Available online at www.sciencedirect.com

SciVerse ScienceDirect

Current Opinion in Neurobiology

Brain networks underlying episodic memory retrieval

Michael D Rugg and Kaia L Vilberg

The importance of the medial temporal lobe to episodic memory has been recognized for decades. Recent human fMRI findings have begun to delineate the functional roles of different MTL regions, most notably the hippocampus, for the retrieval of episodic memories. Importantly, these studies have also identified a network of cortical regions — each interconnected with the MTL — that are also consistently engaged during successful episodic retrieval. Along with the MTL these regions appear to constitute a content-independent network that acts in concert with cortical regions representing the contents of retrieval to support consciously accessible representations of prior experiences.

Address
Center for Vital Longevity and School of Behavioral and Brain Sciences, 1600 Viceroy Drive, Suite 800, Dallas, TX 75235, United States

Corresponding author: Rugg, Michael D (mrugg@utdallas.edu)

Current Opinion in Neurobiology 2013, **23**:255–260

This review comes from a themed issue on **Macrocircuits**

Edited by **Steve Petersen** and **Wolf Singer**

For a complete overview see the Issue and the Editorial

Available online 1st December 2012

0959-4388/$ – see front matter,

http://dx.doi.org/10.1016/j.conb.2012.11.005

Introduction

Episodic memory — consciously accessible memory for unique events — allows us to represent past experiences and to flexibly employ these representations in service of current and future goals [1]. The present review focuses on recent human fMRI findings relevant to the functional neuroanatomy of successful episodic memory retrieval. The majority of the reviewed studies took as their starting point a 'dual-process' model of memory [2,3]. These models posit that a retrieval cue (such as a recognition memory test item) can elicit two qualitatively distinct kinds of mnemonic information: a multi-dimensional *recollection signal* that provides information about qualitative aspects of a prior event, including its context, and a scalar *familiarity signal* that can support simple judgments of prior occurrence. From this perspective, identifying the neural bases of episodic retrieval requires experimental designs that permit recollection-driven and familiarity-driven memory to be dissociated (Box 1). Current evidence suggests that the distinction between recollection and familiarity holds both within the MTL and at the level of the cerebral cortex, where a network of regions that appears to be preferentially engaged during successful recollection can be identified.

Memory signals within the MTL

The MTL — the hippocampus and surrounding perirhinal, entorhinal and parahippocampal cortices — has long been recognized as a key brain area supporting episodic memory. Reminiscent of electrophysiological findings in primates [4], fMRI studies have reported that perirhinal activity covaries inversely with the familiarity of recognition memory test items (*e.g.*, [5]). These fMRI results are consistent with evidence from animal lesion studies [6] and a human single-case study [7] that suggest a pre-eminent role for perirhinal cortex in familiarity-based recognition. Perirhinal cortex is not, however, the only MTL region to demonstrate activity reductions for familiar recognition memory items, with several studies reporting similar findings for the hippocampus, in some cases seemingly in the same hippocampal regions that also manifested recollection-related enhancement (see below) [8]. Hippocampal 'novelty effects' have usually been interpreted as reflecting a bias toward the encoding of novel information [9] rather than as a familiarity signal. In keeping with the idea that perirhinal cortex plays the more important role in familiarity-driven recognition, a recent study [10••] reported that, as indexed by both fMRI and local field potentials, perirhinal activity differentiated familiar and novel test items at an earlier latency than did hippocampal activity.

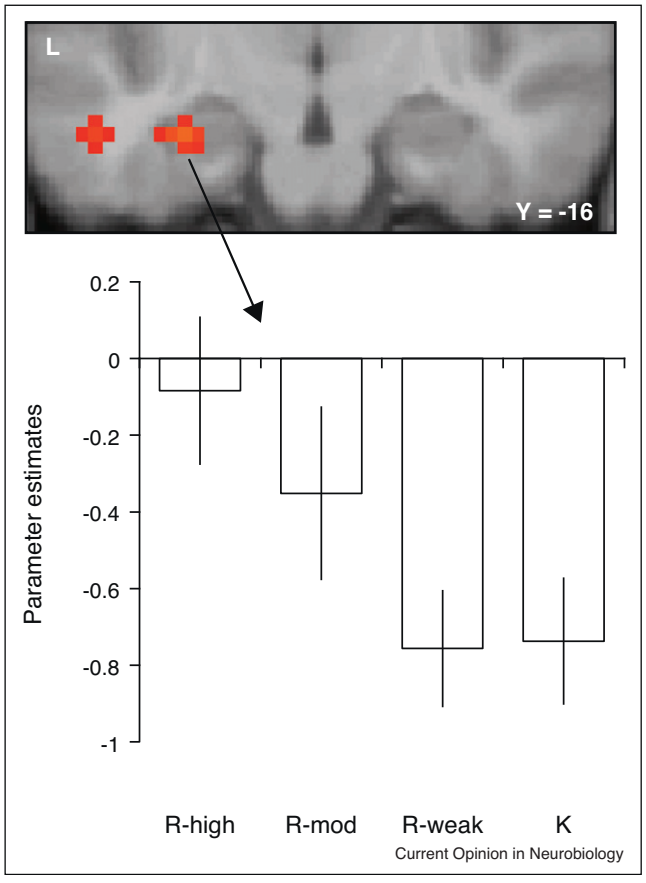
Relative to test items judged to be familiar, but for which recollection seemingly failed, successful recollection is associated with enhancement of fMRI activity in the hippocampus and parahippocampal cortex [11]. These findings converge with some (*e.g.*, [12]), but by no means all (*e.g.*, [13]), human lesion studies to suggest a selective role for the hippocampus in memory for qualitative information. It has been reported that fMRI hippocampal recollection effects are sensitive not to whether a test item elicits a subjective sense of recollection, but to the amount of contextual information retrieved about the study episode ([14•]; see Figure 1).

