

Letter

Visual Working Memory
Storage Recruits
Sensory Processing
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Human visual processing is subject to a dynamic influx of visual information. Visual working memory (VWM) allows for maintaining relevant visual information available for subsequent behavior. According to the dominating view, VWM recruits sensory processing areas to maintain this visual information online (i.e., the ‘sensory recruitment’ hypothesis). In her recent *Trends in Cognitive Sciences* article, however, Xu [1] proposes that VWM storage does not rely on (occipital) sensory processing areas, but rather on specialized frontal and parietal areas that are not involved in sensory processing *per se* [1].

The primary source of evidence for sensory recruitment stems from fMRI studies showing that visual perception and VWM maintenance of a visual object elicit qualitatively similar patterns of neural activity [2,3]. Xu argues, however, that a sensory account of VWM storage is implausible, as it would cause processing of sensory input to interfere with concurrent VWM maintenance, and vice versa. This viewpoint discounts that interactions between VWM content and the processing of concurrent visual input can, in fact, be beneficial. For instance, maintaining task-relevant information in VWM biases perception toward visual input that is relevant to the observer [4]. Similarly, biasing the subsequent percept toward a previously memorized percept can promote perceptual continuity [5].

The author further argues that there is only limited evidence showing that the

content of VWM and the processing of visual input affect one another. In her overview of the literature, however, a line of research is missing that is crucial for the current debate: many studies have revealed how the content of VWM affects the processing of concurrent visual input. For instance, visual stimuli differentially affect saccades, depending on their contingency with the content of VWM [6]. Importantly, the earliest (mostly bottom-up driven) express saccades and late saccades show similar VWM modulation, implying that VWM influences the processing of visual input immediately (as would be expected by sensory recruitment), rather than increasingly (as would be expected by top-down modulation from frontal/parietal storage sites). Moreover, VWM modulates the processing of visual input rendered invisible through perceptual suppression techniques [4,7]. This provides evidence for sensory recruitment, since neural activity elicited by perceptually suppressed visual input is typically confined to a feedforward sweep within visual processing areas [8]. Finally, maintaining oriented gratings in VWM elicits adaptation of subsequently presented gratings in early visual areas [9], providing strong evidence that both processes draw upon the same neural substrate. In sum, such direct modulations of visual processing by VWM content cannot be accounted for by top-down amplification of visual processing areas by frontal/parietal storage sites, but require the VWM content to reside in the same areas that process visual input.

In support of the view that frontal/parietal storage sites underlie VWM maintenance, Xu presents one of her studies showing that visual interference presented during the retention interval disrupts VWM representations in occipital cortex, while leaving representations in parietal areas as well as observers’ memory performance unaffected [10]. From this, the authors concluded that VWM relies on the parietal

storage site, rather than on the occipital storage site. Neural traces of memoranda, however, do not necessarily reflect working memory in the visual modality, but could also reflect non-visual memorization (e.g., the orientation of a grating can also be memorized ‘verbally’ as a rotational angle, or the hand of a clock). It is known that humans can flexibly transfer memoranda from one memory system to the other and back [11]. As such, observers might opt to strategically transfer their memoranda from VWM to non-visual memory stores when visual interference is expected. Bettencourt and Xu indeed showed that it suffices for observers to expect the occurrence of visual interference during the retention interval (even when there is none), to disrupt the memory trace in occipital areas. Thus, an alternative explanation of the findings of Bettencourt and Xu is that VWM storage does occur in sensory processing areas (as predicted by sensory recruitment), but that observers can flexibly shift between different (visual and non-visual) memory stores when this serves the current task demands.

The author also makes the case that the limited capacity of working memory is at odds with sensory recruitment, considering the high capacity of sensory processing. The limited capacity of VWM, however, does not necessarily preclude VWM storage in high-capacity visual processing areas; the bottleneck could depend on the read-out or instigation of the VWM content, rather than on properties of the storage site itself. Alternatively, higher-order visual processing areas (such as the lateral occipital complex) are also candidates for VWM storage, as they have larger receptive fields – and therefore more severe capacity limitations – than lower-level visual areas [12].

Finally, it is important to emphasize that a non-occipital VWM storage, as proposed by Xu, requires the deployment of a secondary (frontal/parietal) visual system,

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.

Acknowledgments

We thank Steve Luck and an anonymous reviewer for valuable contributions during the review process.

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<http://dx.doi.org/10.1016/j.tics.2017.09.011>

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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