1

EVIDENCE FOR, AND CHALLENGES TO, SENSORY RECRUITMENT MODELS OF VISUAL WORKING MEMORY

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We use working memory to temporarily hold information in mind in the service of behavior. A key theme in working memory research is that the type of remembered materials and task-demands will alter where in the brain information gets stored and the format that it is stored in. For example, when you are introduced to someone new and you want to temporarily remember their face and their name, these visual and auditory memories *feel* subjectively different (one you can "see" in your mind's eye, the other you can "hear" rehearsed in your mind). In addition to feeling different, cognitive psychological theories suggest that these memory formats likely rely upon distinct underlying processes. For example, the influential Baddeley and Hitch (1974) model proposes there are separate short-term stores for auditory versus visual stimuli (phonological and visuospatial stores). Indeed, empirical studies of behavioral interference provided key initial evidence for these hypothesized modality-specific stores: Memory items interfere less with one another when items are from different modalities versus from the same modality (e.g., Logie et al., 1990), suggesting separation of the representations during working memory storage (but see Morey, 2018).

Sensory recruitment refers to the hypothesis that the early sensory cortex supports the maintenance of modality-specific information in working memory, and that it would be computationally efficient to use already-specialized neural circuits to temporarily remember detailed sensory information. For example, when remembering the orientation of a line, it would be efficient to temporarily remember the orientation using neurons in early visual cortex that are finely tuned for specific orientations. The idea of sensory recruitment is broadly applicable to many sensory modalities, and there is emerging evidence that analogous mechanisms may

support short-term storage in different domains: The primary auditory cortex for auditory stimuli (Brechmann et al., 2007; Gottlieb et al., 1989; Y. Huang et al., 2016; Linke & Cusack, 2015; Rämä et al., 2004), the primary somatosensory cortex for tactile stimuli (Esmaeili & Diamond, 2019; Harris et al., 2002; Zhao et al., 2018), and the primary olfactory (piriform) cortex for olfactory stimuli (Dade et al., 2001; Zelano et al., 2009). In this review, we examine evidence for a sensory recruitment account of visual working memory.[1] We place a particular focus on the role of *task demands* in determining when the early visual cortex supports working memory maintenance, and we turn a critical eye towards key potential limitations of sensory storage.

Support for "sensory-like" visual working memory representations from psychophysics

The idea of a "sensory-like" format for visual working memory first emerged based on studies of visual perception. Because neurons in the early visual cortex are tuned to basic visual features (e.g., motion direction, spatial frequency, orientation, color), researchers have long been interested in understanding the perception of these features as a way of interrogating the building blocks of visual experience. For example, to study the limits of visual perception, observers are often asked to compare two stimuli to one another and judge if they are the same or different. By manipulating the difference between stimuli (e.g., the orientation difference between two gratings), researchers can estimate the smallest difference that an observer may reliably perceive. Sometimes, these comparisons are made *spatially* (e.g., two stimuli are simultaneously shown at two different locations). However, because many neurons in the early visual cortex are tuned to both a given feature and a specific retinotopic location, an alternative method is to instead use *temporally* separated stimuli (e.g., two stimuli are shown at the same location, but separated in time). Incidentally, the temporal separation of the "sample stimulus" and the "comparison stimulus" introduces an element of memory into perceptual comparison tasks (Laming & Laming, 1992; Laming & Scheiwiller, 1985).

Using these types of paradigms, researchers have found that perceptual judgments of basic visual features are extremely precise, even across time delays. In fact, judgments after a 30+ sec delay were thought to be just as precise as during perception, leading to the hypothesis that such high-fidelity visual memory behaviors may rely on sensory representations (Magnussen et al., 1990; Nilsson & Nelson, 1981; Regan, 1985a, 1985b), but see (Lages & Paul, 2006; Lages & Treisman, 1998; Rademaker et al., 2018; Shin et al., 2017). Mirroring findings earlier found in the

1 Often the term visual short-term memory is used to refer to tasks where visual information is stored without a secondary, intervening processing task (e.g., spatial span task performance is referred to as visual working memory; change detection as visual short-term memory). Here, we use the term visual working memory to describe either type of task, particularly since the line between these tasks blurs when, for example, distractors are introduced into change detection tasks.

