

specifically dedicated to the maintenance of visual information that was initially processed in the conventional visual system. Sensory recruitment, by contrast, provides a parsimonious model of VWM storage, as it decreases redundancy in cortical processing. Imaging studies provide ample support for a shared neural substrate for visual representations of retinal and mnemonic origin, while behavioral studies provide ample support for (either beneficial or detrimental) interactions between VWM content and the processing of concurrent visual input. Based on the current evidence, we should therefore be reluctant to revise the traditional view that VWM recruits sensory processing areas for maintaining visual information available after termination of its sensory input.

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Letter

Reaffirming the Sensory Recruitment Account of Working Memory

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The sensory recruitment theory of working memory (WM) proposes that the same cortical regions that contribute to online perceptual processing of a stimulus are recruited to maintain that information in WM [1,2]. In a recent review, Xu reevaluates and rejects sensory accounts of visual WM storage [3]. We clarify here several principles of sensory recruitment theory and describe how the evidence explored in the review – for instance, the role of top-down signals in sustaining sensory cortex representations – actually supports sensory accounts of WM storage.

Sensory Recruitment Theory Predicts That Regions Engaged for Perception Also Contribute to WM Maintenance

The review [3] describes several observations of stimulus-specific WM information in higher-order areas such as frontoparietal cortex (FP), and argues that these findings undermine sensory accounts. This argument presumes (i) that the existence of stimulus-specific information in FP

precludes an important role for sensory cortex, and (ii) that online perceptual processing is exclusive to early sensory cortex. However, stimulus-specific and functionally important information can be represented in more than one brain area simultaneously. For instance, early sensory areas are clearly crucial during visual perception even though FP can also contain stimulus-specific information about visual stimuli [4]. Sensory recruitment theory by definition predicts that these same distributed regions will contain stimulus-specific WM information [1,2], and substantial evidence supports this prediction [5,6]. In the same way as in perception, therefore, early sensory regions can play crucial roles in WM storage even when stimulus information is also present in FP.

The existence of representations in both early and higher-order cortex suggests that information in these regions serves distinct functions and is maintained at multiple levels of abstraction. For example, FP also contains abstract representations (including rules, goals, and coarse/categorical stimulus representations) during both online visual attention [7] and WM [2,5]. Representations at different levels are complementary: abstract information can support robust maintenance and generalization across modalities, while early sensory regions can provide precise sensory-specific representations. Contrary to the argument in the review [3], information in any one area does not render other areas superfluous; instead this multilevel architecture reflects the flexibility of WM [2,5] (Box 1).

Sensory Recruitment Theory Predicts That FP Provides Top-Down Signals to Sensory Cortex

The review concedes that WM stimulus information is often detected in sensory cortex, but asserts that sensory regions are nonessential to memory storage because top-down signals help to sustain this activity [3]. For example, Xu notes that

Box 1. Occipital Cortex Contributions to WM – A Thought Experiment

Many experiments that could decisively arbitrate between competing theories of WM storage remain implausible. Consider a hypothetical scenario in which participants must precisely remember a visual stimulus: after encoding/consolidation, bilateral occipital cortex is completely inactivated for the remainder of the memory delay, and any memory traces in occipital cortex are erased, then occipital function is reinstated immediately before the test (Figure 1). Although brain stimulation and visual distraction can approximate this imagined experiment, these interventions generally produce temporally/spatially/functionally limited cortical disruption, and thus existing methods provide important but incomplete insight into the role of sensory cortex in WM.

What would be the consequences of this experiment on (i) behavior, and (ii) representations maintained in other areas during the delay? If FP maintains partially redundant but more abstract information, there would be a substantial but not catastrophic decrease in behavioral precision. If occipital cortex is unnecessary for maintenance because high-precision storage occurs in FP, behavior would be no different. Although FP can sometimes exhibit stimulus-specific decoding [3,6], that information may depend on bidirectional interactions with occipital cortex occurring throughout the delay (Figure 1). In this case, inactivating occipital cortex during the delay could also abolish stimulus information in higher-order areas.

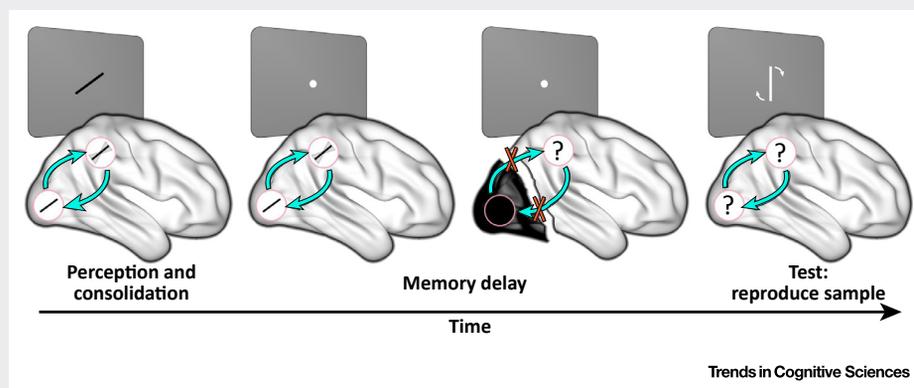


Figure 1. Proposed Thought Experiment and Possible Consequences for Representations in Occipital and Higher-Order Cortex.

feedback from FP reinstates representations in sensory cortex after they are disrupted. However, FP–sensory interactions are a fundamental prediction of sensory recruitment theory, wherein top-down attentional signals from FP drive the privileged processing and maintenance of WM representations in sensory cortex [1,2].

