



Occipital, parietal, and frontal cortices selectively maintain task-relevant features of multi-feature objects in visual working memory

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ABSTRACT

Previous studies have shown that information held in visual working memory is represented in the occipital, parietal, and frontal cortices. However, less is known about whether the mnemonic information of multi-feature objects is modulated by task demand in the parietal and frontal regions. To address this question, we asked participants to remember either color or orientation of one of the two colored gratings for a delay. Using fMRI and an inverted encoding model, we reconstructed population-level, feature-selective responses in the occipital, parietal and frontal cortices during memory maintenance. We found that not only orientation but also color information can be maintained in higher-order parietal and frontal cortices as well as the early visual cortex when it was cued to be remembered. Conversely, neither the task-irrelevant feature of the cued object, nor any feature of the uncued object was maintained in the occipital, parietal, or frontal cortices. These results suggest a highly selective mechanism of visual working memory that maintains task-relevant features only.

Introduction

Visual working memory (VWM) refers to the ability to maintain and manipulate visual information in mind for a brief period of time when it is no longer in view (Curtis and D'Esposito, 2003; Khan and Muly, 2011; Luck and Vogel, 2013). As humans have highly limited cognitive resources, VWM performance is largely influenced by the ability to selectively attend to, memorize, and manipulate information according to task demand. The parietal and frontal cortices have long been considered to play a role in these processes, such as selecting task-relevant information, and ignoring or even suppressing task-irrelevant information, in order to prioritize the current task goals and optimize the deployment of limited cognitive resources (D'Esposito et al., 2000; Miller and Cohen, 2001).

In the neurophysiology literature on non-human primates, there has been ample evidence showing that parietal and frontal neurons can exhibit feature selectivity when the feature is task-relevant (Bichot et al., 1996; Buschman et al., 2012; Toth and Assad, 2002). More recent studies have also shown that such feature-selective tuning can be fine-scaled and modulated by task demand (Ibos and Freedman, 2014). In addition, human neuroimaging work using multi-voxel pattern analysis (MVPA) has shown that the parietal (Albers et al.,

2013; Bettencourt and Xu, 2016; Christophel et al., 2012) and frontal (Albers et al., 2013; Lee et al., 2013) cortices, as well as the early visual cortex (Harrison and Tong, 2009; Serences et al., 2009), can represent the feature-specific information held in VWM. Furthermore, recent work using an encoding technique showed that feature-specific representations can be reconstructed at the population-level from activities in some of the parietal and frontal regions during VWM maintenance (Ester et al., 2015). This work has provided a novel tool of examining feature-selective responses during VWM maintenance in higher-level cortical areas.

However, it remains to be examined if these feature-specific representations can reflect the selective maintenance of task-relevant information, especially when multiple features are presented simultaneously. Although it has been previously shown that manipulation of attention to visual features can modulate feature-selective signals in the early visual cortex (Jehee et al., 2011) as well as in the parietal and frontal cortices (Ester et al., 2016; Liu et al., 2011) during visual attention tasks, few studies have examined how the feature-selective mnemonic representations are modulated by task demand in the parietal and frontal cortices (for early visual cortex see Serences et al., 2009).

In the current study, we aimed to systematically investigate the

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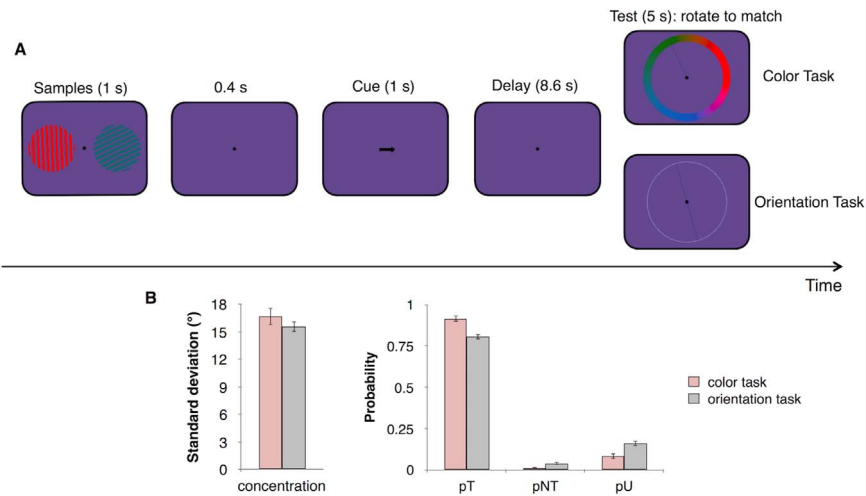


