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Lateral posterior parietal activity during source memory judgments of perceived and imagined events

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ABSTRACT

Memories of real and imagined events are qualitatively distinct, and therefore may be supported by different neural mechanisms. In the present study, we tested whether brain regions are differentially activated during source discriminations of perceived versus imagined events. During the encoding phase, subjects perceived and imagined images of objects in response to a cue word. Then, at test, they made judgments about whether old and new cue words corresponded to items that were previously perceived or imagined, or if they were new. The results demonstrated that the left lateral posterior parietal cortex and dorsolateral prefrontal cortex were significantly more active during source attributions of perceived compared to imagined events. In addition, activity in these regions was associated with successful item memory (hits > correct rejections) for perceived, but not imagined events. These findings of a source-based dissociation of successful retrieval activity have important implications regarding theories of parietal contributions to recognition memory.

1. Introduction

Fundamental to source monitoring theory is the notion that memories of events are comprised of different features, including perceptual, spatial, and temporal details, affective information, and information about the cognitive operations engaged during encoding (Johnson, Hashtroudi, & Lindsay, 1993). It is these contextual details that collectively provide cues that allow us to make decisions about item history (whether information is old or new), as well as the source or origin of memory representations (Johnson, 1997; Johnson & Raye, 1981, 2000; Johnson et al., 1993). Contextual memory models (e.g., Johnson et al., 1993; Schacter, Norman, & Koutstaal, 1998) distinguish between contextual details that were derived through perception (e.g., spatial layout, shape, size, color of objects) and those that were generated internally (e.g., thoughts, feelings). Several brain regions, including regions of the lateral posterior parietal cortex (PPC), appear to be associated with the retrieval of these contextual details (Vilberg & Rugg, 2007; Wheeler & Buckner, 2003; Yonelinas, Otten, Shaw, & Rugg, 2005). However, it is unclear whether these regions are sensitive to the internal/external source detail distinction, or whether they play a more general role in supporting the retrieval of contextual details of memories, regardless of source. The goal of the present experiment was to examine whether there are brain regions that respond more during retrieval of memories of perceptually derived events compared to internally generated events.

Memories from perception and imagination have been shown to differ with respect to the relative amount of different types of qualitative features they contain. Memories of real events tend to contain more perceptually based contextual details than memories of internally generated events (Hashtroudi, Johnson, & Chrosniak, 1990; Johnson, Foley, Suengas, & Raye, 1988; Johnson, Raye, Foley, & Kim, 1982; Johnson, Raye, Foley, & Foley, 1981; Lampinen, Odegard, & Bullington, 2003; Schooler, Gerhard, & Loftus, 1986; Suengas & Johnson, 1988), which instead contain more reflective details, or information regarding the cognitive operations that were engaged during encoding (Johnson et al., 1981, 1988). Reality monitoring, which is a specific form of source monitoring that involves discriminating between the internal/external source of a memory, is thought to be based on a qualitative assessment of the features of memories from perception and imagination (see Johnson et al., 1993; Johnson & Raye, 2000 for reviews). According to source monitoring theory, when a memory is retrieved, it is assessed for the relative amount of these different qualitative details it contains, and then attributed to the source class it most closely resembles (Johnson et al., 1988, 1993).

Given that memories from perception and imagination are qualitatively distinct, and that reality monitoring discriminations are based on these differences, it is plausible that different neural substrates support the representation of these different kinds of contextual details during memory retrieval. Evidence in support of this notion comes from studies demonstrating that regions in the

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medial anterior PFC are more active when attention is focused on the contextual details of episodic memories that were internally generated as opposed to externally derived at encoding. Several studies have demonstrated that medial anterior PFC is more active when subjects make judgments about the task they performed during encoding compared to the spatial location (Simons, Owen, Fletcher, & Burgess, 2005a, temporal order (Simons, Owen, Fletcher, & Burgess, 2005b), or relative size (Dobbins & Wagner, 2005) of encoded stimuli. Other studies examined whether the medial anterior PFC responds more during retrieval of imagined compared to perceived events. While some studies found evidence for this source effect in medial anterior PFC (Turner, Simons, Gilbert, Frith, & Burgess, 2008; Vinogradov et al., 2006) others did not (Lundstrom et al., 2003; Takahashi, Ohki, & Migashita, 2002). Thus, it appears that the anterior medial PFC is more active when attention is focused on the internally generated versus externally derived contextual details of episodic memories. However, it is unclear whether this region is more involved in the control mechanisms involved in directing attention toward these details, or the actual mnemonic representation of these reflective features.

