



The influence of low-level stimulus features on the representation of contexts, items, and their mnemonic associations



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ABSTRACT

Since the earliest attempts to characterize the “receptive fields” of neurons, a central aim of many neuroscience experiments is to elucidate the information that is represented in various regions of the brain. Recent studies suggest that, in the service of memory, information is represented in the medial temporal lobe in a conjunctive or associative form with the contextual aspects of the experience being the primary factor or highest level of the conjunctive hierarchy. A critical question is whether the information that has been observed in these studies reflects notions such as a cognitive representation of context or whether the information reflects the low-level sensory differences between stimuli. We performed two functional magnetic resonance imaging experiments to address this question and we found that associative representations observed between context and item (and order) in the human brain can be highly influenced by low-level sensory differences between stimuli. Our results place clear constraints on the experimental design of studies that aim to investigate the representation of contexts and items during performance of associative memory tasks. Moreover, our results raise interesting theoretical questions regarding the disambiguation of memory-related representations from processing-related representations.

Introduction

Following the discovery that removal of structures within the human medial temporal lobe (MTL) causes amnesia (Scoville and Milner, 1957), decades of research have focused on elucidating the contributions of subregions of the MTL to declarative memory. While there is still debate over the precise nature of the division of labor within the MTL, there is consensus that the MTL sits at the apex of a cortical circuit, which allows it to bind the constituents of an event (e.g., “what”, “where”, “when”) into an associative, conjunctive, or relational representation (e.g., “what-what”, “what-where”; Mishkin et al., 1997; Cohen et al., 1999; Lavenex and Amaral, 2000; Davachi, 2006; Morris, 2006; Diana et al., 2007; Eichenbaum et al., 2007; Wixted and Squire, 2011; Ranganath and Ritchey, 2012; McKenzie et al., 2015). These theories differ in their emphasis of the role of the hippocampus versus adjacent MTL cortical regions in the formation of such representations—i.e., some theories suggest a more exclusive role for the hippocampus with a more domain-specific involvement of MTL cortical regions—and many studies have begun to test these competing hypotheses.

In a series of groundbreaking studies, Eichenbaum and colleagues used a context-guided object association task to explore how the

components of an associative memory such as context, item, position, and valence are represented neurally (Rajji et al., 2006; Komorowski et al., 2009, 2013; Navawongse and Eichenbaum, 2013; Tort et al., 2013; McKenzie et al., 2014; Farovik et al., 2015; Keene et al., 2016). Briefly, animals learn item-reward associations that differ based on the context, which was operationally defined as visually, tactilely, and spatially (side of the apparatus) distinct chambers. Impaired context-guided object association learning has been shown in rats with hippocampal lesions (Komorowski et al., 2013) and in mice with impaired NMDA receptor function in the CA3 subregion of the hippocampus (Rajji et al., 2006), thus establishing a necessary role for the hippocampus in task performance. Recent studies used electrophysiology and representational similarity analysis to investigate patterns of activity across ensembles of cells in the hippocampus (McKenzie et al., 2014) and in MTL cortical regions (Keene et al., 2016). The results of these studies have suggested that subregions of the MTL—including the hippocampus—carry conjunctive representations of the features that comprise an event, including context, item, position, and valence. Moreover, their results suggest that context plays a dominant, organizing role for representations in the MTL, sitting at the highest level of a hierarchy of information (for review see: McKenzie et al., 2015).

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Context is a broad term that encompasses many aspects of an animal's state, including spatial context, temporal context, expectations, and internal state (cf. Nadel and Willner, 1980). Context is an important aspect of memory-driven behavior as it is frequently the case that in one context a certain set of behaviors are appropriate while in another context a different set of behaviors are more appropriate. In many laboratory experiments, context is modeled as a general occasion setter such that the desired behavior or decision to be made is contingent upon or altered if the screen background differs, if the color of the room differs, if the previous time through the corridor you went left (versus right), etc. In the context-guided object association task, the contexts and items are composed of distinct elements (i.e., different visual, olfactory, and tactile cues). Thus a critical issue to address is whether the neural representations of contexts and items reflect the cognitive representation of contexts and items or the low-level sensory differences between stimuli. The use of distinct contexts and items allows animals (e.g., rats, humans) to rapidly discriminate between them (cf. Bulkin et al., 2016); however, as we discovered in the course of the present report, it is virtually inevitable that representational differences will also be present in the relevant primary sensory regions. Given that patterns of activity in the hippocampus (McKenzie et al., 2014) and MTL cortex (Keene et al., 2016) were very dissimilar in response to events that took place in different contexts, we examined whether the representation of context maintains in the absence of low-level sensory differences between contexts. We propose that the cognitive representation of a context should be stable across different versions of the same context (e.g., different viewpoints) so long as the context signals a reliable behavioral outcome (e.g., Context A + Item X + Response 1 = Reward).

