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## The hippocampus is sensitive to the mismatch in novelty between items and their contexts



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#### ABSTRACT

In previous functional magnetic resonance imaging (fMRI) studies of continuous recognition memory it was reported that new items elicit greater hippocampal activity than old (repeated) items (hippocampal 'novelty' effects). Rather than reflecting recency differences between new and old items, hippocampal novelty effects may instead reflect the novelty of the association between test items and the experimental context, or a mismatch in the novelty of the test item and the context. The present continuous recognition study assessed these possibilities by manipulating item-context associations on a trial-by-trial basis. Each trial comprised the presentation of an object-word (context-item) pair. Repeated items were paired either with the same context as on their first presentation, a different but previously presented context, or a new context. The task was to judge whether each item was old or new, regardless of the study status of the associated context. We found no evidence that hippocampal novelty effects reflected either item and context recency, or the novelty of the item-context association. Rather, enhanced hippocampal activity was elicited when the novelty of the item and its context mismatched. These findings support the possibility that hippocampal novelty effects reflect, at least in part, the disjunction in novelty between test items and their contexts.

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#### 1. Introduction

It has been reported in numerous studies that neural activity in the hippocampus is enhanced for novel relative to familiar items (for reviews, see Nyberg, 2005; Rugg et al., 2012). For example, in functional magnetic resonance imaging (fMRI) studies of recognition memory, correctly rejected new items are frequently reported to elicit greater hippocampal activity than correctly recognized old items (e.g., Stark and Okado, 2003; Brozinsky et al., 2005; Daselaar et al., 2006; Johnson et al., 2008; Suzuki et al., 2011a, 2011b; Staresina et al., 2012; Vilberg and Rugg, 2012; for reviews, see Nyberg, 2005; Rugg et al., 2012). Using a continuous recognition memory procedure, Johnson et al. (2008) and Suzuki et al. (2011a) identified novelty-sensitive hippocampal regions where such 'new>old' effects varied monotonically with the number of times a test item was repeated, suggesting that the effects co-vary with a continuously varying 'novelty' or 'familiarity' signal. Following previous proposals (e.g., Duzel et al., 2003; Stark and Okado, 2003; Nyberg, 2005), Johnson et al. (2008) and Suzuki et al. (2011a) suggested

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that these graded effects reflect hippocampally-mediated encoding processes that vary in their level of engagement with the situational novelty of the test item (situational novelty refers to items that, while not necessarily novel in an absolute sense (words, for example), are novel with respect to a given experimental context).

Three variables can potentially contribute to the situational novelty of an item. The first of these is simple recency- the elapsed time since an item was last experienced. The second variable is the novelty of the association between the item and the experimental context. For example, if the MRI scanning environment defines the context, there is not only a difference in the recency of new and old items, but also in the recency and strength of their association with the context. The third variable is the disjunction between the novelty of the item and context. For old items, both the item and the context are familiar. By contrast, for new items, there is a disjunction in familiarity between the item (novel) and the context (familiar). In short, hippocampal novelty effects might depend on the relative novelty of the items, the novelty of an item-context association, or a disjunction between the novelty of the item and the context.

There is evidence to suggest that the hippocampus is sensitive to associative novelty (e.g., Duzel et al., 2003; Kohler et al., 2005; Chen et al., 2011; Howard et al., 2011; Fandakova et al., 2014). For example, in the study of Chen et al. (2011), participants studied face-house associations. At test, participants were cued with a studied face or house and then presented with the original studied associate or an associate from a different studied pair. Correctly rejected novel associates elicited greater hippocampal activity (specifically, in CA<sub>1</sub>) relative to when familiar associates were correctly recognized.

There is also suggestive evidence that hippocampal activity can be modulated as a function of the disjunction in novelty between items (Pihlajamaki et al., 2004; Duncan et al., 2009; Turk-Browne et al., 2012). In the Duncan et al. (2009) study, participants studied a pair of items and, after a short delay, judged whether a probe item pair matched or mismatched the studied pair. The probe pair was either the same two items as the sample stimulus, the same items with interchanged spatial locations, or had had one of the objects replaced with a novel item. Hippocampal activity was greater in this last condition than in the two former conditions. As this study did not have a condition where the sample stimulus contained two novel objects, it is unclear whether the reported effect reflects a mismatch in novelty or a simple item novelty effect (see also, Pihlajamaki et al., 2004). Nevertheless, the finding hints at the possibility that the hippocampus is sensitive to a disjunction in novelty between stimulus elements.

Findings such as those mentioned above lend support to the possibility that previously reported situational novelty effects in the hippocampus during continuous recognition memory (Brozinsky et al., 2005; Viskontas et al., 2006; Johnson et al., 2008; Suzuki et al., 2011a, 2011b) reflect differences between old and new items in their associative novelty, or in the level of disjunction in novelty between an item and its context. In the current study, we assessed these possibilities by manipulating associations between items and their contexts on a trial-by-trial basis. Each trial comprised the presentation of an object-word (context-item) pair. Repeated items were paired either with the same object as on their first presentation (old–Old), a different but previously presented object (old'–Old), or a new object (new–Old). These different pairs are illustrated in Fig. 1.

The task was to judge whether each word was old or new. The task-irrelevant object was assumed to provide the 'local' context for the task-relevant item (cf., Tsivilis et al., 2001, 2003). We assumed that our manipulation of local context would overshadow the influence of the relatively invariant experimental context (see also, Turk-Browne et al., 2012; Kim et al., 2014).

In order to assess the above three accounts of hippocampal novelty effects, we conducted three contrasts. To assess the sensitivity of the hippocampus to the relative recency of



Fig. 1 – Context-item pairs. Repeated items (words in yellow) were paired with either the same context (object) as on their first presentation (old–Old), a different but previously presented context (old'–Old) or a new context (new–Old). The new–New pairs are the initial presentation of each context-item pair and are shown on the left with the relevant old–Old, old'–Old, and new–Old pairs on the right.

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