auditory domain (Deutsch, 1970, 1973), researchers likewise found feature-specific *interactions* between the comparison stimulus and an intervening distractor stimulus (Bennett & Cortese, 1996; Magnussen et al., 1991; Magnussen & Greenlee, 1992). For example, disruption by a distractor occurs only in the same feature-dimension (e.g., an orientation distractor, but not a spatial frequency distractor, produces interference with when remembering an orientation). Moreover, within a feature-dimension, memory precision depends on the similarity between the sample and distractor. From this evidence, the idea emerged that not only are short-term stores modality-specific (i.e., visual vs. auditory), but even within the visual modality, areas of the visual cortex specialized for individual visual features may act as highly specialized stores (e.g., orientation, spatial frequency, etc., Magnussen, 2000; Magnussen & Greenlee, 1999). Much subsequent work has corroborated stimulus- and feature-specific interference effects in visual working memory (Lalonde & Chaudhuri, 2002; McKeefry et al., 2007; Nemes et al., 2011, 2012; Pasternak & Zaksas, 2003; Rademaker et al., 2015) as well as stimulus-specific biases in working memory behaviors (Chunharas et al., 2019; Dubé et al., 2014; J. Huang & Sekuler, 2010; Nemes et al., 2011, 2012). In sum, a "perceptual memory" account of psychophysics data yielded testable predictions that feature-tuned neurons in visual cortex may support memory maintenance for simple visual features.

Early neural evidence for sensory recruitment: Signatures of working memory maintenance in early visual cortex

Although extensive early behavioral evidence supported the idea of sensory-specific short-term stores, direct neural evidence that the visual cortex contributes to working memory emerged much later. This was, in part, due to a historical quirk: Early neuroimaging studies examined only "univariate" effects. Univariate analyses identify groups of voxels which respond to stimuli in a similar manner. For example, a univariate analysis can compare overall activation as a function of task condition, e.g., remembering versus passively viewing stimuli, and find clusters of voxels that are more responsive in one versus the other task condition. With this standard approach, early positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies of working memory revealed univariate signatures of working memory maintenance in regions of the parietal, frontal, and prefrontal cortex (Courtney et al., 1997, 1996; Courtney, Petit, Haxby, et al., 1998; Courtney, Petit, Maisog, et al., 1998; Owen, Doyon, et al., 1996; Owen, Evans, et al., 1996; Ungerleider et al., 1998). These univariate working memory signatures complemented prior findings that prefrontal lesions in both non-human primates and humans lead to profoundly impaired working memory performance (Curtis & D'Esposito, 2004; Harlow et al., 1952; Jacobsen, 1936; Levy & Goldman-Rakic, 1999; Pribram et al., 1952) and findings that neurons in the prefrontal cortex exhibit sustained, elevated delay period activity during working memory maintenance (Funahashi et al., 1989, 1990, 1993; Fuster, 1973; Fuster & Alexander, 1971; Miller et al., 1996). Thus, the role of the prefrontal cortex is well-established, and it has long been hypothesized as the neural substrate of working memory. In

contrast, the visual cortex has shown little or no evidence of sustained, univariate delay period activity, consistent with the assumption that the visual cortex is important for perception but not for working memory maintenance.

With improvements to neuroimaging methods, like better spatial resolution, better signal to noise ratio, and improved computing power, later studies were able to examine multivariate signatures of neural activity to reveal new insights (Cox & Savoy, 2003; Haxby et al., 2001; Spiridon & Kanwisher, 2002). Rather than identifying groups of voxels with similar responses to stimuli, multivariate analyses consider the information contained in groups of voxels which can also be dissimilar with respect to their responses to a given stimulus (i.e., how voxel activity patterns change in response to different stimuli, termed *multi-voxel pattern analysis*). Examining multivariate activity with fMRI revealed that activity *patterns* in the early visual cortex can be used to decode the specific visual feature that a person is viewing (e.g., a particular orientation) and which of two competing features is currently being attended (Kamitani & Tong, 2005). Thus, precise information about what a participant is currently seeing can be decoded from the visual cortex using fMRI blood-oxygen-level-dependent (BOLD) activity, but this multivariate information is not reflected in average activity (e.g., each orientation has the same average activity). The advent of multivariate methods thus raised the possibility that activity in the visual cortex might support working memory but be largely invisible to standard univariate analyses.

