Neuropsychologia 48 (2010) 1089–1095

Contents lists available at ScienceDirect

Neuropsychologia

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

Is the hippocampus necessary for visual and verbal binding in working memory?

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ARTICLE INFO

Article history:
Received 13 May 2009
Received in revised form
25 November 2009
Accepted 7 December 2009
Available online 16 December 2009

Keywords:
Short-term memory
Chunking
Amnesia
Color-shape binding
Verbal redundancy

ABSTRACT

A series of experiments test the recent claim that the hippocampus is necessary for the binding of features in working memory. Some potential limitations of studies underlying this claim are discussed, and an attempt is made to further test the hypothesis by studying a case of developmental amnesia whose extensively investigated pathology appears to be principally limited to the hippocampus, and who shows the expected deficit in episodic long-term memory. One series of experiments studied the short-term visual binding of color and shape under conditions ranging from simple presentation of colored objects through the more demanding task of combining the features when separated in space, or in time. A second set of experiments studied the capacity to use sentence structure to bind words into chunks in short-term verbal memory. Hippocampal pathology did not lead to a decrement on any of these tasks, suggesting that the hippocampus is not essential for short-term binding in working memory.

We process information about the visual world through a series of separate channels, which independently register shape, color, brightness and spatial location. And yet we see a world of integrated visual objects. This clearly requires a process that is capable of binding together the channels into a coherent integrated percept. At a more general level such events are bound into broader episodes, which in turn may be bound into our autobiographical long-term memory.

Analysis of the binding process or processes has therefore become a focus of considerable interest in recent years at a number of levels, notably including the perceptual (Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001; Wheeler & Treisman, 2002) and the linguistic (Allen & Baddeley, 2008; Baddeley, Hitch, & Allen, 2009; Cowan, 2005). The capacity to bind features into integrated episodes has, for example been suggested as one of the prime functions of consciousness, providing the further advantage of serving as a general workspace that facilitates complex cognitive processes such as comprehension and reasoning (Baars, 1997, 2002). A similar function has been proposed by Baddeley (2000, 2007) who attributes it to the operation of the episodic buffer, a recently proposed component of the multicomponent model of working memory that was initially described by Baddeley and Hitch (1974).

A second and possibly related form of binding involves long-term memory and the capacity to link an episodic memory to its context. The ability to retrieve information about a specific event, as opposed to generalized information from multiple events, requires that the memory of a given individual episode can be separately specified and retrieved. One method of doing this is to bind the episode to a rich context which can then be used to access that specific memory. There is abundant evidence to suggest that the hippocampus is involved in this process (Vargha-Khadem et al., 1997; Squire, 2004; Winocur & Mills, 1970). This assumption is consistent with both behavioral evidence, and with the anatomical evidence that suggests that the hippocampus is richly connected to a range of structures involved in perception, attention and long-term memory (Suzuki & Amaral, 1994). Integration of information from these diverse sources is likely to be necessary for multidimensional episodic encoding (Squire, 2004). It has been suggested that such anatomical connections would also make the hippocampus an appropriate structure for the perceptual and linguistic binding attributed to working memory, offering a parsimonious interpretation whereby a number of different functions within long-term and working memory can be explained in terms of a single structure (Ezzyat & Olson, 2008; Hannula, Tranel, & Cohen, 2006; Olson, Page, Sledge-Moore, Chatterjee, & Verfaellie, 2006)

A case for the role of the hippocampus in perceptual binding is made by Olson, Sledge-Moore, Stark, & Chatterjee (2006) who studied a group of patients with hippocampal damage, using a task that required them to bind line drawings of objects to specific locations. They presented their patients with three successive stimuli, each comprising a 3×3 matrix with a line drawing of an object in one of the matrix cells. The patients were then tested for memory of

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0028-3932/$ – see front matter © 2010 Published by Elsevier Ltd.
doi:10.1016/j.neuropsychologia.2009.12.009

the location, or the object, or the combined object and location, the binding condition, after delays of 1 or 8 s. They carried out two experiments, both of which showed their patients to have a particular impairment in the condition demanding object-location binding. Olson et al. then divided their group into two subgroups, those with, and those without extra-hippocampal damage. Those patients for whom damage appeared to be limited to the hippocampus were not significantly less impaired than patients with more extensive lesions, from which they conclude that the crucial factor in the binding deficit is damage to the structure that was compromised in both groups, namely the hippocampus.

There are however a number of reasons why the conclusions drawn should be treated with caution. The task selected has two potential limitations. The first is that the choice of location as one of the features to be bound can be criticized on the grounds that spatial binding may not be typical of feature binding in general. There is extensive evidence for a particular involvement of the hippocampus in spatial processing, extending back to the early work of O'Keefe and Dostrovsky (1971) and O'Keefe and Nadel (1978). Subsequent human neuroimaging work also implicates the hippocampus in allocentric spatial processing (Doeller, King, & Burgess, 2008; Hartley, Maguire, Spiers, & Burgess, 2003). Finally, a neuroimaging study by Piekema, Kessels, Mars, Petersson & Fernández (2006) observed that while the binding of an object to a location involved the hippocampus, the binding of color to shape did not. It could therefore be argued that the decrement observed by Olson, Sledge-Moore, et al. (2006) stems not from binding per se, but from the spatial element of the particular binding task selected. This suggests the need to replicate using non-spatial binding tasks.

