Putting Working Memory to Work

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Abstract

Goal-directed behavior depends on the ability to flexibly change mental representations in working memory. Here, we combined neuroimaging and computational models to test the hypothesis that working memory contents can be transformed in multiple brain regions in service of task demands, including spatial remapping and mental rotation. We found: 1) response amplitudes tracked task-relevant spatial locations both before and after spatial remapping; 2) multivoxel response patterns contained more rotated than original orientation information after mental rotations. Besides, this orientation transformation existed across visual field maps, especially in the fovea. These results suggested that working memory representations can be flexibly transformed to achieve task goals.

Keywords: working memory; cognitive flexibility; mental manipulations; inverted encoding model

Introduction

Human neuroimaging studies of visual working memory (WM) have focused on understanding how visual information is stored (Curtis & D’Esposito, 2003; D’Esposito & Postle, 2015; Harrison & Tong, 2009; Postle, 2006; Serences, 2016; Serences et al., 2009). However, WM has not only storage but also control components. While largely neglected, these control components are essential for goal-directed behaviors as they transform visual representations into codes that can facilitate or ‘work’ to support behavior. For example, recent studies demonstrated that mnemonic codes are more abstract (Duan & Curtis, 2024; Kwak & Curtis, 2022), flexible (Christophel et al., 2015; Iamshchinina et al., 2021; Kandemir et al., 2024), and dynamic (Li & Curtis, 2023) than perceptual codes, indicating the nature of WM is flexible and goal-dependent.

Here, we tested the hypothesis that working memory contents can be transformed to meet different task demands. Human participants (n=14) performed three WM tasks in the fMRI scanner (Figure 1A). In each task, two gratings with randomly assigned orientations were peripherally presented on each side of the screen. A precue indicated which of the two upcoming gratings was task-relevant (cued item). In the ***baseline*** task, participants needed to remember the cued item’s orientation at its original location for a 12s delay. In the ***rotate-only*** task, participants were asked to mentally rotate the item’s orientation counterclockwise 45° and maintain the rotated orientation at its original location. In the ***rotate+remap*** task, participants were instructed to first rotate the cued item’s orientation, then remap it to the other side of the screen. After the delay, a probe with a random orientation appeared at either the original location for baseline and rotate-only tasks or remapped location for rotate+remap task, and participants needed to report the final orientation. Participants were asked to maintain central fixation across the trial and press a button to indicate when they finished the transformation during the delay. We separated the delay into pre- and post-transformation epochs based on the button press.

Each participant also completed a population receptive field (pRF) mapping task to identify each voxel’s receptive field and define regions of interest (ROI) (Mackey et al., 2017). We identified multiple retinotopically organized regions in visual (V1-V3, V3AB) and posterior parietal cortex (IPS). Using pRF parameters of each ROI, we defined three subregions in screen coordinates relative to the cued item (contralateral, ipsilateral, and central; Figure 1B) based on the Euclidean distance between each voxel's pRF center and three circles in the visual field.

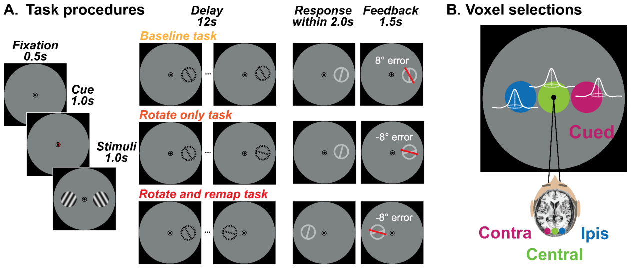

Figure 1: A) Three WM tasks with different demands for orientation rotating and spatial remapping. B) Voxel selections for subregions based on voxel's pRFs and visual stimulus location.

Results: rotate-only task

First, we tested whether and how response amplitudes were modulated by task-relevant spatial locations. We normalized BOLD amplitudes for the three subregions and compared them (Figure 2A). We observed that average BOLD amplitudes were higher for peripheral subregions than the central subregion after stimulus onset, and the contralateral hemisphere had higher amplitudes than the ipsilateral hemisphere, suggesting that both visual inputs and task-relevance modulated population response amplitudes. Moreover, BOLD amplitudes became higher for the central subregion than peripheral subregions later in the delay.