Less work has been devoted to understanding whether there are brain regions that demonstrate the opposite pattern of response as the anterior PFC, responding more during retrieval of perceptually derived compared to internally generated contextual details of memories. Of the studies that compared brain activity during retrieval of internally/externally generated events, the opposite contrast revealing regions that were more active during retrieval of perceived compared to imagined events, regardless of response, was either not reported (Lundstrom et al., 2003; Vinogradov et al., 2006; Takahashi et al., 2002), or did not reveal any regions exhibiting differential activity (Turner et al., 2008). However, in these studies, because the goal was to identify regions that respond more during retrieval of internally generated information, the design was not optimized for observing regions responsive to externally derived mnemonic details. Memories for perceptually derived experiences are distinguishable from memories of internally generated events because they contain greater sensory information. However, in these studies, the presented stimuli were not perceptually rich, which may explain the failure to detect any regions that consistently responded more during retrieval of externally derived compared to internally generated mnemonic information. Perhaps relying on a task that involves the encoding of more perceptually rich visual stimuli might reveal a region or network of regions that respond in this manner.

Other studies have used similar paradigms in order to examine brain activity associated with a particular type of reality monitoring error that occurs when memories of internally generated events are mistakenly thought to reflect reality (false memories). In these studies, subjects perceived and imagined images in response to a cue and then after a delay made internal/external source monitoring judgments (Gonsalves & Paller, 2000; Gonsalves, Reber, Gitelman, Parrish, Mesulam, & Paller, 2004; Kensinger & Schacter, 2006; Okado & Stark, 2003; Simons, Henson, Gilbert, & Fletcher, 2008a; Takahashi et al., 2002). The results revealed that patterns of brain activity associated with both encoding and retrieval of internally generated events differ depending upon whether memories for these events are accurately attributed to internal thought processes or mistakenly thought to be the result of a perceptually experienced event. These findings provide insight regarding the neural processes that lead to accurate versus inaccurate reality monitoring discriminations. However, they do not directly address differences in the neural mechanisms involved in the mnemonic representation of internally generated versus externally derived events, regardless of the accuracy of the response, which was the goal of the present study.

One potential region that might exhibit greater activity during retrieval of externally derived compared to internally generated events is the lateral posterior parietal cortex (PPC). This region has recently received ample attention from memory researchers due to the consistent finding that regions of the lateral PPC are significantly more active during correct recognition of studied items compared to correct rejection of new items (e.g. Kahn, Davachi, & Wagner, 2004; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). This effect, which has been referred to as the parietal old/new effect or the parietal successful retrieval effect, has been observed across a wide range of experimental stimuli and response contingencies (see Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Levy, 2012; Vilberg & Rugg, 2008; Wagner et al., 2005 for reviews). Regions of the lateral PPC are also commonly found to be more active during source memory compared to item memory judgments (Dobbins, Foley, Schacter, & Wagner, 2002; Dobbins & Wagner, 2005; Fan, Snodgrass, & Bilder, 2003; Han, O'Connor, Eslick, & Dobbins, 2012). Because source memory involves the retrieval of greater contextual details than item memory alone, these studies suggest that lateral PPC may contribute to the retrieval of contextual details that are associated with episodic memories. However, it is unclear whether the lateral PPC contributes generally to the mnemonic representation of contextual details, or like the PFC, it plays a more specific role in representing only a subset of these details. The majority of the fMRI studies examining parietal successful retrieval activity have relied on paradigms that involve the external presentation of visual, and occasionally auditory stimuli. Far fewer have investigated memory for internally generated events, and to our knowledge no studies have systematically investigated whether the magnitude of parietal recognition activity varies according to internal/external source. Thus, the lateral PPC may play a prominent role in the retrieval of memories of real versus internally generated events. In support of this notion, although lateral parietal patients do not typically exhibit recognition memory deficiencies, they do tend to report a lack of richness or vividness as well as a lack of confidence in their memories (Ally, Simons, McKeever, Peers, & Budson, 2008; Davidson et al., 2008; Haramati, Soroker, Dudai, & Levy, 2008; Simons et al., 2008b). This suggests that lateral parietal patients may have a deficit in representing the perceptually based contextual details that typically pertain more to memories of real than imagined events.

Evidence that lateral PPC responds more during retrieval of externally derived compared to internally generated memories would provide insight regarding the role of this region in recognition memory. Despite the consistency of observed effects in lateral PPC during recognition memory, the precise functional role of this region remains uncertain. Several hypotheses have been proposed to account for these effects (e.g. Cabeza et al., 2008; Ciaramelli, Grady, & Moscovitch, 2008; Donaldson, Wheeler, & Peterson, 2010; Shimamura, 2011; Vilberg & Rugg, 2008; Wagner et al., 2005). However, fundamental to understanding the contributions of the lateral PPC to recognition memory is deciphering whether this region contributes to processes necessary for successful retrieval; processes such as directing attention or monitoring retrieved information, or whether it plays a role in the actual representation or maintenance of stored information. The present study will provide insight regarding theories of parietal contributions to recognition memory by examining whether parietal activity varies according to internal/external source and source attribution.

In order to examine whether recognition activity in the lateral PPC varies as a function of internal/external source and source attribution, we measured brain activity during a two-part reality monitoring experiment. In the first phase, subjects perceived and imagined images of objects in response to a cue word. Then, at test, they saw old and new cue words and decided whether each