

RUNNING HEAD: SENSORY RECRUITMENT

**Evidence for, and challenges to, sensory recruitment models of visual working memory**

Kirsten C.S. Adam<sup>1</sup>, Rosanne L. Rademaker<sup>2</sup> & John T. Serences<sup>1,3,4</sup>

<sup>1</sup>Department of Psychology, *University of California San Diego*, La Jolla, CA

<sup>2</sup>Ernst Strüngmann Institute (ESI) for Neuroscience in Cooperation with Max Planck Society, Frankfurt, Germany

<sup>3</sup>Institute for Neural Computation, *University of California San Diego*, La Jolla, CA

<sup>4</sup>Neurosciences Graduate Program, *University of California San Diego*, La Jolla CA

**Keywords:** working memory; short-term memory; sensory recruitment;

**Contributions:** KA drafted the manuscript; All authors revised the manuscript.

**Funding:** Research was supported by National Eye Institute grant R01-EY025872 (J.S.). and National Eye Institute grant T32-EY020503 (K.A.).

**ORCIDs:** 0000-0002-4950-327X (K.A.), 0000-0002-2804-8095 (R.R.), 0000-0002-8551-5147 (J.S.)

**Conflicts of interest:** none

**Correspondence to:**

Kirsten C. S. Adam  
University of California San Diego  
9500 Gilman Drive, Mail Code: 0109  
La Jolla, CA 92093-0109  
[kadam@ucsd.edu](mailto:kadam@ucsd.edu)

### **Abstract**

Visual working memory refers to the ability to temporarily hold information in mind in the service of behavior. Often, it is not sufficient to hold an abstract idea in mind to achieve our goals. Rather, we must maintain vivid sensory details. For example, when buying a spool of thread to repair a much-loved shirt, holding an abstract category in mind is not sufficient to buy the correct color (e.g. ‘blue’)—instead, you need a precise visual memory of the color (e.g., a particular gray-ish shade of blue). One proposal for how we maintain vivid, detailed information in mind is the *sensory recruitment hypothesis*. Sensory recruitment proposes that neural circuits already specialized for encoding sensory details during perception are likewise recruited to help maintain this information in working memory. In this review, we recount evidence that is consistent with a key role for early visual cortex in supporting visual working memory, we discuss key debates about the role of early sensory activity in supporting memory maintenance, and we outline a framework in which sensory codes are one part of a flexible, multi-level working memory representation.

### Main Text

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 & 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 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: primary auditory cortex for auditory stimuli (Brechtman et al., 2007; Gottlieb et al., 1989; Y. Huang et al., 2016; Linke & Cusack, 2015; Rämä et al., 2004) primary somatosensory cortex for tactile stimuli (Esmaeili & Diamond, 2019; Harris et al., 2002; Zhao et al., 2018), and 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.<sup>1</sup> We place a particular focus on the role of *task demands* in determining when early visual cortex supports working memory maintenance, and we turn a critical eye towards key potential limitations of sensory storage.

---

<sup>1</sup>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.

## 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 early visual cortex are tuned to basic visual features (e.g., motion direction, spatial frequency, orientation, color), researchers have long been interested in understanding 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 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, judgements 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 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 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 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 task condition versus another. 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 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 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 prefrontal cortex is well-established, and it is long hypothesized as the neural substrate of working memory. In contrast, visual cortex has shown little or no evidence of sustained, univariate delay period activity, consistent with the assumption that 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 even if the individual voxels’ responses are dissimilar from one another (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 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 visual cortex using fMRI BOLD activity, but this multivariate information is not reflected in average activity, as each orientation has similar average activity. The advent of multivariate methods thus raised the possibility that activity in 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 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 early visual cortex throughout the delay period. Replicating prior work, these studies found little or no sustained univariate delay period activity in 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 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; Supér et al., 2001). Such competitive dynamics may yield a net null effect in overall BOLD activity in early visual cortex.

In sum, the sensory recruitment hypothesis proposes that control signals from prefrontal cortex recruit specialized memory stores in 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 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 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 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., 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 of which 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 provides critical constraints for plausible sensory recruitment mechanisms (but also see, Kiyonaga & Egner, 2016). However, these findings do not rule out the involvement of 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 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 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 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 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 occipital cortex<sup>2</sup> 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). 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 visual cortex disrupt consolidation into working memory during the first ~200 milliseconds after stimulus offset (van de Ven et al., 2012; van Lamsweerde &

---

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



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 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) administered TMS 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 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 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 1 item’s location by taking advantage of the topographic organization of 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 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 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 visual cortex are not fully characterized or still unknown. In 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 visual cortex 'multi-task' to support perception and memory?**

Although there is compelling evidence that we can decode the contents of working memory from 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 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 early visual cortex was at chance due to the presence of the flickering pictures. However, decoding remained above chance in a sub-region of parietal cortex. Because visual cortex maintained above-chance in most, but not all, experiments, they concluded that representations in parietal cortex, but not 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 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 early visual cortex, but instead bias or weaken early visual representations.

