

Review

Reevaluating the Sensory Account of Visual Working Memory Storage

Yaoda Xu^{1,*}

Recent human fMRI pattern-decoding studies have highlighted the involvement of sensory areas in visual working memory (VWM) tasks and argue for a sensory account of VWM storage. In this review, evidence is examined from human behavior, fMRI decoding, and transcranial magnetic stimulation (TMS) studies, as well as from monkey neurophysiology studies. Contrary to the prevalent view, the available evidence provides little support for the sensory account of VWM storage. Instead, when the ability to resist distraction and the existence of top-down feedback are taken into account, VWM-related activities in sensory areas seem to reflect feedback signals indicative of VWM storage elsewhere in the brain. Collectively, the evidence shows that prefrontal and parietal regions, rather than sensory areas, play more significant roles in VWM storage.

The Sensory Account of VWM Storage

VWM, also referred to as visual short-term memory, is a memory buffer that allows observers to retain visual information for a short period of time when it is no longer in view. Such an ability allows the formation of a coherent and continuous representation of the external world, otherwise interrupted by factors such as object occlusion and saccadic eye movements [1]. VWM also makes available the relevant visual information needed to support goal-directed behavior and thoughts. Where in the primate brain VWM is stored has thus been of continuous interest in cognitive neuroscience research. Although studies have implicated the prefrontal cortex (PFC) and posterior parietal cortex (PPC) in VWM storage, recent views have predominantly favored early visual areas, the sensory region involved in the initial encoding of visual input, as playing a significant role in VWM storage ([1–7]; also [8]). Initial support for this view came from the distractor interference effect in behavioral studies and sustained neuronal responses in monkey neurophysiology studies. Recent human fMRI multivoxel pattern analysis (MVPA) studies have provided further support for this view by showing that the content of VWM can be successfully decoded in early visual areas during the delay period [9,10]. Sensory regions such as early visual areas are now considered to be the primary storage site for VWM or at least an integral part of VWM storage [1–8].

VWM could be viewed as prolonging the representations formed during sensory processing [11]. Thus, having sensory processing and VWM sharing the exact same neural substrates has the appeal of both decreasing processing redundancy and saving cortical space. Nevertheless, the continuous influx of visual information in everyday vision often requires the storage of information in VWM while concurrently processing new visual input. The very fact that distractors can interfere with VWM performance suggests a need to separate VWM and sensory processing. In this regard, sensory areas seem to be a suboptimal choice to serve as the primary storage site for VWM. In addition, given the high representational capacity of sensory

Trends

Recent findings from human fMRI decoding studies have provided renewed support for the sensory account of VWM storage. This account argues that brain areas involved in sensory processing also play important roles in the temporary storage of information in VWM.

However, a detailed examination of human behavior, fMRI decoding, TMS, and monkey neurophysiology results showed very little support for the sensory account of VWM storage.

Instead, both structural and experimental evidence supports prefrontal and posterior parietal cortices as brain regions playing more significant roles in VWM storage.

¹Department of Psychology, Harvard University, 33 Kirkland Street, Cambridge, MA 02138, USA

*Correspondence: yaodaxu@fas.harvard.edu (Y. Xu).

processing, it is puzzling that VWM should be highly capacity-limited, as shown by an extensive body of studies ([12,13] for recent reviews; also [14]). I review here evidence from human behavioral, fMRI decoding, and TMS studies, as well as from monkey neurophysiology studies, that is relevant to the sensory account of VWM storage (including some that has been used to directly support this account). Detailed analysis of this body of evidence, however, does not provide strong support for the sensory account of VWM storage. Instead, once information is consolidated from sensory processing into VWM, early visual areas play at most an auxiliary rather than an essential role in VWM storage, and the content of VWM seems to be stored elsewhere – in association regions of the brain such as PFC and PPC.

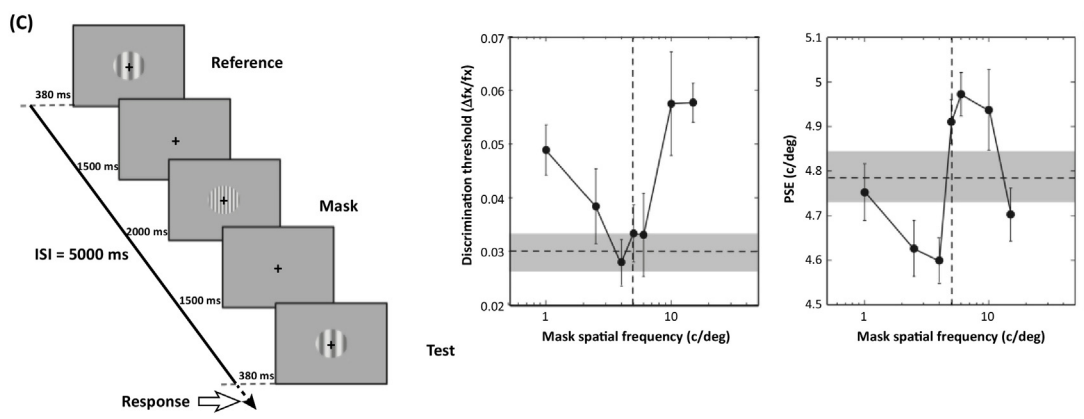
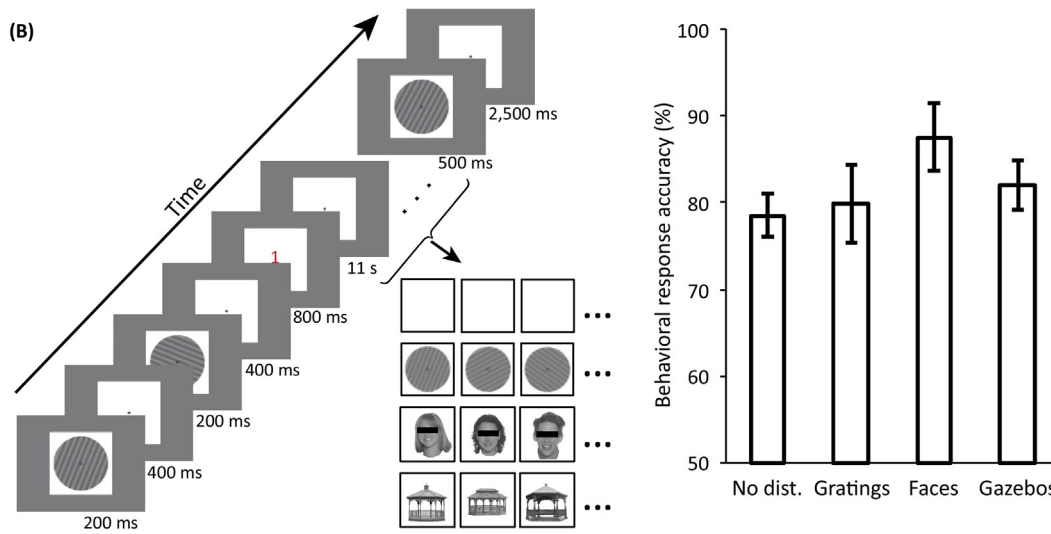
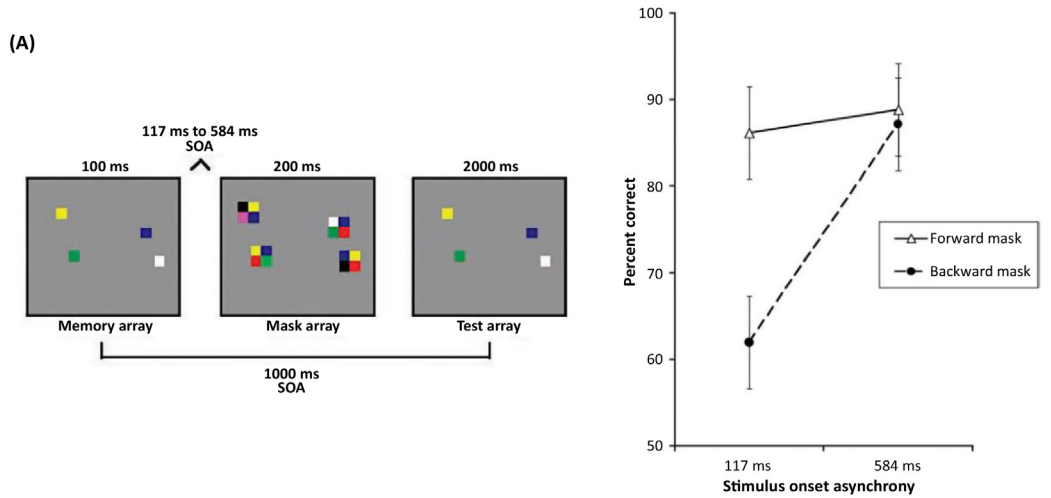
Evidence from Human Behavioral Studies

To understand how sensory processing and VWM storage may interact, behavioral studies have examined the effect of masks or distractors during the VWM delay period. Following the logic of dual task interference, the idea here is that if VWM storage and sensory processing share the same neural substrates, then the presence of masks or distractors during the delay period would significantly interfere with this storage. I review here the results from both change-detection and fine-discrimination studies. I focus on results when the masks/distractors are only passively viewed because any task performed on them would likely introduce interference at multiple stages of processing. The overall evidence shows that once sensory information is successfully transferred and consolidated into VWM, the content of VWM is fairly resilient to distraction. Importantly, given the involvement of several brain regions in VWM storage, the distractor interference effect by itself, whether weak or strong, does not pinpoint the exact locus of interference; it would be equally compatible with regions other than sensory areas serving as the primary storage site for VWM.

