise nature of the impairment caused by damage to the human hippocampus is a topic of much current research. A review of the literature regarding amnesia related to hippocampal damage (Spiers, Maguire, & Burgess, 2001) indicates a clear role in anterograde episodic memory deficits. Hippocampal damage is also associated with retrograde deficits, although their nature and temporal extent are less clear, and the hippocampal role in familiarity-based recognition and semantic memory remains controversial, with more or less involvement reported across different patient groups. The controversy over the hippocampal role in recognition memory extends into the literature on the effects of lesions in monkeys, although it does appear that the deficits that are due to hippocampal lesions are at least smaller than those that are due to perirhinal lesions (Baxter & Murray, 2001; Squire & Zola-Morgan, 1991).

Spatial Memory

It is widely agreed that the hippocampus is required for spatial navigation in animals such as rats, specifically in situations in which following or approaching a simple sensory stimulus or a well-learned route is not sufficient to solve the task (Morris, Garrud, Rawlins, & O'Keefe, 1982; O'Keefe & Nadel, 1978; Pearce, Roberts, & Good, 1998). These types of behaviors can be categorized in terms of relying on an *allocentric* system that can provide a record of an object's location relative to other objects, features, or landmarks in the environment. This contrasts with the many types of behavior for which *egocentric* systems would suffice, providing a record of an object's location relative to some part of the body (retina, head, trunk, etc.; O'Keefe & Nadel, 1978). Evidence has also implicated the human hippocampus in similar spatial behaviors (Abrahams, Pickering, Polkey, & Morris, 1997; Ghaem et al., 1997; Hartley, Maguire, Spiers, & Burgess, 2003; Maguire et al., 1998; Spiers, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001). Although the hippocampal involvement in these tasks is not controversial, different authors chose different interpretations of it. Some authors saw this type of spatial navigation as a specific example of their more general models of memory function: for example, declarative memory (Squire & Zola-Morgan, 1991), flexible-relational (Eichenbaum & Cohen, 2001) or cross-modal associations (Mayes et al., 2001), or episodic memory (Fortin et al., 2002). Other authors saw this type of spatial navigation as a separate function of the hippocampus in its own right (Aggleton & Brown, 1999) or as a primary function that has been

augmented, in humans, by the addition of temporal and linguistic inputs to support the spatiotemporal or narrative context of events (O'Keefe & Nadel, 1978).

Here we specifically consider tests of object-location memory in which the participant's viewpoint is changed between presentation and test (*shifted-view* tests) compared with tests of object-location memory in which the viewpoint remains the same (*same-view* tests). Although either egocentric or allocentric systems would be sufficient to solve a same-view test, a shifted-view task would require an allocentric system for its solution. In recent work (King, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2002), we found a specific deficit in shifted-view object-location memory compared with same-view object-location memory in a developmental case of focal hippocampal damage (see Experiment 2 below). We note that an allocentric system might take several different forms. One form might involve storing an association of the object's location to its environmental context, whereas another might involve reconstruction of the location of the object relative to the current viewpoint by mentally simulating the effect of movement of viewpoint on a stored representation specific to the viewpoint at presentation.

The spatial analysis of the contribution of egocentric and allocentric processes to same- and shifted-view tasks has interesting parallels with the above analysis of the contributions of familiarity and recollection to the tasks of item recognition and context-dependent or associative recognition. In both cases one of the memory tasks (same-view object location; item recognition) can be solved by both postulated processes (egocentric and allocentric; familiarity and recollection), whereas the other memory task (shifted view; context dependent) can be solved by one process (allocentric; recollection) but not the other (egocentric; familiarity). Indeed, there is a direct link between the egocentric and familiarity processes: If the same visual scene is used at test as at presentation, then a process of familiarity-based recognition acting on any egocentric visual or motoric representations of location could be used to solve the task. However, if a shifted viewpoint is used, this will not be the case, and performance will rely on allocentric processes. As noted above, these processes might involve associations between objects and their spatial context or reconstructive processes associated with manipulations of viewpoint. In this article, we explore the nature of these processes in more detail and investigate how they relate to more general context-dependent recognition memory and, finally, episodic recollection.

Jon: A Case of Developmental Amnesia

Jon, who has developmental amnesia, is a prototypical example of the type of patient supporting the hypothesis that the hippocampus is specifically involved in episodic memory and spatial navigation, with, at most, a lesser involvement in semantic and familiarity-based recognition memory. Jon suffered perinatal anoxia and shows a reduction of hippocampal volume of about 50% bilaterally with apparently preserved surrounding cortical tissue (Baddeley et al., 2001; Gadian et al., 2000; Schoppik et al., 2001; Vargha-Khadem et al., 1997). He presented with three types of memory impairment: episodic (forgetting what he had done that day, holidays, conversations, etc.); temporal (forgetting regularly scheduled appointments and events); and spatial (being unable to find his way around, forgetting where he put things; Vargha-Khadem et al., 1997). Neuropsychological investigation showed a deficit in

delayed recall in all episodic tasks compared with a relative preservation of semantic knowledge and good performance in recognition memory (Vargha-Khadem et al., 1997). Two relatively minor impairments in recognition memory were reported involving memory for 20 object–location pairs and memory for 20 voice–face pairs. Jon’s spatial processing, as measured by standard neuropsychological tests, was good: Corsi Blocks task (B. Milner, 1971) score (7 forward, 8 backward), Warrington’s (1996) Topographical Recognition Memory Test (25/30), and Ratcliff’s (1979) Little Man Test (26/32) were all at or above average. His performance IQ was also above average (120 tested at 19; Ravens Advanced Progressive Matrices I [Ravens, 1965], 11/12, which is equivalent to an IQ of 120 when tested at 22).

To test the accuracy of Jon’s navigation we designed a small town using virtual reality (VR), making use of a video game (Duke Nukem, 3D Realms Entertainment, Dallas, TX). Jon is an experienced video game player and was able to move through the town with good dexterity. His navigation was very inaccurate, however, as was his map drawing (Spiers, Burgess, et al., 2001), mirroring his impaired recollection. Slightly more surprising, he was impaired at recognizing scenes from the town compared with foils involving rearrangements of the visual textures from the town. This contrasts with his normal performance on recognizing photographed visual scenes in the Topographical Recognition Memory Test (Warrington, 1996). We speculated that the fact that participants would not have studied the exact scenes from the town used as targets, combined with the similarity of the foils, made familiarity-based recognition difficult in our scene-recognition test and that control participants, but not Jon, could make use of their knowledge of the town’s spatial layout to solve it.

Baddeley and colleagues (2001) followed up the dissociation between Jon’s impaired recall and spared recognition distinction, showing the same pattern in the difficulty-matched Doors and People Test (Baddeley, Emslie, & Nimmo-Smith, 1994). We note again that Jon’s spared recognition memory is characteristic of some other patients with hippocampal damage, but by no means all such patients. Although a cohort of similar developmental cases (Vargha-Khadem, Gadian, & Mishkin, 2001; Vargha-Khadem et al., 1997), adult anoxic cases (Yonelinas, 2002), and a case of adult-onset hippocampal damage (Holdstock et al., 2000) have shown impaired recollection but spared recognition, many cases of presumed hippocampal damage in adulthood do not (Manns & Squire, 1999). The causes of these different patterns of impairment are not yet understood. Two related possibilities are that impaired recognition arises from covert damage to cortical tissue surrounding the hippocampus or that spared recognition results from the presence of some preserved hippocampal function. This latter possibility requires explanation of why any preserved hippocampal function should result in spared recognition but not recall and highlights the need to control for any effects of difficulty that might provide such an explanation. Here we focus on the deficits present in the generally preserved recognition memory of patient Jon and attempt to control for effects of difficulty. If we can characterize the basic mechanisms impaired even within the recognition paradigm in which Jon generally performs well, this might lead us to the basic processes in which failure lies behind the more general impairment in recollection shown by Jon and by the other more globally amnesic cases.

