



Semantic congruence affects hippocampal response to repetition of visual associations



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ARTICLE INFO

Article history:

Received 31 December 2015

Received in revised form

19 July 2016

Accepted 19 July 2016

Available online 20 July 2016

Keywords:

fMRI

Relational memory

Binding

Predictive coding

Novelty

ABSTRACT

Recent research has shown complementary engagement of the hippocampus and medial prefrontal cortex (mPFC) in encoding and retrieving associations based on pre-existing or experimentally-induced schemas, such that the latter supports schema-congruent information whereas the former is more engaged for incongruent or novel associations. Here, we attempted to explore some of the boundary conditions in the relative involvement of those structures in short-term memory for visual associations. The current literature is based primarily on intentional evaluation of schema-target congruence and on study-test paradigms with relatively long delays between learning and retrieval. We used a continuous recognition paradigm to investigate hippocampal and mPFC activation to first and second presentations of scene-object pairs as a function of semantic congruence between the elements (e.g., beach-seashell versus schoolyard-lamp). All items were identical at first and second presentation and the context scene, which was presented 500 ms prior to the appearance of the target object, was incidental to the task which required a recognition response to the central target only. Very short lags 2–8 intervening stimuli occurred between presentations. Encoding the targets with congruent contexts was associated with increased activation in visual cortical regions at initial presentation and faster response time at repetition, but we did not find enhanced activation in mPFC relative to incongruent stimuli at either presentation. We did observe enhanced activation in the right anterior hippocampus, as well as regions in visual and lateral temporal and frontal cortical regions, for the repetition of incongruent scene-object pairs. This pattern demonstrates rapid and incidental effects of schema processing in hippocampal, but not mPFC, engagement during continuous recognition.

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1. Introduction

Many lesion and functional neuroimaging studies indicate that the hippocampus is essential to the encoding and retrieval of relational information, operating to bind and reintegrate elements of an experience such as 'foreground' items and 'background' contexts into a coherent episode (for reviews, see (Diana et al., 2007; Eichenbaum and Cohen, 2014; Ranganath, 2010)). However, the engagement of this hippocampal-dependent binding process may be altered when the experimental or stimulus context provides semantic constraints, such as an appropriate schema, to facilitate encoding or remembering the target (for reviews, see (Preston and Eichenbaum, 2013; van Kesteren et al., 2012)). In such situations,

hippocampal activation is reduced compared to when context and targets are incongruent (van Kesteren et al., 2013) and novel associations learned in the context of a spatial schema rapidly became independent of the hippocampus (Tse et al., 2007). Thus, having pre-existing or experimentally induced schematic context appears to change the degree to which the hippocampus is engaged during associative learning. Conversely, those and other studies suggest that the mPFC is more engaged or critical for encoding and retrieving information or associations that are congruent with pre-existing or newly formed schema (Ghosh et al., 2014; van Kesteren et al., 2010b), suggesting a complementary interplay between medial temporal lobe (MTL) and mPFC representations or processes (Preston and Eichenbaum, 2013; van Kesteren et al., 2012). This differential pattern of neural engagement may help resolve the seeming paradox that memory is enhanced for new information that can be easily assimilated within an existing schema or body of knowledge (Anderson, 1981; Bartlett, 1932; Murty et al., 2013; Poppenk et al., 2010) but also when

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novel or distinctive stimuli are encountered (Kishiyama and Yonelinas, 2003; Tulving and Kroll, 1995).

The schema effects that support this model of hippocampal-mPFC interplay have typically been observed in study-test paradigms in which there is a significant delay (from minutes to days) between encoding and retrieval. Indeed many of the findings have been interpreted with a view toward explaining long-term consolidation of memories in neocortical networks (Winocur and Moscovitch, 2011). Further, the experimental tasks have typically involved direct attention to and intentional linking of the to-be-learned items/associations and the context schema. We were interested here in exploring some of the boundary conditions of this complementary neural engagement. Specifically, we investigated the effects of semantic congruence in a continuous recognition paradigm in which targets repeated at very brief delays (repetition lag of 2–8 intervening items) and there was no explicit requirement to make use of the context. Hippocampal-dependent binding of novel associations has been shown to occur quite rapidly (Hannula et al., 2006; Olson et al., 2006; Yee et al., 2014) and even in the absence of awareness or directed attention to the context that forms part of that novel association (Mayes, 2014; Olsen et al., 2012; Rugg et al., 2012). However, there is little empirical data as to whether the modulation of that hippocampal engagement by congruence follows a similar trajectory. Of note, the concept of memory schema has been applied to a range of different types of knowledge structures, from abstract or gist representations to networks of related events that preserve unit details, and experimental applications range from proverbs to prolonged movie segments to relatively arbitrary A-B A-C experimental pairs of objects (Ghosh and Gilboa, 2014; Preston and Eichenbaum, 2013). Here, a semantically congruent scene was operationalized as the context or schema for encoding a novel target (e.g., a seashell superimposed on a beach scene). To the extent that interplay between medial temporal and medial prefrontal brain regions reflects a fundamental characteristic of associative memory processing, the results obtained in other paradigms should generalise to this situation.

