

Working Memory and the Hippocampus

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Abstract

■ A number of studies suggest an important role for the hippocampus in tasks involving visuospatial or relational working memory. We test the generality of this proposal across tasks using a battery designed to investigate the various components of working memory, studying the working memory performance of Jon, who shows a bilateral reduction in hippocampal volume of approximately 50%, comparing him to a group of 48 college students. We measure performance on four complex working memory span measures based on combining visuospatial and verbal

storage with visuospatial or verbal concurrent processing as well as measuring Jon's ability to carry out the component storage and processing aspects of these tasks. Jon performed at a consistently high level across our range of tasks. Possible reasons for the apparent disparity between our own findings and earlier studies showing a hippocampal deficit are discussed in terms of both the potential differences in the demands placed on relational memory and of the proposed distinction between egocentric and allocentric visuospatial processing. ■

INTRODUCTION

Over the years, the development of cognitive psychology has been strongly influenced by neuropsychological evidence. One of the clearest examples of this is provided by the influence of studies based on patients with dense but pure amnesic deficits on the case for separating long-term memory (LTM) and STM. In a classic study, Milner (1966) described the case of patient HM who, following bilateral lesions to the medial-temporal lobe showed dramatic deficits in new long-term learning while maintaining a normal digit span. This was regarded as strong support for the separation of LTM and STM systems, a conclusion that was reinforced by later studies in which a range of cognitive tasks that were assumed to depend upon STM were shown to be preserved in amnesic patients (Squire, Knowlton, & Musen, 1993; Baddeley & Warrington, 1970).

For many years, the assumption that the hippocampus and the parahippocampal cortex were essential for long-term learning but not for STM was widely accepted. Since this initial formulation, however, knowledge of the hippocampus and its major sensory inputs has substantially grown, and the initial concept of STM has been elaborated, as a result of which, this basic generalization has been questioned. In particular, it has been suggested that the hippocampus may be necessary for certain types of visuospatial STM or working memory tasks involving relational coding. For example, Olson, Page, Moore, Chatterjee, and Verfaellie (2006) conducted two experiments in which patients with hippocampal lesions and controls were required to remember the location of a line-drawn object

within each of a series of three 3×3 matrices. The patients with hippocampal lesions showed a deficit in both studies. Similarly, Olson, Moore, Stark, and Chatterjee (2006) studied the retention of spatial information, color information, and memory for a single face, finding a deficit in their hippocampal patients at delays as short as 4 sec. Face retention was also studied by Ezzyat and Olson (2008), over delays of 1 or 8 sec, again finding a deficit in hippocampal patients.

Other investigators have also found evidence for a hippocampal-based deficit in retention of a single face, although not necessarily at very short intervals. Thus, Nichols, Kao, Verfaellie, and Gabrieli (2006) found a deficit in retention of a single face after 7 sec but not after 1 sec, whereas Shrager, Levy, Hopkins, and Squire (2008) found a deficit in their patients after 14 sec but not after a delay of 2 or 7 sec. Faces were also used in one of the studies by Hannula, Tranel, and Cohen (2006), in which they required their participants to associate a face with a complex scene. Recognition memory for both spatial and nonspatial relationships was impaired in patients with hippocampal lesions even after a brief delay.

In all these cases, it is possible to argue that some form of relational visual or spatial STM might well be involved, although, given the complexity and the range of material used, its exact nature is hard to specify. One obvious question is that of whether, as Olson, Moore, et al. (2006) suggest, the medial-temporal lobes may have a more general role in visual and/or spatial working memory. Further evidence for such a role is provided by Hartley et al. (2007) using a task in which a scene involving a number of mountain peaks was presented from one viewpoint and then tested by showing the scene from an alternative view. Patient Jon, who has developmental amnesia resulting

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from a very substantial but specific hippocampal deficit, was shown to perform poorly on this task, even when no delay was involved.