Forced-Choice Recognition Tests of Memory in a VR Environment

We designed a series of tests to manipulate the use of familiarity-based recognition versus context-dependent retrieval processes (or associative recognition; Yonelinas, 2002) within the same forced-choice recognition paradigm. We used these tasks to probe the extent of Jon’s memory deficits further, focusing on retrieval of episodic events—comparing memory for their content with memory for their context—and retrieval of spatial information—comparing memory for object locations from the same view as at presentation with memory from a shifted viewpoint.

We first developed an episodic memory test within the VR town, in which participants follow a path, meeting virtual characters in different places and receiving a different object each time, for a total of 16 objects. Context-dependent memory for each event (the receipt of an object) was tested by presenting 2 of the received objects next to a location and a character and asking which object had been received in that location or from that character, or which had been received first (see Figure 1). Recognition of the familiarity of an object was tested by presenting a received object and a similar looking foil and asking which had previously been received. Confirming his impaired episodic memory, Jon performed at chance on the context-dependent memory questions but was unimpaired on the object-recognition question (Spiers, Burgess, et al., 2001).

Next, we investigated Jon’s spatial memory within a forced-choice VR paradigm (King et al., 2002). In this task, the participant views an array of placeholders, located in a small town square, while looking down (virtually speaking) from the surrounding rooftops. A series of objects appears on random placeholders, and then participants are tested by presenting each object in random order in its original location, along with a number of copies in foil locations (see Figure 2). The task is to identify the one in the correct original location. Between presentation and testing, the subject either remains in the original position or is moved instantaneously to a new location. The difficulty of a condition can be varied with the number of objects and foils.

We tested Jon using two foil objects at random locations. He showed good performance in the same-view condition for short list lengths, with performance reducing from near ceiling to 50% for List Length 10 (chance performance would be 33%). In the shifted-view condition, he performed at chance for all list lengths greater than 1. Although control participants performed much better than Jon in the shifted-view condition, they also showed a ceiling effect in the same-view condition (even at List Length 10), so that Jon’s relative impairment in the shifted-view versus same-view conditions was not clear. Accordingly, we attempted to reduce control participants’ performance overall, by testing them with five randomly placed foil objects. Now, Jon’s differential deficit at shorter list lengths (4 and 7) became clear: He performed significantly worse than controls in the shifted-view condition and performed better than them in the same-view condition. Jon’s impaired performance from a shifted view indicates impaired allocentric memory. By contrast, his relatively preserved same-view performance on short lists could be due to familiarity-based recognition using preserved egocentric representations. The size of the differential deficit on short lists makes the test a potentially powerful indicator of hippocampal damage, given Jon’s generally spared recognition memory.



Figure 1. An example of a test question from the episodic virtual reality test (Experiment 1). All questions took the same form of two objects with a person in a place, differing only in terms of the question asked. In this case, *place* indicates that the participant must choose which object was received in the pictured location. The test materials were prepared so that the contexts and objects were presented in unique combinations, which were different from combinations seen during encoding except for the context–object association being probed.

Current Investigations

One question regarding the interpretation of these findings concerns differences in difficulty within the episodic memory and the spatial memory tasks, as judged by the average scores of the healthy control participants. The object-recognition task was easier than the context-dependent tasks, and the same-view task easier than the shifted-view task. Thus, it is possible that a nonlinear effect of difficulty might be at work, such that Jon's performance falls much more dramatically than the controls' performance as difficulty increases. To rule out this potential alternative interpretation, we attempted to find performance-matched versions of these tasks. For the object-recognition task we made the foil objects more similar to the target, and for the same-view task we made the foil-objects' locations closer to the target location. We present data from Jon and matched controls on the resulting tasks.

In addition, advances in technology meant that it was now possible to have 20 events in our episodic memory task, all involving distinct characters and places (our previous test contained 16 events involving only two characters and two places). Thus, there was less interference between trials and a wider range of contexts, making the events more naturalistic and the memory for them more like autobiographical memory (see the Discussion section in Burgess, Maguire, Spiers, & O'Keefe, 2001).

A second question concerns the specific nature of the representation that Jon uses to solve the same-view task and the specific nature of his problem with the shifted-view task. Although these are both questions for future research, we have begun to pursue some initial hypotheses in these areas. We present data on Jon's performance in a recent test, the pattern of which is informative in guiding our discussion. We hypothesised that Jon might perform the same-view task in one of two ways. He might store object locations as egocentric vectors (as in representations used for reaching or pointing). Alternatively, he might store sensory-bound representations of the scene (or parts of it) suitable for subsequent pattern matching (as in visual snapshots). The former might be thought of as a dorsal stream representation and the latter a ventral stream representation (see Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). A ventral stream process would be consistent with Jon's preserved visual recognition, whereas a dorsal stream process would be consistent with his preserved performance on the Corsi Blocks task. Both processes use egocentric forms of representation. To investigate this, we changed the visual background between presentation and retrieval, but not the locations of the objects (relative to the individual or to the surround of the display). This would disrupt a visual matching strategy because it could not distinguish between foils without a common background but



Figure 2. Examples of encoding (left) and test (right) stimuli from the difficulty-matched town square test (Experiment 2). In the same-view trials (upper panels), the foil objects are distributed randomly around placeholders close to the target location to increase difficulty for this condition. In shifted-view trials (lower panels), the foils are randomly distributed over all placeholders.

would not disrupt a pointing direction strategy that used individual representations of the egocentric direction of each target (e.g., as described in Georgopoulos, Schwartz, & Kettner, 1986).

Method

Experiment 1: Performance-Matched Context-Dependent and Object-Recognition Tests

A new context-dependent memory task was programmed using the video game Unreal Tournament, Version 4.36 (Epic Megagames, Raleigh, NC; King, Hartley, Spiers, Maguire, & Burgess, 2004). Jon (age 25 years for this and the following experiments) and 12 age- and IQ-matched controls (M age = 23.4 years, SD = 2.2; M IQ = 112, SD = 9.2, on Ravens Advanced Progressive Matrices I) were tested. The experiment took place in two phases; first, the participants explored a virtual town, following marked paths to a series of 20 locations in which they were given an object by a virtual person. Then, memory for each of the 20 events was probed in three conditions using visually matched stimuli consisting of two objects and a character in a spatial scene (see Figure 1). In the place condition, subjects had to decide which of the two objects had been seen in the depicted spatial context. The person condition tested the association of objects with characters, independent of location. Last, the object condition presented a previously seen object next to a similar foil to test object-recognition memory. Each test stimulus took exactly the same form as Figure 1, differing only in terms of the question, and the response was always one of the two presented objects.

