



Special issue: Research report

Subjective recollection independent from multifeatureal context retrieval following damage to the posterior parietal cortex



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ARTICLE INFO

Article history:

Received 23 August 2016

Revised 19 December 2016

Accepted 24 March 2017

Published online 1 April 2017

Keywords:

Source memory

Remember/know judgments

Feature integration

Metamemory

ABSTRACT

This study investigated whether damage to the posterior parietal cortex (PPC) impairs the capacity to retrieve multiple aspects of the encoding context in which items were studied, or whether it impairs the subjective awareness of recollection. Patients with lesions to the PPC (PPC patients) and healthy controls memorized words along with the position in which the words were presented on the screen and the ink color in which they were printed. We studied PPC patients' recognition and source memory performance, as well as subjective recollection as indexed by Remember/Know judgments. PPC patients had preserved recognition memory, and gave a similar number of R responses as did controls. Moreover, PPC patients' source memory performance, including memory for multiple contextual features, was similar to the controls'. However, whereas healthy controls were more likely to select R responses with correct multifeatureal source judgments compared to K responses, PPC patients were not. These findings indicate that the PPC plays a role in the subjective experience and metamnemonic evaluation of memory contents.

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1. Introduction

Episodic memory is the ability to recollect specific past experiences. One prominent – if not defining – property of episodic memory retrieval is the reinstatement of multiple contextual

features characterizing the original event. It is this aspect of episodic memory retrieval that makes it “mental time travel” (Tulving, 1985): re-living a past event with a level of vividness and an experiential richness comparable to that of direct (perceptual) experience. In the laboratory, episodic memory

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<http://dx.doi.org/10.1016/j.cortex.2017.03.015>

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retrieval typically is assessed by investigating individuals' ability to retrieve contextual aspects of the learning episode, such as the original position or color of an item at study (in source memory tasks), or by examining individuals' ability to judge whether memory retrieval is accompanied by a feeling of re-accessing the learning context as opposed to merely having a sense of familiarity (in the Remember (R)/Know (K) paradigm).

Functional neuroimaging (fMRI) and neuropsychological studies of brain-damaged patients converge in showing that the medial temporal lobes (MTLs) and prefrontal cortex are crucial for episodic memory retrieval, orchestrating search, reinstatement and monitoring of past experiences (Cabeza & St. Jacques, 2007; Dobbins, Foley, Schacter, & Wagner, 2002; Gilboa et al., 2005; Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006; Moscovitch, Cabeza, Winocur, & Nadel, 2016; Ranganath, Johnson, & D'Esposito, 2003; Rugg, Fletcher, Chua, & Dolan, 1999; Simons & Spiers, 2003). More recent research has called attention to the posterior parietal cortex (PPC) as an additional neural correlate of episodic memory retrieval. There is, indeed, fMRI evidence of a "retrieval success effect" in PPC, characterized by greater activity for recognition hits compared to correct rejections (for reviews, see Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Gilmore, Nelson, & McDermott, 2015; Vilberg & Rugg, 2008; Spaniol et al., 2009; Wagner, Shannon, Kahn, & Buckner, 2005). Successful autobiographical memory retrieval is also associated with activity in PPC (Cabeza & St. Jacques, 2007; Philippi, Tranel, Duff, & Rudrauf, 2015; Svoboda, McKinnon, & Levine, 2006). The ventral PPC is particularly active during retrieval of memories rich in contextual details (Cansino, Maquet, Dolan, & Rugg, 2002; Dobbins et al., 2002; Kahn, Davachi, & Wagner, 2004) and memories vividly recollected rather than simply familiar (Duarte, Henson, & Graham, 2008; Eldridge, Engel, Zeineh, Bookheimer, & Knowlton, 2005; Wheeler & Buckner, 2004; Yonelinas, Otten, Shaw, & Rugg, 2005).

