NeuroImage 82 (2013) 44–52

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Dynamic changes in parietal activation during encoding: Implications for human learning and memory

Jeremy A. Elman *, Zachary A. Rosner, Brendan I. Cohn-Sheehy, Adelle G. Cerreta, Arthur P. Shimamura

University of California, Berkeley, CA, USA

ARTICLE INFO

Article history:
Accepted 26 May 2013
Available online 31 May 2013

Keywords:
Posterior parietal cortex
Episodic memory
Encoding
fMRI

ABSTRACT

The ventral posterior parietal cortex (vPPC) monitors successful memory retrieval, yet its role during learning remains unclear. Indeed, increased vPPC activation during stimulus encoding is often negatively correlated with subsequent memory performance, suggesting that this region is suppressed during learning. Alternatively, the vPPC may engage in learning-related processes immediately after stimulus encoding thus facilitating retrieval at a later time. To investigate this possibility, we assessed vPPC activity during item presentation and immediately following its offset when a cue to remember was presented. We observed a dynamic change in vPPC response such that activity was negatively correlated with subsequent memory during stimulus presentation but positively correlated immediately following the stimulus during the cue phase. Furthermore, regional differences in this effect suggest a degree of functional heterogeneity within the vPPC. These findings demonstrate that the vPPC is engaged during learning and acts to facilitate post-encoding memory processes that establish long-term cortical representations.

Introduction

Advances in our understanding of the neural bases of human memory have implicated a broad cortical network involved in the encoding, retention, and ultimate retrieval of recently learned information. While early investigations focused on the medial temporal lobe (MTL) and prefrontal cortex (PFC; Scoville and Milner, 1957; Shimamura, 1995; Squire and Alvarez, 1995), recent neuroimaging investigations have identified regions in the posterior parietal cortex (PPC) that are particularly active when an item has been successfully retrieved (Cabeza et al., 2012; Konishi et al., 2000; Shimamura, 2011; Wagner et al., 2005). Retrieval-related activations within the PPC are functionally dissociable such that activity related to low confidence, familiarity based responses are clustered within the dorsal PPC (dPPC), and activity related to high confidence, recollective responses are clustered within the ventral PPC (vPPC) regions (Kim and Cabeza, 2009; Wheeler and Buckner, 2004). Furthermore, these retrieval-related activations appear to be dissociable from attention-related activity such that memory tasks generally elicit left-lateralized activity in the angular gyrus (AnG), whereas activations occurring during attention tasks are clustered in right temporo-parietal junction (TPJ) and supra-marginal gyrus (SMG; Hutchinson et al., 2009).

Although neuroimaging findings suggest an important contribution of the vPPC to successful retrieval, its role during memory encoding is unclear. In some studies, the vPPC was *negatively* correlated with subsequent memory, such that items later remembered elicit greater vPPC deactivation during encoding compared to items later remembered, a phenomenon referred to as a negative subsequent memory effect (SME; see Uncapher and Wagner, 2009). Extant theories of PPC contributions to memory have struggled to explain this apparent conflict between the negative impact during encoding and positive influence during recognition tests, a pattern described as the *encoding/retrieval flip* (Daselaar et al., 2009). One possibility is that the negative influence of vPPC activity during encoding is related to its role as part of the *default mode network* (DMN), which also includes regions within the PFC, MTL, and medial PPC. Initially, the DMN was found to be more active during rest periods and inter-trial intervals compared to moments when participants were engaged in task-relevant activity (Buckner et al., 2008; Raichle et al., 2001). Recent findings suggest that this network is suppressed during perceptually-driven/externally attended conditions and engaged during conceptually-driven/internally attended situations (Guerin et al., 2012; Sestieri et al., 2010). Thus, findings of increased vPPC (i.e., DMN) activity at encoding for subsequently forgotten items suggest that participants during such encoding trials may have been sacrificing stimulus-driven encoding for irrelevant conceptually-driven processing (e.g., mind wandering).

The role of functionally distinct sub-regions within the vPPC may also help explain differential effects associated with the encoding/

* Corresponding author. Department of Psychology, Room 3210, Tolman Hall #1650, University Of California, Berkeley, Berkeley, CA 94720-1650, USA. Fax: +1 510 642 5293.
E-mail address: jelman@berkeley.edu (J.A. Elman).

1053-8119/$ – see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2013.05.113

retrieval flip. The anterior portion of the vPPC, including the TPJ and SMG, are thought to be a part of the *ventral attention network* involved in attentional reorienting (Corbetta et al., 2008; Shulman et al., 2007) and task-switching (Otten and Rugg, 2001; Wagner and Davachi, 2001). During perceptual search, activity within the TPJ/SMG is often suppressed, a phenomenon proposed to reflect filtering (down-regulating) of task-irrelevant stimuli (Shulman et al., 2007). Activation of these areas at encoding is thought to reflect inadvertent bottom–up capture by irrelevant stimulus features or shifts of attention away from task-relevant features (Otten and Rugg, 2001; Uncapher et al., 2011). Either of these possibilities would serve to divert resources away from processes such as elaborative encoding, which would contribute to successful memory formation.