Experiment 2: Performance-Matched Shifted-View and Same-View Object-Location Tests

We attempted to match the difficulty of the same-view and shifted-view conditions of the object-location memory test (using the Quake engine, Version II; Id Software, Mesquite, TX). Small-scale pilot studies indicated that moderate manipulation of the list length or the delay between presentation and test was not sufficient to match the difficulty of the two conditions. The between-subjects manipulation of the number of foil objects that we used previously (King et al., 2002) suffers from varying the chance level of performance so that a more complex measure than proportion correct must be used to compare performance. By contrast, we found that increasing the proximity of the foil locations to the target location reduced performance. We also found that, in the same-view condition, performance was worse for target locations far from the viewing location. Accordingly, we manipulated the proximity of foil locations to the target location, such that foils were closer to the target in the same-view condition than in the shifted-view condition, and preferentially selected distant target locations in the same-view condition. A pilot study (Trinkler, 2004) with 18 volunteers (M age = 26 years, SD = 4.9; M IQ = 117, SD = 10.4, Ravens Advanced Progressive Matrices I) showed that performance could be approximately matched by restricting the foils in the same-view condition to the nearest five locations to the target, while spreading them evenly over all locations apart from the nearest five to the target in the shifted-view condition (viewpoint separation = 152° ; see Figure 2). In addition, in the shifted-view condition, target locations were uniformly distributed over all plinths, whereas in the same-view condition target locations were selected

on the basis of their distance from the viewing location such that the furthest was 10 times likelier to be selected than the nearest.

Jon and 13 male age- and IQ-matched controls (M age = 23.8 years, $SD = 3.2$; Raven's IQ $M = 120.0$, $SD = 6.1$) were tested. Participants performed four trials each of same- and shifted-view conditions at List Length 3, with four foil objects at testing.

Experiment 3: Changing the Background Scene in the Object-Location Test

To investigate the extent of local visual matching supporting Jon's preserved performance in the same-view condition, we produced a new version of the town square test (as before, using Quake Version II; Id Software) involving two completely new towns (King, Hartley, Maguire, & Burgess, 2004). Geometrically, the two towns were roughly similar, but features and textures were changed, allowing us to introduce a different-town condition in which the egocentric locations of the objects remained the same while the surrounding environment was entirely changed (see Figure 3). Participants were told that in the different-town condition, the objects would "move with them"; this instruction was intended to clarify the task without encouraging any particular strategy. There were two viewpoints in each town, and presentation viewpoint and initial town were counterbalanced across conditions. Using a list length of five items and two foils, 14 male

volunteers (M age = 21.7 years, $SD = 2.4$; Raven's IQ $M = 119.0$, $SD = 9.2$) were tested in the same- and shifted-view conditions, as before, and in the novel different-town condition. Participants were given three practice trials of each condition. They received no feedback regarding their performance until after the experiment was completed. Each condition was performed eight times. In the Results section, we present a comparison of the behavioral data from this experiment with Jon's performance (but note that there was no matching of performance across conditions by varying the proximity of foil and target locations in this study).

Results

Experiment 1: Performance-Matched Context-Dependent and Object-Recognition Tests

Performance was well matched across conditions for the control participants, with mean scores ranging from 83% to 86%. Jon showed a different pattern, however (see Figure 4): He was unimpaired on the object-recognition condition ($z = 0.16$) but showed a borderline impairment in the person condition ($z = 2.00$) and a significant impairment in the place condition ($z = 3.20$).

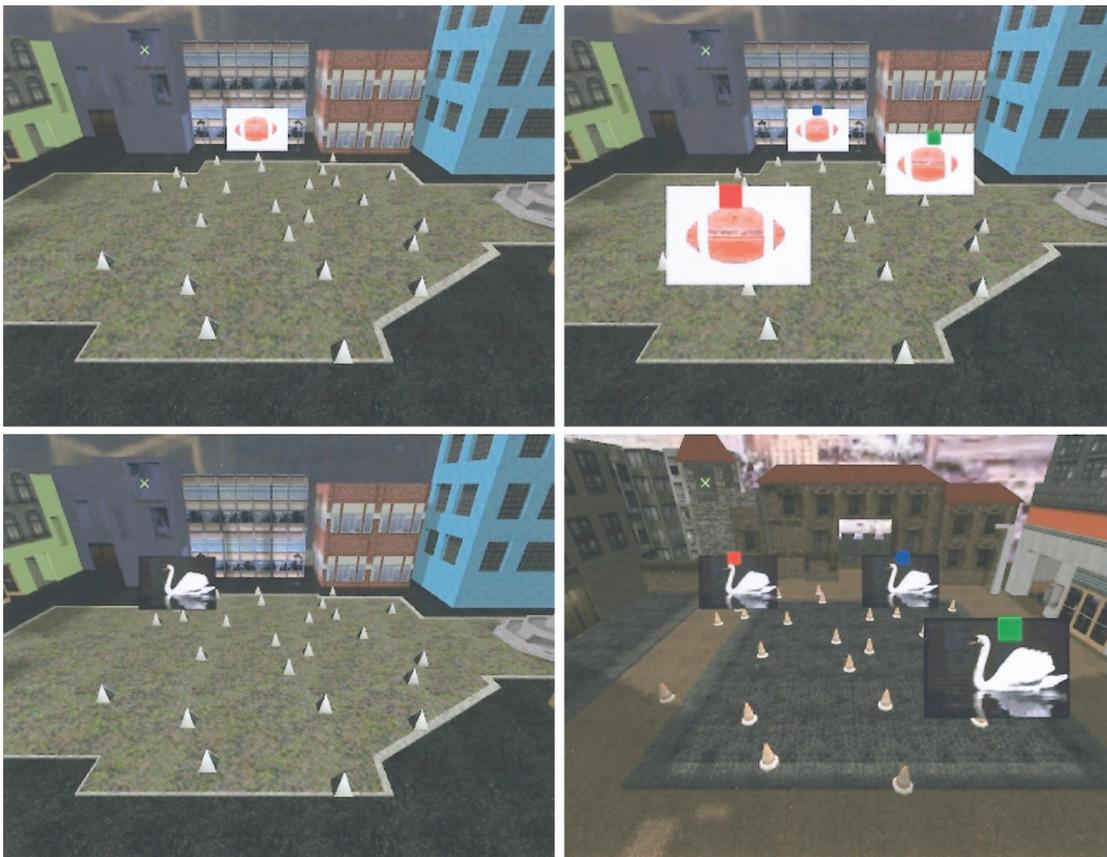


Figure 3. The different-town manipulation of the town square experiment (encoding on the left, testing on the right; see Experiment 3). The upper panels show a same-view trial; Jon's performance was consistent with previous same-view town square results. The lower panels illustrate a different-town trial, in which the targets and placeholders occupy identical egocentric locations but the background scene is changed. Jon's performance on this condition was impaired to a similar degree as his performance on shifted-view tests.

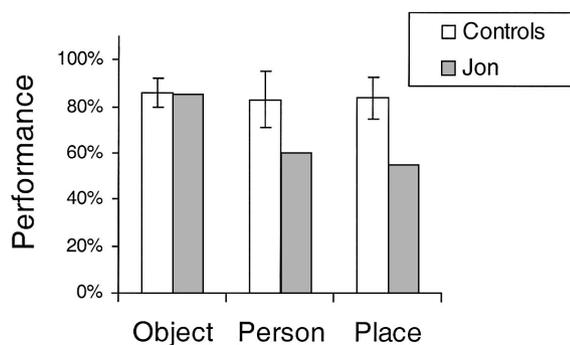


Figure 4. Performance-matched test of recognition of item and context information from events in a virtual reality town (Experiment 1). Patient Jon showed spared memory for the objects received in each event but impaired memory for the context of each event. Columns show Jon's performance and the mean performance of 12 control participants. Error bars show 1 *SD*.

Experiment 2: Performance-Matched Shifted-View and Same-View Object-Location Tests

Volunteers performed the town square test with List Length 3 and four foil object locations. The foil locations were near to the target location in the same-view condition and randomly distributed over the more distant locations in the shifted-view condition. In addition, target locations were uniformly distributed over the plinths in the shifted-view condition, whereas target locations farther away from the viewing position were more likely to be used in the same-view condition. The performance of this participant group in the two conditions was approximately matched in this version of the test (see Figure 5).

