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**Understanding occipital and parietal contributions to visual working memory:
Commentary to Xu (2020)**

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Abstract

In her commentary, Xu (2020) admonishes the reader that “To have a full understanding of the cognitive mechanisms underlying VWM [visual working memory], both behavioral and neural evidence needs to be taken into account. This is a must, and not a choice, for any study that attempts to capture the nature of VWM” (p. 11). Although we don’t disagree with this statement, our overall assessment of this commentary is that it, itself, fails to satisfy several “musts” and, consequently, does not pose a serious challenge for the sensory recruitment framework for understanding visual working memory. These “musts” include accurately characterizing the framework being critiqued, not favoring verbal models and intuition at the expense of formal quantitative models, and providing even-handed interpretation of the work of others. We’ll conclude with a summary of how the sensory recruitment framework can be incorporated into a broader working model of visual working memory.

Keywords: Visual working memory; Visual perception; fMRI; Occipital cortex; Parietal cortex

The Xu (2020) commentary, like two that precede it (Xu, 2017, 2018), is organized as a series of critiques of findings perceived to be inconsistent with the fMRI study of Bettencourt and Xu (2016). This 2020 instantiation focuses in particular on work appearing subsequent to Xu (2018). Many of the specific points raised in Xu (2017, 2018) have already been challenged and, in our view, successfully rebutted (Gayet et al., 2018; Scimeca et al., 2018; Dijkstra et al., 2019), and so we do not revisit those here. Instead, prompted by the admonition from Xu (2020) that we highlighted in the abstract, we have organized this response around more general “musts” that the critiques from Xu (2017, 2018, 2020) have failed to meet. In so doing we hope to clarify several points that are important for understanding the sensory recruitment framework.

An effective critique of a framework must accurately characterize that framework

Modular processing in early visual cortex

Xu (2020) identifies two fMRI studies that reported the decoding of low-level stimulus information from delay-period signals from early visual cortex (areas V1-V4; Harrison and Tong, 2009; Serences et al., 2009), as starting points for sensory recruitment accounts of visual working memory. Although these two studies have, indeed, been highly influential, it is inaccurate to assume, as Xu (2020) does, that they provide the sole conceptual foundation for the sensory recruitment framework. In so doing it portrays a simplistic focus on sensory cortex to the exclusion of other brain systems. To the contrary, however, most advocates of sensory recruitment have articulated perspectives that are considerably more integrative. For example, we have argued that “working memory functions arise through the coordinated recruitment, via attention, of brain systems that have evolved to accomplish sensory-, representation-, and action-related functions. (Postle, 2006; p. 23).” (Indeed, to reflect our emphasis on the broad recruitment of neural systems, our writings typically refer to the framework as “sensorimotor recruitment”¹ e.g., D’Esposito and Postle, 2015; Postle, 2015a; Postle, 2015b; Postle, 2016; Postle, in press; Postle and Oberauer, in press.) Another important example emphasizes the idea that “content-specific information can be flexibly maintained in areas across the cortical hierarchy ranging from early visual cortex to PFC [prefrontal cortex]” and that “recognizing the importance of task-demands and [a] better understanding [of] the operation of non-spiking neural codes may help to constrain new theories about how memories are maintained at different resolutions, across different timescales, and in the presence of distracting information (Serences, 2016; p. 53).” There are many more, but these two examples already make the point that the sensory-recruitment framework of visual working memory cannot be understood in isolation from other principles of brain function. To illustrate with one concrete example, many contemporary accounts of visual perception assume an important role for interactive and recurrent processing between regions (e.g., Kar et al. 2019; Bastos et al. 2012), including for the perception of low-level features (e.g., Sillito et al., 2006; Supér et al., 2001). If one endorses the premise that visual perception requires interareal processing, it wouldn’t make sense to assume that visual working memory for the very same stimulus information does not also require interareal processing, and, indeed, we are not aware of any sensory-recruitment account that makes such an assumption. Thus, many arguments raised by Xu (2020) -- for example, against the notion that V1 “in isolation” could be responsible for the storage of stimulus information –

¹ Because this is a commentary on Xu (2020), not primarily an exposition of our own ideas, we use the label used by Xu (2020): “sensory recruitment”.

strike us as arguments against an assumption of extreme modularity that few cognitive neuroscientists would endorse.

