Acta Psychologica 132 (2009) 221–227

Contents lists available at ScienceDirect

Acta Psychologica

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

Egocentric-updating during navigation facilitates episodic memory retrieval

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ARTICLE INFO

Article history:
Received 12 January 2009
Received in revised form 6 July 2009
Accepted 8 July 2009
Available online 6 August 2009

PsycINFO classification:
2343/2340

Keywords:
Spatial representation
Allocentric
Perspective dependent
Autonoetic consciousness
Hippocampus

ABSTRACT

Influential models suggest that spatial processing is essential for episodic memory [O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. London: Oxford University Press]. However, although several types of spatial relations exist, such as allocentric (i.e. object-to-object relations), egocentric (i.e. static object-to-self relations) or egocentric updated on navigation information (i.e. self-to-environment relations in a dynamic way), usually only allocentric representations are described as potentially subserving episodic memory [Nadel, L., & Moscovitch, M. (1998). Hippocampal contributions to cortical plasticity. *Neuropharmacology, 37*(4–5), 431–439]. This study proposes to confront the allocentric representation hypothesis with an egocentric updated with self-motion representation hypothesis. In the present study, we explored retrieval performance in relation to these two types of spatial processing levels during learning. Episodic remembering has been assessed through Remember responses in a recall and in a recognition task, combined with a "Remember-Know-Guess" paradigm [Gardiner, J. M. (2001). Episodic memory and autonoetic consciousness: A first-person approach. *Philosophical Transactions of the Royal Society B: Biological Sciences, 356*(1413), 1351–1361] to assess the autonoetic level of responses. Our results show that retrieval performance was significantly higher when encoding was performed in the egocentric-updated condition. Although egocentric updated with self-motion and allocentric representations are not mutually exclusive, these results suggest that egocentric updating processing facilitates remember responses more than allocentric processing. The results are discussed according to Burgess and colleagues' model of episodic memory [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*(1413), 1493–1503].

1. Introduction

Data drawn from amnesic patients with hippocampal lesions and from the discovery of hippocampal "place cells", have led to the assumption that episodic memory and spatial processing are linked (Holdstock et al., 2000; King, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2002; O'Keefe & Dostrovsky, 1971; O'Keefe & Nadel, 1978; Spiers, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001; Spiers et al., 2001). To date, however, little is known about how they are functionally related and more specifically which spatial processing underlies Episodic Memory.

Episodic memory was originally described as the memory for information located in time and space. This definition emphasized the access to "what", "when" and "where" information on the event. This definition of Episodic memory has greatly evolved since then. Tulving (2002) now considers that the subjective sense of re-experiencing an event, called autonoetic consciousness, is the hallmark of episodic memory. Autonoetic consciousness relies on the binding of the "what", "where", and "when" of the information learned (De Goede & Postma, 2008; Meiser, Sattler, & Weisser, 2008). To a larger extent, this ability allows one to mentally navigate backwards or project forward along something akin to a personal "movie" (Wheeler, Stuss, & Tulving, 1997).

Here, we distinguish three types of spatial representations, egocentric (i.e. code for static object-to-self relations), allocentric (i.e. code for static object-to-object relations) and egocentric updated with self-motion (i.e. code for self-to-environment relations in a dynamic fashion), that could be linked to long-term memory in different ways (for a recent review see Postma, Kessels, & van Asselen, 2008).

Due to permanent changes in the subjects' localisation and orientation, the static or iconic-egocentric representations (King, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2002), are generally seen as inefficient for long-term memory storage of an episode. In contrast, allocentric representations are considered more stable, independent of subject movement (Burgess, Becker, King, & O'Keefe, 2001). Nadel and Moscovitch (1998), and O'Keefe and Nadel

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doi:10.1016/j.actpsy.2009.07.003

(1978) proposed that the hippocampus would be able to bind all the neocortical representations related to an episode by providing a spatial scaffold for the episode. This theory posits that episodic memory relies on spatial knowledge acquired as a map, thus on relations existing between objects (i.e. allocentric representations). As previously mentioned numerous studies have reported a coincidence of impairments in topographical and episodic memory following hippocampal lesions (Burgess, 2006; Holdstock et al., 2000; Hort et al., 2007; King, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2002; Spiers, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001; Spiers et al., 2001). Although, to our knowledge only two studies have clearly focused their interest on allocentric and egocentric deficits in relation with episodic memory impairments after hippocampal lesions (Holdstock et al., 2000; King, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2002). These experiments opposed iconic-egocentric (i.e. visual pattern matching tasks) to a shifted-view condition, and supported the idea that iconic-egocentric representation cannot be proposed to functionally underlie episodic memory. As acknowledged by its authors, the shifted-view condition might have been concurrently solved using an allocentric processing or an egocentric-updated processing.