To the extent that vPPC activity is involved in internally mediated mnemonic processes, it is possible that this region is suppressed during stimulus presentations, but becomes engaged immediately thereafter. This possibility is consistent with a recent theory of episodic memory which suggests that the vPPC is critical for the *cortical binding of relational activity* (*CoBRA*; Shimamura, 2011). According to CoBRA, the vPPC acts as a convergence zone that enables the binding of event features as an encapsulated episodic representation. Initial binding of event features is established by the MTL, which is also involved in post-encoding strengthening of episodic representations (i.e. consolidation) through reactivation or replay of event features (Eichenbaum et al., 1992; Shimamura and Wickens, 2009). The vPPC participates in cortical binding by establishing more direct links between event features during reactivation (e.g., rehearsal, elaborative encoding). We addressed the role of the vPPC in facilitating memory processes during learning by assessing neural correlates of SME immediately following stimulus presentation. In order to differentially emphasize memory processing during this time period, we presented one of two cues just after stimulus presentation which instructed subjects to either remember the item or ignore it. Later, subjects were given a recognition memory test and the SME was assessed for activity during both stimulus presentation and the cue phase.

Methods

Participants

Nineteen healthy subjects were included in this study (mean age 22.05 years, range 18 to 34 years; 13 females). Recruitment was conducted via advertisement on the UC Berkeley Department of Psychology website (http://psychology.berkeley.edu/rsvp). All subjects were native English speakers and were right-handed. None of the subjects reported a history of neuropsychiatric disorders or brain injury or having recently taken psychoactive medication. Subjects were paid for their participation and gave informed consent according to guidelines approved by the UC Berkeley Office for the Protection of Human Subjects. One subject was excluded from analysis due to below chance performance on the memory test.

Stimuli

Three-hundred and twenty photographs of outdoor scenes were used in this study. Half of the scenes included people and half did not. A total of 160 pictures were used during the encoding session, with the remaining pictures used as new items during the test session. The pictures used in each condition were rotated across subjects such that each picture occurred in all conditions with equal frequency.

Behavioral procedure

All trials were presented using *E-Prime 2 Professional* software (http://www.pstnet.com/eprime.cfm). The encoding session took place in the fMRI scanner and was presented in four functional runs (see Fig. 1). During each run, subjects were presented pictures that they were told would be on a later memory test (Remember items) and pictures that they were told would not be included in the memory test (Ignore items). Trials began with a stimulus presentation slide displaying a photograph of a scene (3 s), during which time subjects

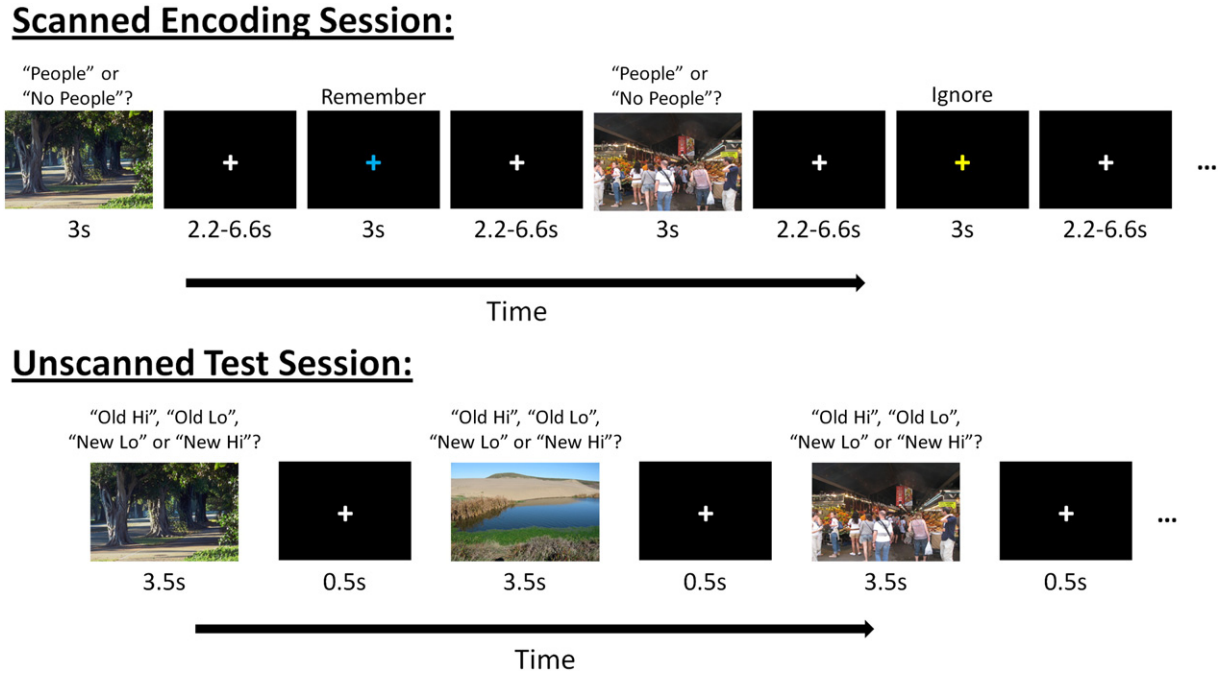

Fig. 1. Behavioral task: During scanned encoding trials, subjects were presented with a picture and responded whether there were people or no people. A cue (represented by colored fixation cross) then indicated whether the previous picture should be remembered for a later memory test or could be ignored. At test, subjects were presented with all pictures from the encoding session (regardless of cue type) along with new items. Subjects responded whether each item was old or new and rated their confidence.