Recollection-related activity in parahippocampal cortex has been interpreted in the light of proposals that it has a central role in the representation of contextual information ([15], see below), retrieval of which is a defining feature of successful recollection. Whereas the information represented in parahippocampal cortex was

Box 1 Dissociating the neural correlates of recollection and familiarity

To identify neural activity selectively associated with successful recollection it is necessary to employ memory tests that allow the activity to be distinguished from the neural correlates of other forms of memory, most notably, familiarity (see text). Two variants of recognition memory tests have frequently been employed in efforts to dissociate recollection and familiarity. In the 'Remember/Know' procedure subjects report whether recognition of a test item is accompanied (Remember) or unaccompanied (Know) by retrieval of one or more contextual details about the study presentation. It is assumed that items endorsed as Remembered were both recollected and familiar, whereas items endorsed Know were recognized on the basis of familiarity alone. Thus, by contrasting the fMRI activity elicited by these two classes of item the neural correlates of recollection can be identified. More complex versions of the procedure have required subjects to respond differentially depending on the number of details recollected (*e.g.*, [57]), or to rate unrecollected items on a confidence (definitely old' to 'definitely new) or familiarity scale (highly familiar to highly unfamiliar), allowing items to be segregated by the strength of the underlying familiarity signal [5,55]. A second popular procedure for identifying recollected items requires an explicit judgment to be made about a specific contextual feature of the study episode (a 'source memory' judgment), for example, whether a test word was studied in a red or a green font. It is assumed that retrieval of source information signifies successful recollection. Failure to retrieve a source feature does not, however, necessarily mean that recollection failed, as it is difficult to discount the possibility that recollection occurred but did not include information diagnostic of the source judgment ('non-criterial recollection').

Figure 1



Retrieval-related hippocampal activity co-varies with amount of retrieved contextual information [56]. The data are shown for test items endorsed as familiar (K) or recollected (R), further segregated by the confidence and accuracy of a subsequent source memory judgment made on recollected items. R-high and R-mod refer to accurate source judgments made with high and moderate levels of confidence respectively. R-weak refers to source judgments made with low confidence or that were inaccurate.

initially conceived of as predominantly spatial, it has been argued that the region may also represent non-spatial contextual information [16]. It has been proposed that the hippocampus acts in concert with the parahippocampal and perirhinal cortices to support recollection, with the hippocampus 'binding' contextual information from the parahippocampal cortex with object information from the perirhinal cortex to form an integrated episodic representation [15,17]. Consistent with this proposal, it was recently reported that hippocampal–perirhinal connectivity is greater during successful than unsuccessful source memory judgments [10••]. In another study, successful recall and recognition were accompanied by enhanced connectivity between the hippocampus and both perirhinal and parahippocampal cortices [18]. Interestingly, the connectivity analyses suggested that the directions of inter-regional influence differed between the two types of test, with perirhinal cortex modulating the hippocampus during recognition, but being modulated by the hippocampus during recall.

The view that fMRI findings indicate a selective role for the hippocampus in recollection has been challenged [19]. According to this alternative proposal retrieval-related hippocampal activity covaries with memory 'strength' — indexed by the accuracy and confidence of simple recognition judgments — regardless of whether memory is based on recollection, familiarity, or a mixture of the two signals. Findings consistent with this proposal were reported in two recent studies [20,21•]. The strategy in each case was to contrast the hippocampal activity elicited by recollected test items with activity elicited by items for which recollection failed but which were equated for memory strength. In both studies hippocampal activity elicited by the two classes of item was of comparable magnitude, and exceeded the activity elicited by studied items misidentified as new (misses). In one of these studies [20] recollection was operationalized by accurate source memory judgments, leaving open the possibility that items designated as unrecollected were associated with recollection of 'non-criterial' details of the study episode (Box 1). This criticism does not apply to the second study [21•], in which items matched for strength were contrasted according to whether they were given a 'Remember' or a 'Know' judgment (Box 1). Two other studies conducted along similar lines reported different