



Item memory, context memory and the hippocampus: fMRI evidence[☆]

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ABSTRACT

Dual-process models of recognition memory distinguish between the retrieval of qualitative information about a prior event (recollection), and judgments of prior occurrence based on an acontextual sense of familiarity. fMRI studies investigating the neural correlates of memory encoding and retrieval conducted within the dual-process framework have frequently reported findings consistent with the view that the hippocampus selectively supports recollection, and has little or no role in familiarity-based recognition. An alternative interpretation of these findings has been proposed, however, in which it is argued that the hippocampus supports the encoding and retrieval of 'strong' memories, regardless of whether the memories are recollection- or familiarity-based. Here, we describe the findings of eight fMRI studies from our laboratory: one study of source memory encoding, four studies of the retrieval of contextual information, and three studies of continuous recognition. Together, the findings support the proposal that hippocampal activity co-varies with the amount of contextual information about a study episode that is encoded or retrieved, and not with the strength of an undifferentiated memory signal.

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1. Introduction

There is a broad consensus that recognition memory is supported by two different processes, usually referred to as *recollection* and *familiarity* (Mandler, 1980; Yonelinas, 2002; Wixted & Mickes, 2010). Recollection occurs when a recognition test item elicits retrieval of qualitative information about the study episode. This information includes not only the identity of the studied item, but also details about the context in which it was studied. By contrast, familiarity supports a sense of past occurrence that is devoid of contextual information. Whereas both recollection and familiarity can support simple 'old/new' recognition judgments, judgments based on the content of an episode – source memory or 'Remember' judgments for example (see below) – depend largely on recollection.

The functional characteristics of recollection and familiarity, and their neural substrates, are currently matters of debate. Contentious issues include the questions of whether the memory signal associated with recollection is better modeled as a thresholded or a continuous process (Wixted & Mickes, 2010; Yonelinas, Aly, Wang, & Koen, 2010), and whether recollection

and familiarity are differentially dependent upon the hippocampus (Eichenbaum, Yonelinas, & Ranganath, 2007; Squire, Wixted, & Clark, 2007). Here, we focus on the second of these issues as it is informed by functional neuroimaging studies, although we touch upon the first issue also.

The proposal that recollection, but not familiarity, is dependent upon the hippocampus has been advanced by numerous authors. Several lines of evidence have been interpreted in favor of the proposal, although none has gone unchallenged. For example, whereas some studies of patients with lesions restricted to the hippocampus have reported disproportionate deficits in estimates of recollection (e.g., Aggleton et al., 2005; Holdstock et al., 2002; Mayes et al., 2004) studies of other, seemingly similar patients have reported that recollection and familiarity are impaired to an equivalent extent (e.g., Cipolotti et al., 2006; Jeneson, Kirwan, Hopkins, Wixted, & Squire, 2010; Manns, Hopkins, Reed, Kitchener, & Squire, 2003; Wais, Wixted, Hopkins, & Squire, 2006). And whereas there is compelling evidence from studies of experimental animals that hippocampal lesions can have little or no impact on recognition memory of single items as assessed by tasks such as delayed non-match to sample (for review, see Brown & Aggleton, 2001) or spontaneous exploration (e.g., Good, Barnes, Staal, McGregor, & Honey, 2007) it is unclear how directly these findings relate to the constructs of recollection and familiarity, which are difficult to operationalize in experimental animals (although see Fortin, Wright, & Eichenbaum, 2004).

[☆] Degrees of freedom corrected for non-sphericity with the Geisser–Greenhouse procedure.

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An important line of evidence in support of the proposal that recollection is disproportionately dependent on the hippocampus comes from functional neuroimaging studies in healthy humans that employed event-related fMRI. Such studies have investigated both the neural correlates of the encoding processes associated with successful recollection on a later memory test, and the correlates of successful recollection at the time of retrieval. In these studies, recollection was almost invariably operationalized either in terms of successful versus unsuccessful memory for a contextual feature of the study episode (source memory), or as the difference in neural activity when recognition of a test item was accompanied by a phenomenal sense of recollection compared with when it was accompanied only by a sense of familiarity ('Remember vs. Know', Tulving, 1985). In studies of both encoding (e.g., Davachi, Mitchell, and Wagner, 2003; Duarte, Henson, and Graham, 2011; Kensinger and Schacter, 2006; Otten, 2007; Ranganath et al., 2004; Uncapher and Rugg, 2005) and retrieval (e.g., Cohn, Moscovitch, Lahat, and McAndrews, 2009; Diana, Yonelinas, and Ranganath, 2010; Eldridge, Knowlton, Furmanski, Bookheimer, and Engel, 2000; Montaldi, Spencer, Roberts, and Mayes, 2006; Yonelinas, Otten, Shaw, and Rugg, 2005) it has been reported that, relative to familiarity-driven recognition, recollection is associated with enhanced hippocampal activity. These findings have been taken as evidence that the hippocampus plays a selective role in supporting recollection, possibly because of its unique ability to bind the different components of a study episode into a cohesive memory representation (Diana, Yonelinas, & Ranganath, 2007; Mayes, Montaldi, & Migo, 2007).