Fig. 1. Color and orientation delay-estimation tasks and behavioral performance. **A.** Participants ($N = 11$) performed a color or orientation delay-estimation task, each of which was conducted in a separate session. On each trial, they viewed two gratings, one in each hemifield, and were cued to remember either color or orientation of one of the gratings. After a delay of 8.6 s, participants adjusted a bar (clockwise or counterclockwise rotation) until it pointed to the cued color or orientation of the cued grating on the color or orientation wheel in 5 s. Images were enhanced for demonstration purposes. **B.** Behavioral performance for the color and orientation VWM tasks, modeled by the mixture model (Bays et al., 2009; Zhang and Luck, 2008). Concentration represented the response variability (standard deviation), and pT , pNT , and pU represented the probabilities of responses to target, non-target, and random guessing, respectively. Error bars indicate ± 1 SEM.

mnemonic representations of both task-relevant and task-irrelevant information in the occipital, parietal, and frontal cortices when multi-feature objects were in view. We measured participants' BOLD activity using fMRI while they performed a delay-estimation task on one of the visual features (color or orientation) of multi-feature objects. We examined mnemonic representations of color in particular because unlike orientation, color does not contain any spatial component; therefore, the memory-related signals in the parietal and frontal cortices are less influenced by spatial attention or motor-related signals which have also been implicated in frontoparietal regions (Kastner et al., 2007; Schluppeck et al., 2005; Silver et al., 2005). Using an inverted encoding model (Brouwer and Heeger, 2009, 2011; Ester et al., 2015; Sprague et al., 2015), we reconstructed population-level feature representations during the delay phase. Our results revealed that VWM representations in the occipital, parietal, and frontal cortices are strongly modulated by task, and that only task-relevant mnemonic representations can be maintained in the early visual and high-level parietal and frontal cortices, suggesting the highly selective nature of VWM representations.

Material and methods

Participants

Eleven participants from Dartmouth College (19–31 years of age, 2 males) participated in the experiment. All had normal or corrected-to-normal vision and normal color vision, and were neurologically intact. Participants provided informed consent in accordance with the Institutional Review Board of Dartmouth College before the experiment and were monetarily compensated for their participation. All participants were naïve to the purpose of the study.

Stimuli and procedure

Stimuli were generated and presented using Matlab and Psychtoolbox 3 (Brainard, 1997; Pelli, 1997). Participants performed a color or orientation delay-estimation task (Wilken and Ma, 2004) in the scanner while fixating at the central dot. Each trial began with the presentation of two square-wave gratings (radius = 5° , spatial frequency = 2 cycles/ $^\circ$, phase angle randomized between 0° and 180°), one in each hemifield (eccentricity = 7°). The orientations of the

gratings were randomly chosen from eight orientations that are equally spaced between 0° and 180° in a step of 22.5° . The colors of the gratings were randomly chosen from eight colors that are equally spaced on the CIEL*a*b color space ($L^* = 45$, $a^* = 0$, $b^* = 0$). All eight colors were isoluminant to the background, determined by a minimum motion task (Cavanagh et al., 1984) prior to scanning of each participant.

The cued and uncued gratings always had different colors and orientations. Each color and orientation was shown four times within a run, twice each in the cued and uncued object in random order. A random jitter of 0 – 3° were added to each orientation and color (0 – 3° on a color wheel) on each trial. The two sample gratings were presented for 1 s, followed by a short blank interval of 0.4 s, and then a black arrow at the center of the screen indicating which of the two gratings to remember (left or right). The likelihood of either grating being cued was equal. Participants only needed to remember the color or orientation of the cued grating, depending on the current task requirement. The cue duration was 1 s, followed by a long retention period of 8.6 s. At the end of the delay period, participants were asked to reproduce the cued color or orientation on a color or orientation wheel (radius = 10°). Specifically, they rotated a bar via button presses until it pointed to the cued color or orientation on the wheel as precisely as possible. The angular change brought by each button press (clockwise or counterclockwise rotation) was 5° for the color task and 2.5° for the orientation task. 5 s was given to complete the adjustment. The color wheel remained identical across trials (Fig. 1A). The memory recall error was measured for each trial as the absolute angular difference (in degrees) between the cued grating and participant's response. The range of recall errors in the color task was $[-\pi, \pi]$, and the range of errors in the orientation task was $[-\pi/2, \pi/2]$. Each run consisted of sixteen trials, which lasted 344 s. Inter-trial-intervals (ITI) varied in 2, 4, 6, or 8 s and there was a 10 s blank fixation period at the beginning of each run. Each participant finished twelve runs each for color and orientation tasks, except one performed ten runs each due to the time limit. Before scanning, each participant practiced the working memory task outside the scanner for 30 min. The color and orientation tasks were performed in separate sessions on different days.

In addition to the main experimental runs, participants also performed several localizer runs, including retinotopic mapping, visual field localizer (two runs of 296 s each) and working memory localizer (two runs of 344 s each). The retinotopic mapping session was

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