

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).

Acknowledgment

We thank members of the laboratory of M.D'E. for helpful discussions.

¹Helen Wills Neuroscience Institute, University of California, Berkeley, CA, USA

*Correspondence: jscimeca@berkeley.edu (J.M. Scimeca).
<http://dx.doi.org/10.1016/j.tics.2017.12.007>

References

1. D'Esposito, M. (2007) From cognitive to neural models of working memory. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 362, 761–772
2. D'Esposito, M. and Postle, B.R. (2015) The cognitive neuroscience of working memory. *Annu. Rev. Psychol.* 66, 115–142
3. Xu, Y. (2017) Reevaluating the sensory account of visual working memory storage. *Trends Cogn. Sci.* 21, 794–815
4. Ester, E.F. *et al.* (2016) Feature-selective attentional modulations in human frontoparietal cortex. *J. Neurosci.* 36, 8188–8199
5. Christophel, T.B. *et al.* (2017) The distributed nature of working memory. *Trends Cogn. Sci.* 21, 111–124
6. Serences, J.T. (2016) Neural mechanisms of information storage in visual short-term memory. *Vision Res.* 128, 53–67
7. Jeong, S.K. and Xu, Y. (2016) Behaviorally relevant abstract object identity representation in the human parietal cortex. *J. Neurosci.* 36, 1607–1619
8. LaRocque, J.J. *et al.* (2017) Within-category decoding of information in different attentional states in short-term memory. *Cereb. Cortex* 27, 4881–4890
9. Wolff, M.J. *et al.* (2017) Dynamic hidden states underlying working-memory-guided behavior. *Nat. Neurosci.* 20, 864–871
10. Knight, R.T. *et al.* (1999) Prefrontal cortex regulates inhibition and excitation in distributed neural networks. *Acta Psychol.* 101, 159–178

11. Kiyonaga, A. and Egner, T. (2016) Center-surround inhibition in working memory. *Curr. Biol.* 26, 64–68

12. Franconeri, S.L. *et al.* (2013) Flexible cognitive resources: competitive content maps for attention and memory. *Trends Cogn. Sci.* 17, 134–141

Letter

Sensory Cortex Is Nonessential in Working Memory Storage

Yaoda Xu^{1,*}

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

playing a role in VWM or claim that online perceptual processing exclusively involves early sensory cortex; neither does it make any specific claim about the nature of VWM contents stored in the PFC and PPC. It simply rejects sensory regions as being essential in VWM storage due to a lack of sufficient supporting evidence. The small behavioral distractor inference effect reported is consistent with VWM representation tracking perceptual representation but is agnostic to where it is stored in the brain.

Scimeca *et al.* further argue that the fact that top-down signals can sustain VWM representation in sensory cortex supports a sensory account of VWM storage [4]. It is unclear how the presence of such an interaction supports the necessity of sensory region in VWM storage, especially in situations in which a decreased VWM representation in sensory cortex does not correlate with a decrement in behavioral performance [7]. Similar evidence can also be found in monkey neurophysiology research [2]. The finding that top-down signals reinstate VWM representations in sensory cortex after they are disrupted further shows that sensory cortex relies on distractor-resilient VWM content stored elsewhere for its representation, making sensory representation and its interaction with top-down signals unnecessary in supporting VWM storage. Although much remains to be learned about the significance of the top-down signals on sensory regions, it likely aids probe detection at the end of the delay period, rather than directly participates in VWM storage [1].

Advantages of VWM Storage in Nonsensory Cortex

Although an overlap between perception and VWM storage in the sensory cortex can save cortical resources [3], it would subject the content of VWM to greater distraction by incoming visual input and make VWM less useful in real world vision

[1]. Moreover, a sensory storage would result in VWM content being scattered across different cortical regions, making an integrated representation less accessible and less able to be manipulated. Having a storage away from the sensory cortex enables better protection, amplification, integration, and manipulation of the VWM content, while freeing up sensory resources and allowing them to be continuously engaged in the processing of incoming visual input [1]. A nonsensory storage account does require PFC and PPC to be directly involved in the representation of visual information initially processed in sensory cortex. Indeed, PFC and in particular PPC have been shown to be capable of representing and holding a diverse array of visual information [10–12].

Concluding Remarks

While both commentaries bring forth additional data and arguments, they do not provide adequate support for the sensory account of VWM storage. Together, the evidence and critiques against the sensory account of VWM storage stand as originally presented [1,2]. That said, the continuous dialogs and debates among researchers are valuable, healthy and welcome forces that will continuously move the field forward.

¹Harvard University, 33 Kirkland Street, Room 780, Cambridge, MA, 02138, USA

*Correspondence: yaodaxu@wjh.harvard.edu (Y. Xu).
<http://dx.doi.org/10.1016/j.tics.2017.12.008>

References

- Xu, Y. (2017) Reevaluating the sensory account of visual working memory storage. *Trends Cogn. Sci.* 21, 794–815
- Leavitt, M.L. *et al.* (2017) Sustained activity encoding working memories: not fully distributed. *Trends Neurosci.* 40, 328–346
- Gayet, S. (2018) Visual working memory storage recruits sensory processing areas. *Trends Cogn. Sci.* 22, 189–190
- Scimeca, J.M. (2018) Reaffirming the sensory recruitment account of working memory. *Trends Cogn. Sci.* 22, 190–192
- Pierrot-Deselligny, C. *et al.* (2004) Eye movement control by the cerebral cortex. *Curr. Opin. Neurol.* 17, 17–25
- Beck, D.M. *et al.* (2001) Neural correlates of change detection and change blindness. *Nat. Neurosci.* 4, 645–650
- Bettencourt, K.C. and Xu, Y. (2016) Decoding under distraction reveals distinct occipital and parietal contributions

to visual short-term memory representation. *Nat. Neurosci.* 19, 150–157

- Vogel, E.K. and Machizawa, M.G. (2004) Neural activity predicts individual differences in visual working memory capacity. *Nature* 428, 748–751
- Xu, Y. and Chun, M.M. (2006) Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature* 440, 91–95
- Christophel, T.B. *et al.* (2017) The distributed nature of working memory. *Trends Cogn. Sci.* 21, 111–124
- Jeong, S.K. and Xu, Y. (2016) Behaviorally relevant abstract object identity representation in the human parietal cortex. *J. Neurosci.* 36, 1607–1619
- Vaziri-Pashkam, M. and Xu, Y. (2017) Goal-directed visual processing differentially impacts human ventral and dorsal visual representations. *J. Neurosci.* 37, 8767–8782

Letter

Seeing Other Minds in 3D

Rebecca Saxe^{1,*}

To be kind or compassionate, or cruel or condescending, a social agent must understand what others are likely to want, feel, and choose. In this issue Tamir and Thornton [1] offer a powerful and parsimonious account of human social knowledge (how we represent the internal states of one another) and social prediction (how we anticipate dynamics in those internal states).

Tamir and Thornton [1] have identified three key dimensions that organize our understanding of other minds. These dimensions (glossed as valence, social impact, and rationality) can capture the similarities and differences between concepts of internal experiences (anger, loneliness, gratitude), and also between concepts of personalities (aggressive, introverted, agreeable). Most impressively, the three dimensions explain the patterns of hemodynamic activity in our brains as we consider these experiences [2] (Box 1). States such as anger and gratitude are invisible, but the patterns evoked in our brain as we think about them are as predictable by the model of Tamir and Thornton as the patterns