Change-Detection Studies

In one of the first studies documenting the characteristics of VWM, using pattern stimuli generated by randomly filling cells in a square matrix and a change-detection paradigm, Phillips [15] reported that although VWM was capacity-limited, it was unaffected by a spatial location change between the sample and test stimuli and was unaffected by pattern masking. With a finer sampling of the temporal interval between the sample and the mask and a manipulation of the display set size, it was found [16] that pattern masking could in fact impact on VWM performance, but only during the early delay period (with a ~25% drop in performance), and had no effect during the mid to late delay period (Figure 1A). Thus, masking seems to be only effective when the sample stimuli are still being consolidated into VWM. Once this process is completed, masking does not seem to affect VWM storage. The time needed for consolidation depends on the display set size and the complexity of the stimuli. It is about 50 ms per item for color stimuli, and much longer for shape and color–shape conjunction stimuli [16,17]. A similar behavioral masking effect has also been observed in Macaque monkeys, such that masking was only effective in a motion WM task during the early, but not the mid to late, delay period [18].

Gazzaley and colleagues did find a small and significant drop in change-detection performance (~3%) in a face VWM task when a distractor face was passively viewed midway through a 6.8 s delay period (experiment 1 of Clapp *et al.* [19], and results for young adults from [20]). However, this effect failed to reach significance in experiment 2 of Clapp *et al.* [19]. Likewise, in a motion VWM task, Berry *et al.* [21] were able to find a small (2%) distractor interference effect, but only in the first block of 40 trials and not in the second block of trials. Perhaps the presence of a single mask or distractor during the mid to late delay period was ineffective in creating a stable negative impact on VWM storage. Feredoes *et al.* [22] presented either a sequence of three face distractors in a scene VWM task or three scene distractors in a face VWM task. They found a small drop in performance (2%) that barely reached significance with a one-tailed *t*-test. Thus,



showing three distractors instead of one did not seem to increase the magnitude of the interference effect.

Perhaps the effect would increase if the distractors are very similar to the memorized items. With that in mind, in a recent study we asked observers to remember the precise orientation of a sample grating and, after an extended delay period, judge whether the test grating rotated slightly either clockwise or counterclockwise compared to the sample grating ([23] and Figure 1B; this task was modeled after [9]). After the sample stimulus was consolidated into VWM, during the delay period, we showed a sequential presentation of either 17 gratings appearing in six different orientations, 17 different faces, or 17 different gazebos. Even with the large number of distractors shown, some highly similar to the memorized item, none of the distractor conditions negatively impacted on VWM performance compared to a control condition with an unfilled delay (Figure 1B). Because performance was ~80% correct, the lack of an interference effect could not be due to either a ceiling or a floor effect. It is also unlikely that the observers simply closed their eyes during the entire delay period because doing so would risk missing the presentation of the test stimulus which lasted only 500 ms. In addition, the same observers performed a version of the task in the MRI scanner, and we were able to decode the content of the distractors during the delay period in early visual areas [23]. The similarity between the sample and distractor also failed to impact on VWM storage accuracy in Sreenivasan and Jha [24], although it did have a small effect on reaction time (~2–3% increase in reaction time).

Together, these change-detection studies showed that a large distractor interference is only present during the early delay period when sensory information is still being transferred and consolidated into VWM. Once this process is completed, the negative impact of distractor appears to be either very small (2–3%) or absent. The content of VWM thus seems to be fairly resilient to distraction once it is consolidated.

Fine-Discrimination Studies

It may be argued that perhaps the change-detection paradigm is not ideal for documenting small effects and that the effect of distractor can be consistently detected with a more sensitive measure. Indeed, when highly controlled psychophysical settings were applied to measure the discrimination thresholds or the points of subjective equality between the sample and test stimuli, or when a detailed modeling of the data was applied, a small effect of distractor interference during the VWM delay period has been found consistently.

Figure 1. The Impact of Distractors on Visual Working Memory (VWM) Storage in Human Behavioral Studies. (A) In a change-detection study conducted by Vogel *et al.* [16], observers were shown four colors and, after the delay period, detected whether a color change occurred in the test display. A pattern mask was shown at various points either before the onset of the sample display (forward mask) or after sample onset during the delay period (backward mask). Only pattern masks shown during the early delay period significantly impaired performance compared to those shown before the sample onset or during the mid to late delay period. (B) In a change-detection study conducted by Bettencourt and Xu [23], observers were shown two gratings and were retro-cued to remember the orientation of only one of the gratings. After the delay period, observers judged whether the test grating rotated slightly either clockwise or counterclockwise. During the delay period, no distractor, 17 gratings appearing in 6 different orientations, 17 faces, or 17 gazebos were shown. VWM performance was not affected by the presence or the type of distractors shown. (C) In a threshold discrimination study conducted by Nemes *et al.* [27], observers were shown a sample (reference) grating and, after a delay period, judged whether the spatial frequency of the test grating matched that of the sample grating. The presence of the distractor grating (mask) halfway through the delay period elevated the spatial frequency discrimination thresholds between the sample and test grating when the two differed. In addition, VWM of the sample spatial frequency was biased towards the distractor spatial frequency. This attractor effect only happened when the distractor spatial frequency was within a range of approximately 1.2 octaves of the sample spatial frequency and disappeared outside this range. Collectively, these results show that once sensory information is successfully transferred and consolidated into VWM, the content of VWM is fairly resilient to distraction. Abbreviations: ISI, interstimulus interval; no dist., no distractor. Figure 1A – Reprinted from [16] with permission by American Psychological Association; Figure 1B – Reprinted with slight modifications from [23] by permission from Macmillan Publishers Ltd: Nat. Neurosci. (<http://www.nature.com/neuro/index.html>), copyright 2016; Figure 1C – Reprinted from [27] with permission from Elsevier: Vis. Res. (<https://www.journals.elsevier.com/vision-research/>).

In a spatial frequency change-detection task, Magnussen *et al.* [25] found that the presence of the distractor halfway through a 10 s delay period elevated the spatial frequency discrimination thresholds between the sample and test stimuli from ~4% to ~8% when the spatial frequency of the distractor differed from that of the sample stimulus by at least an octave (also [26]). Nemes *et al.* [27] replicated this finding and additionally showed that VWM of the sample spatial frequency was biased towards the distractor spatial frequency (also [28,29]). This attractor effect only happened when the distractor spatial frequency was within a range of ~1.2 octaves of the sample spatial frequency, and disappeared outside this range (Figure 1C). This masking bandwidth is in good agreement with those obtained from adaptation and sensory masking experiments (e.g. [30–32]) and those measured in primate V1 neurons [33]. The neural mechanisms supporting VWM for spatial frequency thus seem to follow similar organizational principles to those exhibited by brain regions involved in the sensory processing of this information [27]. Although this agreement is consistent with a sensory account of VWM storage [8], other behavioral evidence challenges this notion. For example, while adaptation to a luminance contrast grating is orientation- and location-dependent [34–37], VWM for spatial frequency is orientation- and location-independent [27,38,39]. In addition, distractor masking in VWM has been shown to be dependent upon perceived as opposed to retinal spatial frequency [26]. These disagreements indicate that, unlike sensory processing, VWM for spatial frequency is likely supported by neural processing at a level beyond early sensory processing.

In addition to spatial frequency, similar results have been obtained for other stimulus features. In a motion VWM task, Magnussen *et al.* [40] observed that a distractor motion stimulus significantly elevated the velocity discrimination thresholds between a sample and a test stimulus when the sample and distractor velocity differed by a factor of two. This masking effect was identical whether or not sample and distractor drifted in the same or different directions [41], again indicating that the interference occurs beyond early sensory processing. Nemes *et al.* [42] found that VWM for a sample color was biased toward the distractor color only when the hue of the distractor fell within a bandwidth of 29–37 degrees of the sample color on the color wheel. In a recent study, Rademaker *et al.* [43] reported that VWM for a sample orientation grating was shifted maximally by about 3° by a distractor orientation shown midway through a 3 s delay period.