Drawing brain-behavior inferences in cognitive neuroscience requires converging methods. Lesion studies, in particular, have the potential to relate brain activity causally with behavior, and constrain the interpretation of the function of target brain regions in a way that is not possible with neuroimaging data alone (Rosenbaum, Gilboa, & Moscovitch, 2014). Despite the fMRI evidence for a role of PPC during episodic memory retrieval, there have been few studies of memory in patients with damage to PPC. In general, such patients show subtle memory deficits, certainly not as severe as those observed in patients with lesions to the MTLs or prefrontal cortex. Nonetheless, the neuropsychological findings align with fMRI evidence implicating PPC in episodic recollection. PPC patients, indeed, do not generally have a recognition memory impairment (Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010; Ciaramelli, Rosenbaum, Solcz, Levine, & Moscovitch, 2010; Haramati, Soroker, Dudai, & Levy, 2008; Simons, Peers, Mazuz, Berryhill, & Olson, 2010), but may show a lower frequency of subjective states of remembering (i.e., R responses; Ciaramelli, Rosenbaum, et al., 2010; Davidson et al., 2008; Drowos, Berryhill, Andre, & Olson, 2010), and reduced confidence in memory (Hower, Wixted, Berryhill, & Olson, 2014; Simons et al., 2010). Surprisingly, PPC patients have

preserved source memory (Davidson et al., 2008; Simons et al., 2008, 2010). Together, these findings have suggested that PPC may be more concerned with the *subjective* experience of one's recollections, rather than the *objective* ability to recollect contextual details of past experiences (Simons et al., 2010). Alternatively, PPC may mediate the automatic capture of attention by vivid memory contents (supposedly associated with remembering states), which remain accessible voluntarily during source memory tasks (Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007; Ciaramelli et al., 2008; see also Berryhill, 2012, and Cabeza et al., 2008, for reviews of competing accounts of the role of PPC in memory retrieval).

As we noted earlier, episodic memory serves retrieval of complex, multi-featural experiences. Source memory tasks, therefore, may be underpowered to detect subtle source memory deficits. This is all the more relevant when focusing on the role of PPC in source memory. The ventral PPC is thought to mediate the integration of perceptual information for attention and action, both within and between sensory modalities. For example, the PPC has been associated with color–form binding in conjunction visual search tasks (i.e., visual search for a target defined by a conjunction of features; Ashbridge, Walsh, & Cowey, 1997; Donner et al., 2002), and patients with bilateral PPC lesions have difficulty in conjoining shape and color (Freidman-Hill, Robertson, & Treisman, 1995). Suppression of PPC excitability with transcranial magnetic stimulation (TMS) decreases individuals' sensitivity in conjunction (but not single feature) visual search tasks (Ashbridge et al., 1997; Muggleton, Cowey, & Walsh, 2008), and impairs the integration of audio-visual (Bertini, Leo, Avenanti, & Làdavvas, 2010) and audio-tactile information (Serino, Canzoneri, & Avenanti, 2011). TMS over the PPC also attenuates the unusual induction of color from graphemes characteristic of some forms of synesthesia (Esterman, Verstynen, Ivry, & Robertson, 2006), further confirming the role of PPC in perceptual feature binding (Robertson, 2003; Seghier, 2013). Shimamura (2011) has recently proposed that the ventral PPC may play a similar integratory role in memory as it does in perception, helping bind and retrieve multiple episodic features, processed in different cortical regions. One prediction of this hypothesis is that the involvement of PPC in source memory (and source memory deficits following PPC damage) should be magnified when the task requires retrieval of ensembles of episodic features as opposed to isolated features, especially if the features rely on processing in disparate brain regions. A recent fMRI study tested this prediction empirically. Bonnici and colleagues investigated brain activity while participants recalled memories for items viewed on a computer screen, heard through headphones, or presented concurrently both auditorily and visually (Bonnici, Richter, Yazar, & Simons, 2016). They showed that the angular gyrus was more engaged during retrieval of audio-visual episodic memories than during retrieval of unimodal auditory or visual memories, supporting the view that ventral PPC may support retrieval of rich, multifeatured episodic memories (Bonnici et al., 2016; Shimamura, 2011).

The fact that PPC may support the integration of multiple features of episodic memories is relevant for interpreting the pattern of results including impaired subjective recollection with preserved source memory observed in PPC patients. This

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