The difficulty-matched version of the town square task was used to test Jon and a matched control group. Jon performed slightly better than controls on the same-view trials but much worse on the shifted-view trials (see Figure 6A). When the difference between scores on the two tasks is compared with the mean control difference, Jon's pattern of performance shows a significant impairment on the shifted-view condition ($z = 2.30$; see Figure 6B).

Experiment 3: Changing the Background Scene in the Object-Location Test

The performance of healthy volunteers in this task indicated similar performance on the same-view and shifted-view conditions

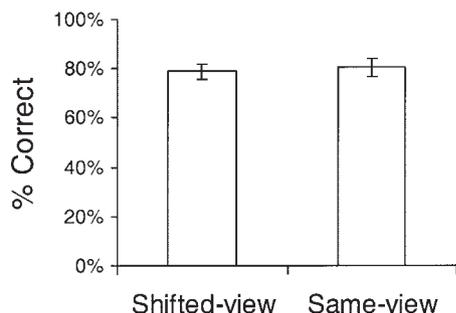


Figure 5. Performance matching between shifted- and same-view conditions of the object-location test (Experiment 2). The proximity of the foil locations to the target location and the distance of target locations from viewer were varied to make the same-view task harder. Columns show mean data from 18 healthy volunteers, List Length 3, and four foils. Error bars show 1 *SEM*.

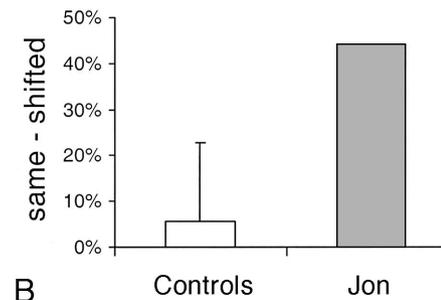
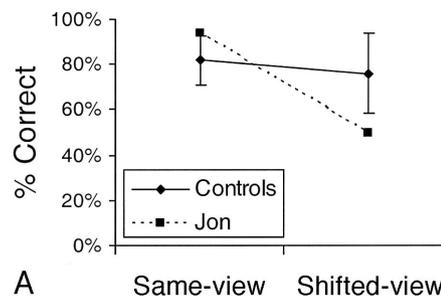


Figure 6. Performance-matched object-location test (Experiment 2). Patient Jon showed a greater decrease in performance in the shifted-view condition compared with the same-view condition than the control group. A: Performance of Jon and mean performance of 13 control participants in the same- and shifted-view conditions (chance is 33.3%). B: Difference in performance between the two conditions. Error bars show 1 *SD*.

in the two new towns, as in our earlier study (King et al., 2002). Performance on the different-town condition was slightly lower than in the same-view condition, with a mean difference of 5.18% (same view: 91.8%; shifted view: 62.9%; different town: 86.6%). Jon's performance in this version of the town square task showed two interesting differences from the controls participants' pattern of performance, which may be suggestive of the mechanisms supporting Jon's performance. As before, Jon performed much worse on the shifted-view than on the same-view conditions; he also performed much worse in the different-town condition than in the same-view condition (same view: 95%; shifted view: 40%; different town: 50%). Compared with the healthy volunteers Jon showed a significantly greater reduction in performance between the same-view condition and the different-town condition ($z = 4.61$; see Figure 7) as well as between the same-view and shifted-view conditions ($z = 2.10$; note that the latter result may have been affected by a floor effect—in the shifted-view condition Jon performed close to chance, 33%, and could not do much worse). These results indicate that changing the visual scene behind the objects was as disruptive to Jon as was changing the viewpoint within the same scene. Thus it is likely that his same-view performance relied on a visual representation rather than on a more motoric egocentric pointing-direction representation.

Discussion

Memory for Context Versus Content and Recognition Versus Recollection

Our context-dependent memory test showed that Jon had impaired memory for the context of an event (where he received the

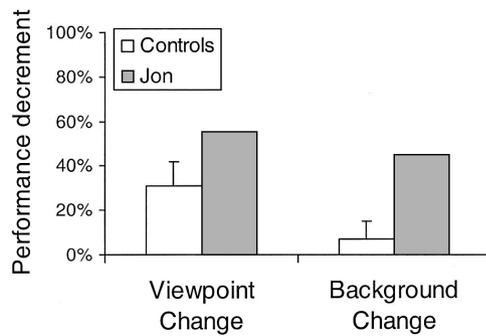


Figure 7. Effect of changing the viewpoint and the background scene in an object-location test (Experiment 3). Control participants performed slightly worse when the background scene changed to show a different town while the object locations did not change relative to the view (or to the edge of the computer screen; see Figure 3). A change of viewpoint produced a much greater decrement in participants' performance. Patient Jon's performance decreased significantly more than control participants' performance in both cases. (Note that a floor effect limited the apparent size of Jon's performance decrement with viewpoint change relative to control participants; see text.) Columns show the difference in performance in the two conditions (same view–shifted view and same view–different town), and error bars show 1 *SD*.

object or who he received it from) and showed spared performance at recognizing the content of the event (i.e., which object was familiar). In this type of test, item recognition and context-dependent memory, or *associative recognition* (Yonelinas, 2002), can be tested for the same events using identical procedures (paired forced choice of objects presented in a context in an interleaved fashion; see also Burgess, Maguire, et al., 2001; Spiers, Burgess, et al., 2001). These precautions make us more secure in supposing that differences in performance are due to differences in the type of mnemonic information being probed than due to procedural differences (as in findings of spared recognition compared with impaired free recall). In addition, and unlike our previous study, control performance was also matched across the different question types, ruling out difficulty effects. However, the procedural equivalence between conditions and the fact that the various aspects of memory were probed for the same event come at a price. The most obvious problem is that the objects must be re-presented during testing, so that later in testing, any process of familiarity-based recognition might rely on familiarity built up during testing rather than during the initial event. In fact, of the three errors made by Jon in the familiarity condition, one was at the beginning and two were at the end of the experiment, suggesting that this potential confound did not influence his performance and that Jon does indeed have a specific impairment in retrieving the context of an event.

Viewpoint Dependence in Spatial Memory

In our previous study of viewpoint dependence (King et al., 2002), we showed that Jon had a differential impairment in the shifted-view condition compared with the same-view condition. By making both conditions easier for Jon (testing him with two foils while testing the control participants with five foils), we showed that, for List Lengths 4 and 7, he performed as well as or better than controls in the same-view task and significantly worse

than them in the shifted-view task (being at chance for list lengths greater than 1). For List Lengths 10 and above, Jon performed significantly worse on the same-view task, notwithstanding the advantage afforded to him by the lower number of foils. We hypothesized that performance of the same-view task could be supported by both an egocentric system and an allocentric system, whereas the shifted-view task requires an allocentric system. We further hypothesized that the egocentric system might store each item's location individually, whereas the allocentric system might form a combined representation. This would be consistent with Jon's preserved performance in the same-view task for short list lengths but impaired performance in the shifted-view task at all list lengths above 1 (for which alternative [e.g., verbal] strategies might be available). It would also be consistent with his impaired performance in the same-view task for longer lists, for which he would have to use many separate egocentric representations, whereas control participants could use a single allocentric representation.

However, in our previous study we could not directly compare Jon's same-view performance with that of control participants (because of the different numbers of foils used), and we could not rule out a nonlinear effect of difficulty (because performance was not matched across tasks). In our current study we found that, for short lists (of three items) tested with four foils, Jon's absolute performance level on the same-view task was unimpaired relative to controls. We also showed that his impairment on the shifted-view task at these list lengths was unlikely due to an effect of difficulty because control participants performed at approximately the same level in both conditions (although not identically; see Figure 6A).