Neural codes

A second incorrect assumption about the sensory recruitment framework that is advanced in Xu (2020) is captured in this assertion: “Because the key idea of the sensory account of VWM storage is that the same neural substrates supporting perception in sensory regions may support the retention of the perceived sensory information for a prolonged period of time in VWM, this account explicitly argues that the same sensory code is used for both perception and VWM in early visual areas. (p. 9)” Not only has this argument never been made explicitly in any writing about sensory recruitment of which we are aware, such an argument could only be tenable if one were to endorse the more general proposition that a given brain area can only support one code, itself a tenet that is demonstrably not true. At the level of populations of single units, it has been observed in nonhuman primates that representational codes supported by a population of neurons can be dynamic despite the presumed stability of the putative mental representation being held by the experimental animal (e.g. Meyers et al., 2008; Crowe et al., 2010), and that the stimulus-representing code employed by a group of neurons in mouse auditory cortex can change to a different code supported by those same neurons in response to a change in sensory input (Libby and Buschman, unpublished). In human visual working memory, in the same set of voxels in early visual cortex, the pattern that represents a stimulus can change across the delay period, as demonstrated by failures of cross-temporal generalization (e.g. Riggall and Postle, 2012; Emrich et al., 2013). Finally, the same sets of voxels in early visual cortex (Yu, Teng, and Postle, 2020; Olmos-Solis et al., 2021), in category-selective posterior fusiform gyrus (Van Loon et al., 2018), and in IPS (Yu et al., 2020; Olmos-Solis et al., 2021), can represent the same stimulus in different representational formats as a function of whether that information is needed for the in-the-moment behavior or, instead, for a subsequent behavior. Thus, Xu (2020) illogically portrays as “essential to establish the validity of [the sensory recruitment] account” (p. 9), a proposition that can, in fact, be ruled out by some of the very studies that support this account.

An effective critique of a framework must not favor verbal models and intuition at the expense of formal quantitative models

There are several arguments in Xu (2020) that rely on verbal models and/or intuitive reasoning, that is inconsistent with, and therefore would need to be reconciled with, formal quantitative models and/or computational simulations. These include arguments about the factors underlying capacity limitations, the problem of resistance to distraction, and the signal that corresponds to recognition decisions.

Capacity limitations

When considering capacity limitations, Xu (2020) points to the fact that fMRI signal intensity in superior IPS tracks individual differences in this behavioral measure (e.g., Jeong & Xu, 2013; Todd and Marois, 2004, 2005; Xu 2007, 2009, 2010; Xu and Chun, 2006, 2007), and that “these results show that PPC [posterior parietal cortex] contains a more robust VWM code than early visual areas ...” (p. 3). This reasoning depends on the intuition that capacity limitations in visual working memory must arise due to direct competition between stimulus representations.

However, there is an increasing number of quantitative models and simulations that suggest alternatives, and drawing from these might lead to a different interpretation of the phenomenon

of load sensitivity in IPS. One of these is a neural network model that represents the identity of a stimulus and the context in which it was presented (e.g., its location or ordinal position) in two different layers. In it, capacity limitations arise due to interference between the context representations of the multiple items being held in working memory (Oberauer and Lin, 2017). A second model accomplishes retention in working memory as a transient “conjunctive representation” comprising a linkage between units in any of several tuned bump-attractor sensory networks and units in an untuned random-recurrent network. In this model it is interference between overlapping connections in the random-recurrent network that gives rise to capacity limitations and explains load-sensitive increases in activity that saturate at behavioral capacity (Bouchacourt and Buschman, 2019). A third computational model similarly accounts for capacity limitations as a consequence of interference within a “binding pool” (Swan and Wyble, 2014). If the context layer, random network, or binding pool of these models is construed as carrying out functions of an IPS-based priority map, an alternative to the memory storage interpretation of load sensitivity in IPS emerges. (We will elaborate on this idea in the final section of this commentary.)

