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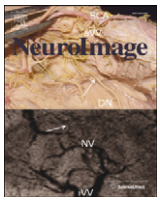

Parietal activity in episodic retrieval measured by fMRI and MEG

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ABSTRACT

Understanding the functional role of the left lateral parietal cortex in episodic retrieval requires characterization of both spatial and temporal features of activity during memory tasks. In a recent study using magnetoencephalography (MEG), we described an early parietal response in a cued-recall task. This response began within 100 milliseconds (ms) of the retrieval cue and lasted less than 400 ms. Spatially, the effect reached significance in all three anatomically defined left lateral parietal subregions included in the study. Here we present a multimodal analysis of both hemodynamic and electrophysiologic responses in the same cued-recall paradigm. Functional MRI (fMRI) was used to more precisely reveal the portion of the parietal cortex with the greatest response. The MEG data set was then reanalyzed to show the early MEG time course of the region identified by fMRI. We found that the hemodynamic response is greatest within the intraparietal sulcus. Further, the MEG pattern in this region shows a strong response during the first 300 ms following the cue to retrieve. Finally, when individual-dipole MEG activity is analyzed for the left cortical surface over the early 300-millisecond time window, significant recall-related activity is limited to a relatively small portion of the left hemisphere that overlaps the region identified by fMRI in the intraparietal sulcus.

Introduction

Recent efforts to assign a functional role for the prominent activations in left lateral parietal cortex during episodic retrieval tasks have produced competing hypotheses. One hypothesis holds that retrieved information is stored in an "episodic buffer" supported by the left parietal cortex (Baddeley, 2000; Vilberg and Rugg, 2008a; Wagner et al., 2005). Another hypothesis states that left parietal cortex participates in directing attention internally to memory search (Cabeza, 2008; Ciaramelli et al., 2008). Others have proposed that parietal cortex does not directly participate in retrieval and instead reflects the subjective experience of recollection (Ally et al., 2008).

The relatively high spatial resolution of functional magnetic resonance imaging (fMRI) has provided evidence for a further functional dissociation between left hemisphere dorsal parietal and ventral parietal cortex. In particular, ventral parietal activity has been associated with the episodic buffer. Some have questioned dorsal parietal involvement in retrieval, suggesting it may only reflect "processes downstream of retrieval" (Vilberg and Rugg, 2008a,b). Under the attention to memory hypothesis, however, ventral parietal activity arises from attentional capture by retrieved information in an automatic, bottom-up process, and dorsal parietal activity supports goal-driven, top-down direction of attention to retrieval (Cabeza, 2008; Ciaramelli et al., 2008).

We recently proposed that these functional hypotheses could be distinguished by the timing of the parietal response (Seibert et al., 2011). Episodic buffer, subjective experience of recollection, and bottom-up attention all require that at least some information has already been retrieved. Top-down attention to memory search, on the other hand, must begin prior to retrieval, and is consistent with an early parietal response. Using magnetoencephalography (MEG) in a cued-recall task, we observed a response in left posterior parietal cortex that began within 100 milliseconds (ms) of the cue and resolved in less than 400 ms. This early and transient activity increase is most consistent with an attentional role. However, the pattern of activity in the three anatomically-defined subregions probed in the study was fairly similar and did not show a dissociation of dorsal and ventral parietal cortices.

Both location and timing are required to characterize parietal activity in retrieval paradigms and improve understanding of its function. Dissociable spatial patterns within the parietal cortex have been observed with fMRI, but the hemodynamic response offers very limited information on timing. Conversely, our MEG results have revealed an early parietal response, but no clear dissociation was observed between the superior and inferior anatomical subregions probed in the study. While fMRI and MEG may measure different aspects of brain activity, both modalities provide important functional insights. The advantage of

Abbreviations: dSPM, dynamic statistical parametric mapping; BOLD, blood oxygenation level dependent.

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a multimodal approach is the opportunity to leverage both the spatial resolution of fMRI and the temporal resolution of MEG to investigate retrieval activity in the same region of parietal cortex.

In this manuscript, we present results from a combined analysis of a previously unpublished fMRI data set and our MEG data. We acquired BOLD functional data from subjects performing the same paradigm used in our previous MEG study (Seibert et al., 2011). We expected the hemodynamic response would reveal one or more significant activations within the left lateral posterior parietal cortex. Those regions could then be used as masks for our MEG data to give insight into the temporal dynamics of neural activity in the functional regions of interest (ROI). We hypothesized that this multimodal analysis would confirm MEG findings of recall-associated activity in dorsal and ventral parietal subregions, while painting a more precise picture of the spatiotemporal dynamics of the left lateral parietal response in episodic retrieval.

Material and methods

Participants

Sixteen healthy, right-handed adults participated in this study. Twelve subjects (mean age: 23.8 ± 3 years; five male) participated in the fMRI study, and eleven subjects (mean age: 23.7 ± 3 years; six male) participated in the MEG study. Seven subjects participated in both the fMRI and MEG studies; of these, four had fMRI first. These studies were approved by the institutional review board of the University of California, San Diego. The subjects gave informed consent prior to the experiment and received $40 for their participation.

