



Research report

Consolidation and reconsolidation of object recognition memory



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HIGHLIGHTS

- PRH and IC are necessary to consolidate object, but not object-in-context recognition memory.
- HIPP is necessary to consolidate object-in-context, but not object recognition memory.
- D₁ dopamine receptors activity in the PRH but not in the HIPP is needed for ORM consolidation.
- Muscarinic receptor activity is required for LTM in the PRH but not in the HIPP.
- Retrieval is not necessary to reconsolidate ORM in the PRH.

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ABSTRACT

In the first part of this review, we will present evidence showing a functional double dissociation between different structures of the medial temporal lobe in the consolidation of object and object-in-context recognition memory. In addition, we will provide evidence to support this differential participation through protein synthesis inhibitors and neurotransmitters antagonists and agonists. This evidence points out that the perirhinal, prefrontal and insular cortices consolidate the information of individual stimuli, *i.e.*, objects, while the hippocampus consolidates the contextual information where the objects were experimented. In the second part of this review, we will present evidence that shows that the perirhinal cortex is also necessary for reconsolidation of ORM; the destabilization/re-stabilization memory process upon its activation. In the final part of this review, we will present evidence that shows that ORM reconsolidation is an independent process from its retrieval in the perirhinal cortex. Altogether, this review depicts part of the mechanisms by which the medial temporal lobe processes the functional components of recognition memory, in both consolidation and reconsolidation.

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1. Introduction

Recognition memory has been described as the ability to know that something has been previously experienced (individual stimulus or a whole event) [1,2]. At least two components of the recognition process have been identified: one is the judgment of stimulus familiarity and the other is the recollection of contextual information (spatial and/or temporal); *i.e.*, where and when items were experienced [1,3]. Recognition memory has been associated to a network of medial temporal lobe regions, including the perirhinal, parahippocampal, entorhinal and insular cortices, as well as

the hippocampus [4–6]. In the first part of this review, we will present evidence for the contribution of different temporal-lobe regions in memory consolidation for object and object-in-context recognition tasks. These two tasks allow us to dissociate the two above-mentioned components of recognition memory, the identity of the object (a whole representation of the stimulus), and the spatial context where the object was found. Object recognition task is based on the discrimination between familiar and novel stimuli; the subject needs to remember “what” stimulus experimented previously [7]. Conversely, object-in-context task is based on the association of a specific stimulus with a spatial arrangement and for this, the subject needs to remember “where” the stimulus was experimented [8,9].

Recognition memory tasks have been utilized to demonstrate the role of the temporal lobe regions in memory formation [10,11]. Earlier demonstrations were done by ablations of the medial temporal lobe in monkeys. This study suggested that combined lesions of the hippocampus and amygdala accounted for a severe recognition memory impairment [10]. However, more recent findings

Abbreviations: PRH, perirhinal cortex; HIPP, hippocampus; IC, insular cortex; ORM, object recognition memory; STM, short-term memory; LTM, long-term memory.

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showed that recognition impairment was not directly related to damage to those structures but, rather, to damage to the anterior and posterior portions of the perirhinal and entorhinal cortices induced by the aspiration of the amygdala and the hippocampus [11].

2. Dissociation between the hippocampus and rhinal cortices in stimulus familiarity and context

The perirhinal cortex is a multimodal association region that is densely interconnected with sensory areas specific to different sensory modalities [1]. Several studies have shown that multiple sensory systems related to stimulus recognition activate the perirhinal cortex [1,12–17], supporting the idea that association of individual features that represent a stimulus as a whole (within-stimulus association of components) are represented in the perirhinal cortex. On the other hand, complex associations between stimuli and environment (context) may be represented in the hippocampal formation [1]. One of the first reports on this topic was done by Winters et al.; they found that hippocampus lesions impair spatial but not object recognition memory. Conversely, periposterior cortex lesions disrupt object recognition but not spatial memory [18]. Similar results were found by Eacott et al., who demonstrated that lesions of the perirhinal cortex disrupt memory of a non-contextual object recognition task without affecting the object-in-context task [19]. Contrary, it has been reported that perirhinal lesions impair an object-in-place task, where animals have to recognize that a specific object has changed position with respect to another. However, detailed histological analysis revealed that both perirhinal and lateral entorhinal cortices were lesioned in these experiments [20]. In this regard, it has been reported that excitotoxic lesions of the lateral entorhinal cortex do not disrupt the recognition of either novel objects or novel places, but clearly impair the discrimination of familiar objects in familiar places, suggesting that memory for new associations between objects and places is processed in the lateral entorhinal cortex [21–23].

