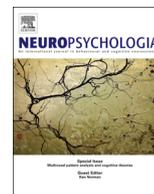




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The posterior parietal cortex: Comparing remember/know and source memory tests of recollection and familiarity

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ABSTRACT

Numerous neuroimaging studies have shown a dissociation within the left posterior parietal cortex (PPC) between recollection and familiarity, with dorsal regions routinely active during familiarity and ventral regions active during recollection. The two most common methods for separating the neural correlates of these retrieval states are the remember/know paradigm and tests probing source memory. While relatively converging results have been found using these methods, the literature is lacking an adequate and direct comparison of the two procedures. We directly compared these two methodologies and found differences in both the magnitude and extent of activation within the left PPC. During familiarity, dorsal PPC regions were more strongly activated by the source test, while the remember/know test led to stronger recollection-related activations within the ventral regions of the PPC. This modulation of PPC activity is particularly important because it suggests that the neural correlates of familiarity and recollection depend on how they are operationalized. Previous assumptions that remember/know and source memory tests are functionally equivalent should therefore be re-evaluated. Additionally, any theories attempting to explain the functional role of the PPC during memory retrieval must take these differences into account.

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1. Introduction

Both recollection and familiarity can be used to guide memory decisions during a standard recognition memory test (Mandler, 1980). Recollected memories are described as containing information about the study episode, are often contextually rich and vivid, and can involve mentally traveling back in time to the original encoding event (Tulving, 1983). Familiarity on the other hand, refers to memories that are lacking information about the study episode, are without contextual detail, and are often based on an undifferentiated, strength-like memory signal (Mandler, 1980). To isolate the neural regions uniquely associated with recollection and familiarity, one must be able to differentiate which items were retrieved via recollection and which relied on familiarity. By far, the two most common strategies for operationalizing recollection and familiarity during neuroimaging studies are the remember/know test and tests probing source memory. During a remember/know test, the subject is asked to identify what retrieval state (recollection or familiarity) was experienced on a trial-to-trial basis (Tulving, 1985). Source tests

take a much more objective approach, operationalizing the retrieval state according to whether or not recognition was accompanied by the recovery of a specific piece of contextual information (Johnson, Hashtroudi, & Lindsay, 1993). Both methods have been criticized in the literature, the remember/know test for its subjective nature and exclusive reliance on the subject's ability to correctly classify their retrieval state (Rotello, Macmillan, Reeder, & Wong, 2005; Donaldson, 1996; Dunn, 2004, 2008; Wixted, 2007; Wais, Mickes, & Wixted, 2008), and the source test for being too restrictive on what qualifies as a recollected response (i.e. the 'non-criterial problem') (Yonelinas & Jacoby, 1996). Despite these differences in procedural methodology, there seems to be a general assumption that these methods are essentially functionally equivalent, and as a result are often used interchangeably to separate familiarity and recollection. This ostensible equivalence has been described both at the behavioral level (Yonelinas & Jacoby, 1995) and at the neural level using evidence from event-related potentials (ERP) (Rugg, Schloerscheidt, & Mark, 1998; Mark & Rugg, 1998). In regards to the parietal lobe, both methods have found recollection to be associated with the so called 'parietal old/new effect' which is a positive going deflection that occurs around the 400–800 ms time window (Vilberg & Rugg, 2006; Curran, 2004; Wilding, 2000). Results from functional magnetic resonance imaging (fMRI) studies have also shown a general convergence between these two approaches as to

