Reverse Spatiotemporal Hierarchy during Cross-modal Memory Recall and Imagery

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Abstract

Recalling past events is often accompanied by mental imagery of those experiences. Based on previous research, this process engages memory- and sensory-related brain areas. However, the underlying spatiotemporal dynamics remain poorly investigated. Here, we used naturalistic videos of audiovisual events and recorded fMRI data during the tasks in which human participants recalled visual contents when hearing associated sounds and recalled sounds when watching silent videos, after they had well memorized the video contents. With time-resolved fMRI multivariate pattern analyses, we observed reverse spatiotemporal hierarchy during the visual memory recall and imagery: the neural activity in primary visual cortex was delayed compared with high-order visual areas. A similar trend was found during auditory memory recall and imagery, where the activity of the high-level superior temporal gyrus was earlier than the mid-level planum temporale. However, the primary auditory area was not involved, suggesting modality differences in the role of primary sensory areas in corresponding memory recall. We also observed the activity of the hippocampus, the parahippocampal cortex, the retrosplenial cortex, and the precuneus. We found their associated temporal dynamics were consistent across sensory modalities during memory recall, which were distinct from that during memory encoding. Overall, our study provided both spatial and temporal accounts of neural activity during the cross-modal memory recall and imagery.

Keywords: Memory Recall; Mental Imagery; fMRI; Spatiotemporal Dynamics

Introduction

When we recall past events, we often create mental imagery to re-experience aspects of the original events. Many people can recreate the visual experience from their memory in their "mind's eye", although some populations cannot (Zeman et al., 2015). For example, recalling a vacation might bring up visualizations of the visited place.

This process first involves memory recollection, which recruits a network of brain regions to retrieve past information (Dickerson & Eichenbaum, 2010; Rugg & Vilberg, 2013), including the hippocampus and the parahippocampal cortex (PHC) in the medial temporal lobe, as well as areas in the default mode network (Raichle et al., 2001), such as the retrosplenial cortex (RSC), the precuneus (PCu), and the ventromedial prefrontal cortex (vmPFC).

This process also involves mental imagery to reconstruct past experiences. Previous findings show that mental imagery engages sensory brain areas as original sensory perceptions (Wheeler et al., 2000). Visual mental imagery involves the visual cortex to create the internal visual experience (Dijkstra et al., 2019). Similarly, auditory imagery, although less studied, has also been found to activate the auditory cortex (Bunzeck et al., 2005; Kraemer et al., 2005).

However, little is known about the temporal hierarchy in these brain areas during memory retrieval and imagery. Although previous studies show that the level of information flow is reversed during memory reconstruction or mental imagery (Dijkstra et al., 2020; Linde-Domingo et al., 2019), we still lack direct evidence characterizing the time course of neural activity in specific brain regions during this process. To this end, we applied time-resolved fMRI multivariate decoding analysis (Turner et al., 2012) to assess whether reverse temporal hierarchy can be observed at the one-second temporal resolution of the fMRI signals.

Results

In our experiment (Figure 1), we used naturalistic audio-video stimuli and recorded fMRI data when participants (n=16) passively viewed the stimuli and performed both visual and auditory memory recall and imagery triggered by associated cross-modal information, after they had well memorized the video contents. We examined brain areas associated with visual and auditory processing as well as memory retrieval. We applied time-resolved multivariate analysis to decode the stimuli category at the temporal resolution of one second (TR=1s). We also evaluated univariate activations in contrast to the resting baseline without time-resolved beta estimation.

Reverse hierarchy in visual areas during visual memory retrieval and imagery

To examine visual areas of different levels, we selected primary visual cortex (V1) as the low-level, V4 as the middle-level, the lateral occiptal cortex (LOC) and the fusiform gyrus (FG) as the high-level regions (Figure 2). We found that during the audiovisual perception task and visual-induced auditory memory recall task, all visual areas examined were sig-

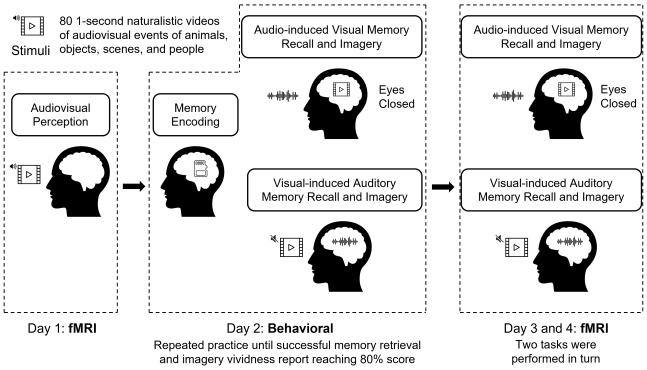

Figure 1: Experiment design.

nificantly activated above baseline and showed similar temporal patterns of categorical decoding, reflecting the perceptual processing of visual information in visual brain areas. For the task of audio-induced visual memory recall and imagery, we did not observe any significant activations in V1, V4, and LOC, except for FG. This is consistent with the meta analysis showing that only the fusiform area was activated during visual imagery (Spagna et al., 2021). However, categorical information can be decoded in V1, LOC, and FG, suggesting that the low-level visual area V1 was involved during visual memory recall and imagery even with the low magnitude of activation. Prominently, we found that the onset of significant decoding accuracy in V1 was one second delayed compared with high-level visual areas. This demonstrate that the V1 was involved later in time after the activity in high-level visual areas, suggesting the top-down processing during the visual memory recall (Pearson, 2019).