First, very brief disruptions do not weaken decoding from early visual cortex. For example, when participants were shown two items and were then retro-cued 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 & 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 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 & Xu study (photographs of faces/gazebos were included, and distractors were made to flicker on-and-off) and found that memory decoding in early visual cortex was significantly reduced with distraction. However, unlike the Bettencourt & 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 & 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 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 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, 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 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 visual cortex (Rademaker & Serences, 2019) .

### **Evidence for multiple representational formats revealed by changing task demands**

Task demands play an important role in determining whether 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 early visual cortex (LaRocque et al., 2016; Riggall & Postle, 2012; Rose et al., 2016; Wolff et al., 2017). To assess how active maintenance within visual cortex is flexibly recruited depending on task demands, a ‘dual retro-cue’ task is often used. In a 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 2 items will be tested. Critically, after the participants perform the first test, they are given a *second* retro-cue about which of the 2 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 early visual cortex (Christophel et al., 2018). Despite the loss of decoding for the unattended memory item in early visual cortex, both items may still be decoded from 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 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 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).

## Conclusions

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 visual cortex in supporting working memory.

The evidence reviewed here argues against two extreme possible accounts of early sensory codes. On one extreme, one could hypothesize that sensory activity during working memory is epiphenomenal, emerging as a byproduct of other memory-related computations elsewhere in 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). On 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 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 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 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.

## References

- Aberra, A. S., Wang, B., Grill, W. M., & Peterchev, A. V. (2020). Simulation of transcranial magnetic stimulation in head model with morphologically-realistic cortical neurons. *Brain Stimulation: Basic, Translational, and Clinical Research in Neuromodulation*, 13(1), 175–189. <https://doi.org/10.1016/j.brs.2019.10.002>
- Abrahamyan, A., Clifford, C. W. G., Arabzadeh, E., & Harris, J. A. (2011). Improving visual sensitivity with subthreshold transcranial magnetic stimulation. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 31(9), 3290–3294. <https://doi.org/10.1523/JNEUROSCI.6256-10.2011>
- Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, 5(3), 119–126. [https://doi.org/10.1016/S1364-6613\(00\)01593-X](https://doi.org/10.1016/S1364-6613(00)01593-X)
- Baddeley, A. D., & Hitch, G. (1974). Working Memory. In *Psychology of Learning and Motivation* (Vol. 8, pp. 47–89). Elsevier. <http://linkinghub.elsevier.com/retrieve/pii/S0079742108604521>
- Barbosa, J., Soldevilla, D. L., & Compte, A. (2021). *Unattended short-term memories are maintained in active neural representations*. <https://doi.org/10.31234/osf.io/qv6fu>
- Beckers, G., & Hömberg, V. (1991). Impairment of visual perception and visual short term memory scanning by transcranial magnetic stimulation of occipital cortex. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, 87(2), 421–432. <https://doi.org/10.1007/BF00231859>
- Bennett, P. J., & Cortese, F. (1996). Masking of spatial frequency in visual memory depends on distal, not retinal, frequency. *Vision Research*, 36(2), 233–238. [https://doi.org/10.1016/0042-6989\(95\)00085-e](https://doi.org/10.1016/0042-6989(95)00085-e)
- Bettencourt, K. C., & Xu, Y. (2016). Decoding the content of visual short-term memory under distraction in occipital and parietal areas. *Nature Neuroscience*, 19(1), 150–157. <https://doi.org/10.1038/nn.4174>
- Beukers, A. O., Buschman, T. J., Cohen, J. D., & Norman, K. A. (2021). Is Activity Silent Working Memory Simply Episodic Memory? *Trends in Cognitive Sciences*. <https://doi.org/10.1016/j.tics.2021.01.003>
- Bloem, I. M., Watanabe, Y. L., Kibbe, M. M., & Ling, S. (2018). Visual Memories Bypass Normalization. *Psychological Science*, 29(5), 845–856. <https://doi.org/10.1177/0956797617747091>
- Boettcher, S. E. P., Gresch, D., Nobre, A. C., & van Ede, F. (2021). Output planning at the input stage in visual working memory. *Science Advances*, 7(13). <https://doi.org/10.1126/sciadv.abe8212>
- Bosch, S. E., Jehee, J. F. M., Fernandez, G., & Doeller, C. F. (2014). Reinstatement of Associative Memories in Early Visual Cortex Is Signaled by the Hippocampus. *Journal of Neuroscience*, 34(22), 7493–7500. <https://doi.org/10.1523/JNEUROSCI.0805-14.2014>
- Brechmann, A., Gaschler-Markefski, B., Sohr, M., Yoneda, K., Kaulisch, T., & Scheich, H. (2007). Working Memory-Specific Activity in Auditory Cortex: Potential Correlates of Sequential Processing and Maintenance. *Cerebral Cortex*, 17(11), 2544–2552. <https://doi.org/10.1093/cercor/bhl160>
- Breitmeyer, B. G., Ro, T., & Ogmen, H. (2004). A comparison of masking by visual and transcranial magnetic stimulation: implications for the study of conscious and unconscious visual processing. *Consciousness and Cognition*, 13(4), 829–843.