A second issue concerns the likelihood that the matrix binding task selected, involves a long-term memory component. Indeed, such a task is used as a standardized test of long-term memory deficit (Bucks, Willison, & Byrne, 2000). It could therefore be argued that the Olson, Sledge-Moore, et al. (2006) results are simply demonstrating the widely accepted association between amnesia, the hippocampus and long-term episodic binding, rather than demonstrating the importance of the hippocampus for binding in working memory.

A final point of potential criticism stems from the patient sample used, where very little anatomical evidence is provided for the specificity of the lesions of the various patients. In particular, it is crucial that those patients for whom the damage is claimed to be purely hippocampal are not suffering from more extensive lesions. This is also a potential problem with two other studies from Olson's group (Ezzyat & Olson, 2008; Olson, Page, et al. (2006)), both of which focus on three patients who clearly do have relatively widespread damage, and a level of verbal intelligence that it marginally significantly lower than their control group ($p = .065$). Hence, although they clearly observe impaired performance in this group, there is a danger that this could be attributable to the presence of brain damage of any type, rather than being specific to the hippocampus.

One further study is cited by Ezzyat and Olson (2008) as providing evidence for the role of the hippocampus in working memory. Hannula, Tranel and Cohen (2006) studied the capacity of amnesic patients to learn to associate a single face with a complex visual scene, finding impairment even at short delays. However, as Hannula et al. acknowledge, long-term memory may contribute to performance, even at brief delays, potentially explaining the deficit in their amnesic patients who may be showing a deficit in the long-term rather than the working memory component.

This point is emphasized in a recent study by Shrager, Levy, Hopkins, and Squire (2008), who use a concurrent task procedure to disrupt working memory. They argue that a comparison between performance with and without the concurrent task should allow the relative contribution of long-and short-term components both to be assessed. If the task is followed by a delay containing a rehearsal-preventing task, this should eliminate the short-term component while leaving the long-term component relatively intact. Shrager et al. studied eight carefully selected patients with clear hippocampal damage and moderate or severe amnesia. In one study, patients were required to recognize either three names or a single face either immediately or after a 14 s delay. The delay period was either unfilled, or filled with distracting material of either a verbal or a visual nature. In the case of names, the patient and control groups were equivalent after an unfilled delay. There was however a very substantial decrement in the hippocampal group when the delay was filled with a concurrent verbal task that prevented the use of working memory. No such decrement occurred for the control group who could presumably supplement the disrupted short-term component from their preserved long-term memory. In the case of face memory, the controls showed an advantage over the patients, as in previously described Olson studies. However, performance was not impaired by the concurrent task, suggesting that unlike the verbal task, face memory was dependent on long-term memory.

A further study by Shrager, Levy, Hopkins, and Squire (2008) used the object location task employed by Olson, Page, et al. (2006) again comparing retention of three and six object locations. With an unfilled delay, the two groups were equivalent in performance with a three object load, whereas a substantial impairment was found in the case of the patients when rehearsal was prevented by a concurrent task, leading Shrager et al. to conclude that the performance of the Olson, Sledge-Moore, et al. (2006) and Olson, Page, et al. (2006) patients was dependent on a combination of impaired LTM and preserved working memory, suggesting that it was the long-term component rather than working memory that was impaired following their hippocampal damage.

However, a single disconfirming investigation is unlikely to be regarded as sufficient to settle the issue. We therefore describe a study that aims to avoid some of the difficulties raised by the Olson studies and the complexities of dual task methodology, focusing on a single well-studied case with a limited and clearly defined hippocampal deficit. We use methods that have been developed to study binding of both perceptual and linguistic features in working memory, attempting to ensure that our results do not depend heavily on either spatial or long-term memory. Our study falls into two parts, the first is concerned with the binding of shape and color, and the second with the impact of linguistic factors on the binding of words within sentences.

1. Case description

Jon, who was 28 years old at time of testing, was born prematurely at 26 weeks of gestation. He weighed less than 1 kg, suffered breathing problems and during his first 6 weeks of life required incubation and positive pressure ventilation for severe apnea (Gadian et al., 2000). He showed steady improvement and normal development, but about the age of five, memory problems were noted, and have since continued to be prominent. Consistent with his hippocampal deficit, Jon has difficulty in reliably finding his way. He is impaired on complex spatial tasks such as judging the appearance of a three-dimensional scene when the viewpoint is changed (King, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2002), and recalling the spatial layout of an explored virtual reality town (Spiers, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001). He also tends to forget where belongings are normally kept and makes many prospective memory errors, even for regularly scheduled events. He has difficulty remembering everyday events such as TV programmes just seen and is typically