At the same time as our understanding of the functions of the hippocampus was developing, the concept of STM was evolving into the more complex concept of working memory. In addition to simple temporary storage, working memory is assumed to be a system for combining the storage and manipulation of information to perform complex cognitive activities (Baddeley, 2007; Baddeley & Hitch, 1974), and although the terms are sometimes used as broadly equivalent (e.g., Olson, Page, et al., 2006), there are important differences at a conceptual level between STM and working memory. The differences lie principally in the assumption that working memory involves the simultaneous and interacting influences of temporary storage and attentionally based executive control. It is this assumption that underpins measures such as working memory span (Daneman & Carpenter, 1980) in which participants must process a series of sentences at the same time as remembering the last word of each. This measure correlates strongly, not only with the measures of language comprehension originally studied by Daneman and Carpenter (Daneman & Merikle, 1996), but also with many other cognitive activities ranging from complex reasoning through learning a new programming language to performance on the antisaccade task (Engle, Kane, & Tuholski, 1999). Given the evidence that the hippocampus clearly does play a role in a number of tasks that almost certainly involve working memory, the question arises as to how general this role might be.

The strongest evidence appears to be for an involvement of the hippocampus in the processing of visuospatial relationships, and as Olson, Page, et al. observed, “relational processing is important in many working memory tasks especially tasks using visual stimuli” (Olson, Page, et al., 2006, page 4596). The generality of such a claim for the role of the hippocampus might seem unlikely, given the literature suggesting that “pure” but dense amnesia appears to be able to occur in the absence of the general cognitive impairment that might be expected from a working memory deficit (e.g., Squire et al., 1993; Baddeley & Warrington, 1970; Milner, 1966). It could, however, be argued that such patients were tested at a time before the concept of working memory was elaborated and may have had subtle deficits that were simply not detected by existing cognitive measures. Such a possibility is reinforced by the proposal of a fourth component to the tripartite working memory model initially proposed by Baddeley and Hitch (1974), namely the episodic buffer. This is assumed to be a temporary store using a multidimensional code to integrate information from perception, LTM, and the various components of working memory (Baddeley, 2000). The buffer is assumed to play a crucial role in binding features into integrated episodes and, as such, requires access to perception, LTM, and executive control. Although Baddeley (2000) did not postulate a specific anatomical

location for this system, it has been suggested that the hippocampus might fulfill this integrative function (Eysenck & Keane, 2010, page 222; Berlingeri et al., 2008; Rudner, Fransson, Ingvar, Nyberg, & Ronnberg, 2007). The study that follows attempts to test this hypothesis, namely that the hippocampus plays an important role within this broader-based concept of working memory, using tasks that have been shown to predict individual differences in cognitive capacity. It is important to note that our aim was not to test specific hypotheses as to the nature of any deficit but to explore its generality across a broadly based behavioral test battery.

We do so by studying the performance of a single patient, Jon, with a clear deficit in hippocampal function, on a battery of tests that were explicitly designed to assess the various components of working memory. The battery (see Bayliss, Jarrold, Gunn, & Baddeley, 2003) was designed to tease apart and measure the various subcomponents of working memory, namely STM and processing efficiency, as well as their combination within working memory paradigms. In addition, the domain (verbal or visuospatial) of both storage and processing tasks was manipulated to examine the capacity for cross-modal storage and for the complex manipulation of visual and verbal stimuli. Importantly, Bayliss et al. (2003) demonstrated that performance on this battery reflected separate factors for speed of processing, separate visual and verbal STM systems, and a multimodal executive component. This latter component was correlated with performance on Raven’s matrices, reading comprehension and mathematics, validating these tasks as working memory span measures (see also Jarrold & Bayliss, 2007).

We compare Jon’s performance on this battery with the large undergraduate student group on which the initial analysis of the test battery was based. Our aim was, therefore, to investigate the possibility of a general involvement of the hippocampus in working memory.