The effect of distractor interference has also been examined in spatial VWM. Van der Stigchel *et al.* [44] found a distractor attractor effect such that there was a small but significant shift of 0.153° of the memorized location towards the distractor location. However, this effect was only present when the distractor was close in space to the memory representation. Marini *et al.* [45] reported a small but significant increase in error in polar angle estimation of a sample dot when a distractor was shown 12–18° away from the sample dot at the same eccentricity during the delay period. However, this effect was only significant relative to a distractor-absent condition, but not to a condition in which the distractor was shown at the sample location (which, exactly as the distractor-absent condition, did not impact on performance). The effect of distraction thus did not appear to be robust.

Thus, even with highly controlled psychophysical settings, these results show that distractors shown during the mid to late delay period do not severely impact on VWM representation as they do if shown during the early delay period. The overall distractor interference effect is relatively small, the range in which the distractors are effective is limited, and the effect may not be obtained if highly controlled psychophysical settings are not applied (e.g., [46]). Most importantly, the distractor interference effect does not completely align with characteristics observed in sensory processing.

Together, results from both change-detection and fine-discrimination studies show that once sensory information is successfully transferred and consolidated into VWM, the content of VWM is fairly resilient to distraction. This is at odds with an intuitive understanding of the sensory account, which would predict a large interference between VWM storage and sensory processing of the distractor as a result of shared neural resources. At the very least, these weak interference effects do not provide strong support for the sensory account. Given the involvement of PFC and PPC in VWM storage, the distractor interference effect could also arise from processing within those regions. As such, the distractor interference effect by itself, whether weak or strong, does not pinpoint early visual areas as the primary storage site for VWM; it would be equally compatible with other regions serving as the primary storage site for VWM.

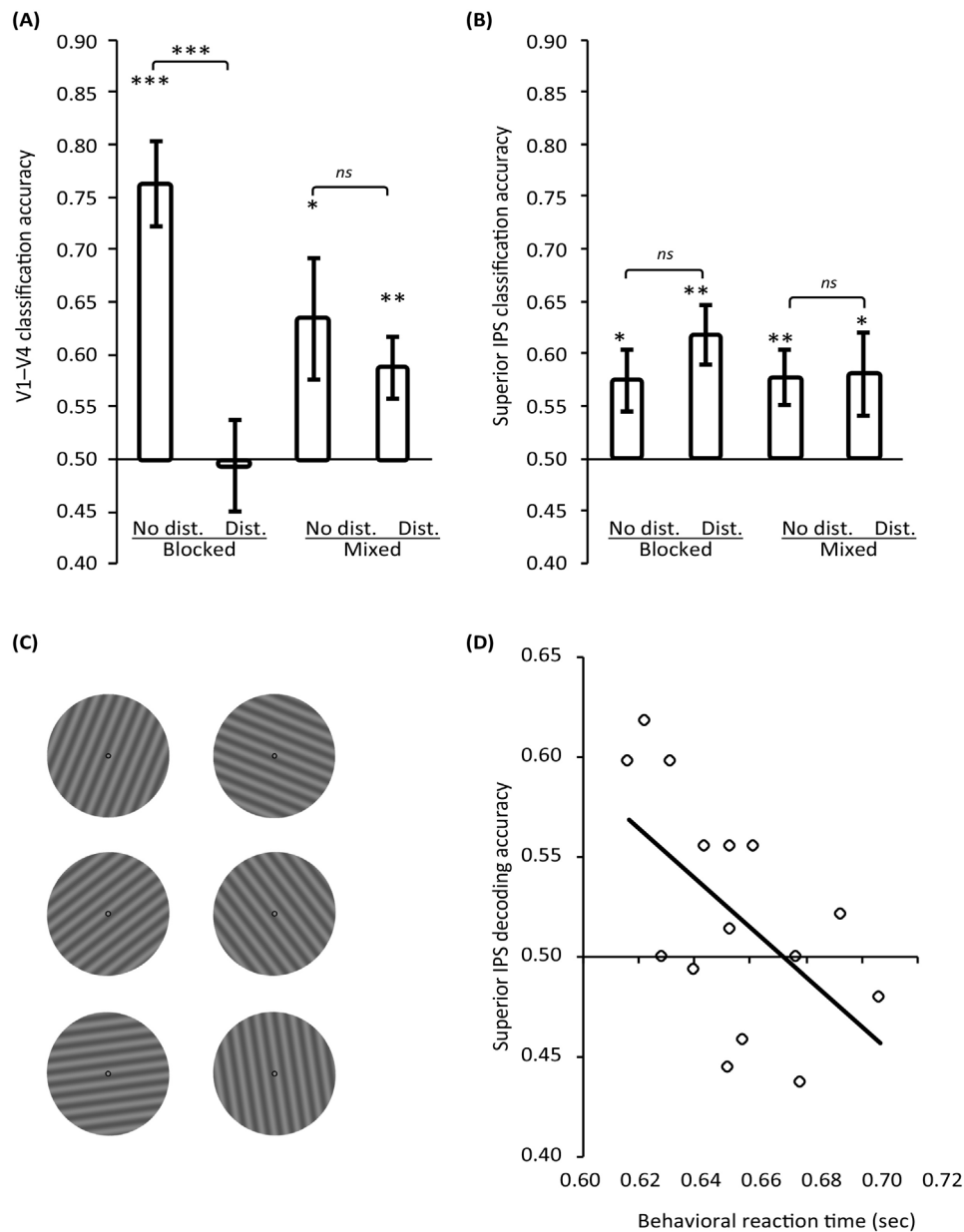
Evidence from Human fMRI and TMS Studies

Instead of seeking indirect evidence from human behavioral studies, with the development of fMRI MVPA and TMS methods, researchers have directly examined the representational content of sensory areas during VWM delay period and the impact of temporary stimulation of sensory areas on VWM storage. Although fMRI decoding studies have demonstrated the existence of robust VWM representation in early visual areas, such a representation is susceptible to distraction, making early visual areas unlikely to serve as the primary storage site for VWM. Similarly, once information has been consolidated into VWM, TMS of early visual areas does not seem to affect VWM storage.

Human fMRI MVPA Studies

The development of fMRI MVPA has allowed researchers for the first time to examine whether the content of VWM can be stored in human early visual areas. Harrison and Tong [9] asked observers to remember the orientation of a grating; they were able to decode the remembered orientation successfully during the VWM delay period in early visual areas (also [10]). Since then this finding has been replicated multiple times across different laboratories [23,47–57]. These results have provided a new wave of evidence supporting the sensory account of VWM storage.

Despite these robust findings, it is worth noting that VWM decoding was obtained when the entire delay period was unfilled. This is very unlike our real-world visual experience when, as we try to hold onto information stored in VWM, we are at the same time bombarded by the continuous influx of new visual information. Can early visual areas still store the content of VWM when the delay period is filled with distractors? To address this question, we used the orientation VWM task described in Figure 1B and compared decoding for trials with an unfilled delay and those with a filled delay with face and gazebo distractors. In a first experiment, we made distractor presence in a trial completely predictable by blocking trials with and without distractors. In trials without distractors, VWM decoding in early visual areas was high and comparable to what was previously reported [9] (Figure 2A). However, in trials with distractors, VWM decoding in early visual areas dropped significantly and became indistinguishable from chance-level performance ([23] and Figure 2A). Meanwhile, distractor presence had no impact on behavioral performance, consistent with Phillips [15] and Vogel *et al.* [16]. These results show a discrepancy between VWM decoding in early visual areas and behavioral performance, and suggest that the representations held in early visual areas may not support the actual storage of VWM. In a second experiment, instead of making the distractor presence predictable by blocking trials with and without distractors, we randomly intermixed the two types of trials. Again, we found no effect of distractors on behavioral performance. Interestingly, we were able to obtain significant and comparable VWM decoding in early visual areas for both trial types during the delay period (Figure 2A). However, decoding for trials without distractors was significantly lower for those in the second than in the first experiment. In other words, even when distractors were not shown, knowing that distractors might be present significantly



Trends in Cognitive Sciences

Figure 2. The Impact of Distractors on Visual Working Memory (WWM) Storage in a Human fMRI Decoding Study [23]. Using a paradigm similar to that shown in Figure 1B, it was found that WWM delay period decoding in early visual areas was significantly impacted by the presence and predictability of the distractors (A), even though distractor presence and predictability had no impact on behavioral performance. Specifically, when trials with and without distractors were blocked, decoding was robust when observers knew that distractors would never be present (blocked-no dist); however, decoding dropped significantly and became indistinguishable from chance performance when observers knew that distractors would always be present (blocked-dist). When trials with and without distractors were randomly intermixed, significant and comparable decoding was obtained for both trials with and without distractors (labeled as mixed-dist and mixed-no dist, respectively). Nevertheless, decoding for trials without distractors was significantly lower for those in the mixed than in the blocked condition. Thus, even when distractors were not shown, knowing that distractors might be present significantly weakened WWM decoding in early visual areas. By contrast, mirroring behavioral performance, successful WWM delay period decoding was obtained in superior intraparietal sulcus (IPS) and was unaffected by the presence and predictability of the distractors (B). When six different orientation gratings were used as stimuli in a WWM task (C), using a representational similarity measure, a significant correlation was found between WVM representation in superior IPS and behavioral performance, such that the more similar the two orientation representations were in superior IPS, the slower it was to tell them apart in a behavioral change-detection task (D). Together, given the lack of consistent WVM decoding in early visual areas under distraction, these results indicate that early visual areas are unlikely to serve as the primary storage site for WVM. Instead, areas such as superior IPS may play a more significant role in WVM storage. Abbreviation: *ns*, not significant.

