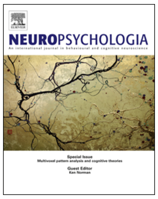
Neuropsychologia 59 (2014) 74–84

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia



Item-location binding in working memory: Is it hippocampus-dependent?

Richard J. Allen [a,*], Faraneh Vargha-Khadem [b], Alan D. Baddeley [c]

[a] Institute of Psychological Sciences, University of Leeds, Leeds, LS2 9JT, UK
[b] Institute of Child Health, University College London, UK
[c] Department of Psychology, University of York, UK

ARTICLE INFO

Article history:
Received 23 January 2014
Received in revised form
16 April 2014
Accepted 19 April 2014
Available online 28 April 2014

Keywords:
Working memory
Binding
Hippocampus
Long-term memory

ABSTRACT

A general consensus is emerging that the hippocampus has an important and active role in the creation of new long-term memory representations of associations or bindings between elements. However, it is less clear whether this contribution can be extended to the creation of temporary bound representations in working memory, involving the retention of small numbers of items over short delays. We examined this by administering a series of recognition and recall tests of working memory for colour-location binding and object-location binding to a patient with highly selective hippocampal damage (Jon), and groups of control participants. Jon achieved high levels of accuracy in all working memory tests of recognition and recall binding across retention intervals of up to 10 s. In contrast, Jon performed at chance on an unexpected delayed test of the same object-location binding information. These findings indicate a clear dissociation between working memory and long-term memory, with no evidence for a critical hippocampal contribution to item-location binding in working memory.

1. Introduction

The hippocampus has been consistently identified as having a key role in associative or relational memory, that is, memory for how different elements within episodes are bound together (e.g. Cohen & Eichenbaum, 1993; Cohen et al., 1999; Horner et al. 2012; Mayes, Montaldi, & Migo, 2007; Moses & Ryan, 2006). While there is still debate concerning the precise forms of associative processing in which the hippocampus is involved, these claims typically refer to long-term memory formation, often requiring encoding of numerous associated features and retention over substantial delays. For example, Moses and Ryan (2006) argue for a hippocampal role in the formation of long-term relational associations between distinct elements, as opposed to the rapid creation of unitary representations over the short-term. These approaches typically assume that binding within working memory is independent of the hippocampus and wider medial temporal lobes (MTL), reflecting a commonly held distinction drawn between short-term memory and long-term memory (e.g. Squire, Stark, & Clark, 2004).

This view has been challenged more recently, however (see Jonides et al., 2008; Kumaran, 2008; Ranganath & Blumenfeld, 2005; for reviews). Studies have suggested that patients with MTL damage show impairments on tests of visual working memory (Ezzyat & Olson, 2008; Olson, Moore, Stark, & Chatterjee, 2006). More specifically, it has been claimed that the hippocampus might have a key role in binding in working memory. For example, Henke (2010) suggested that the hippocampus is important in the rapid formation of associations, for short-term retention as well as long-term memory. In line with this, Hannula, Tranel, and Cohen (2006) observed that hippocampal amnesic patients showed deficits on memory for object-location associations within complex 3D scenes (see also Hannula & Ranganath, 2008; Yee, Hannula, Tranel, & Cohen, 2014). Similarly, Olson, Page, Moore, Chatterjee, and Verfaellie (2006) examined MTL patients' recognition memory for sequences of three objects, locations, and object-location conjunctions within a simple 3 × 3 grid. Their patient group showed particular impairments on the object-location binding trials, relative to controls (though this decrement was somewhat more consistent for 8 s than 1 s retention intervals).

Imaging studies have complemented the apparent patterns of impairment on binding tasks in hippocampal patients. For example, Mitchell, Johnson, Raye, and D'Esposito (2000; see also Giovanello & Schacter, 2011) proposed a prefrontal-hippocampal circuit to be involved in the binding of object to location in working memory, and to be responsible for deficits they observed in healthy aging on this task. Piekema, Kessels, Mars, Petersson, and Fernández (2006) examined maintenance of three letter-colour or letter-location associations over variable delays of 9–20 s, and found right-lateralized hippocampal activation in the

---

* Corresponding author.
E-mail address: r.allen@leeds.ac.uk (R.J. Allen).

http://dx.doi.org/10.1016/j.neuropsychologia.2014.04.013
0028-3932/

letter-location recognition task, but not for letter-colour binding. However, Piekema et al. (2006) noted the possibility that the hippocampal activation they observed in object-location binding may actually represent active formation of long-term memory traces, rather than a working memory contribution per se. In line with this, Schon et al. (2004); see also Axmacheret al., 2008) demonstrated that MTL involvement in working memory predicts later long-term memory formation. More recently, Piekema and colleagues failed to observe increased MTL activation in face-location binding (Piekema, Rijpkema, Fernánde, & Kessel 2010), instead identifying parietal and prefrontal areas as being critical (though see Luck et al. 2010). Jeneson and Squire (2012) have recently developed further the argument that evidence for a hippocampal contribution to binding in working memory may actually reflect LTM involvement. They claim that imaging and patient studies previously suggesting a working memory-based involvement have implemented experimental techniques that increase LTM contributions, through a combination of the type of material, memory load, complexity, and retention duration used. In support of this, Shrager, Levy, Hopkins, and Squire (2008) found recognition memory deficits on object-location binding tasks in MTL patients only at the highest memory load (six items, rather than three items), thus exceeding working memory capacity (e.g. Cowan, 2001). Similarly, Jeneson, Maudlin, and Squire (2010) examined MTL patients' ability to relocate objects to their locations in a real-world task, and found that impairments emerged once again only with higher memory loads (though see Watson et al., 2013).