Studies by Harrison and Tong (2009) and Serences et al. (2009) demonstrated that it is possible to decode an orientation held in working memory by leveraging multivariate activity in the early visual cortex. In Harrison and Tong (2009), participants viewed two oriented gratings and then were given a cue to remember either the first or second grating. The remembered grating could be decoded throughout the working memory delay period in visual areas V1–hV4. In Serences et al. (2009), participants viewed a colored grating and were instructed to remember either the color or the orientation. The remembered feature, but not the ignored feature, could be decoded from the early visual cortex throughout the delay period. Replicating prior work, these studies found little or no sustained univariate delay period activity in the early visual cortex (e.g., Courtney et al., 1997; Offen et al., 2009; Postle et al., 2000), despite the presence of decodable information. The lack of a univariate response may be due to the properties of the visual cortex itself: When neuronal responses tuned to the attended/remembered item are enhanced, other neuronal responses are suppressed (Martinez-Trujillo & Treue, 2004; Scolari et al., 2012; Serences et al., 2009; Supèr et al., 2001). Such competitive dynamics may yield a net null effect in overall BOLD activity in the early visual cortex.

In sum, the sensory recruitment hypothesis proposes that control signals from the prefrontal cortex recruit specialized memory stores in the sensory cortex (Awh & Jonides, 2001; D'Esposito, 2007; D'Esposito & Postle, 2015; Jonides et al., 2005; Pasternak & Greenlee, 2005; Postle, 2006). This hypothesis emerged from twin findings: (1) neuroimaging evidence that the contents of working memory can be decoded from the early visual cortex (Christophel et al., 2012; Emrich et al., 2013; Ester et al., 2009; S.A. Harrison & Tong, 2009; LaRocque et al., 2016;

Riggall & Postle, 2012; Serences et al., 2009) and (2) long-standing evidence of the importance of sustained activity in the prefrontal cortex for working memory. Combining prefrontal control signals with sensory representations would be advantageous for a number of reasons. For example, the size of receptive fields in later visual areas is relatively broad and imprecise; perhaps top-down recruitment of earlier visual areas is needed to make comparisons between perception and memory or to maintain precise visual representations (Merrikhi et al., 2017), but see (Favila et al., 2020; Park & Serences, 2020)

Challenges to sensory recruitment and the potential role of task demands

Although much behavioral and neural evidence is consistent with a sensory recruitment account of visual working memory, some behavioral studies have found effects that challenge this framework. As discussed above, new visual inputs can bias or interfere with remembered items in a feature-specific way (e.g., Magnussen & Greenlee, 1999). Likewise, an item held in working memory can bias attentional selection toward features in the environment that match the remembered item (Downing, 2000; Gayet et al., 2017; Olivers et al., 2006; Pashler & Shiu, 1999; Soto et al., 2005). While this bidirectional link between memory and perception aligns with a sensory recruitment account, on the other hand, recent studies have found that visual working memory representations only inconsistently exhibit key features of perceptual representations (e.g., crowding; normalization).

In perception, when two items are shown near each other they are also represented close together in the cortex and can interfere with one another (a phenomenon known as "spatial crowding"). Likewise, when items are presented simultaneously and encoded into working memory, crowded displays produce larger working memory errors and/or higher swap rates (Fang et al., 2019; Tamber-Rosenau et al., 09/2015). However, Harrison and Bays (2018) found that when items were presented *sequentially*, they no longer produced crowding effects. The failure to observe spatial competition effects within memory suggests that the working memory items were either not maintained in a retinotopically organized fashion, or else these retinotopically organized codes were kept segregated in time (e.g., Lisman & Idiart, 1995; Lundqvist et al., 2018). Further work has suggested that task demands for spatial context binding might play a role in determining whether working memory representations are stored in a retinotopically organized fashion (Teng & Postle, 2021; Yörük et al., 2020). Such flexibility to store remembered features in a spatially local or global format could likewise explain conflicting fMRI decoding results, some of which have found a cross-hemisphere spread of remembered features (Ester et al., 2009) and others have found more spatially localized decoding (Pratte & Tong, 2014).