Figures 2A, 2B, and 2D - Reprinted with slight modifications from [23] by permission from Macmillan Publishers Ltd: Nat. Neurosci. (<http://www.nature.com/neuro/index.html>), copyright 2016.

weakened VWM decoding in early visual areas. These results show that VWM representation in early visual areas is heavily modulated by both the presence and the predictability of the distractors. Meanwhile, because behavioral performance was unaffected, early visual areas are unlikely to have served as the primary storage site for VWM. These findings are at odds with the sensory account of VWM storage.

If early visual areas are unlikely to serve as the primary storage site for VWM, why do we observe VWM-related decoding in these brain regions at all? It is possible that the low task demand of the long VWM delay period encourages observers to activate regions nonessential for the task via mental imagery [47]. Alternatively, feedback to early sensory areas could play a functional role, and facilitate the comparison between VWM content and the upcoming test probe at the end of the delay period [1]. Either way, feedback to early visual areas has been observed in both fMRI and neurophysiology studies. Using fMRI decoding, Ester *et al.* [48] reported a dissociation between cortical areas involved in sensory processing and VWM storage such that although sensory processing only engaged area V1 contralateral to stimulus presentation, VWM content could be decoded from both contralateral and ipsilateral V1. More direct evidence of feedback from neurophysiology studies is presented later.

Thus, although fMRI decoding studies have demonstrated the existence of robust VWM representation in early visual areas, such a representation is susceptible to distraction. In everyday vision, a continuous influx of new information is always expected, similar to the presence of predictable distractors in Bettencourt and Xu [23]. Sensory regions such as early visual areas are thus unlikely to serve as the primary storage site for VWM to support real-world visual cognition.

Human TMS Studies

The location of early visual areas is easily accessible by TMS. This has provided researchers with an opportunity to examine a causal connection between the function of early visual areas and VWM storage. Two studies have found that TMS of early visual areas during a VWM task significantly impaired performance [58,59]. These two studies have been cited as providing key evidence supporting the sensory nature of VWM storage [1,2]. A closer examination of these two TMS studies, however, revealed a different story. In a VWM task involving observers remembering a clock face, Cattaneo *et al.* [58] found that applying TMS over the occipital cortex resulted in a negative effect during the early delay period, but no negative effect during the late delay period. Similarly, in a VWM task involving abstract geometric shapes (Figure 3A), van de Ven *et al.* [59] observed a negative effect of TMS over the occipital cortex only at 200 ms, but not at 100 ms or 400 ms post stimulus presentation (Figure 3B). The null effect at 400 ms is crucial because it suggests that, once information is consolidated into VWM, occipital cortex plays no further role in VWM information storage. This is consistent with the behavioral masking effects described earlier [16,17]. Indeed, when van de Ven *et al.* [59] placed a visual mask at the same time-points as TMS, they obtained very similar effects to those produced by TMS (Figure 3C). In a most recent study involving VWM for colors, van Lamsweerde and Johnson [60] administered TMS at 0, 100, and 200 ms post stimulus presentation and found that the negative effect of TMS was greatly reduced or entirely absent at the longer stimulation interval, consistent with the findings of van de Ven *et al.* [59]. Likewise, Rademaker *et al.* [61] also found in an orientation VWM task that recall error was larger when TMS was applied at the tail-end of encoding than at midway during the delay. These results indicate that, once information has been consolidated into VWM, TMS to early visual areas does not affect VWM storage.

A few TMS results have been obtained that on the surface do not appear to subscribe to the above view. However, a detailed examination reveals that these results either tap into a different processing stage or are ambiguous/debatable. Cattaneo *et al.* [58] applied TMS at the end of

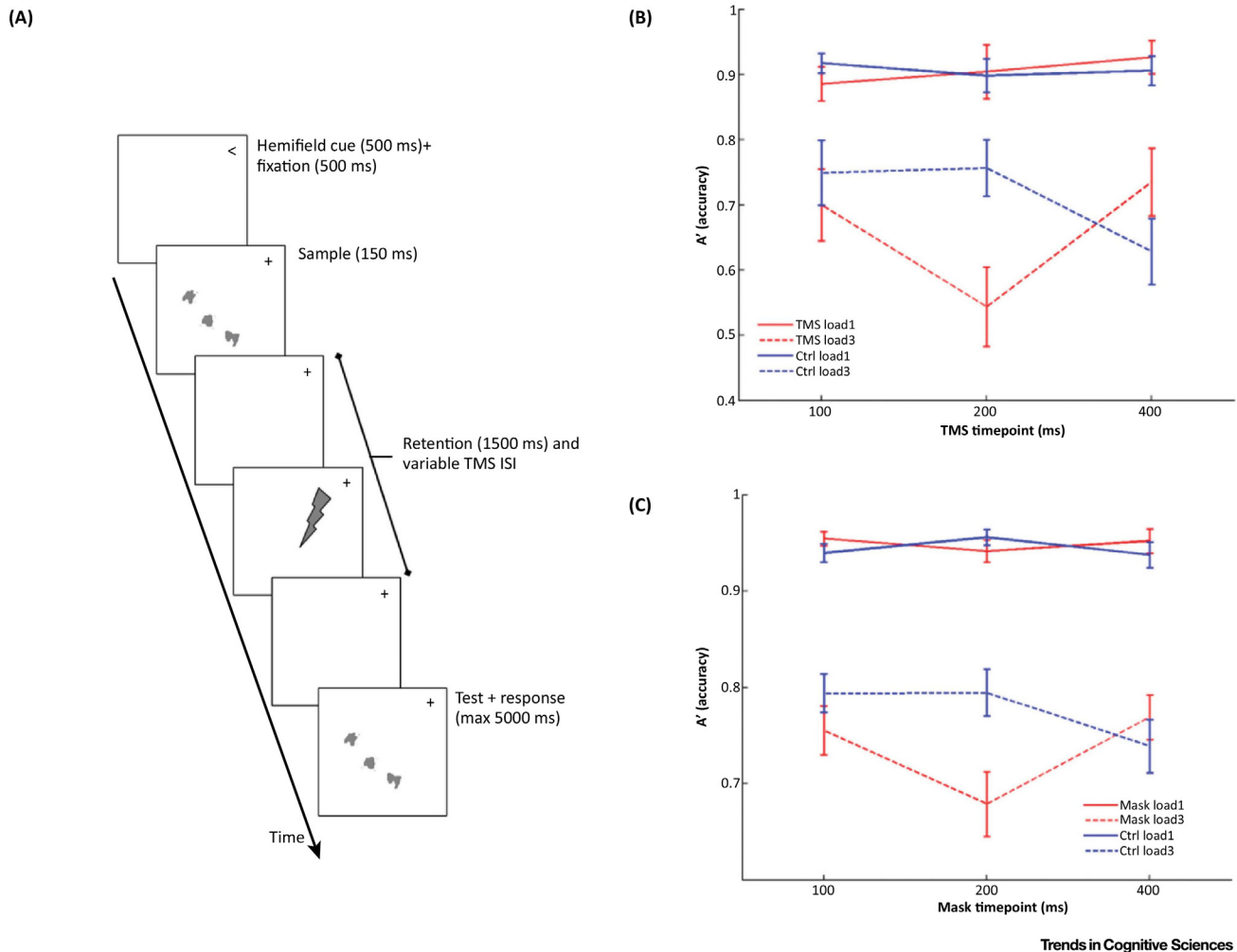


Figure 3. The Effect of TMS on VWM Storage in Human Occipital Cortex. In a change-detection study, van de Ven *et al.* [59] asked observers to remember in a sample display either one or three abstract geometric shapes and, after a delay period, judge whether a change occurred in the test display (A). During the delay period, TMS was applied over the occipital cortex at 100 ms, 200 ms, or 400 ms after sample presentation. When the sample contained three shapes, a negative effect of TMS was found at the 200 ms but not at the other stimulation time-points (B). Presenting a visual mask at the same time-points resulted in very similar effects to those produced by TMS (C). Together, these results show that once information is consolidated into VWM, TMS of occipital cortex does not impact on VWM retention. Abbreviations: Ctrl, control; ISI, interstimulus interval; TMS, transcranial magnetic stimulation; VWM, visual working memory. Reprinted from [59] with permission of SOCIETY FOR NEUROSCIENCE in the format Republish in a journal/magazine via Copyright Clearance Center.