- <https://doi.org/10.1016/j.concog.2004.08.007>
- Carandini, M., & Heeger, D. J. (2012). Normalization as a canonical neural computation. *Nature Reviews. Neuroscience*, 13(1), 51–62. <https://doi.org/10.1038/nrn3136>
- Cattaneo, Z., Vecchi, T., Pascual-Leone, A., & Silvanto, J. (2009). Contrasting early visual cortical activation states causally involved in visual imagery and short-term memory: Visual imagery and memory. *The European Journal of Neuroscience*, 30(7), 1393–1400. <https://doi.org/10.1111/j.1460-9568.2009.06911.x>
- Christophel, T. B., Hebart, M. N., & Haynes, J.-D. (2012). Decoding the Contents of Visual Short-Term Memory from Human Visual and Parietal Cortex. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 32(38), 12983–12989. <https://doi.org/10.1523/JNEUROSCI.0184-12.2012>
- Christophel, T. B., Iamshchinina, P., Yan, C., Allefeld, C., & Haynes, J.-D. (2018). Cortical specialization for attended versus unattended working memory. *Nature Neuroscience*, 21(4), 494–496. <https://doi.org/10.1038/s41593-018-0094-4>
- Christophel, T. B., Klink, P. C., Spitzer, B., Roelfsema, P. R., & Haynes, J.-D. (2017). The Distributed Nature of Working Memory. *Trends in Cognitive Sciences*, 21(2), 111–124. <https://doi.org/10.1016/j.tics.2016.12.007>
- Chunharas, C., Rademaker, R. L., Brady, T. F., & Serences, J. (2019). *Adaptive memory distortion in visual working memory*. <https://doi.org/10.31234/osf.io/e3m5a>
- Cooper, H., DeNeve, K., & Charlton, K. (1997). Finding the missing science: The fate of studies submitted for review by a human subjects committee. *Psychological Methods*, 2(4), 447–452. <https://doi.org/10.1037/1082-989X.2.4.447>
- Courtney, S. M., Petit, L., Haxby, J. V., & Ungerleider, L. G. (1998). The role of prefrontal cortex in working memory: examining the contents of consciousness. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 353(1377), 1819–1828. <https://doi.org/10.1098/rstb.1998.0334>
- Courtney, S. M., Petit, L., Maisog, J. M., Ungerleider, L. G., & Haxby, J. V. (1998). An area specialized for spatial working memory in human frontal cortex. *Science*, 279(5355), 1347–1351. <https://doi.org/10.1126/science.279.5355.1347>
- Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1997). Transient and sustained activity in a distributed neural system for human working memory. *Nature*, 386(6625), 608–611. <https://doi.org/10.1038/386608a0>
- Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1996). Object and spatial visual working memory activate separate neural systems in human cortex. *Cerebral Cortex*, 6(1), 39–49. <https://doi.org/10.1093/cercor/6.1.39>
- Cox, D. D., & Savoy, R. L. (2003). Functional magnetic resonance imaging (fMRI) “brain reading”: detecting and classifying distributed patterns of fMRI activity in human visual cortex. *NeuroImage*, 19(2 Pt 1), 261–270. [https://doi.org/10.1016/s1053-8119\(03\)00049-1](https://doi.org/10.1016/s1053-8119(03)00049-1)
- Curtis, C. E., & D’Esposito, M. (2004). The effects of prefrontal lesions on working memory performance and theory. *Cognitive, Affective & Behavioral Neuroscience*, 4(4), 528–539. <https://doi.org/10.3758/cabn.4.4.528>
- Dade, L. A., Zatorre, R. J., Evans, A. C., & Jones-Gotman, M. (2001). Working Memory in Another Dimension: Functional Imaging of Human Olfactory Working Memory. *NeuroImage*, 14(3), 650–660. <https://doi.org/10.1006/nimg.2001.0868>
- D’Esposito, M. (2007). From cognitive to neural models of working memory. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 362(1481),