Stimuli

Stimuli were 256 color drawings of common objects selected from Rossion and Pourtois color Snodgrass images (Rossion and Pourtois, 2004). Drawings were paired randomly into 128 pairs. Pairs were screened to remove those with obvious visual or semantic relationships.

Task

The behavioral task for fMRI sessions was identical to that previously described for MEG sessions (Seibert et al., 2011). Subjects were tested on 128 pairs of drawings of common objects and animals (which they had studied approximately 45 min prior to the experiment) while activity was recorded using either fMRI or MEG. In all test phase trials, a single drawing from one of the studied pairs was presented for 500 ms in one of two boxes (Fig. 1), followed by an additional 2750-ms response period. During "classify" trials, subjects simply indicated by a finger response whether the presented stimulus was a living or non-living object. During "recall-classify" trials, subjects indicated whether the absent associate of the presented stimulus was a living or non-living object, requiring recall of the paired associate. A colored box, present from 1000 ms prior to stimulus onset, designated the trial type—green for classify and red for recall-classify. A fixation cross presented between two black boxes was shown for the first 250 ms of each trial. Subjects were instructed to respond as quickly and accurately as possible.

The test phase comprised 256 trials, presented in eight runs of 32 trials each. Order of presentation of stimulus pairs was pseudorandomized to create 'trial list A' and 'trial list B,' each containing all pairs. The item presented from each pair, the side of the screen it was presented on, and the condition associated with each pair were all pseudorandomly determined separately for each trial list. All pairs were the same in each list. In the MEG experiment, five subjects were given trial list A and six subjects were given trial list B. In the fMRI experiment, six subjects were given trial list A, and six subjects were given trial list B. Of the seven subjects who participated in both the

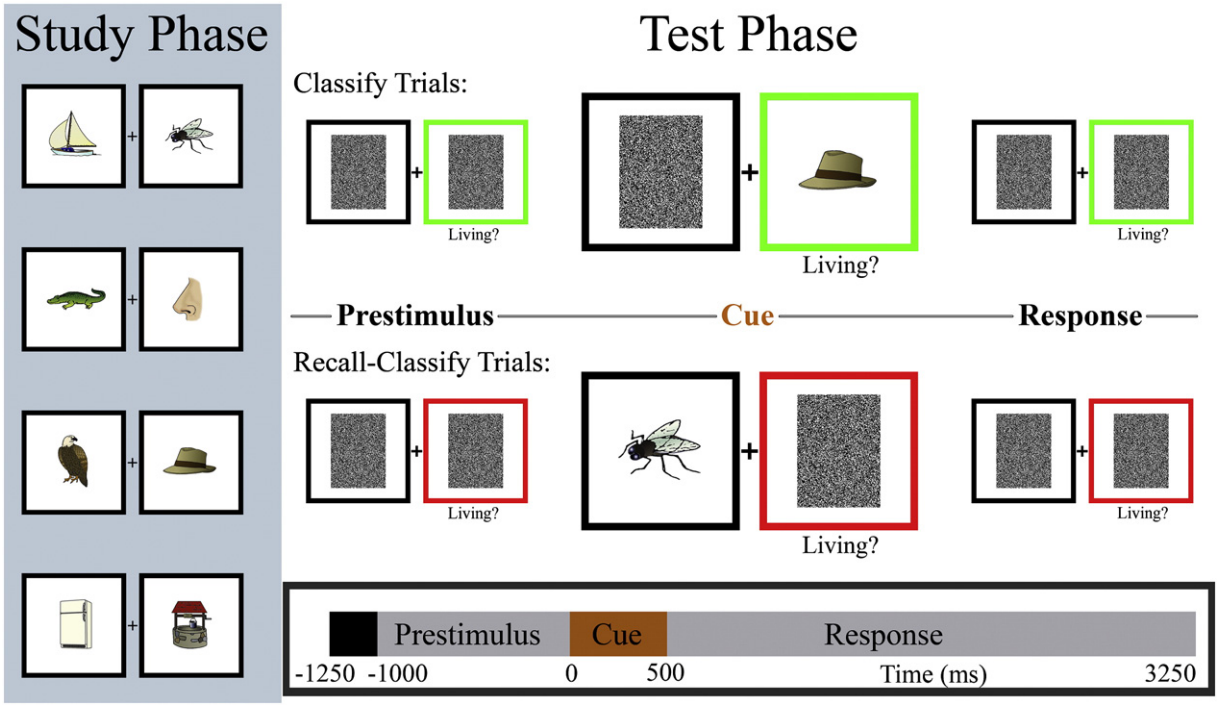

Fig. 1. Pair-cued recall task. Subjects viewed each pair for 3 s during the study phase (repeated in random order three times). MEG or fMRI recordings were acquired during the test phase (timeline on bottom of figure). In classify trials subjects made a simple living/nonliving judgment on the presented item. In recall-classify trials subjects retrieved the absent associate and then made a living/nonliving judgment on the item in memory. In both conditions the test item was equally likely to appear on the left and right sides. A fixation cross and two black boxes were presented during the initial 250 ms of the trial. The cue period is enlarged only for display in the figure.
Reproduced with permission from Seibert et al. (2011).