the VWM retention period and found a facilitation effect with a decreased reaction time in performance. However, this effect could be caused by an enhancement in either test probe detection via neural priming or reactivation of the memory item (via top-down feedback) to facilitate memory item and test probe comparison. This enhancement thus may be more related to probe detection/comparison than to VWM storage. In another study, Silvanto and Cattaneo [62] applied TMS to the middle temporal (MT) area midway during the delay period and reported an interference between TMS-induced phosphene motion direction and that maintained in VWM. Although this finding has been used to support the sensory account of VWM [3], it could instead reflect the position that top-down signals to sensory areas affect visual perception [63]. Because higher cortical regions are necessarily involved in conscious interpretation of phosphene motion, any interference observed could occur in these higher cortical regions rather than in MT. Silvanto and Cattaneo [62] did not directly examine the effect of TMS on VWM storage, but rather the effect of TMS-induced phosphene on VWM storage. This is in

essence a distractor interference manipulation which, as discussed earlier, cannot pinpoint the locus of the interference. Rademaker *et al.* [61] recently reported an improvement in VWM for orientation shown at the TMS site of early visual area V1/V2 compared to that shown diagonally from the TMS site. They further reported that this effect was present at both early and late TMS during the delay period. The validity of this TMS effect, however, is debatable, given that a similar effect appears to exist with sham TMS (Figure 4 of [61]). The effect likely reflects better VWM performance at the lower than upper visual field given that TMS was applied at the dorsal portion of V1/V2, thereby always targeting stimuli shown at the lower visual field.

Collectively, the available TMS evidence indicates that, once information has been consolidated into VWM, TMS to early visual areas does not affect VWM storage. Thus, contrary to what has been argued, TMS results do not provide key evidence supporting the sensory nature of VWM storage.

Evidence from Monkey Neurophysiology Studies

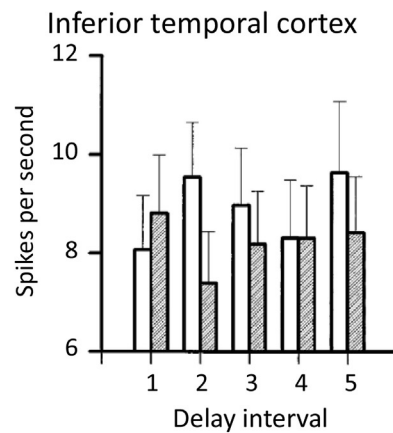
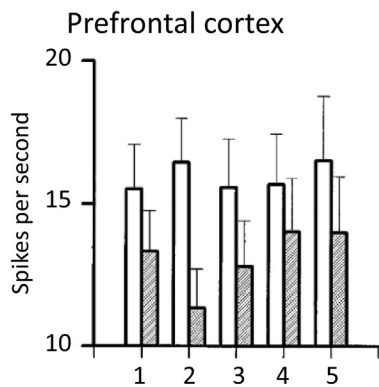
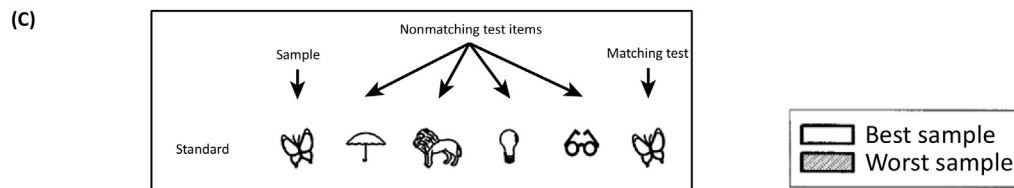
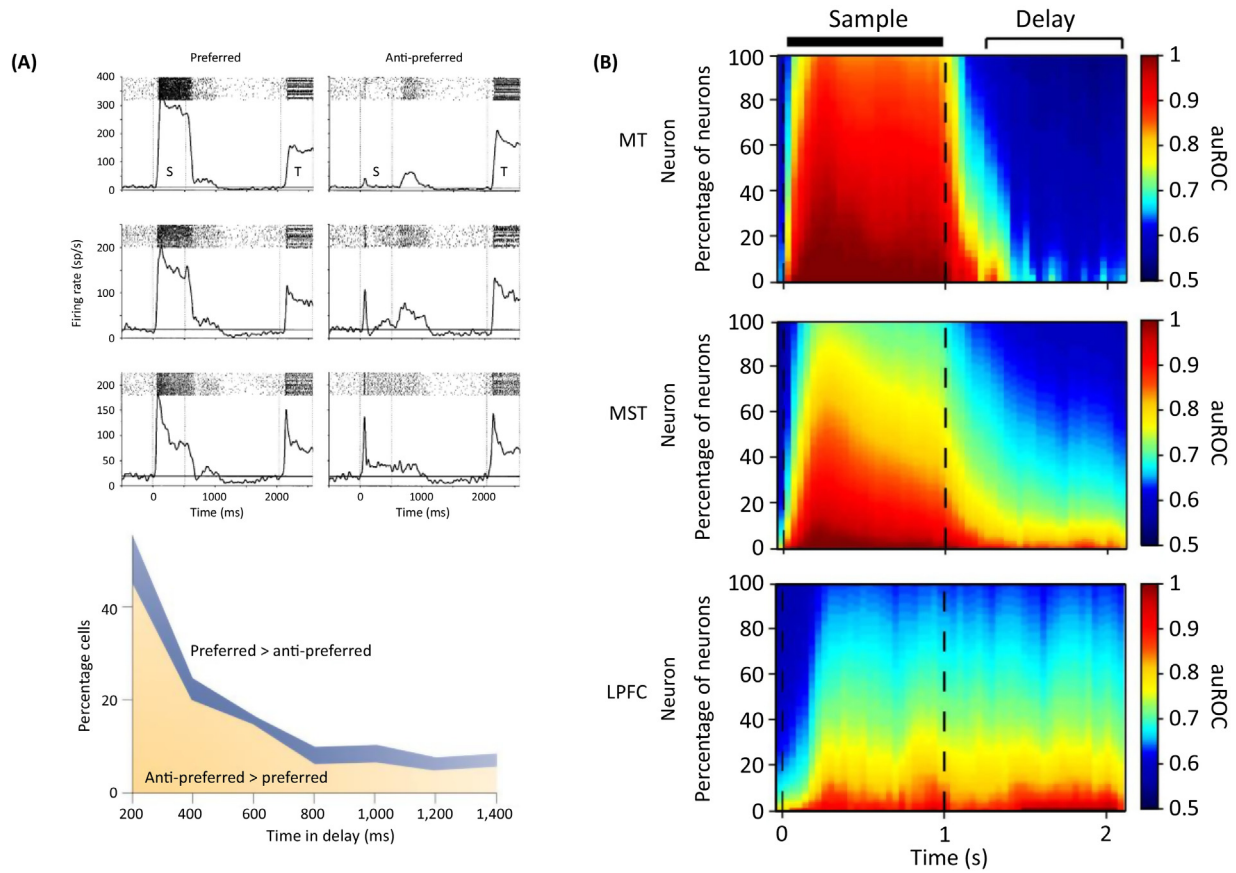
Monkey neurophysiology studies have continuously played a leading role in shaping our understanding of the neural mechanisms underlying VWM. A detailed examination of these results, however, also produces very little support for the sensory account of VWM storage.

Sustained Responses and Neural Synchrony

Past monkey neurophysiology studies have used the presence of robust delay period activity as an indicator of the involvement of a brain region in VWM storage. By examining 90+ monkey neurophysiological studies on VWM that have been published in the past four decades [63], Martinez-Trujillo and colleagues recently reported that ‘WM-related sustained activity in early sensory areas are rare, and typically lack stimulus specificity’ and argued that ‘robust sustained activity that can support WM coding arises as a property of association cortices downstream from the early stages of sensory processing’ (p.111).

For example, in a VWM study for motion, Bisley *et al.* [64] did not observe in MT sustained delay period neuronal activity (also [65]). Instead, they reported a burst of MT activity during the early delay period, followed by a prolonged period of activity suppression, with the suppression being greater for the preferred than the anti-preferred direction (Figure 4A). Such activity suppression was believed to limit further sensory encoding during the delay period to protect the stored VWM content, and to decrease background noise so as to enhance neuronal responses to the upcoming test stimulus. A decrease in response amplitude during the VWM delay period has also been reported in V1 in human fMRI studies, suggesting that a similar suppressive mechanism may be at play in the human brain [48]. It is worth noting that such delay period activity suppression was not observed in PFC neurons [66]. In a more recent study, Mendoza-Halliday *et al.* [67] also failed to find VWM delay period activity in MT. Instead, such activity was found in a downstream associative area, the medial superior temporal (MST) area and in PFC (Figure 4B). While the behavioral performance of the animals was correlated with the sustained activity in both lateral prefrontal cortex (LPFC) and MST, the correlation was greater in LPFC than MST, suggesting the existence of a more prominent VWM signal in LPFC than in MST.