- 761–772. <https://doi.org/10.1098/rstb.2007.2086>
- D’Esposito, M., & Postle, B. R. (2015). The Cognitive Neuroscience of Working Memory. *Annual Review of Psychology*, 66(1), 115–142.  
<https://doi.org/10.1146/annurev-psych-010814-015031>
- Deutsch, D. (1970). Tones and numbers: specificity of interference in immediate memory. *Science*, 168(3939), 1604–1605. <https://doi.org/10.1126/science.168.3939.1604>
- Deutsch, D. (1973). Interference in memory between tones adjacent in the musical scale. *Journal of Experimental Psychology*, 100(2), 228–231. <https://doi.org/10.1037/h0035440>
- Downing, P. E. (2000). Interactions Between Visual Working Memory and Selective Attention. *Psychological Science*, 11(6), 467–473. <https://doi.org/10.1111/1467-9280.00290>
- Dubé, C., Zhou, F., Kahana, M. J., & Sekuler, R. (2014). Similarity-based distortion of visual short-term memory is due to perceptual averaging. *Vision Research*, 96, 8–16.  
<https://doi.org/10.1016/j.visres.2013.12.016>
- Dwan, K., Altman, D. G., Arnaiz, J. A., Bloom, J., Chan, A.-W., Cronin, E., Decullier, E., Easterbrook, P. J., Von Elm, E., Gamble, C., Gherzi, D., Ioannidis, J. P. A., Simes, J., & Williamson, P. R. (2008). Systematic Review of the Empirical Evidence of Study Publication Bias and Outcome Reporting Bias. *PloS One*, 3(8), e3081.  
<https://doi.org/10.1371/journal.pone.0003081>
- Emrich, S. M., Riggall, A. C., LaRocque, J. J., & Postle, B. R. (2013). Distributed Patterns of Activity in Sensory Cortex Reflect the Precision of Multiple Items Maintained in Visual Short-Term Memory. *Journal of Neuroscience*, 33(15), 6516–6523.  
<https://doi.org/10.1523/JNEUROSCI.5732-12.2013>
- Esmaili, V., & Diamond, M. E. (2019). Neuronal Correlates of Tactile Working Memory in Prefrontal and Vibrissal Somatosensory Cortex. *Cell Reports*, 27(11), 3167–3181.e5.  
<https://doi.org/10.1016/j.celrep.2019.05.034>
- Ester, E. F., Rademaker, R. L., & Sprague, T. C. (2016). How Do Visual and Parietal Cortex Contribute to Visual Short-Term Memory? [Review of *How Do Visual and Parietal Cortex Contribute to Visual Short-Term Memory?*]. *eNeuro*, 3(2).  
<https://doi.org/10.1523/ENEURO.0041-16.2016>
- Ester, E. F., Serences, J. T., & Awh, E. (2009). Spatially Global Representations in Human Primary Visual Cortex during Working Memory Maintenance. *Journal of Neuroscience*, 29(48), 15258–15265. <https://doi.org/10.1523/JNEUROSCI.4388-09.2009>
- Ester, E. F., Sprague, T. C., & Serences, J. T. (2015). Parietal and Frontal Cortex Encode Stimulus-Specific Mnemonic Representations during Visual Working Memory. *Neuron*, 87(4), 893–905. <https://doi.org/10.1016/j.neuron.2015.07.013>
- Fang, M. W. H., Ravizza, S. M., & Liu, T. (2019). Attention induces surround suppression in visual working memory. *Psychonomic Bulletin & Review*, 26(6), 1925–1932.  
<https://doi.org/10.3758/s13423-019-01624-7>
- Favila, S. E., Kuhl, B. A., & Winawer, J. (2020). Perception and memory have distinct spatial tuning properties in human visual cortex. In *bioRxiv* (p. 811331).  
<https://doi.org/10.1101/811331>
- Ferguson, C. J., & Heene, M. (2012). A Vast Graveyard of Undead Theories: Publication Bias and Psychological Science’s Aversion to the Null. *Perspectives on Psychological Science: A Journal of the Association for Psychological Science*, 7(6), 555–561.  
<https://doi.org/10.1177/1745691612459059>
- Franco, A., Malhotra, N., & Simonovits, G. (2014). Social science. Publication bias in the social