Jon's impaired same-view performance on longer lists indicates an advantage for allocentric systems over egocentric systems at long list lengths. This might relate to the suggestion that allocentric systems are naturally preferred for long-term memory, because the subject's viewpoint will change over time, whereas egocentric systems are more useful for short-term or working memory, because action and perception are egocentric (Burgess, Becker, et al., 2001; A. D. Milner, Dijkerman, & Carey, 1999). It might also be that an allocentric system has a greater ability to store several sequentially presented locations within a single coherent representation. Note that the relatively mild deficit on the same-view task at longer list lengths closely matches Jon's performance on a two-dimensional object-location task, similar to that used by Vargha-Khadem et al. (1997). Thus, his deficit on previous two-dimensional object-location tasks may not result purely from their cross-modal nature because there was no impairment at short list lengths, unlike the shifted-view tasks. Instead, his deficit might reflect a capacity limitation on a single-modality egocentric system.

Manipulation of the Background Scene

Jon's preserved performance in the same-view task in our earlier study (King et al., 2002) implies the presence of an intact egocentric system. However, we could not tell what type of representation was being used to support this behavior. Use of a sensory-bound representation might enable visual matching, consistent with Jon's good visual recognition in previous studies (Baddeley et al., 2001; Spiers, Burgess, et al., 2001). Meanwhile, Jon's good Block Span results might indicate use of an action-based egocentric represen-

tation. Here, we changed the background scene between presentation and test while leaving the target locations in the same positions relative to the viewer and the display surround. The severe reduction in Jon's performance implies that visual matching contributed to his preserved same-view performance. It is possible that egocentric representations from both dorsal and ventral streams contributed to Jon's performance of the same-view task. In this case, the reduction in Jon's performance when the background was changed (disrupting only the visual representations) should be less than the reduction caused by a change in viewpoint (disrupting the use of either type of egocentric representation).

We found that the size of the impairment caused by changing the background scene was comparable with that caused by shifting the viewpoint (both manipulations reduced performance nearly to chance). Thus, Jon's performance of the same-view task probably relied primarily on visual matching of the scene local to an object, with little role for motoric representations such as pointing vectors. These visual representations might well rely on the ventral visual stream and his intact parahippocampal gyrus in particular (see Burgess et al., 2002, for a discussion), whereas motoric representations might rely on the dorsal stream, although we note the highly speculative nature of these anatomical attributions.

A previous study investigated recall of locations defined either egocentrically or allocentrically in a patient, "YR," with selective hippocampal damage (acquired in adulthood) and relatively preserved recognition memory (Holdstock et al., 2000). In this study, both egocentric and allocentric conditions involved indicating the previous location of an illuminated LED in a lightboard on a table, using a laser pointer. As with the same- and shifted-view tasks, the participant moved to a new position between presentation and retrieval in the allocentric condition but not in the egocentric condition. Unlike the same- and shifted-view tasks, the allocentric condition took place with the room lights on, to accentuate the presence of visual cues in the testing room, whereas the egocentric condition took place in the dark, to minimize the use of visual cues. In addition, there was a filled delay of 5 s or 60 s between presentation and test. The intention of the experimenters was to ensure that the egocentric condition was solved by remembering the location of the LED relative to the subject, and this was confirmed by the subjective reports of the participants.

Patient YR was found to have a greater impairment in the allocentric task than in the egocentric task, although this difference was significant only for the longer delay period (and the allocentric deficit was not quite significant in a recognition version of the task). The relatively weak dissociation between egocentric and allocentric conditions found in YR might relate to the use of a single location in each trial of the test. Jon was unimpaired at immediate recognition of a single object location from a shifted view but impaired at longer list lengths, whereas YR only showed a relative impairment in remembering a single location after a filled delay. Thus, it may be that both increasing list lengths and increasingly long filled delays favor the use of an allocentric system compared with an egocentric one. That is, an allocentric memory system may have an advantage in terms of both capacity and longevity. A second factor contributing to the strength of the dissociation found in Jon might be the ease with which visual matching of scene fragments could be used to solve the same-view task. By contrast, the use of darkness in the egocentric test performed by YR would put more reliance on nonvisual memory for locations relative to the body.

Relating Jon's Spatial Deficits to Theories of Hippocampal Function

How does Jon's performance on the various tasks presented here relate to the various theories of hippocampal function outlined in the introduction? First, his shifted-view impairment is consistent with the cognitive map theory (O'Keefe & Nadel, 1978), in which the flexibility of a hippocampal allocentric system to manipulations like novel starting positions was stressed. Jon's deficit in context-dependent memory is also consistent with O'Keefe and Nadel's (1978, chap. 14) suggested involvement of the human hippocampus in episodic memory. Note, however, that Jon's equal impairments in retrieving the spatial and nonspatial context of an event (e.g., the person who gave the object) questions the proposed mechanism underlying hippocampal involvement in (nonverbal) episodic memory: that of providing a spatiotemporal context within which events could be stored. We come back to the mechanisms underlying episodic recollection at the end of this section.

As with the cognitive map, Jon's pattern of performance is also consistent with a hippocampal role in supporting flexible relational memory (Cohen & Eichenbaum, 1993; Eichenbaum & Cohen, 2001). This theory explicitly includes the spatial aspects of the cognitive map, in which allocentric representations are regarded as more flexible than egocentric ones, consistent with Jon's impaired shifted-view performance. In addition, his impairment that was due to varying the background is also consistent with poor flexibility. For example, this impairment can be characterized in terms of preserved visual scene information but an inability to extract the object locations from it. Jon's deficit in context-dependent recognition compared with item recognition is also consistent with the idea that associating the item to its context is more relational than simply recognizing the item itself. Distinguishing this theory from others, such as the cognitive map, relates to whether behaviors not accounted for by other theories (e.g., transitive inference) turn out to depend on the hippocampus or on other areas such as prefrontal cortex.

Jon's pattern of performance is not compatible with the declarative memory theory (Squire & Zola-Morgan, 1991), because the spared item recognition and egocentric tasks are as explicit or declarative as the impaired context-dependent and allocentric tasks. Note, however, that other patients with hippocampal damage do not show the spared recognition memory shown by Jon, YR, and others (e.g., Manns & Squire, 1999; see also Spiers, Maguire, & Burgess, 2001). It is not clear why these patients show different patterns of performance or whether and how these differences might relate to differences in etiology and extent of pathology. Notwithstanding these remaining questions, Jon's results strengthen the case for dissociations between familiarity-based recognition and episodic recollection and between egocentric and allocentric systems, which are not accommodated in the declarative theory of memory.

How does Jon's pattern of performance compare with the idea that the hippocampus is required to perform cross-modal association of stimuli represented in different brain areas (Alvarez & Squire, 1994; Marr, 1971; Mayes et al., 2001; McClelland et al., 1995; McNaughton & Nadel, 1990; Rolls, 1996)? A strict interpretation of this idea in terms of sensory modality is not compatible with our results, because all of the tests here were visual. However, if Jon's unimpaired same-view and object-recognition performance depends on information encoded within a single

visual representation, presumably in a single visual area, this is consistent with the idea that information from a single area can be retrieved without the hippocampus. Equally, one might argue that context-dependent recognition and shifted-view object-location memory require association of the identity of the object to the various aspects of the context of its receipt and to its environmental location, respectively, each of which might be represented in a different area. However, this argument for the involvement of the hippocampus in the shifted-view task is slightly undermined by the finding that YR was unable to remember a place (i.e., one that did not have to be associated to a specific object; Holdstock et al., 2000).