Recently, an alternative account of these fMRI findings has been advanced (Squire et al., 2007; Wixted, Mickes, & Squire, 2010). By this account, encoding- and retrieval-related hippocampal activity are neural correlates not of recollection, but of 'strong' memory – as operationalized by the accuracy and confidence of recognition judgments – regardless of whether the strength of the memory is due to recollection, high familiarity, or a combination of the two memory signals. In support of this account, Wixted et al. (2010) argued that contrasts intended to identify the neural correlates of recollection (for example, contrasts between items attracting correct versus incorrect source judgments, or items endorsed 'Remember' versus 'Know'), are invariably confounded with differences in item recognition accuracy and hence memory strength. Wixted et al. (2010) noted that even in studies in which confidence judgments were employed to segregate 'unrecalled' test items according to their level of familiarity (Cohn et al., 2009; Montaldi et al., 2006; Ranganath et al., 2004; Yonelinas et al., 2005), recognition accuracy was invariably higher for items endorsed as recollected than it was for highly familiar items (but see Montaldi & Mayes, 2010). Wixted et al. (2010) argued that it was this difference in item accuracy, and not the distinction between recollection and familiarity, that was responsible for the differential hippocampal activity reported in those studies.

In the following sections, we describe the findings from a series of studies from our laboratory that bear directly on the question of whether the construct of memory strength is sufficient to account for modulation of encoding- and retrieval-related hippocampal activity, as this activity is assessed with fMRI. On the basis of these findings, we argue that hippocampal activity is sensitive neither to variation in the strength of an undifferentiated memory signal, nor to whether a test item elicits a subjective sense of recollection. Instead, hippocampal activity reflects the amount of contextual information that is encoded during a study episode, or that is retrieved in response to a test item.

2. Measurement of memory strength and recollection

Before turning to our empirical findings we briefly review the behavioral measures that we and others have employed to

estimate memory strength and recollection in studies of recognition memory. As the construct is employed in the literature cited above (e.g., Squire et al., 2007; Wixted et al., 2010), strength is operationalized in terms of the accuracy ($p_{\text{Hit}}/(p_{\text{Hit}}+p_{\text{False Alarm}})$) and confidence with which recognition memory test items are correctly endorsed as studied, and we follow that practice below. We defer discussion of the value of the construct of memory strength in understanding the neural correlates of memory performance until later.

We have employed two different procedures to operationalize recollection. The first is the 'Remember/Know' procedure, introduced by Tulving (1985). In its simplest form, the procedure requires subjects to signal whether recognition of a test item is accompanied (Remember judgment) or is not accompanied (Know judgment) by the retrieval of a contextual detail or details about the item's study presentation. Remember and Know judgments are assumed to map onto the constructs of recollection and familiarity, respectively. The procedure has been criticized on the grounds that it merely distinguishes between relatively strong and relatively weak memories (e.g., Donaldson, 1996). Recent evidence suggests however that this is not necessarily the case. Rather, independently of differences in memory strength, Remember and Know judgments can indeed segregate test trials according to whether or not contextual (source-specifying) information was retrieved (Ingram, Mickes, & Wixted, 2012; Wixted & Mickes, 2010). The second procedure adopted to operationalize recollection requires subjects to make an explicit judgment about a specific contextual feature of the study episode, for example, whether a test word was presented at study in a red or a green font. It is typically assumed that accurate retrieval of such 'source' information is indicative of the recollection of the relevant contextual feature, and hence of the retrieval of qualitative information about the study episode. It is important to note, however, that failure to retrieve source information does not necessarily mean that recollection failed; the possibility that recollection occurred, but that it did not include retrieval of contextual features relevant to the source judgment ('non-criterial recollection', see Yonelinas and Jacoby, 1996), cannot easily be discounted.

In several of the experiments described below, we employed variants of the Remember/Know and source memory procedures to identify and characterize recollection-related hippocampal activity. Additionally, we estimated the memory strengths of 'recollected' and 'unrecollected' test items when this was possible.

3. Hippocampal activity and the encoding of source and item information

Below, we describe data drawn from a larger study of the effects of age on the neural correlates of source memory encoding (unpublished data), focusing on findings from the 17 young participants (ages 18–27, 6 male, all right-handed with no reported neurological or psychiatric histories). During the scanned study phase, subjects viewed a series of 180 color pictures of objects, each of which was preceded by a cue that signaled whether the object should be judged as to whether it would be more likely to be found indoors or outdoors, or was smaller or larger than a shoebox. fMRI data were acquired and analyzed according to our standard methods (e.g., Gottlieb and Rugg, 2011). In an unscanned test phase that began approximately 25 min after exiting the scanner, subjects viewed the 180 critical study pictures intermixed with 90 new items. The requirement was to first make an 'old/new' judgment on each picture and, for each item endorsed 'old', to then judge whether

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