Participants

Our study focused on Jon, an extensively studied patient with a substantial and highly specific hippocampal deficit. Jon’s case is described in detail by Baddeley, Vargha-Khadem, and Mishkin (2001) and Gadian et al. (2000). Briefly, he was born prematurely with breathing problems and severe apnea, requiring intubation and ventilation for the first 6 weeks of life. Memory problems were noted from the age of 5 years and persist, particularly when these involve recall. His score on the Rivermead Behavioural Memory Test (Wilson, Cockburn, & Baddeley, 1985) was 3, clearly impaired. His LTM performance on the California Verbal Learning Test II (Delis, Kramer, Kaplan, & Ober, 1987) was at the first percentile. He was severely impaired on the recall component of the Doors and People Test (Baddeley, Emslie, & Nimmo-Smith, 1994) but was in the normal range on recognition (Baddeley et al., 2001). In general, his recognition performance is at or slightly below

average, consistent with the assumption that he is unimpaired on the major familiarity component of recognition, but has little capacity to supplement this by recollection. MRI scans showed a reduction of about 50% in the volume of both left and right hippocampal regions, with no apparent pathology in the rest of the medial-temporal lobe (Gadian et al., 2000). He was 28 years old when tested.

We compared Jon's performance to a baseline group taken from the initial Bayliss et al. (2003) study. The group consisted of 48 students from Bristol University who were undertaking the tasks either for remuneration or as a course requirement. Jon was given the same tasks as employed in the Bayliss et al. study, and these were presented in the same manner as in the original article. Consequently, brief procedural details are given below, and the reader is referred to Bayliss et al. (2003) for full methodological information.

METHODS

Complex Working Memory Span

Four tasks were created by combining the demand for visual or verbal storage with visual or verbal processing. However, each was presented using the same display screen that showed an array of nine different colored squares scattered across a touch-sensitive VDU screen. For each presentation, four of the squares were "big" (3.4-cm square) and five were small (2.3-cm square). Three of the small squares and one of the big squares were also presented with a 3-D "bevel" effect. Each square had one of the numbers 1–9 shown in its center (see Figure 1).

Depending on the task (see below), participants performed a processing operation to locate and touch the target square. If participants had not located the target within 3 sec, it was highlighted automatically, but regardless of when the participant detected the target, the task moved on to the next presentation phase immediately

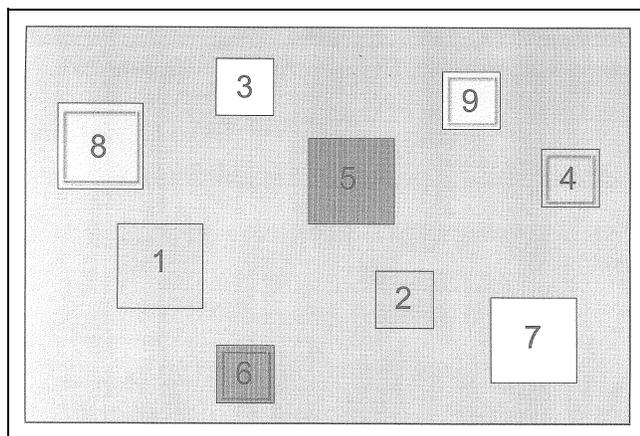


Figure 1. The visual display used in the working memory battery device by Bayliss et al. (2003). Each square was a different color.

after 4 sec had elapsed since the start of the current presentation phase. For each presentation of the display, the precise arrangement of the squares changed, although they were always shown in the same fixed nine locations.

A span procedure was used to administer the tasks, with a maximum of three trials at each of list lengths of 3–8. However, if participants were unable to recall all of the storage items in correct serial order on any of the trials at a given list length, then testing stopped at that point. Performance was scored as a mean "span score" that was derived from averaging the list length of the last three correctly recalled trials.

Visual Processing–Visual Storage: At each presentation, participants were required to find the single square that was both large and beveled, which they touched to signal that they had located it. Participants had to remember this location for subsequent recall before moving on to the next presentation phase. Final recall was by touching the locations of the target squares on the screen in the appropriate order.