It is therefore possible that hippocampal involvement in tasks that ostensibly measure binding in working memory may be more likely to emerge when these tasks have a substantial LTM component. Given the conflicting evidence that exists, however (e.g. Watson et al., 2013; Yee et al., 2014), it is important to explore further whether evidence can be found to indicate that item-location binding within working memory is hippocampus-dependent. The current study attempts to address this, examining the ability of a patient with selective hippocampal damage on tasks that require binding of item to location in working memory while minimizing potential LTM involvement. We have previously examined this patient (Jon) on tasks measuring binding between shape and colour (and also chunking within sentences), and found him to be intact on these measures (Baddeley, Allen, & Vargha-Khadem, 2010). While this supports the notion that the hippocampus is not crucial for certain forms of working memory binding, the tasks used in that study were not primarily spatial in nature, and did not directly assess binding to location. As the hippocampus is widely accepted to have an important role in processing spatial information (e.g. Burgess, Maguire, & O'Keefe, 2002; O'Keefe & Nadel, 1978), it is possible that binding explicitly involving such information loads on this area (e.g. Postma, Kessels, & van Asselen, 2008). We examined this question using a range of tests (recognition, reconstruction, cued recall) measuring working memory for colour-location binding (Studies 1 and 2) and object-location binding (Study 3). As our primary focus in the current work was to establish whether hippocampal damage impinges on item-location binding within working memory, each study used memory loads typically considered to be within working memory capacity of 3–4 items (e.g. Cowan, 2001). In addition, Study 3 directly contrasted accuracy in working memory with performance on a later long-term memory test for the same binding information.

2. Case description

Jon was aged 34 years at time of Study 1, and 35 years during Studies 2 and 3. He was born prematurely at 26 weeks of gestation, weighing less than 1 kg, and suffered repeated breathing problems during the first 6 weeks of life (requiring intubation and positive pressure ventilation for severe apnoea), leading to hypoxic-ischaemic injury (Gadian et al. 2000). His memory problems were first noted at five years of age and continue to be prominent, alongside steady improvement and normal development in other domains.

Jon shows frequent prospective memory problems, for both regular and novel events, and is typically unable to recount the details of events earlier in the day. He also has spatial awareness problems and shows difficulty in reliably finding his way, consistent with his hippocampal deficit. In line with this, he demonstrates impairment in empirical investigations measuring recall of spatial layouts of an explored virtual reality town (Spiers, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001), and on forced choice recognition tasks concerning relational configurations within complex three-dimensional scenes when viewpoint is shifted, even at short delays (Hartley et al. 2007; King et al., 2002), though these deficits generally only emerge with larger memory loads. Jon also performs poorly on a range of standardized memory tests. Thus, whereas his immediate memory supraspan on the California Verbal Learning Test: II (Delis, Kramer, Kaplan, & Ober, 1987) was at the 73rd percentile, his LTM recall (as reflected in list learning, immediate and delayed recall) was at the 1st percentile on all measures. In terms of visual memory, Jon's immediate Rey Figure copy score was normal at 24/36 but he was severely impaired after a delay, with no scoreable reproduction (Baddeley, Vargha-Khadem, and Mishkin 2001; see also Fig. 1D in Vargha-Khadem et al. 1997). His profile score on the Rivermead Behavioural Memory Test (Wilson et al., 1999) was 3, in the severely impaired range.

In comparison to his performance on recall measures, however, his recognition performance is relatively well preserved. Baddeley et al. (2001) found that Jon achieved a set of recall scores at the 5th percentile on the Doors and People visual and verbal tests (Baddeley, Emslie, & Nimmo-Smith, 1994), alongside recognition scores in the 50th–75th percentile range. Similarly discrepant performance levels on recall and recognition tests were also found in empirical investigations using verbal material and news videos. More recently, a slightly lower level of performance on other empirical tests of delayed recognition (for encyclopaedic facts) has been observed (Gardiner, Brandt, Vargha-Khadem, Baddeley, & Mishkin, 2006). This general pattern of severely impaired delayed recall alongside relatively intact recognition is consistent with the assumption that recognition draws on two separate processes – episodic recollection and familiarity judgments (Yonelinas, 1999) – with Jon being more adept at the latter (Brandt, Gardiner, Vargha-Khadem, Baddeley, & Mishkin, 2009; Düzel, Vargha-Khadem, Heinze, & Mishkin, 2001; Maguire, Vargha-Khadem, & Mishkin, 2001)

These deficits prevail despite Jon's full scale IQ of 118 (high average) as measured at age 33, and his consistently normal performance on standardized tests of reading, syntax, semantics and vocabulary (see Baddeley et al. 2001; Vargha-Khadem et al., 1997). His performance on working memory tasks is at the level of normal-to-high functioning control participants. This has been as observed on standard neuropsychological tests such as forwards and backwards digit and Corsi block recall (Vargha-Khadem et al., 1997). Convergent findings have also emerged in empirical investigations using immediate recognition memory for coloured shapes and recall of short sentences (Baddeley et al., 2010) and simple and complex span tasks measuring verbal, visuospatial, and relational memory (Baddeley, Jarrold, & Vargha-Khadem, 2011).

Direct measurement of Jon's MRI scans indicated a reduction of about 50% in the volume of both left and right hippocampus, with no evident pathology in the rest of the medial temporal lobe (Gadian et al. 2000; Vargha-Khadem et al., 1997).