- sciences: unlocking the file drawer. *Science*, 345(6203), 1502–1505.  
<https://doi.org/10.1126/science.1255484>
- Funahashi, S., Bruce, C. J., & Goldman-Rakic, P. S. (1989). Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex. *Journal of Neurophysiology*, 61(2), 331–349.  
<https://doi.org/10.1152/jn.1989.61.2.331>
- Funahashi, S., Bruce, C. J., & Goldman-Rakic, P. S. (1990). Visuospatial coding in primate prefrontal neurons revealed by oculomotor paradigms. *Journal of Neurophysiology*, 63(4), 814–831. <https://doi.org/10.1152/jn.1990.63.4.814>
- Funahashi, S., Chafee, M. V., & Goldman-Rakic, P. S. (1993). Prefrontal neuronal activity in rhesus monkeys performing a delayed anti-saccade task. *Nature*, 365(6448), 753–756.  
<https://doi.org/10.1038/365753a0>
- Fuster, J. M. (1973). Unit activity in prefrontal cortex during delayed-response performance: neuronal correlates of transient memory. *Journal of Neurophysiology*, 36(1), 61–78.  
<https://doi.org/10.1152/jn.1973.36.1.61>
- Fuster, J. M., & Alexander, G. E. (1971). Neuron activity related to short-term memory. *Science*, 173(3997), 652–654. <https://doi.org/10.1126/science.173.3997.652>
- Gayet, S., Guggenmos, M., Christophel, T. B., Haynes, J.-D., Paffen, C. L. E., Van der Stigchel, S., & Sterzer, P. (2017). Visual Working Memory Enhances the Neural Response to Matching Visual Input. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 37(28), 6638–6647. <https://doi.org/10.1523/JNEUROSCI.3418-16.2017>
- Gayet, S., Paffen, C. L. E., & Van der Stigchel, S. (2018). Visual Working Memory Storage Recruits Sensory Processing Areas [Review of *Visual Working Memory Storage Recruits Sensory Processing Areas*]. *Trends in Cognitive Sciences*, 22(3), 189–190.  
<https://doi.org/10.1016/j.tics.2017.09.011>
- Gottlieb, Y., Vaadia, E., & Abeles, M. (1989). Single unit activity in the auditory cortex of a monkey performing a short term memory task. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, 74(1).  
<https://doi.org/10.1007/BF00248287>
- Hallenbeck, G. E., Sprague, T. C., Rahmati, M., Sreenivasan, K. K., & Curtis, C. E. (2021). Working Memory Representations in Visual Cortex Mediate the Effects of Distraction. In *bioRxiv* (p. 2021.02.01.429259). <https://doi.org/10.1101/2021.02.01.429259>
- Harlow, H. F., Davis, R. T., Settlage, P. H., & Meyer, D. R. (1952). Analysis of frontal and posterior association syndromes in brain-damaged monkeys. *Journal of Comparative and Physiological Psychology*, 45(5), 419–429. <https://doi.org/10.1037/h0056634>
- Harris, J. A., Miniussi, C., Harris, I. M., & Diamond, M. E. (2002). Transient Storage of a Tactile Memory Trace in Primary Somatosensory Cortex. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 22(19), 8720–8725.  
<https://doi.org/10.1523/JNEUROSCI.22-19-08720.2002>
- Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, 458(7238), 632–635. <https://doi.org/10.1038/nature07832>
- Harrison, W. J., & Bays, P. M. (2018). Visual Working Memory Is Independent of the Cortical Spacing Between Memoranda. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 38(12), 3116–3123.  
<https://doi.org/10.1523/JNEUROSCI.2645-17.2017>
- Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal

- cortex. *Science*, 293(5539), 2425–2430. <https://doi.org/10.1126/science.1063736>
- Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex. *Visual Neuroscience*, 9(02), 181–197. <https://doi.org/10.1017/S0952523800009640>
- Henderson, M. M., Rademaker, R. L., & Serences, J. T. (2019). Complementary visual and motor-based strategies for encoding information in working memory. *Journal of Vision*, 19(10), 91–91. <https://doi.org/10.1167/19.10.91>
- Henning, G. B., & Wichmann, F. A. (2007). Some observations on the pedestal effect. *Journal of Vision*, 7(1), 3. <https://doi.org/10.1167/7.1.3>
- Huang, J., & Sekuler, R. (2010). Distortions in recall from visual memory: two classes of attractors at work. *Journal of Vision*, 10(2), 24.1–27. <https://doi.org/10.1167/10.2.24>
- Huang, Y., Matysiak, A., Heil, P., König, R., & Brosch, M. (2016). Persistent neural activity in auditory cortex is related to auditory working memory in humans and nonhuman primates. *eLife*, 5. <https://doi.org/10.7554/eLife.15441>
- Iamshchinina, P., Christophel, T. B., Gayet, S., & Rademaker, R. L. (2021). Essential considerations for exploring visual working memory storage in the human brain. *Visual Cognition*, 1–12. <https://doi.org/10.1080/13506285.2021.1915902>
- Jacobsen, C. F. (1936). Studies of cerebral function in primates. I. The functions of the frontal association areas in monkeys. *Comparative Psychology Monographs*, 13, 3, 1–60.
- Jonides, J., Lacey, S. C., & Nee, D. E. (2005). Processes of Working Memory in Mind and Brain. In *Current Directions in Psychological Science* (Vol. 14, Issue 1, pp. 2–5). <https://doi.org/10.1111/j.0963-7214.2005.00323.x>
- Kamitani, Y., & Tong, F. (2005). Decoding the visual and subjective contents of the human brain. *Nature Neuroscience*, 8(5), 679–685. <https://doi.org/10.1038/nn1444>
- Kiyonaga, A., & Egner, T. (2016). Center-Surround Inhibition in Working Memory. *Current Biology: CB*, 26(1), 64–68. <https://doi.org/10.1016/j.cub.2015.11.013>
- Lages, M., & Paul, A. (2006). Visual long-term memory for spatial frequency? *Psychonomic Bulletin & Review*, 13(3), 486–492. <https://doi.org/10.3758/bf03193874>
- Lages, M., & Treisman, M. (1998). Spatial frequency discrimination: visual long-term memory or criterion setting? *Vision Research*, 38(4), 557–572. [https://doi.org/10.1016/s0042-6989\(97\)88333-2](https://doi.org/10.1016/s0042-6989(97)88333-2)
- Lalonde, J., & Chaudhuri, A. (2002). Task-dependent transfer of perceptual to memory representations during delayed spatial frequency discrimination. *Vision Research*, 42(14), 1759–1769. [https://doi.org/10.1016/s0042-6989\(02\)00111-6](https://doi.org/10.1016/s0042-6989(02)00111-6)
- Laming, D., & Laming, J. (1992). F. Hegelmaier: on memory for the length of a line. *Psychological Research*, 54(4), 233–239. <https://doi.org/10.1007/BF01358261>
- Laming, D., & Scheiwiller, P. (1985). Retention in perceptual memory: a review of models and data. *Perception & Psychophysics*, 37(3), 189–197. <https://doi.org/10.3758/bf03207563>
- LaRocque, J. J., Riggall, A. C., Emrich, S. M., & Postle, B. R. (2016). Within-Category Decoding of Information in Different Attentional States in Short-Term Memory. *Cerebral Cortex*, cercor.bhw283v1. <https://doi.org/10.1093/cercor/bhw283>
- Lawrence, S. J. D., Norris, D. G., & de Lange, F. P. (2019). Dissociable laminar profiles of concurrent bottom-up and top-down modulation in the human visual cortex. *eLife*, 8, e44422. <https://doi.org/10.7554/eLife.44422>
- Lawrence, S. J. D., van Mourik, T., Kok, P., Koopmans, P. J., Norris, D. G., & de Lange, F. P. (2018). Laminar Organization of Working Memory Signals in Human Visual Cortex. *Current Biology: CB*, 28(21), 3435–3440.e4. <https://doi.org/10.1016/j.cub.2018.08.043>