Visual Processing–Verbal Storage: In this case, participants again searched for the single large square with the beveled edge on each presentation phase of the task, but having located this target they then had to remember the digit that was located within it for subsequent serial recall at the end of the trial.

Verbal Processing–Visual Storage: At each presentation phase, the participant heard 1 of 105 object names that pilot testing had shown to be reliably associated with a particular color (e.g., "banana" = yellow). They then located the square of that color and had to remember its location for subsequent serial recall at the end of the task.

Verbal Processing–Verbal Storage: Again a spoken word required identification of the appropriate colored square, but this time, it was necessary to remember the digit within the square. Again verbal serial recall of all of the digits that had been located was required at the end of the trial.

Speed of Processing

Two tasks assessed participants' ability to carry out the processing involved in the complex working memory span tasks, but in the absence of any concurrent storage load. Each involved a similar presentation screen to that employed in the complex span tasks but employed a visual search procedure, such that three, six, or nine of the nine possible squares were displayed, with unactivated squares remaining blank. On any trial, a mix of small and big squares was shown, with approximately half having a beveled edge. However, only one big square with a beveled edge was ever displayed on any trial.

In the visual processing task, the participant was required to identify the single large square with a beveled edge and respond by touching it. In the verbal processing task, a word that evoked one of the nine colors was spoken, whereupon the participant touched the appropriately

colored square. There were 27 trials in each task, 9 at each display size. Any RTs that were >2.5 *SD* longer than the mean RT for controls were Windsorized by replacement of the upper cutoff for that task, and performance was then calculated as the average of the median RT for each display size (see Bayliss et al., 2003).

Storage

Two tasks indexed the storage requirements of the complex span tasks in the absence of any processing load. The visual storage task took the form of a Corsi span test and employed a similar display to that used in the complex span tasks, with the exception that all squares were small squares. On any trial, the prespecified number of squares was highlighted sequentially for 1 sec with a 300-msec gap in between items. At the end of the trial, the participant touched the corresponding locations in correct serial order. The verbal storage task was a digit span task and involved the sequential visual presentation of digits in the center of the screen, with items displayed for 1 sec each with a 300-msec gap in between them. At the end of the trial, the participant was instructed to recall the presented digits in correct serial order.

In both tasks, list length was varied from 1 to a maximum of 9, with three trials at each level. Testing stopped when the participant was unable to successfully recall all of the items on at least one trial of a given level. The span score taken from each task was the average of the length of the last three correctly recalled trials.

Raven's Matrices

In addition, we measured fluid intelligence using Sets D and E of the standard progressive matrices (Raven, Court, & Raven, 1977).

RESULTS

We compared Jon's performance with the original sample of 48 university students slightly younger than Jon, but with more years of education. In many cases, they were performing the tasks for obligatory credit points and were likely to be less highly motivated than Jon, who is a very keen participant. For that reason, in addition to the mean

Table 1. Performance of Jon and Control Participants ($n = 48$) on Raven's Matrices (Max = 24) and the Storage-only Simple Span Tests

	Jon	Controls (<i>SD</i>)	Range
Raven's matrices (max = 24)	20	16.40 (4.17)	5.00–23.00
Digit span	7.33	6.24 (1.06)	4.33–8.33
Corsi span	7.33	6.41 (1.21)	3.33–8.66

Table 2. Performance of Jon and Controls on the Visual and Verbal Processing Tasks

	Jon	Controls (<i>SD</i>)	Range
Verbal processing	1594	1710 (172)	1261–2033
Visual processing	1483	1282 (185)	906–1744

Mean search time (msec) per stimulus array.

and standard deviation of their scores, we also include the range and use this as further information in interpreting Jon's performance.