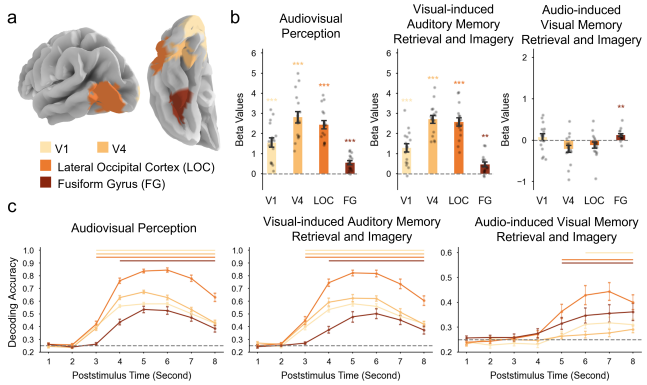

Figure 2: Univariate responses and multivariate decoding in visual areas.

Reverse hierarchy in auditory areas during auditory memory retrieval and imagery

We selected the Heschl's gyrus (HG) as the low-level, the planum temporale (PT) as the middle-level, and the posterior superior temporal gyrus (pSTG) as the high-level auditory areas. During the audiovisual perception and audio-induced visual memory recall task, we observed significant activations in these auditory ROIs and no temporal difference in one-second resolution on the onset time was found across these regions (Figure 3), consistent with previous findings on the temporal speed of auditory processing. During auditory memory retrieval and imagery, we found no involvement of HG because no significant positive activation or categorical decoding was observed. Instead, we observed significant decoding accuracy in PT and pSTG, despite no significant activations above baseline. The significant decoding onset of PT was delayed compared with that of pSTG, again reflecting the reversed hierarchical processing during auditory memory recall and imagery.

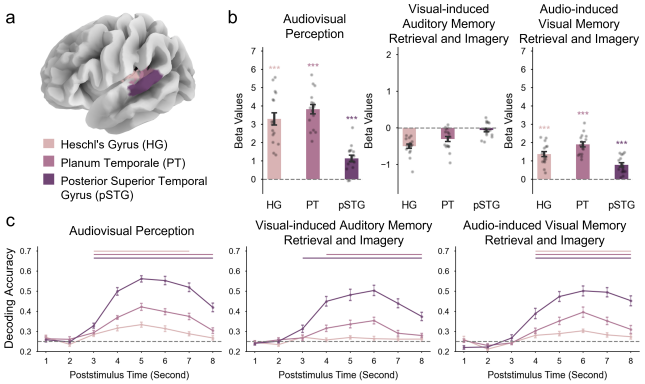

Figure 3: Univariate responses and multivariate decoding in auditory areas.

Consistent temporal dynamics in the medial temporal and parietal cortex across sensory modalities during memory recall

We selected the hippocampus, the parahippocampal cortex (PHC), the retrosplenial cortex (RSC), and the precuneus (PCu) as ROIs associated with memory retrieval (Figure 4). Because the resting state is not a proper baseline to examine the univariate activations in the medial temporal lobe during memory tasks, we did not interpret the univariate activations in these areas (Stark & Squire, 2001). Using multivariate approaches, we found that categorical information can be successfully decoded in all examined areas for three different tasks. Regarding the onset time of significant decoding during memory recall, we found that the temporal patterns were consistent across two sensory modalities. The PHC and PCu were involved first, at the same second with the high-order sensory areas (LOC and FG for visual recall, pSTG for auditory recall). The neural activity in the hippocampus and RSC was delayed for one second, at the same timing with the lower-level sensory areas (V1 for visual recall, PT for auditory recall). In contrast, the temporal order of the significant onset in these ROIs during audiovisual perception were distinct from those during memory recall. The onset of PHC was in the same second with all sensory areas, while the onset of the hippocampus and PCu was delayed for 1 second, and the onset of RSC was delayed for 2 seconds.

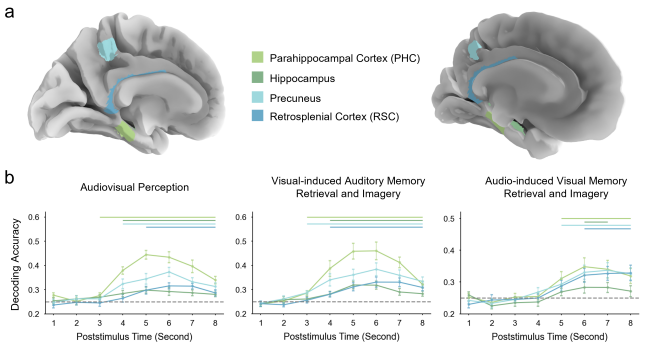

Figure 4: Multivariate decoding in the medial temporal and parietal areas.

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