Divisive normalization refers to the finding that the neural response to a particular stimulus within the receptive field is attenuated when a similar stimulus is present and evoking a response from a nearby pool of neurons (Carandini & Heeger, 2012; Heeger, 1992). To test whether working memory representations

show effects of divisive normalization, Bloem and colleagues (2018) used a center-surround contrast normalization paradigm. Typically, the presence of a high-contrast surround will lower the perceived contrast of the target stimulus at the center. Bloem et al. found normalization of the remembered feature when the center and surround stimulus were encoded simultaneously, but not when the center and surround were encoded sequentially. Thus, it appears that, in the absence of direct perceptual competition, normalization does not operate within working memory. The findings that working memory contents can bypass crowding and normalization (but also see Kiyonaga & Egner, 2016) provide critical constraints for plausible sensory recruitment mechanisms. However, these findings do not rule out the involvement of the visual cortex in working memory maintenance. For example, in line with recent layer-specific accounts of working memory performance (van Kerkoerle et al., 2017), one hypothesis is that spatial crowding and normalization operate during feedforward encoding (e.g., layer 4) but not during recurrent maintenance in deep and superficial layers of the visual cortex.

In sum, many studies have found interactions between working memory and perception. However, extant evidence also suggests that perceptual and working memory representations are not perfectly synonymous, and key behavioral differences between perception and memory provide important constraints for plausible neural implementations of sensory recruitment. In addition, it seems that task demands may likewise critically shape the role of the visual cortex in supporting working memory. For example, task demands may dictate when participants store features in a spatially global versus retinotopically organized fashion, and they might nudge participants to switch freely between detailed but fragile sensory codes and sparse but robust abstracted codes (Rademaker et al., 2019; Serences, 2016).

Manipulating visual cortical activity during working memory with TMS

To determine the causal role of the visual cortex in visual working memory we need to be able to manipulate visual cortical activity in a rapid, reversible fashion. Classic lesion approaches are not feasible for testing the role of the visual cortex in maintaining visual working memory, because an intact visual cortex is needed to encode the items. Recently, transcranial magnetic stimulation (TMS) has provided a means to selectively, temporarily perturb ongoing activity in visual cortex to test whether this impacts working memory behaviors.

Studies of TMS and visual working memory have consistently found that TMS to the occipital cortex[2] shortly after stimulus onset (0–200 ms) disrupts the consolidation of sensory information into working memory (Cattaneo et al., 2009; Rademaker et al., 2017; van de Ven et al., 2012; van Lamsweerde & Johnson, 2017).

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2 Typically, these working memory studies have used single-pulse TMS or small bursts (e.g., a 10 Hz triplet).

During the early consolidation period, the non-specific excitatory input of a TMS pulse acts similarly to non-specific excitatory input from a large visual distractor: Both visual masking stimuli and TMS pulses to the visual cortex disrupt consolidation into working memory during the first ~200 milliseconds after stimulus offset (van de Ven et al., 2012; van Lamsweerde & Johnson, 2017; Vogel et al., 2006). This result is consistent with the broader finding that both masking stimuli and TMS pulses to visual cortex can impair visual perception (Beckers & Hömberg, 1991; Breitmeyer et al., 2004).

Although it is clear that TMS targeting the early visual cortex impairs perception and the consolidation of information into working memory, it is less clear whether TMS impacts working memory storage during the delay. One possible prediction is that the non-specific input from TMS could perturb ongoing maintenance, and that disruption would impair visual working memory performance. A study by Becker and Hömberg (1991) found a working memory impairment when TMS was administered shortly before or after the onset of the test probe, and found that TMS slowed down "memory scanning", such that the RT slope across set sizes was steeper with TMS pulses than without. The authors thus concluded that the visual cortex is important for scanning through the contents of working memory when making comparisons to the probe.

Counter to a simple story of any TMS intervention disrupting working memory, many subsequent studies have found *improvements* to visual working memory performance with TMS pulses to the occipital cortex during the delay. In particular, these working memory improvements with TMS seem to occur either when (1) a single item is held in working memory (Cattaneo et al., 2009; Silvanto & Cattaneo, 2010; Soto et al., 2012) or (2) when TMS is targeted to just one item's location by taking advantage of the topographic organization of the visual cortex (Rademaker et al., 2017). Authors have proposed a variety of explanations for why TMS might sometimes be detrimental to working memory performance (e.g., early in the delay) but other times beneficial (e.g., late in the delay). For example, some have proposed that TMS may serve as a "noisy pedestal", and that by injecting noise equally into all sensory channels, the signal needed to overcome a fixed activity threshold is lowered (Abrahamyan et al., 2011; Henning & Wichmann, 2007). Thus, TMS, by injecting some noise, could lead to facilitatory effects (depending on the strength of the TMS pulse). Another possibility is that the different effects of TMS may depend on the initial state of the system, whereby less active neurons might be *more* affected by the TMS pulse (Cattaneo et al., 2009; Siebner et al., 2009). Such a dynamic could explain the effect of TMS when participants are holding two, differentially prioritized memory items in mind. For example, Zokaei and colleagues (2014) found that TMS hurt memory precision of the prioritized item while improving precision of the non-prioritized item. Likewise, both global visual stimulation (Wolff et al., 2015, 2017) and TMS (Rose et al., 2016) can "revive" active working memory signals from an unattended state.