How do our spatial memory results relate to the idea that the hippocampus and related structures along Papez's circuit (Papez, 1937) support episodic recollection, whereas a separate circuit including perirhinal cortex supports familiarity-based recognition (Aggleton & Brown, 1999; Baxter & Murray, 2001; Gaffan & Parker, 1996)? This picture has much experimental support, including our finding of impaired context-dependent recognition and spared item recognition in Jon (but see also Manns & Squire, 1999). However, it does not provide a mechanistic account of the processes underlying episodic recollection and familiarity-based recognition, or of why they should have the suggested anatomical distribution. Jon's preserved performance in the same-view task but impaired performance when the background scene changes is compatible with an extrahippocampal process of familiarity-based recognition using visual representations. What processes are involved in the shifted-viewpoint task, and can they tell us anything about the processes involved in episodic recollection?

We noted above that the allocentric system responsible for solving the shifted-view task might store a direct representation of the object's location relative to the environment (an allocentric representation) or might allow the manipulation of viewpoint using egocentric information encoded at presentation. In this latter case, the system must provide a three-dimensional spatial framework within which the effects of arbitrary movements of viewpoint can be calculated (i.e., the system provides a mechanism for producing viewpoint independence rather than explicitly storing a viewpoint independent representation). Evidence for this latter mechanism comes from an increase in reaction times with the angle of viewpoint change between presentation and retrieval (Diwadkar & McNamara, 1997; King et al., 2002), although this does not preclude the additional presence of an allocentric representation. The process of imagining the effect of a movement of viewpoint on a spatial scene is different from the process of imagining the effect of a rotation of the scene itself. There appear to be specific mechanisms supporting efficient calculation of the effects of movement of viewpoint, enabling faster or more accurate responses following real or imagined movement of viewpoint than following equivalent real or imagined movements of the scene (Easton & Sholl, 1995; Farrell & Robertson, 1998; Presson & Montello, 1994; Rieser, 1989; Wang & Simons, 1999; Wraga, Creem, & Proffitt, 2000).

In Jon's case, we believe his bilateral hippocampal lesion prevents him from using an allocentric system, so that he is incapable of accessing remembered spatial knowledge of the scene from a different point of view. Although apparently critical to the shifted-view task, this ability is not required in the same-view task. In principle this can be solved on the basis of familiarity—by a process of matching the current scene with a stored representation

that is sensory-bound and whose viewpoint is fixed. Our results on a test manipulating the background visual scene indicate that Jon's preserved same-view performance depends on a (ventral stream-like) visual matching process rather than on (dorsal stream-like) stored egocentric vectors.

Do the processes required by the allocentric system relate to the hippocampal contribution to context-dependent recognition and episodic recollection? First, the ability to calculate the appearance of a scene from a new viewpoint would certainly facilitate recognition of the spatial context of an event in our context-dependent memory test. In this test, the participant had to indicate which of two objects had been received in a given location; however, the view of the location was not identical at presentation and test. Beyond this, the relationship between the ability to manipulate viewpoints in memory and the ability to perform episodic recollection necessarily becomes more speculative. It may be that one way of indexing the vast amount of different types of stored information relating to personal experiences is by the location at which the information was experienced. This would correspond to models suggesting that the hippocampus provides an associative memory for information stored in disparate cortical locations (Alvarez & Squire, 1994; Marr, 1971; McClelland et al., 1995; McNaughton & Nadel, 1990; Mishkin, Suzuki, Gadian, & Vargha-Khadem, 1997; Recce & Harris, 1996; Rolls, 1996; Teyler & DiScenna, 1986) and that this function derives from a prior role in representing spatial location (O'Keefe & Nadel, 1978). Given this type of model, a natural way to search for stored information concerning a specific event is to move the location so as to maximize the match between retrieved information and the retrieval cue. Obviously, the ability to manipulate points of view in memory would facilitate this type of search.

The speculative model outlined above would also provide the beginnings of an explanation for why the suggested circuit (Papez's) should be involved in this process. In rats (Muller, 1996; O'Keefe & Nadel, 1978; Wilson & McNaughton, 1993) and, more recently, in humans (Ekstrom et al., 2003), *place cells* in the hippocampus have been found to provide a representation of the animal's current location, whereas cells representing the animal's head direction (e.g., Taube, 1998) have been found along the rest of Papez's circuit (mammillary bodies, anterior thalamus, subicular complex, and cingulate cortex).¹ These cells, combined with a (presumably parietal) means for translating information into egocentric reference frames, would be able to simulate the subject's movement and so organize the retrieval of spatial information (see Becker & Burgess, 2001, for details). Consistent with these ideas is the remarkable similarity of the network of areas (including

¹ In open environments, place cells in freely moving rats represent the rat's location, independent of its orientation (McNaughton, Barnes, & O'Keefe, 1983; Muller, Bostock, Taube, & Kubie, 1994; O'Keefe & Nadel, 1978; Wilson & McNaughton, 1993), and their firing corresponds to the rat's behavioral choices in spatial memory paradigms (Lenck-Santini, Muller, Save, & Poucet, 2002; Lenck-Santini, Save, & Poucet, 2001; O'Keefe & Speakman, 1987; Pico, Gerbrandt, Pondel, & Ivy, 1985). Head-direction cells provide the complementary representation of head direction independent of location (Taube, Muller, & Ranck, 1990). Both of these types of cells reflect influences of internal (path integrative) signals as well as visual landmarks and do not simply reflect the current view (e.g., maintaining their firing in the absence of visual stimuli; Knierim, Kudrinski, & McNaughton, 1998; O'Keefe & Conway, 1978; Taube, 1998).

those mentioned above) activated in autobiographical (Maguire & Mummery, 1999; Maguire, Mummery, & Buchel, 2000) and context-rich episodic retrieval (Burgess, Maguire, et al., 2001) on one hand and spatial navigation on the other (Hartley et al., 2003; Maguire et al., 1998). How this mechanism would retrieve non-spatial data is a matter of conjecture, but a neural level understanding in the spatial domain will at least allow a quantitative computational investigation.

Conclusion

We investigated spatial and context-dependent memory in a single case of developmental amnesia associated with focal perinatal hippocampal damage (Vargha-Khadem et al., 1997), using forced-choice recognition paradigms. Recognition memory for the items received in a VR episodic memory test was unimpaired, whereas memory for the context in which they were received was impaired. The tests concerned the same events, were interleaved, used identical stimuli, and were matched for difficulty. Memory for object locations presented in a virtual town square was unimpaired when tested from the same viewpoint as presentation but impaired when tested from a shifted viewpoint. These tests were also interleaved and matched for difficulty by varying the proximity of the foil locations.

We postulate that Jon's deficits in spatial memory from new viewpoints reflect an inability either to store object locations in an allocentric framework or to perform allocentric manipulations on stored egocentric representations. In our context-dependent memory task, we would expect the ability to reconstruct stored spatial information and make arbitrary manipulations of the viewpoint to play a role in recognizing the spatial context of an event. The absence of this ability could help to explain Jon's context-dependent memory deficit. The results thus lead us to the hypothesis that episodic recollection involves the same allocentric system as the shifted-viewpoint object-location recognition task. The postulated transformation of stored spatial information into an egocentric reference frame compatible with imagery during recollection might also help to explain its characteristic vividness when compared with familiarity-based recognition.

