NeuroImage 68 (2013) 141–153

Contents lists available at SciVerse ScienceDirect

NeuroImage

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

Multimodal imaging reveals the spatiotemporal dynamics of recollection

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ARTICLE INFO

Article history:
Accepted 21 November 2012
Available online 28 November 2012

Keywords:
Episodic
Recollection
PFC
Precuneus
Multimodal
MEG
fMRI

ABSTRACT

Functional MRI research suggests that different frontal and parietal cortical regions support strategic processes that are engaged at different stages of recollection, from pre-retrieval processing of a cue to post-retrieval maintenance and evaluation of recollected information. Whereas some of these regions respond in a domain-general way, other regions are sensitive to the type of information being recollected. However, the low temporal resolution of fMRI cannot distinguish component processes at the time-scale at which recollection occurs. We therefore combined fMRI with the excellent temporal resolution of source localised EEG/MEG to investigate the spatiotemporal neural dynamics of recollection. fMRI and EEG/MEG data were collected from the same participants in two sessions while they retrieved different types of episodic information. This multimodal imaging approach revealed striking consistency between the regions identified with fMRI and EEG/MEG, providing novel evidence of how these brain areas interact over time to support source recollection. For domain-general recollection, results from both modalities converged in showing the strongest activations in medial parietal cortex, which according to EEG/MEG was reliable at a late retrieval stage. Domain-specific source recollection increased fMRI and EEG/MEG activation in the left lateral prefrontal cortex, which EEG/MEG indicated also to be recruited during a post-recollection stage. The findings suggest that although medial parietal and left lateral prefrontal regions mediate functionally different retrieval processes, they are both engaged at a late stage of episodic retrieval.

Introduction

Intentional recollection of past experiences involves a series of successive stages, from initial targeted analysis of a retrieval cue that biases retrieval towards a particular type of memory information, to monitoring the retrieved information for diagnostic qualitative characteristics and evaluating these against response criteria (Fletcher and Henson, 2001). Whereas the hippocampus is critical for matching information in a cue with a stored episodic trace, pre- and post-retrieval processes are thought to be mediated by a network of cortical regions that interact with the hippocampus during recollection (Moscovitch, 1992; Simons and Spiers, 2003). Previous fMRI research has consistently shown enhanced activation in posterior parietal (PPC) and left lateral prefrontal (LPFC) cortical regions during tasks that require retrieval and monitoring of contextual information, such as source memory judgements (Johnson et al., 1993), compared to simple item recognition tasks (Dobbins et al., 2002; Mitchell and Johnson, 2009). These findings suggests that PPC and left LPFC regions are particularly recruited to facilitate intentional recollection and are less involved when behaviour is based on more automatic forms of memory. PPC activation is often domain-general, that is, independent of the type of information retrieved (Duarte et al., 2011; Hornberger et al., 2006). In contrast, left LPFC activity is often enhanced when people are asked to recollect conceptual/verbal compared to perceptual/non-verbal details of an event, indicating a domain-specific role in recollection (Dobbins and Wagner, 2005; Simons, Owen et al., 2005).

Different hypotheses associate PPC and left LPFC with either pre- or post-retrieval stages. For example, one hypothesis suggests that both medial and lateral parts of the dorsal PPC are involved in top-down attention to memory during pre-retrieval search (Cabeza et al., 2008). In contrast, other research has indicated that PPC activation may be related to metacognitive reflection on the quality of retrieved memories (Chua et al., 2006), which may involve elaborative processing of already recollected information (Daselaar et al., 2008). Left LPFC has been suggested to support the conceptual processing of retrieval cues at a pre-retrieval stage of recollection in order to bias the retrieval search process towards conceptual information in memory (Cabeza et al., 2003). An alternative view suggests that left LPFC activations reflect systematic monitoring of highly differentiated information during memory judgements (Nolde et al., 1998). Each of these accounts makes a prediction about the relative time-courses of PPC and left LPFC during

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http://dx.doi.org/10.1016/j.neuroimage.2012.11.030

retrieval; however, interpreting temporal information from fMRI data is problematic because the haemodynamic response effectively integrates several seconds of neural activity, whereas each stage of recollection likely unfolds over fractions of a second. Thus, previous attributions of left LPFC and PPC to particular stages of retrieval have tended to be based on indirect task manipulations rather than direct evidence of neural activation timing.

Event-related potentials (ERPs) measure neural activity at a millisecond scale, and have revealed retrieval-related neural effects that have been tentatively attributed to LPFC and PPC based on functional profiles and topographic distributions over sensors. Because of their temporal characteristics, some of these effects are interpreted as correlates of early versus late retrieval stages (Johansson and Mecklinger, 2003; Rugg and Wilding, 2000). The earliest ERP signs of episodic recollection emerge from around 450 ms after stimulus presentation in the form of an enhanced parietal positive peak, typically left lateralised, referred to as the "parietal old/new effect" because it is often observed during recognition memory tasks when comparing correctly recognised "old" items with correctly rejected "new" items (Rugg and Curran, 2007). This effect shows similar functional characteristics to fMRI activations in the left inferior lateral PPC, and has therefore been hypothesised to generate from this region (Vilberg and Rugg, 2008).