Ultimately, although extant TMS data are suggestive of a relationship between visual cortical activity and successful working memory maintenance, future pre-registered and/or methods-focused studies will be needed to better explain when

and why beneficial versus detrimental effects of TMS are observed. First, publication biases may lead to only positive results being submitted, and the file drawer of null results or confusing results might be large in this field (Cooper et al., 1997; Dwan et al., 2008; Ferguson & Heene, 2012; Franco et al., 2014; Rosenthal, 1979). Second, many basic aspects of single-pulse TMS's effects on the visual cortex are not fully characterized or are still unknown. In the motor cortex, for example, detailed modeling studies of TMS-evoked motor cortex potentials suggest that TMS pulses may differentially activate neurons in each cortical layer (Aberra et al., 2020; Seo et al., 2016). An intriguing but highly speculative possibility is that TMS could, for example, more strongly influence activity in Layer 4 neurons carrying the feedforward visual signal. Such layer-specific perturbation could disrupt sensory consolidation into WM early in the delay but benefit working memory maintenance later in the delay (by dampening activity related to competing sensory input).

Key debate: Can the visual cortex 'multi-task' to support perception and memory?

Although there is compelling evidence that we can decode the contents of working memory from the visual cortex, one valid criticism is that this has only been shown in artificial laboratory studies. In fMRI experiments, people typically keep their eyes perfectly fixated on a blank, gray screen while they are remembering the item. This is a laboratory contrivance to reduce noise and increase experimental control. In the real world, we would almost never stare at a perfectly still, blank gray void while remembering something (unless you are really really hungover and trying to recall what happened the night before without evoking nausea). Rather, we would be continually receiving new visual inputs as our eyes move around our environment (and things in our environment move as well). A critical question naturally arises: Can the visual cortex "multi-task" and concurrently support working memory maintenance while also processing new incoming visual information (Ester et al., 2016; Gayet et al., 2018; Lorenc et al., 2021; Xu, 2017, 2018, 2020)?

To test whether memory representations in visual cortex can persist in the presence of concurrent visual input, Bettencourt and Xu (2016) flickered pictures of faces or gazebos on-and-off during the delay period. In one of four experiments, Bettencourt and Xu (2016) found that decoding of the remembered orientation based on activation patterns in the early visual cortex was at chance due to the presence of the flickering pictures. However, decoding remained above-chance in a sub-region of the parietal cortex. Because the visual cortex maintained above-chance in most, but not all, experiments, they concluded that representations in the parietal cortex, but not the visual cortex, were essential to support working memory in the face of concurrent visual inputs. Bettencourt and Xu proposed a strong version of visual cortical multitasking, whereby the early visual cortex is unable to support working memory because of its susceptibility to incoming visual inputs. Counter to this strong view, a breadth of evidence suggests that competing

visual inputs do not obligatorily wipe out working memory representations in the early visual cortex, but instead bias or weaken early visual representations.

First, very brief disruptions do not weaken decoding from the early visual cortex. For example, when participants were shown two items and were then retrocued about which item to remember (S.A. Harrison & Tong, 2009), the onset of the second memory item did not disrupt decoding of the first item. Rather, decoding was equivalent for both cue conditions (first vs. second item cued). Second, in a follow up to Bettencourt and Xu (2016), Rademaker et al. (2019) found that even strong visual distractors (e.g., large phase-reversing noise stimuli that lasted 11 seconds) did not wipe out working memory signals in the early visual cortex. Rather, in an initial experiment, Rademaker et al. observed robust decoding from early visual cortex throughout the delay, regardless of concurrent visual input. In a second experiment, Rademaker et al. used procedures that more closely replicated the original Bettencourt and Xu study (photographs of faces/gazebos were included, and distractors were made to flicker on-and-off) and found that memory decoding in the early visual cortex was significantly reduced with distraction. However, unlike the Bettencourt and Xu study, Rademaker et al. *also* found a loss of behavioral precision when the sensory code was negatively impacted. This behavioral decrement suggests that early visual codes may allow for extra behavioral fidelity compared to parietal codes alone. The original Bettencourt and Xu study used a coarse behavioral task that is not well-suited for the measurement of fine-grained disruptions to behavior, so this explanation should be further tested in future work. At the least, it seems that reviving a working memory representation in the early visual cortex is useful for performing comparisons at test. Even when the early visual code is weakened or eliminated by distractors, participants revive this code after the distraction has ended (Hallenbeck et al., 2021; Rademaker et al., 2019) or whenever the representation is needed to perform a comparison (e.g., dual retrocue studies, LaRocque et al., 2016).