- Lee, S.-H., Kravitz, D. J., & Baker, C. I. (2013). Goal-dependent dissociation of visual and prefrontal cortices during working memory. *Nature Neuroscience*, 16(8), 997–999. <https://doi.org/10.1038/nn.3452>
- Levy, R., & Goldman-Rakic, P. S. (1999). Association of storage and processing functions in the dorsolateral prefrontal cortex of the nonhuman primate. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 19(12), 5149–5158. <https://www.ncbi.nlm.nih.gov/pubmed/10366648>
- Linke, A. C., & Cusack, R. (2015). Flexible Information Coding in Human Auditory Cortex during Perception, Imagery, and STM of Complex Sounds. *Journal of Cognitive Neuroscience*, 27(7), 1322–1333. [https://doi.org/10.1162/jocn\\_a\\_00780](https://doi.org/10.1162/jocn_a_00780)
- Lisman, J., & Idiart, M. (1995). Storage of 7 +/- 2 short-term memories in oscillatory subcycles. *Science*, 267(5203), 1512–1515. <https://doi.org/10.1126/science.7878473>
- Logie, R. H., Zucco, G. M., & Baddeley, A. D. (1990). Interference with visual short-term memory. *Acta Psychologica*, 75(1), 55–74. [https://doi.org/10.1016/0001-6918\(90\)90066-o](https://doi.org/10.1016/0001-6918(90)90066-o)
- Lorenc, E. S., Mallett, R., & Lewis-Peacock, J. A. (2021). Distraction in Visual Working Memory: Resistance is Not Futile. *Trends in Cognitive Sciences*. <https://doi.org/10.1016/j.tics.2020.12.004>
- Lorenc, E. S., & Sreenivasan, K. K. (2021). Reframing the debate: The distributed systems view of working memory. *Visual Cognition*, 1–9. <https://doi.org/10.1080/13506285.2021.1899091>
- Lorenc, E. S., Sreenivasan, K. K., Nee, D. E., Vandenbroucke, A. R. E., & D'Esposito, M. (2018). Flexible Coding of Visual Working Memory Representations during Distraction. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 38(23), 5267–5276. <https://doi.org/10.1523/JNEUROSCI.3061-17.2018>
- Lundqvist, M., Herman, P., Warden, M. R., Brincat, S. L., & Miller, E. K. (2018). Gamma and beta bursts during working memory readout suggest roles in its volitional control. *Nature Communications*, 9(1), 394. <https://doi.org/10.1038/s41467-017-02791-8>
- Magnussen, S. (2000). Low-level memory processes in vision. *Trends in Neurosciences*, 23(6), 247–251. [https://doi.org/10.1016/s0166-2236\(00\)01569-1](https://doi.org/10.1016/s0166-2236(00)01569-1)
- Magnussen, S., & Greenlee, M. W. (1992). Retention and disruption of motion information in visual short-term memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, 18(1), 151–156. <https://doi.org/10.1037/0278-7393.18.1.151>
- Magnussen, S., & Greenlee, M. W. (1999). The psychophysics of perceptual memory. *Psychological Research*, 62(2-3), 81–92. <https://doi.org/10.1007/s004260050043>
- Magnussen, S., Greenlee, M. W., Asplund, R., & Dyrnes, S. (1990). Perfect visual short-term memory for periodic patterns. *The European Journal of Cognitive Psychology*, 2(4), 345–362. <https://doi.org/10.1080/09541449008406212>
- Magnussen, S., Greenlee, M. W., Asplund, R., & Dyrnes, S. (1991). Stimulus-specific mechanisms of visual short-term memory. *Vision Research*, 31(7-8), 1213–1219. [https://doi.org/10.1016/0042-6989\(91\)90046-8](https://doi.org/10.1016/0042-6989(91)90046-8)
- Mallett, R., & Lewis-Peacock, J. A. (2019). Working memory prioritization impacts neural recovery from distraction. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, 121, 225–238. <https://doi.org/10.1016/j.cortex.2019.08.019>
- Martinez-Trujillo, J. C., & Treue, S. (2004). Feature-Based Attention Increases the Selectivity of Population Responses in Primate Visual Cortex. *Current Biology: CB*, 14(9), 744–751. <https://doi.org/10.1016/j.cub.2004.04.028>