In fact, spatial memory cannot be reduced to only allocentric and iconic-egocentric representations (Avraamides & Kelly, 2008; van Asselen et al., 2006; Waller, Lippa, & Richardson, 2008). Behavioural, electrophysiological and fMRI data suggest that it could be useful to consider another type of representation involved in navigation (Burgess & O'Keefe, 1996; Farrell & Robertson, 1998; Maguire et al., 2003; Mellet et al., 2000; Nardini, Burgess, Breckenridge, & Atkinson, 2006; Wang & Spelke, 2000; Whishaw, McKenna, & Maaswinkel, 1997). This egocentric updated with self-motion representation would be automatically constructed from both ideothetic (i.e. sensorial information extracted from stable stimuli) and allothetic information (i.e. sensorial information acquired through self-movement). This representation would remain egocentric in the sense that it uses a coordinate system centred on the observer. Nevertheless, it would encode self-to-environment relations in a dynamic fashion due to continuous vestibular, proprioceptive, and visual flow inputs, during navigation.

Moreover, although episodic information of an event can be simultaneously represented in an allocentric and an egocentric way, allocentric representations alone cannot account for self-centred visuo-spatial re-experiencing, in a direct way (Burgess, Becker, King, & O'Keefe, 2001). A translation from the allocentric reference frame to an egocentric reference frame would be necessary. Crawley and French (2005) explored the link between points of view and autonoetic consciousness by using the "Remember-Know-Guess paradigm" (RKG) (Gardiner, 2001; Gardiner, Ramponi, & Richardson-Klavehn, 1998). They observed that Remembered (R) information induced viewer-centred recall, whereas Known (K) information was independent of viewer perspective, like allocentric relations. R information refer to event retrieved through an "autonoetic consciousness" of the original event, a central feature of episodic memory. Instead, K information induce no re-experiencing of the event and are related to the semantic memory. In a similar vein, congruent body posture has been observed to facilitate access to and retention of remote episodic memories (Dijkstra, Kaschak, & Zwaan, 2007). Thus, episodic memory appears to be linked with viewer-centred recall.

We acknowledge that egocentric-updated information could simply reflect the possible translation of allocentric information representations into egocentric iconic ones. Nonetheless, we wondered if a memory of allocentric processing alone could account for episodic memories or if egocentric-updated processing performed during learning is crucial for re-instantiating an episodic memory. Indeed, if iconic-egocentric representations do not underlie long-term memory, it remains unclear in the literature which of these last two spatial representations, allocentric or egocentric updated with self-motion, plays a more important role for long-term episodic memory. The aim of this experimental study is to directly compare these two types of spatial representation by testing whether egocentric-updated processing helps subsequent episodic remembrance more than allocentric processing alone.

To investigate this issue, we designed two experimental conditions emphasizing either object-to-object processing (i.e. allocentric) or dynamic self-to-environment processing (i.e. egocentric-updated) by changing the spatial context-task performed during incidental encoding of items into long-term memory. Free recall, and recognition of item names were then measured 4 h later. This global memory performance emphasized only the "what" component of episodic memories. To strictly assess episodic memory, a "Remember-Know-Guess" paradigm was used to insure that the measured effects were associated with autonoetic consciousness (i.e. R responses). An additional source-monitoring task was proposed after the recognition task. By evaluating memories of the stimuli encoding context, this task provides further corroboration on the effects measured through R responses. In the present study, we attempted to disentangle two hypotheses describing the link between episodic memory and spatial processing. The first hypothesis that we will call the allocentric hypothesis, supposes that allocentric representations are sufficient and essential for episodic memory (Nadel & Moscovitch, 1998). The allocentric hypothesis presumes that learning words while emphasizing allocentric representation rather than egocentric updated with self-motion representation facilitates retrieval performance, especially when related to autonoetic consciousness (i.e. R responses). The second hypothesis, that we will call the egocentric-updated hypothesis, predicts the opposite pattern of results (i.e. retrieval facilitation in the egocentric-updated condition, especially for R responses). This hypothesis does not exclude a potential functional implication of the allocentric representation within the Episodic Memory.

2. Materials and methods

In the first part of the following procedure, participants learnt to spatially process the environment layout then they spatially processed the layout when it included test pictures (which were here learnt incidentally). In the second part, 4 h later, they were unexpectedly tested on recall and recognition for the pictures alone (and not on any of the spatial relations that appeared to be the test in the first part).

2.1. Participants

Twenty-two undergraduate and graduate students in psychology (1 male and 21 females), aged from 18 to 37 years (mean age of 22 years and 2 months) participated in the experiment for course credit. They all gave written informed consent to the experiment.

2.2. Stimuli

To capture the true dynamism of navigation while maintaining an appropriate degree of experimental control, participants accessed the environment via pre-processed data, instead of interacting freely with a real environment (see Fig. 1a).

The items-to-be-remembered consisted of 28 names and pictures of birds, matched with 28 other bird names for the recognition task. These items were embedded in "close viewpoint object" images by placing them on a goal object (see Fig. 1b). "Contextual snapshots" were taken from a more distant viewpoint, to provide contextual information on the "goal object" (see Fig. 1c).