Recent studies have also focused on evaluating simultaneous sensory and mnemonic processing in the early visual cortex by examining how competing visual input can bias working memory representations and behavior. The link between distractor-induced neural biases and biases in behavior points toward a functional role of early visual codes in supporting working memory. For example, when distracting information is in the same feature space as a remembered item (e.g., both the memory item and the distractor are oriented gratings), neural representations in early visual cortex are biased toward the distractor item (Hallenbeck et al., 2021; Lorenc et al., 2018; Rademaker et al., 2019). In contrast, representations in later visual areas such as IPS0 show less or no bias toward the distractor feature (Lorenc et al., 2018). Furthermore, recent trial-by-trial analyses suggest that neural bias in V1, but not in other visual areas like IPS, predicts behavioral biases (Hallenbeck et al., 2021). Together, these studies imply a link between behavioral bias and distractor-induced bias of neural representations in visual cortex. However, future work will need to disentangle true bias in the memory representation *per se* from a failure of neural decoding methods to separate the memory item and distractor representations.

One hypothesis has emerged that may offer a resolution to the multi-tasking debate: Perhaps the potential ability of visual cortex to concurrently support perception and memory may not truly be "multi-tasking", but rather, may rely on segregated layer-specific signals. In this account, incoming visual information is shuttled through feedforward pathways via layer 4, whereas recurrent processing related to attention and working memory is represented in deep and superficial layers (van Kerkoerle et al., 2017). Our ability to resolve layer-specific signals with fMRI is still nascent, but initial evidence is consistent with this layer-specific account of perception versus working memory signals in V1 (Favila et al., 2020; Lawrence et al., 2018, 2019). Furthermore, this account raises interesting predictions for the role of attention. For example, working memory representations in the visual cortex may be diminished when attention is directed to distractors versus when distractors are ignored, due to competition between concurrent top-down attentional and mnemonic signals targeting superficial and deep layers of the visual cortex (Rademaker & Serences, 2019) .

Evidence for multiple representational formats revealed by changing task demands

Task demands play an important role in determining whether the sensory cortex is recruited to aid working memory performance. For example, if participants choose to remember verbal versus visual features of an object, then this will dictate whether a sensory code is required and recruited (Lee et al., 2013). Likewise, when participants have a motor plan available, they can rely less on sensory representations as they are no longer as relevant to the task (Boettcher et al., 2021; Henderson et al., 2019).

When an item in memory is not immediately task relevant, the withdrawal of attention typically leads to a large drop in decoding performance from the early visual cortex (LaRocque et al., 2016; Riggall & Postle, 2012; Rose et al., 2016; Wolff et al., 2017). To assess how active maintenance within the visual cortex is flexibly recruited depending on task demands, a "dual retro-cue" task is often used. In the typical dual retro-cue task, participants are shown two items. After a brief delay where both items are held in mind, participants are given a retro-cue indicating which of the two items will be tested. Critically, after the participants perform the first test, they are given a *second* retro-cue about which of the two items will be tested in a second memory test. After the first retro-cue, the initially non-cued item (or "unattended memory item") is presumably deprioritized, and decoding performance has been shown to drop to baseline in the early visual cortex (Christophel et al., 2018). Despite the loss of decoding for the unattended memory item in the early visual cortex, both items may still be decoded from the parietal and frontal cortex (IPS and FEF, respectively; Christophel et al., 2018). However, more recent analyses show that even "unattended memory items" can be decoded when using more powerful model training approaches (Iamshchinina et al., 2021), or by looking at a different type of neural signal (Barbosa et al., 2021;

but see Wolff et al., 2021), which demonstrates how care is needed when interpreting null findings.