In the current experiment, we examined activation in the hippocampus and mPFC as a function of repetition and semantic congruence between objects and background scenes. Participants were instructed that recognition decisions were to be based on the central target objects only, and were not alerted to the fact that half the background scenes were semantically related to the targets. Context scenes were displayed for 500 ms prior to the target onset which then appeared as an overlay in the middle of the scene. We hypothesised that for congruent trials the context scene would provide an appropriate schema for encoding the target and, more importantly, would enable prediction or facilitate retrieval of the related object at second presentation. That process would be indicated by stimulus repetitions in which recognition speed was facilitated, and which recruited regions of interest in the hippocampus to a lesser degree and mPFC to a greater degree for congruent compared with incongruent items. In addition to comparing different cohorts of 'old' stimuli, we were also interested in comparing activation to first vs second presentations of the identical target-scene pairs. Repeated presentation of single items typically results in decreased hippocampal activity (i.e., 1st > 2nd presentation), known as the repetition suppression effect (Brozinsky et al., 2005; Johnson et al., 2008; Rugg et al., 2012; Viskontas et al., 2006), and we hypothesised this might be expressed differently for items that had been encoded in the context of congruent schema. Exploratory whole brain analyses were also conducted to examine whether congruence or repetition effects would be observed in other cortical regions.

2. Methods

2.1. Participants

Fifteen healthy adults (mean age 32.3 yrs, sd 8.60 yrs) participated in this study. Each provided written informed consent and reported having no significant psychiatric or neurological disorder.

2.2. Continuous recognition memory paradigm

The paradigm was conducted during fMRI scanning after engaging in a brief practice session. On each trial, a context scene appeared for 500 ms and then a target object in a red box was overlaid on that scene for 2000 ms, for a total trial duration of 2500 ms. Participants were instructed to look at the background context but that their response should be based only on the target object in the box. They should respond 'yes' (pressing the response key with their right index finger) if the target had been presented before and 'no' (pressing the key with the right middle finger) if the target was new. Response times were calculated from the onset of the target object; note that the stimulus remained in view after the response until the full 2000 ms had elapsed. Each target and accompanying context scene was repeated only one time, at lags of 2–8 intervening stimuli, and trials were separated by an interval that was randomly jittered by 1000, 1500 or 2000 ms.

There were four trial types based on the combined nature of the context and target stimuli (see Fig. 1). The first dimension reflected semantic congruence between context and target, with either related scene-object pairs (congruent) or ones with no such relation (incongruent). The second dimension referred to initial versus second presentation of the stimuli. There were 20 instances of each of these four conditions (Con1, Con2, Inc1, Inc2). The scenes and targets were taken from purchased databases and relatedness was confirmed by consensus of several raters. Of note, the experimental paradigm included several other conditions that are not part of the current analysis: 40 additional stimuli were constructed by re-arranging targets and backgrounds (all these were incongruent) and 40 targets were presented against a grey background (used as fillers to ensure appropriate study-test lags for critical stimuli).

2.3. fMRI acquisition

Anatomical and functional data were acquired on a 3-T Sigma MR System (GE Medical Systems, Milwaukee). Anatomical scans, for co-registration of functional data, were acquired first (T1-weighted sequence, 120 slices, FOV=220 mm, slice thickness=1 mm, 0 gap, 256 × 256 matrix, resulting in a voxel size of .9 × 0.9 × 1.0 mm³). The functional data were acquired in an interleaved order (EPI, TR=2 s; 30–32 slices to cover the whole brain, FOV=240 mm, slice thickness=5 mm, 0 gap, 64 × 64 matrix, resulting in a voxel size of 3.75 × 3.75 × 5.0 mm³). Functional images were taken in an oblique orientation with each slice being perpendicular to the long axis of the hippocampus. The other full fMRI protocol also included two other experimental tasks that are not part of the current analysis.

2.4. Data analyses

A 2 (Congruence) × 2 (Presentation) ANOVA was conducted on both accuracy and reaction times. For both behavioural and fMRI data, we explored congruence effects for cohorts of items (e.g., 2nd presentation of congruent vs incongruent target-context pairs) and for repetition of specific items (e.g., 1st vs 2nd presentation of congruent trials compared to 1st vs 2nd presentation of incongruent trials).

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