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what brain regions within the left posterior parietal cortex (PPC) are sensitive to recollection and familiarity. Specifically, both methods have shown a dorsal/ventral dissociation within this area, with familiarity activating more dorsal regions centered around the intraparietal sulcus (IPS) and extending dorsally into the superior parietal lobule (SPL), and recollection activating more ventral regions within the inferior parietal lobule (IPL) (for reviews see: Ciaramelli, Grady, & Moscovitch, 2008; Hutchinson, Uncapher, & Wagner, 2009; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). This apparent convergence is informative because it suggests that the neural representations of familiarity and recollection are the same regardless of the methodology used to index them. While this convergence is somewhat reassuring, the fMRI literature is lacking a direct and adequate comparison of the neural correlates of recollection and familiarity between these two methods. Without this, there remains a possibility that this apparent convergence is merely an illusory finding. If results of such a comparison concluded that different PPC regions were active depending on the test used, this would suggest that these two methods are not as equivalent at measuring recollection and familiarity as is currently assumed. In particular, it would suggest that these divergent brain regions may be representing either a difference in retrieved memory content or a difference in the cognitive demands associated with retrieval depending on what method was used to operationalize recollection and familiarity. Specifically, it could be the case that recollected memories from the source task may be more constrained than memories retrieved via the remember/know task. Additionally, it may be relatively effortful to search for the specific contextual information required by the source test. This increased search effort may engage the top-down attentional system to a greater degree than during the remember/know test. Regardless of what theory is used to explain any differences that might be found, this result would be informative to the field since the standard view is to treat remember/know and source memory tests as equivalent measures of recollection and familiarity. While some fMRI comparisons have been made between the two methods, the vast majority have been conducted between experiments (Ciaramelli et al., 2008; Hutchinson et al., 2009; Vilberg & Rugg, 2008; Wagner et al., 2005). Thus, comparisons have been made across a wide range of stimuli, variations in experimental design, differences in analysis technique, and perhaps most detrimentally, between different subjects. Without controlling for these confounding variables, neural differences between remember/know and source memory tests may be difficult, if not impossible to detect. In other words, even if specific sub-regions of the parietal cortex were more sensitive to one test than the other, co-varying differences in experimental designs may attenuate or even completely mask this effect. Take for instance, the type of stimulus used during testing. Variations in the specific location of neural activity have been found within the left ventral PPC depending on the stimulus type that was used to invoke the activity (Elman, Cohn-Sheehy, & Shimamura, 2013; Klosterman, Loui, & Shimamura, 2009). Research investigating individual differences during recognition memory tests has shown extensive yet reliable differences in brain activity patterns between individuals (Miller et al., 2002, 2009). If variables such as these are free to vary during comparisons of the remember/know and source memory tests, one could imagine how any true differences in neural activity between the two methods may go undetected. Although most fMRI comparisons have been conducted with this between-experiment approach, there have been a few comparisons utilizing a within-subjects design (Duarte, Henson, & Graham, 2008; Vilberg & Rugg, 2007; Yu, Johnson, & Rugg, 2012). The goal of these studies, however, was not to directly compare the two methodologies, but instead to focus on how the amount of recollected information modulates activity within the PPC. While successful in tackling their

specific goal, the designs of these studies were not optimal for a direct comparison between remember/know and source tests. First of all, none of these studies directly compared the neural correlates of familiarity between these two methods. Instead, they focused exclusively on recollection-related comparisons. While lately much focus has been made to elucidate the neural correlates of recollection, familiarity-related activity is still far from understood. Therefore, when comparing PPC activations between remember/know and source tests, it is just as important to investigate familiarity-related activity as it is activity related to recollection. Furthermore, none of these studies used the traditional testing methodologies, but instead used variants of the remember/know paradigm to find brain regions that were active during the remember/know task and were additionally modulated by the source task. Therefore, when identifying regions that were sensitive to source recollection, analysis was constrained to regions that were additionally active during recollection in the remember/know task. As a result, no independent measure of objective recollection was/could be reported. Although helpful in highlighting brain regions that are modulated by the *amount* of information recollected (Vilberg & Rugg, 2007; Yu et al., 2012), without an independent measure of source recollection they cannot speak to the apparent convergence between remember/know and source memory tests. In an effort to avoid the limitations of between-subject designs, the current study will have the same group of subjects participate in both a remember/know test and a source memory test. Additionally, the same stimuli (words), scanner protocol, and analysis parameters will be used for both tests. To obtain independent measures of subjective and objective recollection and familiarity, the remember/know test and source test will be taken independent of each other (as opposed to a combined procedure where subjects make a remember/know and/or a source judgment on each trial). The results from these two tests will be directly compared so that potential differences in neural activation may be found, with specific focus on activation within the left PPC. The results of this direct comparison may reveal something important about the assumed equivalence of the remember/know and source memory tests at indexing recollection and familiarity. If neural differences are found between testing methods, then the generally-held assumption that these methods are tapping into functionally equivalent memory processes would need to be readdressed. Additionally, attempts to attribute any particular functional role to PPC activity during memory retrieval would need to take these differences into account.

2. Materials and methods

2.1. Subjects

Twenty-five healthy subjects (7 female) took part in this study. Subjects ranged in age from 19 to 35 years old ($M=24.8$, $SD=4.6$). Data from eight additional subjects were not included in any reported analyses (one due to a failure to complete the experiment in its entirety, two due to an insufficient number of trials of interest < 20, and five for excessive movement). All subjects were native English speakers and all except one reported their right hand to be dominant. All subjects gave informed consent as approved by the UCSB Institutional Review Board and were paid for their participation.

2.2. Stimuli

Stimuli consisted of 608 nouns selected using the MRC Psycholinguistic Database (www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm). For counterbalancing purposes, words were pseudorandomly divided into two lists of 304 words each. These lists were matched (as closely as possible) on ratings of concreteness, familiarity, imagability, Kucera Francis written frequency, number of letters and number of syllables. Words were back projected onto a screen at the head of the scanner bore and were visible to the subject by a mirror mounted on the head coil. Words were presented in the center of the screen in black 85-point Times New Roman font against a white background. Stimulus presentation was controlled by a

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