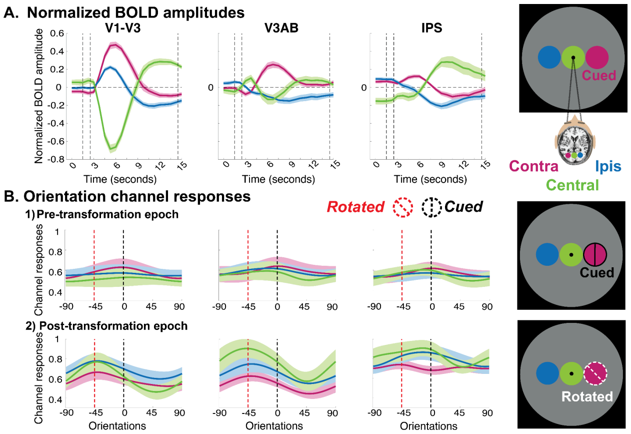

Figure 2: Results for rotate-only task.

Next, we tested if subregions with different response amplitudes form different WM contents, by reconstructing orientation information using an inverted encoding model (IEM) (Brouwer & Heeger, 2009, 2011). The model first estimates the orientation profile for each voxel as a weighted sum of several modeled information channels using activation patterns from the baseline task. Then, it inverts the weight matrix to transform activation patterns from the rotate-only task into orientation channel responses. A channel response that peaks at 0° reflects the cued item's original orientation, while a channel response that peaks at -45° suggests a rotated orientation.

For the pre-transformation epoch, channel responses peaked at 0° for all ROIs (Figure 2B, top). However, for the post-transformation epoch, channel responses were shifted toward -45° for visual ROIs (V1-V3, V3AB), and for IPS, channel responses peaked somewhere in between 0° and -45° (Figure 2B, bottom). These results were similar for all three subregions, suggesting a transformed WM representation spread beyond the neural populations with receptive fields containing the stimulus.

Results: rotate+remap task

Next, we tested how WM contents changed during both orientation rotating and spatial remapping. Importantly, we found that the amplitude of BOLD responses tracked remapping; the initial increase at the cued location flipped during the delay to the remapped location (Figure 3A). Moreover, we found a mix of both the cued (0°) and the rotated orientation (-45°) for the pre-transformation epoch, but rotated toward -45° for the post-transformation epoch (Figure 3B). Intriguingly, the central ROI showed both a large BOLD response and represented the rotated orientation later in the delay.

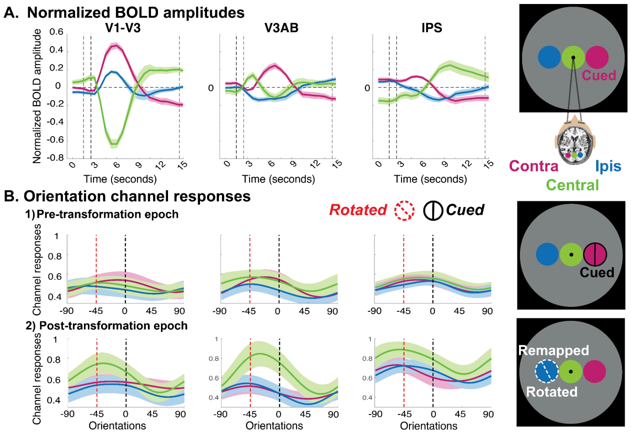

Figure 3: Results for rotate+remap task.

In summary, leveraging pRF parameters and encoding models we demonstrated 1) the amplitude of BOLD responses tracked the spatial position of task relevant items in WM, even when those positions were remapped to the other hemifield, 2) WM orientation information, even after mental rotation, spread across the visual field, and 3) surprisingly strong spatial and feature responses in the central visual field around fixation. Thus, memory transformations take place in early and mid-level visual areas and may depend on remapping peripheral visual features in WM to a workspace in central vision.

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