In their study, Mendoza-Halliday *et al.* [67] additionally reported a synchrony between MT local field potential (LFP) and LPFC neuronal spikes during the VWM task. This indicates that the sustained activity in LPFC could modulate synaptic activity in MT via a top-down feedback mechanism. Indeed, van Kerkoerle *et al.* [68] reported that the sustained spiking activity in V1 neurons during VWM delay was mainly seen in the superficial layers and layer 5 of area V1, a laminar pattern consistent with feedback from higher areas to V1. Synchrony has also been observed between LPFC and V4 in monkeys performing a VWM task, with enhanced phase



synchronization in theta frequencies in LFP and elevated phase locking in spiking between these two brain regions [69]. LPFC was additionally shown to be more involved than V4 in generating and sustaining such oscillations during VWM retention, again suggesting an asymmetric relationship and a top-down role of LPFC in controlling the inter-region neural synchrony [69].

Together, the combination of a top-down feedback mechanism and a suppressive mechanism [64] can also explain why in Super *et al.* [70] the overall V1 neuronal responses were well below baseline but there was still a difference between the remembered direction of motion and background during the delay period. Although this finding has been used to support the sensory account of VWM, this effect may not imply a direct involvement of V1 in VWM storage. Mendoza-Halliday *et al.* [67] also noted paradigm differences between Super *et al.* [70] and traditional VWM tasks that could account for the result obtained by Super *et al.*

Because fMRI signal has been shown to mainly reflect LFP [71,72], it has been argued that feedback-driven LFPs in sensory areas could account for successful fMRI decoding of VWM content in the absence of sustained activities [67]. This could explain the discrepancy between robust VWM decoding found in human fMRI studies and the lack of sustained activities found in monkey neurophysiology studies.

Despite the omnipresence of distractors in everyday vision, few monkey neurophysiology studies have examined the impact of distractors on the WM delay period activity in sensory regions. Using a delayed-match-to-sample paradigm, Miller *et al.* [73] found, when the delay period was filled with non-matching stimuli (i.e., distractors), that sustained response to the sample was no longer present in inferior temporal area (IT) neurons (Figure 4C; also [74]). Similarly, van Kerkoerle *et al.* [68] reported that a briefly appearing mask temporally abolished the spiking activity in V1 during the delay period; it was then restored via top-down feedback.

Overall, these results show that there is a lack of consistent and robust delay period activities in early visual areas in VWM tasks, and that feedback from downstream regions greatly impacts on activities in these areas. This suggests that regions other than sensory areas play a significant role in VWM storage. In addition, exactly as with human fMRI decoding [23], sample-selective delay period activity in sensory neurons could be easily abolished by the presence of distractors, making the sensory storage of VWM content a suboptimal choice if VWM is to play a functional role in real-world visual information processing.

Lesion and Microstimulation

In addition to recording studies, lesion and microstimulation studies have been used to support the sensory account of VWM storage [8]. For example, Bisley and Pasternak [75] reported that

Figure 4. Delay Period Activity from Monkey Neurophysiology Studies. (A) In a delayed-match-to-sample motion task, Bisley *et al.* [64] failed to observe sustained delay period activity in MT neurons. Instead, they reported a burst of MT activity during the early delay period, followed by a prolonged period of activity suppression (top graph). In a majority of the neurons recorded, the suppression was greater for the preferred than for the anti-preferred direction of motion (bottom graph) of the neurons. (B) In a more recent delayed-match-to-sample motion task, Mendoza-Halliday *et al.* [67] also failed to find VWM delay period activity in area MT. Instead, such an activity was found in MST and LPFC. Shown here is the average area under the receiver operating characteristics curve (auROC) across MT, MST, and LPFC neurons over time as a function of the percentage of averaged neurons. (C) In a delayed-match-to-sample object task, Miller *et al.* [73] found that, when non-matching stimuli (i.e., distractors) were shown during the delay period, PFC neurons still maintained a difference in activity between the 'best' and the 'worst' samples during the delay period between the presentation of successive distractors. Such a difference, however, was not seen in IT neurons. Overall, these results show that sustained delay period activities are not always found in early visual areas in VWM tasks, and that the delay period activities may additionally be subjected to distraction. Abbreviations: IT, inferior temporal area; LPFC, lateral prefrontal cortex; MST, medial superior temporal area; MT, middle temporal area; PFC, prefrontal cortex; VWM, visual working memory.

Figure 4A top – Reprinted from [64] with permission by American Physiological Society; Figure 4A bottom – Reprinted from [8] by permission from Macmillan Publishers Ltd: Nat. Rev. Neurosci. (<http://www.nature.com/nm/index.html>), copyright 2005; Figure 4B – Reprinted from [67] by permission from Macmillan Publishers Ltd: Nat. Neurosci. (<http://www.nature.com/neuro/index.html>), copyright 2014; Figure 4C – Reprinted with slight modifications from [73] with permission of SOCIETY FOR NEUROSCIENCE in the format Republish in a journal/magazine via Copyright Clearance Center.

lesion to MT/MST impaired WM retention of a low-coherence motion stimulus (also [76]). However, because MT/MST lesion also impaired the sensory encoding of such stimuli, and possibly the transfer and consolidation of sensory information into WM, such a lesion result does not pinpoint the role of MT/MST in VWM storage.

Bisley *et al.* [77] reported that microstimulation of area MT during VWM encoding biased the direction of the remembered motion stimulus to the preferred direction corresponding to the stimulated site. It is as if sensory processing itself was altered by microstimulation. However, microstimulation during the delay period did not result in the same effect, but instead resulted in chance-level performance when the to-be-remembered stimulus was in the opposite direction to the preferred direction corresponding to the stimulated site. Although this result has been used to support a causal role of MT in VWM storage, it is also possible that microstimulation generated a competing representation that was relayed to downstream regions and created interference there.

Activity-Silent VWM Mechanisms

Recently, activity-silent WM mechanisms have been put forward as alternatives to a sustained activity-driven WM mechanism (e.g., [78–81]). Evidence supporting these mechanisms has mainly come from PFC. For example, in a memory-guided saccade task, Watanabe and Funahashi [79] observed that WM delay period signal in PFC was substantially attenuated when an attentional task was performed during the delay period. However, WM delay signal reappeared after the completion of the attentional task. This result has been used to argue for the existence of activity-silent WM maintenance in PFC neurons [81]. It is worth noting that, even when distractors were passively viewed during the delay period, both Miller *et al.* [73] and Jacob and Nieder [82] also observed the disappearance of WM delay signal in PFC during the presence of the distractor, and subsequent restoration of this signal after the distractor was removed.

In a recent study, Rose *et al.* [83] applied TMS to reactivate VWM items that were maintained outside the focus of attention, presumably via activity-silent WM mechanisms. Interestingly, in experiment 3 of the study in which TMS elicited both fMRI and behavioral effects, the site of TMS stimulation was the parietal cortex (Figure 4 of [83]). If anything, this suggests that activity-silent VWM storage is in parietal cortex and not in occipital cortex. No evidence is presently available supporting the role of sensory regions in VWM storage via activity-silent WM mechanisms.

It is worth noting that, even when activity-silent WM mechanisms might be at play in PFC, Watanabe and Funahashi [79] reported the presence of weak but noticeable WM delay-period activities in PFC. They cautioned ‘it is premature to conclude that working memory is not maintained by LPFC delay-period activity’ (p. 610). They additionally pointed out that VWM-related signals in PFC could be maintained by sustained activities elsewhere in brain regions such as PPC. As such, activity-silent WM mechanisms may not be necessary to account for the observed results. Consistent with this view, Jacob and Neider [82] reported that, although the presence of distractors abolished WM delay signal in PFC, it did not affect WM delay signal in PPC. Leavitt *et al.* [63] additionally noted that activity-silent VWM signal cannot travel between cortical regions to coordinate between brain regions in VWM-related activities. Thus, activity-silent WM mechanisms, even if they exist, may play very limited roles in VWM tasks.

In human behavioral studies, VWM items that are maintained outside the focus of attention are remembered with lower precision than those maintained in the focus of attention [84,85]. This suggests that maintaining items in the focus of attention, possibly via a sustained neuronal response, likely plays a functional role in boosting the quality of VWM storage, and is an

important component of VWM maintenance. Consistent with this view, in mice performing a VWM task, lower delay period activity of medial prefrontal cortex (mPFC) neurons has been associated with incorrect trials; similarly, when thalamus–mPFC projection is suppressed to lower mPFC delay period activity, VWM performance is impaired [86].