Resistance to distraction

When considering the problem of distraction, Xu (2020) writes “It is unclear how the unreliable VWM representations in early visual areas could play an essential role in WM storage in ... situations [of constant distraction] in real world vision” (p. 3). This echoes the statement from Xu (2017) that “the content of VWM is fairly resistant 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” (p. 799). These statements are based on the intuition that working memory representation is stored in literally the same format in which it was perceived, and that would therefore be expected to be degraded upon the arrival additional sensory input. We would protest, however, that this intuition may not hold up when confronted with more formal approaches to the problem of the degradation of the contents of working memory. This line of argumentation takes us back to the question of coding in working memory. Recent theoretical and empirical work has employed principles from Shannon’s (1959) noisy channel coding theorem in a way that we think could address Xu’s concerns about this aspect of the sensory recruitment framework. Specifically, Koyluoglu et al. (2017) have noted that the problem of maintaining information in a noisy substrate (i.e., the brain) is equivalent to that of transmitting a message over a noisy channel. Comparing a direct storage model versus a channel coding model, the authors found that the latter, which posited additional encoding and decoding stages, provided a better fit to memory performance. Thus, it may be that information can be stored (“transmitted”) with highest fidelity if it is recoded at the time of encoding (“transmitting”) then decoded at the time of retrieval (“receiving”). Although this study mainly addresses how memory representation deals with internal noise, a recoding/transformation operation like this may also be a candidate mechanism for protecting memory representations from external noise/distraction (Note that the subsection on *Neural Codes* has reviewed studies offering empirical evidence for representational transformations in sensory cortex that may be consistent with predictions from Koyluoglu et al., 2017.).

We would also note that, in Xu’s review, memory-perception interactions have been depicted as deleterious for behavior. In real life, however, there is heavy and constant demand for

computation and integration of past and current visual information. Indeed, state-dependent computational models have shown that memory and sensory processing can happen simultaneously in the same circuits in a dynamical system in which spatiotemporal information is encoded in multidimensional dynamic trajectories, allowing for the separation of current and past information for downstream read-out neurons (Buonomano and Maass, 2009; Gangili et al., 2008). Consistent with these models is the empirical finding from cat visual cortex that activity of a population of neurons not only contained information of the current visual stimuli, but also stimuli from the past (Nikolic et al., 2007).

Recognition decisions

As an alternative to the storage, per se, of information by regions in early visual cortex, Xu (2020) advances a “template matching account of the role of early visual areas in VWM,” whereby these regions receive feedback from higher brain regions to facilitate decision processes during recognition. Although we agree that this is a plausible account of one working memory-related function that may be supported by early visual cortex, we need to note that it is challenged by a recent finding from a dynamic neural field model of the change detection task, which suggests that this function may instead be supported by IPS. In it, Buss et al. (2020) simulated the results from two fMRI studies of delayed recognition with arrays of colored squares that studied the effects of varying memory load on signal in the IPS. One, which featured a short delay period (1200 msec), found that activity in IPS asymptoted at a load that corresponded to an individual’s estimated capacity (Todd and Marois, 2004). A second, which featured a longer delay period (6 sec), found that activity in IPS increased monotonically for loads ranging from 1 to 7 (i.e., no asymptote; Magen et al., 2009). The simulations, which related load-related effects on fMRI signal and on behavior to the dynamics of their model, indicated that “key areas in the dorsal attention network such as the intraparietal sulcus play a central role in change detection [i.e., in the recognition decision] rather than working memory maintenance.”

An effective critique of a framework must provide even-handed interpretation of the work of others.

Relation to Bettencourt and Xu (2016)

We find many of the summation statements in Xu (2020) to be misleading. One example: “The detailed analyses provided above [of Christophel et al. (2018), Lorenc et al. (2018), and Rademaker et al. (2019)] are more consistent with our original finding that early visual areas may not play a key role for VWM storage” (p. 7). Statements like this are clearly at odds with the results of at least some of these papers. We are confident that most would endorse a different contemporaneous assessment, from a group not directly implicated in these studies, as more balanced: “... based on findings by Bettencourt and Xu (2016) and Christophel et al. (2018), we might expect prospective information to be withdrawn from visual cortex and stored in higher areas instead ... In contrast, Rademaker [et al.] (2019) and Lorenc [et al.] (2018) showed that visual cortex still contained information on the memorandum in the wake of interfering stimuli ...” (Olmos-Solis et al., 2021). (Note that Olmos-Solis et al. (2021), itself, provides yet more evidence for distractor-resistant stimulus representation in early visual cortex.)