Overall, our studies indicate a surprisingly close relationship between the mechanisms of episodic and spatial memory, in which the hippocampus appears to play a key role. This role seems to hinge on the requirement to store context-rich memories in a form that permits both the identification of a familiar place from a novel viewpoint and the reconstruction of a viewpoint-specific, quasi-perceptual experience of past events.

References

- Abrahams, S., Pickering, A., Polkey, C. E., & Morris, R. G. (1997). Spatial memory deficits in patients with unilateral damage to the right hippocampal formation. *Neuropsychologia*, *35*, 11–24.
- Aggleton, J. P., & Brown, M. W. (1999). Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behavioural Brain Science*, *22*, 425–490.
- Alvarez, P., & Squire, L. R. (1994). Memory consolidation and the medial temporal lobe: A simple network model. *Proceedings of the National Academy of Sciences, USA*, *91*, 7041–7045.
- Baddeley, A. D., Emslie, H., & Nimmo-Smith, I. (1994). *The Doors and People Test*. Bury St Edmunds, England: Thames Valley Test Company.
- Baddeley, A., Vargha-Khadem, F., & Mishkin, M. (2001). Preserved recognition in a case of developmental amnesia: Implications for the acquisition of semantic memory? *Journal of Cognitive Neuroscience*, *13*, 357–369.
- Baxter, M. G., & Murray, E. A. (2001). Opposite relationship of hippocampal and rhinal cortex damage to delayed nonmatching-to-sample deficits in monkeys. *Hippocampus*, *11*, 61–71.
- Becker, S., & Burgess, N. (2001). A model of spatial recall, mental imagery and neglect. *Advances in Neural Information Processing Systems*, *13*, 96–102.
- Bogacz, R., & Brown, M. W. (2003). Comparison of computational models of familiarity discrimination in the perirhinal cortex. *Hippocampus*, *13*, 494–524.
- Burgess, N., Becker, S., King, J. A., & O'Keefe, J. (2001). Memory for events and their spatial context: Models and experiments. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *356*, 1493–1503.
- Burgess, N., Maguire, E., & O'Keefe, J. (2002). The human hippocampus and spatial and episodic memory. *Neuron*, *35*, 625–641.
- Burgess, N., Maguire, E. A., Spiers, H. J., & O'Keefe, J. (2001). A temporoparietal and prefrontal network for retrieving the spatial context of lifelike events. *Neuroimage*, *14*, 439–453.
- Cohen, N. J., & Eichenbaum, H. (1993). *Memory, amnesia and the hippocampal system*. Cambridge, MA: MIT Press.
- Delay, J., & Brion, S. (1969). *Le syndrome de Korsakoff [Korsakoff's syndrome]*. Paris: Masson.
- Diwadkar, V. A., & McNamara, T. P. (1997). Viewpoint dependence in scene recognition. *Psychological Science*, *8*, 302–307.
- Easton, R. D., & Sholl, M. J. (1995). Object-array structure, frames of reference, and retrieval of spatial knowledge. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 483–500.
- Eichenbaum, H., & Cohen, N. J. (2001). *From conditioning to conscious recollection: Memory systems of the brain*. Oxford, England: Oxford University Press.
- Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., et al. (2003, September 11). Cellular networks underlying human spatial navigation. *Nature*, *425*, 184–188.
- Farrell, M. J., & Robertson, I. H. (1998). Mental rotation and the automatic updating of body-centered spatial relationships. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *24*, 227–233.
- Fortin, N. J., Agster, K. L., & Eichenbaum, H. B. (2002). Critical role of the hippocampus in memory for sequences of events. *Nature Neuroscience*, *5*, 458–462.
- Gadian, D. G., Aicardi, J., Watkins, K. E., Porter, D. A., Mishkin, M., & Vargha-Khadem, F. (2000). Developmental amnesia associated with early hypoxic-ischaemic injury. *Brain*, *123*, 499–507.
- Gaffan, D., & Parker, A. (1996). Interaction of perirhinal cortex with the fornix-fimbria: Memory for objects and "object-in-place" memory. *Journal of Neuroscience*, *16*, 5864–5869.
- Gardiner, J. M., & Java, R. I. (1993). Recognizing and remembering. In A. Collins, S. Gathercole, & P. Morris (Eds.), *Theories of memory* (pp. 168–188). Hillsdale, NJ: Erlbaum.
- Georgopoulos, A. P., Schwartz, A. B., & Kettner, R. E. (1986, September 26). Neuronal population coding of movement direction. *Science*, *233*, 1416–1419.
- Ghaem, O., Mellet, E., Crivello, F., Tzourio, N., Mazoyer, B., Berthoz, A., et al. (1997). Mental navigation along memorized routes activates the hippocampus, precuneus, and insula. *Neuroreport*, *8*, 739–744.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience*, *15*, 20–25.
- Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. *Neuron*, *37*, 877–888.