Overall, both the existence and the usefulness of activity-silent VWM storage mechanisms are still under debate. It is presently unknown whether such a mechanism exists in sensory regions.

Together, the results reviewed in this section show that, with a lack of consistent and robust sustained activity during the delay period, and reliance on top-down feedback and susceptibility to distraction, early visual areas are not supported by the available monkey neurophysiology evidence as the primary storage site for VWM. Instead, the results reviewed indicate a functional distinction between early visual areas, which encode sensory inputs, and downstream association areas, which process sensory inputs and store VWM representations [67].

Where Could VWM Be Stored Instead?

If early visual areas are nonessential, then where would VWM be stored instead? Both PFC and PPC have been highlighted in their involvement in VWM storage in monkey neurophysiology and human fMRI studies.

Some Structural Characteristics of PFC and PPC

Before reviewing the relevant evidence, it is important to highlight a few structural advantages of involving PPC and PFC in VWM storage compared to sensory areas. Having the content of VWM stored in brain regions other than sensory areas would free up sensory areas and allow them to continuously monitor the incoming visual input, a function that could be vital to the survival of an organism. Unlike laboratory testing, real-world VWM storage is rarely about retaining features from a single stimulus dimension. Instead, it often involves an integrated representation, for example tracking the identity of an object that is momentarily occluded. A sensory account of VWM storage will result in VWM content being scattered across different cortical regions, making an integrated representation less accessible and less able to be manipulated.

At the network level, PFC and PPC are tightly coupled, such that cooling either region in a monkey neurophysiological study resulted in a significant change of neuronal firing rate in the other region in a delayed saccade task [87]. PPC and PFC are parts of the task-positive/multiple demand network [88,89], a set of brain regions long known to be involved in the performance of a variety of tasks. Network analysis further shows that the frontoparietal network (FPN) in particular has among the highest global connectivity with other regions than other networks in the brain [90,91]. Moreover, FPN changes its functional connectivity with other regions depending on the task being performed, enabling FPN to coordinate multiple brain regions during task performance [92]. Such an ability makes PPC and PFC ideal candidates in which task-relevant VWM information may be rapidly stored and integrated to guide thoughts and behavior.

At the circuit level, recent research has discovered mixed selectivity in PFC neurons [93]. This offers a significant computational advantage over fixed selectivity in sensory neurons, and increases the number of distinctive and diverse representations that can be carried by PFC neurons. Other work has identified longer intrinsic timescales in PFC and PPC neurons than in sensory neurons ([94]; also [95]). Given the temporal variability in sensory input, it is advantageous for sensory areas to have shorter intrinsic timescales and relatively uncoupled activities to allow them to effectively track the fast-evolving and changing sensory stimuli. On the other hand, longer intrinsic timescales and highly coupled activities in PPC and PFC enable the formation of stable, consistent, and integrated signals that are better suited to guide behavior

and thoughts [148]. Indeed, in recent studies it has been argued that longer-timescale dynamics may give rise to the emergence of short-term memory in PPC [148,96]. Other crucial features at the circuit level that can contribute to sustained activity in PFC but are absent in V1 have been highlighted in a recent view [63].

Overall, these structural advantages suggest that PPC and PFC may be better suited than sensory areas for VWM storage.

Evidence Supporting PFC and PPC Involvement in VWM

The involvement of PFC in VWM tasks has long been documented by neurophysiology and human fMRI studies. Recent MPVA decoding studies further reported the representation of both low-level visual features, such as orientation, and high-level features, such as verbal semantic category, in PFC during the VWM delay period [50,52,97]. Computational modeling of PFC neuron activity further supports the role of PFC in VWM storage [98]. Several recent publications provide a detailed review of this extensive literature (e.g., [1,3,99]; also [6,7,100–102]).

The involvement of PPC in VWM storage has been noted by both monkey neurophysiology and human fMRI studies over the past two decades. In monkey neurophysiology studies, sustained VWM delay activities have been reported in parietal neurons in lateral intraparietal (LIP) area, ventral intraparietal (VIP) area, and area 7a (e.g., [82,103–112]). For example, Sereno and Manuell [107] reported that shape selectivity in LIP neurons persisted during the delay period of a WM delayed match-to-sample task. Likewise, Freedman, Assad and colleagues found sustained LIP activities during the delayed match-to-category task for abstract motion and shape categories [109,111]. Similar sustained responses in PPC neurons have also been reported for spatial locations during WM delay period [105,106,110,112]. In a recent study, Jacob and Nieder [82] reported sustained delay period activity in VIP in a numerosity VWM task.

In human fMRI studies, behavioral VWM capacities for color, orientation, and shape have been shown to be tightly correlated with fMRI response amplitudes in a region in human intraparietal sulcus (IPS) [113]. This VWM-related IPS response is sensitive to individual observer VWM capacity [114] and to the complexity of the items encoded and stored in VWM [115]. We have localized this VWM capacity-related activity to the superior part of IPS, and referred to it as superior IPS for simplicity [115]. In further studies we documented that the response amplitude of this brain region tracks the total amount of information stored in VWM and shows more resistance to distraction than a lower IPS region and the lateral occipital complex (a region involved in object shape processing) ([116–120]; also [121]). Using fMRI MVPA, we additionally showed that not only could visual information be directly decoded from superior IPS but also these representations tracked perception and behavior [122,123].

In our VWM task with distractors (Figure 1B and [23]), while the presence of predictable distractors significantly reduced VWM decoding in early visual areas, and made it no longer different from chance-level performance as described earlier, successful VWM decoding was obtained in superior IPS irrespective of the presence and predictability of the distractors, exactly as behavioral performance (Figure 2B). In other words, VWM decoding in superior IPS, but not early visual areas, mirrored behavioral performance. When six orientation gratings were used in the VWM task (Figure 2C), using a representational similarity measure [124], we found a close correlation between orientation representation in superior IPS during the delay period and behavioral performance, such that the more similar two orientation representations were in superior IPS, the slower it was to tell them apart in a behavioral change-detection task (Figure 2D). Given the lack of consistent VWM decoding in early visual areas under distraction (Figure 2A), these results indicate that superior IPS likely plays a more significant role in VWM

storage. Consistent with these results, distractor-resistant delay period activity has also been reported in monkey VIP in a numerosity VWM task [82].

In addition to our study, others have also reported successful VWM-related decoding for a variety of visual information in human PPC, including spatial position, color, orientation, shape, abstract pattern, and view-invariant abstract shape [6,7,50,54,55,57,97,125–128]. Weber *et al.* [128] further showed that, in left parietal area 7A, lower fMRI decoding of WM content was correlated with lower precision and higher precision variability measured in behavioral VWM performance. This correlation was not seen in V1. Thus, the precision of VWM representations in a PPC, but not a sensory area, was found to correspond to VWM capacity limitations. As expected, the precision of VWM also depends on functional connectivity strength between occipital and parietal regions because successful transfer of visual information from sensory encoding to VWM is crucial for VWM performance [129]. Consistent with the role of PPC in VWM storage, TMS of PPC has been shown to affect VWM capacity [130].

It is worth noting that, although we defined superior IPS using a VWM task following Todd and Marois [113], others have not done so. Although superior IPS occupies a portion of PPC and overlaps with several IPS topographic maps [131], parietal regions defined anatomically and by IPS topographic maps [132] did not exhibit the same consistent VWM decoding under distraction in our study [23]. As such, the presence of VWM representation in a subregion of PPC should not be considered as reflecting a general function of the entire PPC. This may explain why some have failed to find successful VWM decoding in PPC (e.g., [51–53]) or failed to find VWM decoding when examining the brain as a whole [83,133].

It has been argued that, in the absence of sustained activities in sensory areas, feedback-driven LFPs contribute to fMRI decoding success in VWM tasks in those areas [67]. Because LFP could reflect feed-forward, feedback, and local neuronal interactions, in the presence of sustained activities in PFC and PPC during VWM tasks, fMRI decoding studies can inform us of the actual neural computations carried out and the representations formed in those areas that are not entirely feedback-driven.

Functional Distinctions between PPC and PFC in VWM Tasks

Is there a functional distinction between PPC and PFC in their involvement in VWM? Differences between the involvement of PFC and PPC in VWM have been noted in terms of the strength of VWM representation [134] and the ability to resist distraction. In spatial VWM tasks, better distractor resistance has been reported in PFC than LIP [112] and 7a ([110,135]; also [136]). For example, Suzuki and Gottlieb [112] showed that the presence of a distractor during the delay period was more suppressed in PFC than in LIP, and inactivation of PFC resulted in greater distractor interference than inactivation of LIP. In non-spatial VWM, as described earlier, both Miller *et al.* [73] and Jacob and Nieder [82] reported that WM delay signal in PFC disappeared during the presence of passively viewed distractor, and reappeared when the distractor was removed. By contrast, delay signal in VIP persisted even during distractor presence [82]. Thus, for non-spatial VWM, PPC may provide more robust VWM storage than PFC.