Table 1 shows performance on Raven's matrices and the two storage (simple span) tasks. As expected, Jon scored highly on matrices, reflecting his above average intelligence. He performs approximately 1 *SD* above the student average. It is clear from the range however, that not all participants were performing at a level consistent with a highly selective undergraduate body. The main point to note therefore is that Jon is performing at the higher end of the student range. The same conclusion can be drawn from his digit span and Corsi span, both of which reflect a high level of performance.

Table 2 shows performance on visual and verbal processing. Jon made no errors on the visual processing task and one on the verbal task. Seven of his responses in the visual task and two in the verbal task were Windsorized because they were excessively long. In the verbal processing task, Jon's performance is approximately 1 *SD* faster than the control mean, and in the visual processing task, it is approximately 1 *SD* slower. However, both values are clearly well within the normal range.

Performance on the four complex working memory span tasks is shown in Table 3. The subtests are categorized on the basis of processing and storage modality. On three of the four complex span measures, Jon scores above the mean and toward the top of the range, whereas in the fourth verbal processing–visual storage condition, he is very marginally below the mean. Indeed, the most striking feature of Table 3 is the poor performance of the controls in the verbal–verbal condition. This involved associating a word with a color, locating the square of that color, and remembering the digit within it. The lower performance by the control group is assumed to reflect interference

Table 3. Performance of Jon and Controls on the Complex Working Memory Span Tasks (Max = 8)

Task		Jon	Controls (<i>SD</i>)	Range
Processing Mode	Storage Mode			
Visual	Visual	7.66	6.00 (1.35)	3.33–8.00
Visual	Verbal	6.33	6.06 (1.06)	3.00–8.00
Verbal	Visual	6.00	6.17 (1.37)	2.66–7.66
Verbal	Verbal	7.66	4.97 (0.95)	3.00–7.00

between verbal storage and verbal processing (cf. Jarrold, Tam, Baddeley, & Harvey, 2011). Jon appears to cope particularly well with this task, complementing his excellent performance on the overall battery.

DISCUSSION

Our results are clear in showing no suggestion of impaired performance on any of the tasks comprising our working memory battery. Indeed, the only task on which Jon shows any sign of being below average is on the visual processing search task, which is clearly not a working memory task. On the complex span measures, he tends to show above average performance. It is, of course, important to note that he has good visual and verbal STM (see Table 1) and is highly motivated, something that cannot necessarily be assumed of all the 48 students in the comparison group. However, he performs well, even when compared with the top of the range. Jon's excellent performance was at a similarly high level when tested on tasks involving binding in visual and verbal working memory (Baddeley, Allen, & Vargha-Khadem, 2010), in a study for which the control group comprised individual students from the University of York (Baddeley et al., 2010). Jon does appear to have an excellent working memory, as measured by these tasks.

Given the amount of evidence discussed in the introduction in favor of a role for the hippocampus in tasks involving visuospatial working memory, it is perhaps surprising that we find no evidence of a deficit in performance on our more general battery. Our study was not set up to investigate the nature of the visuospatial deficit, but given that it has both visual and spatial components, the absence of a deficit merits further discussion.

One possibility is that our tasks simply fail to tap the relational aspect of working memory that is seen by Olson et al. (Olson, Moore, et al., 2006; Olson, Page, et al., 2006) as crucially dependent on the hippocampus. At a superficial level at least, some of our tasks would appear to require relational coding, as in the case where a word is presented and used to cue a color, which maps onto a target within a complex array, which subsequently has to be recalled. Our data do not, of course, refute the relational coding hypothesis but do suggest a need for further development and specification. We should, however, also consider the possibility that earlier studies might be explained in other ways.

The first point to note is that many of the studies involve memory for faces, a type of material that does not feature strongly within the extensive working memory literature, perhaps because faces appear to behave in a rather different way from the spatial and verbal material that make up the main body of behavioral literature in this area. Warrington and Taylor (1973) found that perfect performance was limited to a single face, with no effect of a brief delay on performance. Once beyond a single item, they found impaired performance in a group of

amnesic patients, a result they interpret as reflecting a probable contribution of LTM to performance, even after a short delay.