- Holdstock, J. S., Mayes, A. R., Cezayirli, E., Isaac, C. L., Aggleton, J. P., & Roberts, N. (2000). A comparison of egocentric and allocentric spatial memory in a patient with selective hippocampal damage. *Neuropsychologia*, *38*, 410–425.
- King, J. A., Burgess, N., Hartley, T., Vargha-Khadem, F., & O'Keefe, J. (2002). The human hippocampus and viewpoint dependence in spatial memory. *Hippocampus*, *12*, 811–820.
- King, J. A., Hartley, T., Maguire, E. A., & Burgess, N. (2004). *Spatial context and the hippocampal role in object-location memory*. Manuscript in preparation.
- King, J. A., Hartley, T., Spiers, H. J., Maguire, E. A., & Burgess, N. (2004). *Lateral and anterior prefrontal involvement in episodic retrieval is associated with contextual interference*. Manuscript submitted for publication.
- Kinsbourne, M., & Wood, F. (1975). Short-term memory processes and the amnesic syndrome. In D. Deutsch & J. A. Deutsch (Eds.), *Short-term memory* (pp. 257–291). New York: Academic Press.
- Knierim, J. J., Kudrimoti, H. S., & McNaughton, B. L. (1998). Interactions between idiothetic cues and external landmarks in the control of place cells and head direction cells. *Journal of Neurophysiology*, *80*, 425–446.
- Knowlton, B. J., & Squire, L. R. (1995). Remembering and knowing: Two different expressions of declarative memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 699–710.
- Lenck-Santini, P. P., Muller, R. U., Save, E., & Poucet, B. (2002). Relationships between place cell firing fields and navigational decisions by rats. *Journal of Neuroscience*, *22*, 9035–9047.
- Lenck-Santini, P. P., Save, E., & Poucet, B. (2001). Evidence for a relationship between place-cell spatial firing and spatial memory performance. *Hippocampus*, *11*, 377–390.
- Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S., Frith, C. D., & O'Keefe, J. (1998, May 8). Knowing where and getting there: A human navigation network. *Science*, *280*, 921–924.
- Maguire, E. A., & Mummery, C. J. (1999). Differential modulation of a common memory retrieval network revealed by positron emission tomography. *Hippocampus*, *9*, 54–61.
- Maguire, E. A., Mummery, C. J., & Buchel, C. (2000). Patterns of hippocampal-cortical interaction dissociate temporal lobe memory subsystems. *Hippocampus*, *10*, 475–482.
- Manns, J. R., & Squire, L. R. (1999). Impaired recognition memory on the Doors and People Test after damage limited to the hippocampal region. *Hippocampus*, *9*, 495–499.
- Marr, D. (1971). Simple memory: A theory for archicortex. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *262*, 23–81.
- Mayes, A. R., Isaac, C. L., Holdstock, J. S., Hunkin, N. M., Montaldi, D., Downes, J. J., et al. (2001). Memory for single items, word pairs, and temporal order of different kinds in a patient with selective hippocampal lesions. *Cognitive Neuropsychology*, *18*, 97–123.
- Mayes, A. R., & Roberts, N. (2001). Theories of episodic memory. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *356*, 1395–1408.
- McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychological Review*, *102*, 419–457.
- McNaughton, B. L., Barnes, C. A., & O'Keefe, J. (1983). The contributions of position, direction, and velocity to single unit activity in the hippocampus of freely-moving rats. *Experimental Brain Research*, *52*, 41–49.
- McNaughton, B. L., & Nadel, L. (1990). Hebb-Marr networks and the neurobiological representation of action in space. In M. A. Gluck & D. E. Rumelhart (Eds.), *Neuroscience and connectionist theory* (pp. 1–63). Hillsdale, NJ: Erlbaum.
- Milner, A. D., Dijkerman, H. C., & Carey, D. P. (1999). Visuospatial processing in a case of visual form agnosia. In N. Burgess, K. J. Jeffery, & J. O'Keefe (Eds.), *The hippocampal and parietal foundations of spatial cognition* (pp. 443–466). Oxford, England: Oxford University Press.
- Milner, B. (1971). Interhemispheric differences in the localization of psychological processes in man. *British Medical Journal*, *27*, 272–277.
- Mishkin, M., Suzuki, W. A., Gadian, D. G., & Vargha-Khadem, F. (1997). Hierarchical organization of cognitive memory. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, *352*, 1461–1467.
- Morris, R. G. M., Garrud, P., Rawlins, J. N., & O'Keefe, J. (1982, June 24). Place navigation impaired in rats with hippocampal lesions. *Nature*, *297*, 681–683.
- Muller, R. U. (1996). A quarter of a century of place cells. *Neuron*, *17*, 813–822.
- Muller, R. U., Bostock, E., Taube, J. S., & Kubie, J. L. (1994). On the directional firing properties of hippocampal place cells. *Journal of Neuroscience*, *14*, 7235–7251.
- O'Keefe, J., & Conway, D. H. (1978). Hippocampal place units in the freely moving rat: Why they fire where they fire. *Experimental Brain Research*, *31*, 573–590.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford, England: Oxford University Press.
- O'Keefe, J., & Speakman, A. (1987). Single unit activity in the rat hippocampus during a spatial memory task. *Experimental Brain Research*, *68*, 1–27.
- O'Reilly, R. C., & Norman, K. A. (2002). Hippocampal and neocortical contributions to memory: Advances in the complementary learning systems framework. *Trends in Cognitive Sciences*, *6*, 505–510.
- Papez, J. W. (1937). A proposed mechanism of emotion. *Archives of Neurology and Psychiatry*, *38*, 724–744.
- Pearce, J. M., Roberts, A. D., & Good, M. (1998, November 5). Hippocampal lesions disrupt navigation based on cognitive maps but not heading vectors. *Nature*, *396*, 75–77.
- Pico, R. M., Gerbrandt, L. K., Pondel, M., & Ivy, G. (1985). During stepwise cue deletion, rat place behaviors correlate with place unit responses. *Brain Research*, *330*, 369–372.
- Presson, C. C., & Montello, D. R. (1994). Updating after rotational and translational body movements: Coordinate structure of perspective space. *Perception*, *23*, 1447–1455.
- Ratcliff, G. (1979). Spatial thought, mental rotation and the right cerebral hemisphere. *Neuropsychologia*, *17*, 49–54.
- Ravens, J. C. (1965). *Progressive matrices*. London: H. K. Lewis.
- Recce, M., & Harris, K. D. (1996). Memory for places: A navigational model in support of Marr's theory of hippocampal function. *Hippocampus*, *6*, 735–748.
- Rieser, J. J. (1989). Access to knowledge of spatial structure at novel points of observation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *15*, 1157–1165.
- Rolls, E. T. (1996). A theory of hippocampal function in memory. *Hippocampus*, *6*, 601–620.
- Rugg, M. D., & Yonelinas, A. P. (2003). Human recognition memory: A cognitive neuroscience perspective. *Trends in Cognitive Sciences*, *7*, 313–319.
- Schoppik, D., Gadian, D. G., Connelly, A., Mishkin, M., Vargha-Khadem, F., & Saunders, R. C. (2001). Volumetric measurement of the subhippocampal cortices in patients with developmental amnesia [Abstract]. *Society for Neuroscience Abstracts*, *27*, 1400.
- Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery, and Psychiatry*, *20*, 11–21.
- Spiers, H. J., Burgess, N., Hartley, T., Vargha-Khadem, F., & O'Keefe, J. (2001). Bilateral hippocampal pathology impairs topographical and episodic memory but not visual pattern matching. *Hippocampus*, *11*, 715–725.
- Spiers, H. J., Maguire, E. A., & Burgess, N. (2001). Hippocampal amnesia. *Neurocase*, *7*, 357–382.

- Squire, L. R., & Zola-Morgan, S. (1991, September 20). The medial temporal lobe memory system. *Science*, 253, 1380–1386.
- Taube, J. S. (1998). Head direction cells and the neuropsychological basis for a sense of direction. *Progress in Neurobiology*, 55, 225–256.
- Taube, J. S., Muller, R. U., & Ranck, J. B., Jr. (1990). Head-direction cells recorded from the postsubiculum in freely moving rats: I. Description and quantitative analysis. *Journal of Neuroscience*, 10, 420–435.
- Teyler, T. J., & DiScenna, P. (1986). The hippocampal memory indexing theory. *Behavioral Neuroscience*, 100, 147–154.
- Trinkler, I. (2004). *The structure of hippocampal-dependent spatial and episodic memories*. Manuscript in preparation, University College London, London.
- Tulving, E. (1972). Episodic and semantic memory. In E. Tulving & W. Donaldson (Eds.), *Organization of memory* (pp. 382–403). New York: Academic Press.
- Tulving, E. (1983). *Elements of episodic memory*. Oxford, England: Clarendon Press.
- Tulving, E. (1993). What is episodic memory? *Current Perspectives in Psychological Science*, 2, 67–70.
- Tulving, E. (2001). Episodic memory and common sense: How far apart? *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 356, 1505–1515.
- Ungerleider, L. G. & Mishkin, M. (1982). Two cortical visual systems. In M. A. Goodale & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.
- Vargha-Khadem, F., Gadian, D. G., & Mishkin, M. (2001). Dissociations in cognitive memory: The syndrome of developmental amnesia. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, 356, 1435–1440.
- Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A., Van Paesschen, W., & Mishkin, M. (1997, July 18). Differential effects of early hippocampal pathology on episodic and semantic memory. *Science*, 277, 376–380.
- Wang, R. F., & Simons, D. J. (1999). Active and passive scene recognition across views. *Cognition*, 70, 191–210.
- Warrington, E. K. (1996). *The Camden memory tests*. New York: Psychology Press.
- Wilson, M. A., & McNaughton, B. L. (1993, August 20). Dynamics of the hippocampal ensemble code for space. *Science*, 261, 1055–1058.
- Wraga, M., Creem, S. H., & Proffitt, D. R. (2000). Updating displays after imagined object and viewer rotations. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 26, 151–168.
- Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, 46, 441–517.
- Yonelinas, A. P., Kroll, N. E., Quamme, J. R., Lazzara, M. M., Sauve, M. J., Widaman, K. F., et al. (2002). Effects of extensive temporal lobe damage or mild hypoxia on recollection and familiarity. *Nature Neuroscience*, 5, 1236–1241.

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