Working Memory Enhances Cortical Representations via Spatially Specific Coordination of Spike Times

Highlights

- WM increases the power of αβ oscillations and spike phase locking within MT cortex
- WM-induced increase in αβ power in MT correlates with behavioral performance
- WM increases the visual information conveyed by spike timing relative to αβ phase
- These changes in spike timing could account for WM-induced sensory enhancement

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In Brief

When examining primate extrastriate visual responses, Bahmani et al. find that, in the absence of rate changes, working memory mainly affects αβ oscillations and spike timing. These changes are associated with better visual processing, suggesting how working memory benefits sensory areas.
Working Memory Enhances Cortical Representations via Spatially Specific Coordination of Spike Times

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SUMMARY
The online maintenance and manipulation of information in working memory (WM) is essential for guiding behavior based on our goals. Understanding how WM alters sensory processing in pursuit of different behavioral objectives is therefore crucial to establish the neural basis of our goal-directed behavior. Here we show that, in the middle temporal (MT) area of rhesus monkeys, the power of the local field potentials in the αβ band (8–25 Hz) increases, reflecting the remembered location and the animal’s performance. Moreover, the content of WM determines how coherently MT sites oscillate and how synchronized spikes are relative to these oscillations. These changes in spike timing are not only sufficient to carry sensory and memory information, they can also account for WM-induced sensory enhancement. These results provide a mechanistic-level understanding of how WM alters sensory processing by coordinating the timing of spikes across the neuronal population, enhancing the sensory representation of WM targets.

INTRODUCTION
Working memory (WM) is an integral part of our daily life, determining how we interact with the world around us based on our goals (D’Esposito and Postle, 2015). WM helps us guide our actions based on current goals, in part by altering the processing of sensory information (Postle, 2005). Attention and WM share overlapping mechanisms: items held in WM are better processed, and attention facilitates the entrance of items into WM (Awh and Jonides, 2001). Understanding the neural basis and circuitry by which WM engages sensory areas and alters representation within them is therefore crucial to establish the basis of our goal-directed behavior. Sensory areas have been recently shown to receive a WM-rich signal from the frontal eye field (FEF) part of the prefrontal cortex (Merrikhi et al., 2017). In the presence of this top-down WM signal, the ability of neurons in visual areas, including V4 and the middle temporal (MT) cortex, to represent and discriminate between stimuli appearing near the location held in memory increases. Considering the mounting evidence regarding the FEF’s role in attention (reviewed in Clark et al., 2014), the WM-rich signal sent from the FEF to visual areas corroborates the idea that one purpose of WM signals is to alter neural processing within sensory areas based on goals held in WM (Gazzaley and Nobre, 2012; Postle, 2006).

Despite receiving a robust WM signal from the prefrontal cortex, neurons in visual areas such as V4 or the MT cortex show almost no change in their firing rate during the delay period of WM tasks (Lee et al., 2005; Mendoza-Halliday et al., 2014; Zak-sas and Pasternak, 2006). The finding that a WM signal fails to alter the firing rate in visual areas but enhances the processing of visual signals there (Merrikhi et al., 2017) suggests that a WM signal drives subthreshold modulations. Indeed, previous studies have shown changes in local field potential (LFP) signals in the extrastriate cortex, including the MT cortex, during maintenance of WM (Lee et al., 2005; Mendoza-Halliday et al., 2014). Most models of attention presume a WM module to alter sensory processing based on current goals, but little is known about how WM contributes to visual processing and visual attention. How this subthreshold input results in enhanced visual processing is crucial for understanding the mechanism by which WM alters sensory processing—in other words, the neural basis for the interdependence of attention and WM. We specifically assessed the subthreshold and supra-threshold effects of WM on visual areas by simultaneously recording the spiking activity and LFPs from multiple sites within the MT cortex, where WM-related enhancement of location representation has already been shown during a spatial WM task (Merrikhi et al., 2017). We quantified the receptive fields (RFs) in the MT cortex and altered the location held in WM relative to each RF to study the effect of a top-down WM signal on oscillations and spike timing in the MT cortex, both alone and in the presence of visual stimuli. This systematic investigation revealed a robust increase in the αβ power of LFPs within the MT cortex when remembering a location near the MT RF. We found that these changes in LFP power not only correlated with WM performance, but they also altered the temporal pattern of spiking activity in the MT cortex even though the overall firing rate remained unchanged. These WM-induced changes in oscillatory power and spike timing were specific to the αβ band and were sufficient to enhance
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