Working memory is fundamentally used to guide behavior. To do so, we need to use our internal goals to guide our attention in the external world. Perhaps a robust but abstracted code in the prefrontal cortex is suboptimal or even insufficient for making comparisons with the external world. Even when we revive long-dormant information from long-term memory into working memory, we observe signatures of sensory recruitment (e.g., Bosch et al., 2014). So, perhaps we should think of sensory recruitment not as a simple tool for the continued maintenance of lingering perceptual inputs, but rather as a "translation device": We use sensory codes to temporarily hold information in mind in a format that is useful for determining whether our abstracted, visual goals relate to the world around us (Iamshchinina et al., 2021; Rademaker et al., 2019).

Conclusion

The sensory recruitment hypothesis proposes that early sensory regions are recruited in the service of working memory. Here, we reviewed the emergence of the sensory recruitment hypothesis with psychophysics and the advent of multivariate decoding techniques in neuroimaging; we considered evidence of visual cortical involvement in working memory from behavior and TMS; and we outlined key challenges to the functional role of the visual cortex in supporting working memory.

The evidence reviewed here argues against two extreme possible accounts of early sensory codes. At one extreme, one could hypothesize that sensory activity during working memory is epiphenomenal, emerging as a byproduct of other memory-related computations elsewhere in the cortex. We argue that within- and between-subjects correlational links between behavior and sensory maintenance signatures are in opposition to an epiphenomenal account (Christophel et al., 2018; Hallenbeck et al., 2021; Iamshchinina et al., 2021; Lorenc et al., 2018; Rademaker et al., 2019). At the other extreme, one could argue that for sensory cortices to be meaningfully involved in working memory, they must be entirely self-sufficient for maintenance (Xu, 2020). This account seems unlikely, given the multitude of studies (lesion, single cell recordings, and neuroimaging) showing the involvement of frontal and parietal cortices in working memory maintenance (e.g., Curtis & D'Esposito, 2004; Ester et al., 2015; Funahashi et al., 1989; Ungerleider et al., 1998). Counter to this self-sufficient account, we argue that sensory codes are one part of a flexible, multi-level working memory representation (Christophel et al., 2017; Ester et al., 2016; Gayet et al., 2018; Lorenc & Sreenivasan, 2021). A hierarchical code with partial redundancies and different representational formats can accommodate coarse or fine memories, immediately relevant or irrelevant memories, etc., depending on task demands. A hierarchical code also allows for more resilient representations because even if relatively fragile sensory codes are disrupted, less precise but more robust representations may persist.

A hypothesized multi-level model raises an important point: If information maintained in visual codes is fully redundant with information maintained elsewhere in the cortex, then why do we bother with sensory codes at all? And, why might these sensory codes become more prominent at test? Our working hypothesis is that sensory codes allow for enhanced behavioral precision and/or for more direct comparison between our internal goals and our external environment. First, recent evidence suggests that purely top-down signals (i.e., in the absence of precise bottom-up input) are less precise than bottom-up signals (Favila et al., 2020; Park & Serences, 2020). But, if a top-down biasing signal can "latch on" to a precise, bottom-up stimulus drive and then maintain this initial bottom-up signal, this could confer a benefit to both neural precision and behavior. Conversely, if the code that was initially formed from the confluence of bottom-up stimulus drive and top-down attention is temporarily lost, then behavioral precision suffers. We think this is exemplified in findings from distraction: When sensory codes are free of distortions or disruptions by competing visual stimuli, then a slight behavioral benefit can be conferred. Second, sensory codes may facilitate the comparison between internal goals and external task demands. This is exemplified by the dynamic, involuntary interplay between working memory and attentional guidance: Holding a feature in working memory can involuntarily guide attention toward matching information in the environment, perhaps via a shared, spatially organized priority map in the early visual cortex. However, sensory recruitment in this context is, perhaps, a double-edged sword: Sensory-format representations are needed to make comparisons with stimuli in the world, but these sensory representations are also more susceptible to distortion by competing visual inputs (e.g., Mallett & Lewis-Peacock, 2019).

Future work is needed to tackle a host of interesting questions related to the role of sensory activity in working memory maintenance. For example, we need a more concrete understanding of *how* sensory codes wax and wane with changing task demands (e.g., via episodic long-term memory, Beukers et al., 2021; or via activity silent working memory, Stokes, 2015). Tracking working memories as they are shuttled back and forth between high-resolution sensory codes, abstracted prefrontal codes, and hippocampus-dependent long-term memory will allow us to probe how multi-level working memory formats are distinct (e.g., in abstraction, in resilience) but fundamentally intertwined.

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