Following the parietal old/new effect, intentional recollection is also often associated with enhanced negative slow-drifts over posterior electrodes (e.g. Friedman et al., 2005; Mecklinger et al., 2007; Senkfor and Van Petten, 1998; Wilding, 1999) that have been suggested to reflect processes that are engaged when task-relevant memory features are not readily recovered or need continued evaluation (Johansson and Mecklinger, 2003; see also Herron, 2007). The late posterior negativity (LPN) is enhanced when participants report that they vividly remember an episode as opposed to have a feeling of familiarity (Leynes and Phillips, 2008), and when participants make metamemory judgements rather than old/new recognition decisions (Wolk et al., 2007), similar to the PPC fMRI activations described above (Chua et al., 2006). The parietal distribution and functional profile of the LPN has led researchers to suggest that it may also originate in domain-general PPC (e.g. Johansson and Mecklinger, 2003). In contrast, domain-specific ERP effects are typically seen over frontal electrode sites relatively late after stimulus presentation. Similarly to frontal fMRI activations, late frontal ERP slow-drifts have been found to distinguish between intentional retrieval of conceptual and perceptual contextual information (Mecklinger et al., 2007; Wilding, 1999).

One might be tempted to assume that frontal and parietal ERP effects originate from directly underlying cortical regions and thus are generated by the same frontal and parietal regions that show recollection-related fMRI activations. However, EEG scalp distributions cannot be easily interpreted because it is impossible to determine uniquely the underlying neural generators of scalp-recorded electrophysiological effects (the "inverse problem"; Nunez and Srinivasan, 2006). Furthermore, EEG fields are distorted by passing through skull and scalp tissue, and the resulting scalp distributions are highly sensitive to choice of reference site, so the maximum site of an EEG effect will differ depending on this arbitrary choice. Finally, on a more fundamental level, the relationship between neural firing as measured by electrophysiology and the haemodynamic fMRI signal is not yet fully understood (Logothetis, 2008). Since these techniques are measuring complementary aspects of neural activity, there are many possible situations where effects in one modality may be invisible in the other (e.g. Ekstrom, 2010). Links between imaging modalities have therefore been highly speculative, with attributions of EEG/MEG sensor effects to specific brain regions based on uncertain evidence.

Methods for mathematically estimating the underlying cortical generators of scalp-level EEG effects have become increasingly sophisticated over recent years. It is advantageous to combine EEG with magnetoencephalography (MEG) recordings in these studies (Sharon et al., 2007), since the latter have the additional benefit of being reference-free and are not distorted by passing through tissue. Solving the inverse problem is non-trivial, but constraining the localisation of activation to participants' cortical sheet as estimated by their individual structural MRI (Mattout et al., 2007), coupled with various other methodological advances such as fusing of EEG and MEG information during the inverse reconstruction (Henson et al., 2009) has produced highly promising results. For early perceptual processes such as object recognition, results with these novel source localisation techniques show high spatial overlap with fMRI activations (e.g. Bar et al., 2006). Because EEG/MEG localisation techniques require untestable starting assumptions to solve the inverse problem, inevitably affecting the outcome (Pascual-Marqui, 1999), demonstrating spatial convergence between independent imaging modalities is particularly strong evidence for isolating the neural correlates of a task or cognitive process. No previous study has demonstrated converging fMRI and EEG/MEG source localisation of domain-general and domain-specific strategic recollection processes, as investigated here.

We collected fMRI and EEG/MEG data from the same group of participants in two separate sessions while they undertook an intentional recollection task where they had to remember different types of source information about a previously presented item. During non-scanned study phases, participants viewed pictures of famous faces presented either on the left or the right of the screen, and made either pleasantness or semantic judgements about each face. fMRI and EEG/MEG data was collected during subsequent test phases while participants were shown the faces again and asked to remember either the location where the face picture had been presented (focusing retrieval towards visuospatial memory information), or which task they had undertaken on the picture (focusing retrieval towards conceptual memory information). In a control condition, participants made semantic judgements about pictures of famous faces that were novel in the experimental context. Within each imaging modality, we looked for common activation during both types of recollection when contrasted against the control condition in order to investigate domain-general retrieval processes. Brain activity associated with the different recollection tasks was contrasted in order to investigate the neural basis of domain-specific retrieval processes.

We then estimated the cortical generators of scalp level EEG/MEG effects, seeking convergence with fMRI to characterize the spatio-temporal dynamics of recollection. The fMRI data were predicted to show domain-general activation in PPC and domain-specific activation in left LPFC. Regions associated with "early" pre-retrieval stages should show EEG/MEG effects during the first few hundred milliseconds after cue presentation, before the first ERP signs of conscious recollection (i.e. the parietal "old/new" effect, Rugg and Curran, 2007). Effects in regions mediating "late" post-retrieval processing should emerge after the first ERP signs of conscious recollection have occurred.

Material and methods

Participants

Eighteen right handed participants (8 males, mean age 25, age range 19–35) completed the fMRI and EEG/MEG versions of the experiment in two separate sessions, at a minimum of 7 days apart. Half the participants completed the fMRI session first and the other half completed the EEG/MEG session first. Task design was identical across the sessions but each used a different set of stimuli (counterbalanced across participants). Written informed consent was obtained from participants in a manner approved by the University of Cambridge Psychology Research Ethics Committee.