WM activity in sensory cortex is modulated by shifts of internal attention – whereas unattended items are stored in states that are ‘hidden’ with respect to current recording methods, attended items are stored in decodable activity patterns [8,9]. ‘Hidden’ states could be realized via short-term synaptic changes or dynamic activity traces distributed across neural populations. These traces can act as a history-dependent matched filter that allows abstract representations in FP to reinstate fine-grained representations in sensory cortex via top-down signals [8,9], enabling

sensory cortex to serve as an essential substrate for WM storage even without sustained decodable activity. Moreover, FP–sensory interactions make sensory WM representations robust to perturbations (e.g., distraction, attentional shifts, or brain stimulation) that transiently disrupt sensory activity (Box 1). Thus, the FP–sensory interactions marshaled by the review to discount sensory recruitment theories instead affirm them.

Sensory Recruitment Theory Predicts Interactions between WM and Perceptual Content

The review reports that irrelevant visual distraction has minimal impact on WM, and argues that this precludes sensory regions as a substrate for WM storage [3]. However, the fact that a passively perceived distractor can impact on WM to any extent supports the idea that

perception and WM rely on overlapping areas. Furthermore, sensory recruitment theory predicts that the top-down signals that modulate sensory representations during WM also mitigate distractor interference. In the same way as attention modulates perceptual interference by prioritizing a subset of visual information, FP attentional signals provide a sensory-gating mechanism to segregate mnemonic and perceptual information [10]. While irrelevant distractors pose minimal demand on this filtering process, distractors that require increased attentional processing, or are more perceptually similar to WM content, should (and do) produce increased interference [11]. The tuning of distractor effects by similarity to WM content, framed by the review as a weak distractor influence, is actually the precise pattern predicted by sensory recruitment theory: more similar distraction should be more disruptive to WM

because the representations overlap more in cortex [11,12].

Conclusion

After delineating several key principles, we contend that sensory recruitment theory remains the most parsimonious account of extant data. Nevertheless, the ideas explored in the review highlight important open questions: future WM models must consider the extent to which representational codes in different areas are redundant or distinct, how representations in different areas vary across the delay and as a function of task demands, and how areas interact through recurrent feedback/feedforward mechanisms to shape and sustain memory representations throughout the brain (Box 1).

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Letter

Sensory Cortex Is Nonessential in Working Memory Storage

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Despite the initial supporting evidence and the popularity of the sensory account of visual working memory (VWM) storage, the overwhelming negative evidence presented in my review [1] and a related review [2] show that sensory regions are unlikely to play an essential role in VWM storage. In commentaries, Gayet *et al.* [3] and Scimeca *et al.* [4] put forth new arguments in defense of the sensory account of VWM storage. However, the evidence and arguments presented do not provide support for this account or address the negative evidence. Given the lack of sufficient supporting evidence, we should accept the null hypothesis, no matter how appealing or popular the alternative idea may be.

Interaction between VWM and Perception

Gayet *et al.* contest that the sensory account of VWM storage is supported by findings that VWM content may bias or benefit perception [3]. However, such evidence is agnostic as to where VWM may be stored, as attention- and VWM-related processing in posterior parietal cortex (PPC) and prefrontal cortex (PFC) can also impact perception. Similarly, given that brain circuits involved in saccade planning and execution reside within PPC and PFC and conscious visual perception engages PFC and PPC [5,6],

VWM-biased saccades and VWM modulation of conscious visual perception could arise from an interaction within PPC and PFC and do not provide support for the sensory account of VWM storage either. Lastly, although VWM signals in early visual areas could induce a small orientation tilt after-effect, such VWM signals do not appear to be essential for VWM storage [7].

Gayet *et al.* argue that a visual and a possibly verbal code for VWM may be used by the early visual areas and PPC, respectively [3]. I disagree. In our study in which the content of VWM was decoded from PPC, observers made a fine orientation comparison between the memoranda and the probe (a small $\pm 3^\circ$ or $\pm 6^\circ$ difference) [7]. Such VWM precision could only be represented by a visual and not a verbal code.

To address the discrepancy between high-capacity sensory processing and limited-capacity VWM storage, Gayet *et al.* propose that VWM capacity limitation could come from a bottleneck in VWM content read-out or instigation. However, electrophysiological measures of VWM during the delay period argue against this view and instead show a capacity-limited representation for simple features such as color before the read out of VWM content occurs [8]. A similar result is also found with functional magnetic resonance imaging measures during the extended VWM delay period [9]. The existence of limited VWM storage capacity is at odds with a sensory account of VWM storage that poses no severe limitation on capacity.

Interaction between Top-Down Signals and Sensory Cortex in VWM Storage

Contrary to the argument presented by Scimeca *et al.* [4], a PFC and PPC-centered VWM storage account does not *a priori* preclude sensory cortex from