The earliest models of STM assumed that processing involved a sequence of memory stores whereby information was first held in STM and only then passed on to LTM. Most current models, however, assume that immediate memory is likely to contain a contribution from both STM and LTM, with the contribution from STM decreasing after a delay, as described above. Furthermore, when the load exceeds span, the reliance on LTM is also likely to increase (see Baddeley et al., 2010, for further discussion). Consistent with this latter point is the observation of greater hippocampal involvement with higher loads in the study by Shrager et al. (2008). Although not necessarily conclusive, the evidence from Shrager et al. suggests that a contribution from LTM may be an important confounding factor in this area.

A further potential problem stems from the detailed characteristics of the patients on which some of these studies were based; in some cases, lesions extending beyond the hippocampus may complicate interpretation (see Baddeley et al., 2010, for further discussion of this point). However, this is unlikely to provide an adequate account of the difference between our results and earlier studies, some of which have included the patient on which our own conclusions are based.

So why should Jon show clear problems in some types of visuospatial processing and yet perform normally on our complex working memory tasks that include substantial visual and spatial components? Our earlier studies show that Jon is unimpaired on the capacity to bind the visual features of shape and color (Baddeley et al., 2010), whereas our own and other studies indicate normal performance on the Corsi block task (Vargha-Khadem, Gadian, & Mishkin, 2001), which, at a superficial level at least, would appear to depend on encoding the relationship between the blocks to encode and remember the sequence. A more direct and adequate test of the relational hypothesis is clearly desirable but will require a more detailed specification of the concept of relational coding.

One possible version of a relational coding explanation is offered by the proposed distinction between egocentric and allocentric space, with the former referring to space around the body, processed from the viewpoint of the perceiver, whereas the latter refers to space more broadly considered that can potentially be viewed from a range of different directions (Goodale & Milner, 1992), two different forms of visuospatial relationship. Milner and Goodale (1995) propose that egocentric processing does not require information about the object's identity, whereas allocentric processing involves "a kind of 'boot strapping' operation" requiring "an interplay between feature analysis and spatial coding." The results of this process can then "be incorporated into a 'cognitive map' that is independent of the observer's movements and viewpoint. The storage of such maps may involve structures such as the medial-temporal

cortex and the hippocampus" (Milner & Goodale, 1995, page 91).

The mapping of objects onto their location within a matrix is, of course, the task shown by Olson and colleagues to be impaired in their patients with hippocampal damage (Olson, Moore, et al., 2006; Olson, Page, et al., 2006). Allocentric processing is also central to the task used by Hartley et al. (2007), in which the participant sees a representation of an array of mountains and then must recognize it from a different viewpoint, a task that Jon finds extremely difficult, leading Hartley, King, and Burgess (2003) to conclude that Jon's "topographical memory (and thus navigation) normally depends on allocentric processes that are damaged in his case." They also suggest that "many spatial and mnemonic functions may depend on snapshot-like representations (intact in Jon) in the medial-temporal lobe outside the hippocampus proper" (Hartley et al., 2003, page 159). It is also possible that the paradigm used by Hannula et al. (2006), in which faces must be linked to scenes, might also encourage an allocentric coding strategy. At this point, however, we cannot rule out the possibility that the hippocampus plays a role in some more general form of relational processing that is yet to be specified.

In conclusion, although existing evidence does suggest that the hippocampus plays a role in a range of tasks involving visuospatial processing, many of which almost certainly do involve working memory, our own data suggest that this is not a general deficit. The hippocampus does not appear to be necessary for performance on the type of complex working memory tasks that play a central role in current behavioral studies of individual differences in cognitive capacity.

Acknowledgments

We thank Jon for his enthusiastic participation, Mortimer Mishkin and Tom Hartley for helpful discussion, and two anonymous referees for their constructive comments on an earlier draft. F. V. K. is grateful for support from Medical Research Council grant G0300117/65439.

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