Consistent with this view, in a VWM task involving object shapes and simultaneous recording from both PFC and PPC, Salazar, *et al.* [137] observed widespread, task-dependent, and content-specific frontoparietal synchronization during VWM delay period. There is an asymmetry in this synchronization, such that information transmission seems to be governed by influences arising in PPC, with parietal neurons (especially those from LIP) exhibiting a greater effect than those from PFC. Similarly, in a delayed-match-to-category visual motion categorization task, Swaminathan and Freedman [138] found stronger, more reliable, and shorter latency category signals during the delay period in LIP than in PFC. Likewise, in the VWM task

on numerosity, in addition to showing distractor-resistant delay period activity in VIP, Jacob and Nieder [82] also reported that neuronal activity correlating with behavioral VWM performance appeared much earlier in VIP than in PFC. These results indicate that delay period signals in PPC are not triggered by feedback originated from PFC, but may by themselves play a crucial role in VWM storage. These results argue against a PFC-centered view of VWM storage [99]. Given the role of PFC in cognitive control [102] and the lack of VWM-related activities also reported in a few other studies (e.g., [139,140]), PFC may be involved in the online control of VWM storage rather than the actual storage, a view that has also been expressed by others ([2,3,141]; also [142]). However, given the distinction between spatial and non-spatial aspects of VWM, it is also possible that PFC and PPC interact differently to support spatial and non-spatial aspects of VWM, a topic that deserves more detailed investigation (see Outstanding Questions).

It has also been argued that anterior and posterior regions may differ in the level of information they could hold, with anterior regions representing more abstract and higher-level visual features, and posterior regions (including sensory regions) representing lower-level visual features [6,7,52]. As reviewed in the previous section, sensory regions such as early visual areas do not appear to play a significant role in VWM storage. The anterior–posterior distinction, however, also does not readily apply to the difference between PFC and PPC because both lower- and higher-level visual features can be represented in VWM in both regions in monkey and human studies (Figure 1 of [6]). For example, the representation of lower-level visual features, such as motion, shape, orientation, and color, have been reported in monkey and human PFC during the VWM delay period [50,57,67,73,97,143–145]. Meanwhile, abstract and high-level visual feature representations such as motion and shape categories and view-invariant abstract shapes have been shown to exist in monkey and human PPC during the VWM delay period ([6,7,109,111,138,146]; also [122]). Thus, the anterior–posterior VWM storage gradient account does not provide an accurate depiction of the available empirical data.

Collectively, the results reviewed here suggest one possible scenario for the respective roles of PPC and PFC and how they may interact with sensory regions in VWM tasks (Figure 5): during

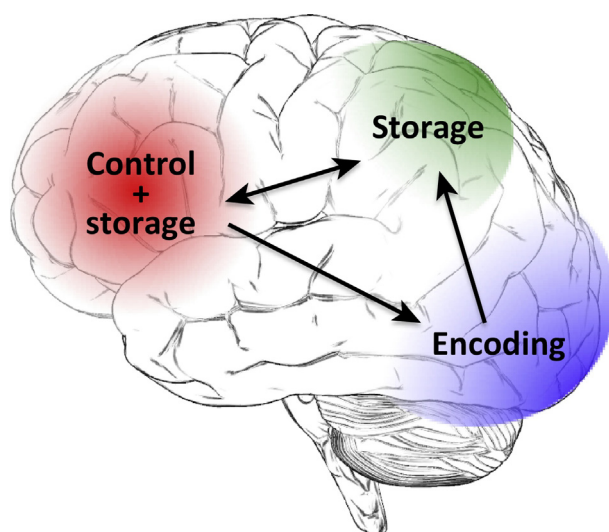


Figure 5. A Possible Scenario of How PFC, PPC, and Sensory Areas May Interact During a VWM Task. During encoding, PFC interacts with sensory regions and PPC via top-down control to ensure that task relevant information is properly encoded by sensory regions and transferred to PPC for storage. PFC may also store some VWM information. PFC additionally communicates with sensory regions via top-down control during the delay period to facilitate the upcoming comparison between the stored VWM content and the test probe. Under this scenario, the primary function of the sensory regions is VWM encoding, that of PPC is VWM storage, and that of PFC is both VWM control and storage. Abbreviations: PFC, prefrontal cortex; PPC; posterior parietal cortex; VWM, visual working memory.

Trends in Cognitive Sciences

encoding, PFC interacts with sensory regions and PPC via top-down control to ensure that task-relevant information is properly encoded by sensory regions and transferred to PPC for storage. PFC may also store some VWM information. PFC additionally communicates with sensory regions via top-down control during the delay period to facilitate the upcoming comparison between the stored VWM content and the test probe. Under this scenario, the primary function of the sensory regions is VWM encoding, that of PPC is VWM storage, and those of PFC are VWM control and storage. Thus, unlike the prevalent view arguing for a sensory account or a distributed view of VWM storage, this view highlights the involvement of PFC, and especially PPC, in VWM storage.

Concluding Remarks

Here I reevaluate the sensory account of VWM by reviewing relevant evidence from human behavior, fMRI pattern decoding, and TMS studies, as well as from monkey neurophysiology studies. The behavioral evidence reviewed so far shows that distractor interference is mostly effective during the early delay period when visual information is still being consolidated into VWM. Once this process is completed, distractor interference is small and may not be obtained if highly controlled psychophysical settings are not applied. Regardless of its magnitude, the distractor interference effect by itself does not pinpoint early visual areas as the primary storage site for VWM; it would be equally compatible with other regions being the primary VWM storage site and the interference effect occurring there. The finding that distractor interference in VWM does not completely align with that in perception further supports this view. Although fMRI decoding has revealed that VWM contents are represented in early visual areas during the delay period, such decoding deviates significantly from behavior when distractors are shown during the delay period. Given the continuous influx of irrelevant visual information in the everyday visual world, early visual areas are unlikely to serve as a primary and reliable storage site for VWM if VWM is to play a functional role in real-world visual information processing. Consistent with this idea, causal evidence from TMS showed that only TMS during the early, but not mid to late, delay period impacts on VWM storage, again indicating that early visual areas are unlikely to be essential for VWM storage. Similarly, results from monkey neurophysiology studies also fail to provide strong support for the sensory account of VWM storage. Instead, early visual areas exhibit a lack of consistent and robust sustained activities during the delay period, a reliance on top-down feedback, and susceptibility to distraction. Together, the available evidence indicates that VWM-related activities observed in sensory areas largely reflect feedback signals indicative of the storage of VWM content elsewhere in the brain. Sensory areas are thus unlikely to serve as the primary storage site for VWM. Instead, the evidence points to PFC and PPC as playing more significant roles in VWM storage.

One may argue that perhaps some information can only be stored in visual areas because it may be visually so complex that there is no other way but to use visual areas to keep it active. However, it is unclear that we are capable of holding such complex visual information in VWM. Change-detection studies have demonstrated that, despite our subjective experience of seeing and encoding everything from a complex visual scene, we actually remember very little of it such that we often miss obvious changes in the scene [147]. If VWM indeed relies on the detailed representation held in visual areas, then we should not be so deficient in change-detection tasks. The discrepancy between the high representational capacity of sensory processing and the limited capacity of VWM further shows that sensory areas are unlikely to play primary roles in VWM storage.

Although the evidence reviewed here indicates that early visual areas may not be involved in VWM storage, these brain areas are nevertheless crucial for VWM tasks in the initial encoding of sensory input and the transfer of this information for VWM storage. In addition, feedback to early visual areas from higher regions during VWM delay may play a functional role in facilitating the

Outstanding Questions

What is the relationship between PFC and PPC in VWM storage? How do they interact to protect the content of VWM from distraction?

To what extent do spatial and non-spatial VWM involve similar and distinctive neural mechanisms?

What is the functional role of the feedback to early visual areas from higher regions during VWM delay? How does this feedback facilitate the comparison between the content of VWM and the test probe at the end of the delay period?

comparison between the content of VWM and the test probe. More research will be necessary to understand this process (see Outstanding Questions).

Moving forward, we are left with two options. Either we should downplay the role of sensory regions in VWM storage and refocus our attention on PFC and PPC, or we need to come up with a better version of the sensory storage account, one that can incorporate and address all the available evidence, especially that presented here. Although much remains to be discovered and learned, a continuous effort of collecting new evidence and refining our existing theories will ultimately bring us a more complete understanding of the cognitive and neural mechanisms underlying VWM, and of how it may support real-world visual information processing.

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