Working memory-perception interactions

Of studies of working memory-perception interactions, Xu (2020) concludes that “any interference observed ... between perception and VWM tasks could come from interference at PPC and/or PFC and the results of these studies cannot be used to support the involvement of sensory areas in VWM storage” (p. 11). To explain why this claim is problematic, we must first quickly review some pertinent literature. Visual distractors often bias and/or degrade the precision of information held in working memory (e.g. Magnussen and Greenlee, 1999; Nemes et al., 2012; Rademaker et al., 2015). In the other direction, the contents of working memory can influence perceptual sensitivity of low-level visual stimuli (e.g. Teng and Kravitz, 2019; Teng and Postle, in press), can override bottom-up salience cues in visual search (Dowd and Mitroff, 2013), and can modulate how visual input gains access to visual awareness (e.g. Gayet et al., 2013). Importantly, the extent of overlap in feature space between remembered and perceived stimuli determines the magnitude of interference (e.g. Kiyonaga and Egner, 2016; Teng and Kravitz, 2019). These memory-perception interactions thus suggest shared representational bases for these two functions, and early visual cortex is often assumed to be the substrate. Xu (2020) does not deny the empirical findings, but argues that they might reflect interactions at higher levels, because activity related to perceptual processing can also be observed in PFC and PPC. We see at least two problems line of reasoning. The first appeals to parsimony: because PFC and PPC aren’t necessary for visual perception (lesions not associated with profound impairments), why would a system that can flexibly optimize information processing “choose” to recruit these systems for perceptual processing if doing so results in interference? The second appeals to logical consistency: this argument undercuts one of the pillars of the author’s stance against the sensory recruitment framework, which is that “separated VWM and perception processing in different brain regions ... would be more adaptive and flexible in information processing and manipulation” (Xu, 2020; p. 3).

Working memory functions of occipital and parietal cortex from a sensory recruitment perspective

Having defended the sensory recruitment framework from the critiques of Xu (2020), we will conclude by summarizing how it can offer a foundation from which one can begin to build a broader understanding of working memory. The emphasis will be on two themes that have been prominent throughout this commentary: What are the working memory functions of IPS?; and How are “sensory” representations in working memory controlled?

Manipulating load to study visual cortex and IPS

Comparing results with signal intensity versus with multivariate analyses is informative. In visual cortex, although delay-period signal returns to baseline and is insensitive to load, the strength of decoding from this signal, a proxy for the integrity of a neural representation, varies monotonically with memory load, and in a manner that predicts load-related effects on behavior. In IPS, in contrast, it is delay-period signal intensity that varies with load, while multivariate evidence for stimulus representation, although often present at a load of 1, is typically absent at higher loads (Emrich et al., 2013; Gosseries et al., 2018; Cai et al., 2019; Cai et al., in press). Closer investigation of IPS indicates that its load sensitivity is only observed when high-load memory sets contain items drawn from the same category. For example, delay activity in IPS is higher for memory for 3 orientations than for one, but not for *one orientation + one color + one luminance* (Cai et al., in press; c.f. Gosseries et al., 2018). This suggests sensitivity to demands on the need to individuate items by binding each to its unique context.

The control of sensory representations

In situations like the 3-orientations trial from Cai et al. (in press), failure to bind context to content can result in a “swap error,” in which one mistakenly recalls the wrong item from the memory set. We have proposed that IPS-mediated binding of context to (sensory) content in working memory may be similar to the attentional control ascribed to the frontoparietal priority map (e.g., Bisley and Mirpour 2019). Initial results consistent with a content (visual cortex) versus context (IPS) division of labor are seen after sorting the subjects by individual differences in swap-error rates: In occipital cortex, the neural strength of the representation of orientation (content) is stronger for low swap-error than for high swap-error subjects, whereas, in IPS, the strength of the delay-period representation of the location (context) of the to-be-probed item is negatively related to the behavioral swap error rate (Cai et al., in press), suggesting distinct contributions of visual cortex and IPS to the operation of context-binding in working memory.

A second class of control needed for working memory is the prioritization of and/or among its contents. Indeed, consideration of the studies that were the primary focus of the Xu (2020) highlights an important question, which is whether protection from distraction (e.g., Bettencourt and Xu, 2016; Lorenc et al., 2018; Rademaker et al., 2019) engages mechanisms that are qualitatively different from those needed to prioritize one item among many (e.g., Christophel et al., 2018; c.f. Yu et al., 2020; Olmos-Solis et al.; 2021).

In parting, we note that all the work considered here has been concerned with questions of stimulus representation. An important next step will be to couple this approach with explicit reinforcement learning models of selective gating mechanisms (e.g., Chatham and Badre, 2014; Kruijne et al., 2020), models that typically explain selection and control at level of abstraction that does not incorporate the dynamics of stimulus representation.

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