We developed two human versions of the context-guided object association task for functional magnetic resonance imaging (fMRI) to investigate the representation of context, items, order, and their conjunctions within subregions of the MTL, including the hippocampus, parahippocampal cortex (PHC), and perirhinal cortex (PRC). Additionally, we investigated representations in retrosplenial cortex (RSC), a subregion of the posterior cingulate cortex (PCC), which has been hypothesized to be involved in processing scenes and contexts (Chen et al., 1994; Ennaceur et al., 1997; Cho and Sharp, 2001; Vann and Aggleton, 2002; Bar and Aminoff, 2003; Parron and Save, 2004; Park and Chun, 2009; Walther et al., 2009; Auger and Maguire, 2013; Alexander and Nitz, 2015; Auger et al., 2015; Wing et al., 2015) in addition to playing a role in declarative memory, spatial memory, and the formation of stimulus-stimulus associations (Valenstein et al., 1987; Vann et al., 2009; Aggleton, 2010; Ranganath and Ritchey, 2012; Bucci and Robinson, 2014). In Experiment 1, we used distinct stimuli for our contexts and objects, similar to the rodent studies (Rajji et al., 2006; Komorowski et al., 2009, 2013; Navawongse and Eichenbaum, 2013; Tort et al., 2013; McKenzie et al., 2014; Farovik et al., 2015; Keene et al., 2016). In Experiment 2, we matched the low-level visual features of our stimulus set to test for context and object representation in the absence of the confounding effect of low-level sensory differences between stimuli.

The results of Experiment 1 are consistent with the representation of context in the MTL. Additionally, the results of Experiment 1 are consistent with the notion that RSC/PCC carries context and conjunctive item-in-context information and such representations correlated with behavioral performance (a traditional means of enhancing our confidence that the observed signals are mnemonic in nature). However, the results of Experiment 1 are also consistent with the representation of context, item-in-context, and item-in-order-in-context in primary visual cortex. Further, the relationship between such representations and behavior was at least as strong in primary visual cortex as in RSC/PCC. Therefore, our results provide a clear demonstration of the importance of controlling for low-level feature differences between contexts and objects. Moreover, these results raise interesting questions about how to distinguish between memory-

related representations and processing-related representations. In Experiment 2, we matched the low-level features between our contexts and objects, and we found that the evidence for context and associative representations disappeared, suggesting that the results from Experiment 1 were influenced by differences in the low-level features that comprised the events. In contrast, we observed evidence for fine-grained object representation in PRC in the absence of a low-level confound, thus corroborating theories that suggest that PRC contains fine-grained semantic representations of objects (e.g., Clarke and Tyler, 2015).

Materials and methods

Participants

Thirty-five participants were recruited from the community at the University of California, Irvine. Participants were between 18 and 31 years of age, were right handed, and screened negative for neurological and psychiatric disease. Five participants were excluded due to excessive motion. Twenty participants were included in the analysis in Experiment 1 (10 females) and 10 in Experiment 2 (5 females). Participants consented to the procedures in accordance with the Institutional Review Board of the University of California, Irvine, and received monetary compensation for their participation.

Stimuli

Experiment 1: Distinct stimulus set

In Experiment 1, the stimulus set consisted of two time-lapse videos (clips from Timestorm Films: <https://vimeo.com/93003441>) and two object pairs (Fig. 1A).

Experiment 2: Low-level image matching

In Experiment 2, the two contexts consisted of grayscale images (600×600 pixels) of Saint Peter's Basilica and the U.S. Capitol Building and the objects consisted of grayscale images (256×256 pixels) of car and house keys (Fig. 2A). We used a combined approach of image manipulation and model testing to diminish the presence of category information from the low-level visual features. First, we used the SHINE toolbox (Willenbockel et al., 2010) to equate luminance histograms across all of the scene stimuli and across all of the object stimuli. Second, we used a modeling approach to select images that were devoid of low-level category features.

For our scene images, similar to Marchette et al. (2015), we used pixel-wise correlation, the GIST computational model (Oliva and Torralba, 2001), and the HMAX computational model (two variants, one that used all images from the Fifteen Scene Categories dataset (Lazebnik et al., 2006) as prototypes and one that used a superset of our scene images as prototypes; we used the model from: Theriault et al., 2011). Additionally, similar to Kriegeskorte et al. (2008a), we used two models of V1 (one that included both simple and complex cells from HMAX and another that included only complex cells; Theriault et al., 2011), low-pass pixel-wise correlation (low frequency image features), high-pass pixel-wise correlation (high frequency image features), and Radon transform. We iteratively looped over a superset of our scene images and selected images for which all nine models showed no sign of a relationship between the scene images and the context matrix for both the selected stimulus set (40×40 matrix with 780 unique entries) and across the odd/even split (20×20 matrix with 400 unique entries; $-0.012 < \text{Spearman's rank correlation} < 0.011$, all p 's > 0.77). As a final control, we simulated an object being presented on top of each scene image by placing a black square (256×256 pixels) at the center of the image; importantly, similar results were obtained using this method.

For the object images, we used the same nine models as well as binary-silhouette correlation (similar to Kriegeskorte et al., 2008a).

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