Studies using electrophysiological recordings in the anterior temporal lobe cortex showed that visual stimuli produce noticeable neuronal changes in the perirhinal cortex [24–26]. The authors observed that cellular responses were considerably decreased between the first and second exposure to the same visual item. In addition, they demonstrated that the decremented neuronal activity persisted for at least one day after stimulation and was specific to a particular item; accordingly, exposure to another novel item induced a normal response. Thus, they identified neurons whose response is shaped by the relative familiarity of discrete visual stimuli. Furthermore, the decrement in neuronal activity to a specific item persisted even if several other items were presented in-between [27–29]. These findings suggest that the reduced responsiveness in the perirhinal cortex reflects long-term memory [30–32]. Interestingly, no significant changes in neuronal responses were found in the hippocampus after exposure to visual stimuli [25]. Accordingly, studies using Fos activation have reported that more neurons are activated by novel stimuli than by familiar items in the perirhinal cortex but not in the hippocampus. By contrast, hippocampal, lateral entorhinal and postrhinal, but not perirhinal cortices activity was enhanced when a new spatial arrangement of familiar objects was presented to rats [21,33–35]. In agreement with these results, considerable evidence have shown that neuronal responses in the hippocampus were related to spatial components, such as self-position in space or information concerning stimuli in particular places [36,37].

Although particular attention has been paid to the perirhinal cortex in object recognition, it is clear that other cortical regions are also important in recognition memory processing. In this regard,

we have reported that the insular cortex (IC) is required for both object and taste recognition memory consolidation [38–40]. The IC is located in the lateral temporal lobe deep within the Sylvian fissure in primates and humans. In rodents (Krieg's areas 13 and 14) the IC is located along the confluence of the rhinal sulcus and the medial cerebral artery [41]. Due to reciprocal connectivity with several limbic structures and sensory areas of the cortex, the IC is involved in several cognitive functions, including memory formation for several appetitive and aversively motivated learning tasks [38,41]. Therefore, the temporal cortical structures located along the rhinal sulcus are critical for recognition memory storage. In the next section, we will describe experiments that by inhibiting protein synthesis, activating or blocking different neurotransmission systems, strongly support a double dissociation between the rhinal cortices and the hippocampus in object and object-in-context recognition memory consolidation.

3. The role of the rhinal cortices and hippocampus in recognition memory consolidation

As mentioned, pharmacological manipulations have provided evidence suggesting that the perirhinal and insular cortices store recognition memory for different sensory modalities [14,38,42,43]. In a previous study, we investigated the contribution of different temporal-lobe regions to recognition memory consolidation of objects and objects in context.

In the ORM protocol after habituation to the context, rats were allowed to freely explore two identical objects (A_1 and A_2). Memory was tested 90 min (short-term memory) or 24 h later (long-term memory). In the memory test, rats were allowed to explore freely one copy of the previously presented object (A_3) together with a new one (B) (see Fig. 1a). In our object-in-context protocol the objects and contexts were familiar in the test phase, but the relation between them was novel [39] (see Fig. 1c). In this protocol after habituation to two different contexts (1 and 2), rats were placed in the context 1 and were allowed to explore two different objects (A_1 and B_1). Sample phase 2 was conducted 24 h later and rats were placed in context 2 together with two identical objects [copies of one of the previously presented objects, (A_2 and A_3)]. Therefore, object A was familiar in both contexts but object B was only presented in context 1. Memory was tested 90 min (short-term memory) or 24 h (long-term memory) later. In the test, rats were reintroduced to context 2 and were allowed to explore one copy of each of the objects presented before (A_4 and B_2). Thus, the combination object B in context 2 is novel and allows evaluation of the context component of recognition memory. Together, these behavioral protocols were employed to separately assess the two components of recognition memory in the short and long term [39] (see Fig. 1a and c).

In a series of experiments using these protocols, we demonstrated that object but not object-in-context recognition memory consolidation was impaired when the protein synthesis blocker anisomycin was infused into the perirhinal or insular cortices after the sample phase (see Fig. 1b). Conversely, administration of anisomycin into the dorsal hippocampus blocked the consolidation of object-in-context, but not object recognition memory (see Fig. 1d). It is important to highlight that anisomycin infusions in the hippocampus, perirhinal or insular cortices did not disrupt memory when tested 90 min after sample phase (see Ref. [39]), suggesting this is a suitable time point to evaluate memories in the short-term for object and object-in-context [39]. Our findings provide additional information concerning the participation of distinct structures of the temporal lobe required for recognition memory processing, and make it clear that the hippocampus and the cortex have specific and different roles in long-lasting recognition

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