- McKeefry, D. J., Burton, M. P., & Vakrou, C. (2007). Speed selectivity in visual short term memory for motion. *Vision Research*, 47(18), 2418–2425. <https://doi.org/10.1016/j.visres.2007.05.011>
- Merrikhi, Y., Clark, K., Albarran, E., Parsa, M., Zirnsak, M., Moore, T., & Noudoost, B. (2017). Spatial working memory alters the efficacy of input to visual cortex. *Nature Communications*, 8(1), 15041. <https://doi.org/10.1038/ncomms15041>
- Miller, E. K., Erickson, C. A., & Desimone, R. (1996). Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 16(16), 5154–5167. <https://www.ncbi.nlm.nih.gov/pubmed/8756444>
- Morey, C. C. (2018). The case against specialized visual-spatial short-term memory. *Psychological Bulletin*, 144(8), 849–883. <https://doi.org/10.1037/bul0000155>
- Nemes, V. A., Parry, N. R. A., Whitaker, D., & McKeefry, D. J. (2012). The retention and disruption of color information in human short-term visual memory. *Journal of Vision*, 12(1), 26. <https://doi.org/10.1167/12.1.26>
- Nemes, V. A., Whitaker, D., Heron, J., & McKeefry, D. J. (2011). Multiple spatial frequency channels in human visual perceptual memory. *Vision Research*, 51(23–24), 2331–2339. <https://doi.org/10.1016/j.visres.2011.09.003>
- Nilsson, T. H., & Nelson, T. M. (1981). Delayed monochromatic hue matches indicate characteristics of visual memory. *Journal of Experimental Psychology. Human Perception and Performance*, 7(1), 141–150. <https://doi.org/10.1037/0096-1523.7.1.141>
- Offen, S., Schluppeck, D., & Heeger, D. J. (2009). The role of early visual cortex in visual short-term memory and visual attention. *Vision Research*, 49(10), 1352–1362. <https://doi.org/10.1016/j.visres.2007.12.022>
- Olivers, C. N. L., Meijer, F., & Theeuwes, J. (2006). Feature-based memory-driven attentional capture: Visual working memory content affects visual attention. *Journal of Experimental Psychology. Human Perception and Performance*, 32(5), 1243–1265. <https://doi.org/10.1037/0096-1523.32.5.1243>
- Owen, A. M., Doyon, J., Petrides, M., & Evans, A. C. (1996). Planning and spatial working memory: a positron emission tomography study in humans. *The European Journal of Neuroscience*, 8(2), 353–364. <https://doi.org/10.1111/j.1460-9568.1996.tb01219.x>
- Owen, A. M., Evans, A. C., & Petrides, M. (1996). Evidence for a two-stage model of spatial working memory processing within the lateral frontal cortex: a positron emission tomography study. *Cerebral Cortex*, 6(1), 31–38. <https://doi.org/10.1093/cercor/6.1.31>
- Park, S., & Serences, J. (2020). Top-down and stimulus-driven influences jointly determine precision of spatial attention. *Journal of Vision*, 20(11), 978–978. <https://doi.org/10.1167/jov.20.11.978>
- Pashler, H., & Shiu, L.-P. (1999). Do images involuntarily trigger search? A test of Pillsbury's hypothesis. *Psychonomic Bulletin & Review*, 6(3), 445–448. <https://doi.org/10.3758/BF03210833>
- Pasternak, T., & Greenlee, M. W. (2005). Working memory in primate sensory systems. *Nature Reviews. Neuroscience*, 6(2), 97–107. <https://doi.org/10.1038/nrn1603>
- Pasternak, T., & Zaksas, D. (2003). Stimulus specificity and temporal dynamics of working memory for visual motion. *Journal of Neurophysiology*, 90(4), 2757–2762. <https://doi.org/10.1152/jn.00422.2003>
- Postle, B. R. (2006). Working memory as an emergent property of the mind and brain.

- Neuroscience*, 139(1), 23–38. <https://doi.org/10.1016/j.neuroscience.2005.06.005>
- Postle, B. R., Berger, J. S., Taich, A. M., & D'Esposito, M. (2000). Activity in human frontal cortex associated with spatial working memory and saccadic behavior. *Journal of Cognitive Neuroscience*, 12 Suppl 2, 2–14. <https://doi.org/10.1162/089892900564028>
- Pratte, M. S., & Tong, F. (2014). Spatial specificity of working memory representations in the early visual cortex. *Journal of Vision*, 14(3), 22–22. <https://doi.org/10.1167/14.3.22>
- Pribram, K. H., Mishkin, M., Rosvold, H. E., & Kaplan, S. J. (1952). Effects on delayed-response performance of lesions of dorsolateral and ventromedial frontal cortex of baboons. *Journal of Comparative and Physiological Psychology*, 45(6), 565–575. <https://doi.org/10.1037/h0061240>
- Rademaker, R. L., Bloem, I. M., De Weerd, P., & Sack, A. T. (2015). The impact of interference on short-term memory for visual orientation. *Journal of Experimental Psychology. Human Perception and Performance*, 41(6), 1650–1665. <https://doi.org/10.1037/xhp0000110>
- Rademaker, R. L., Chunharas, C., & Serences, J. T. (2019). Coexisting representations of sensory and mnemonic information in human visual cortex. *Nature Neuroscience*, 22(8), 1336–1344. <https://doi.org/10.1038/s41593-019-0428-x>
- Rademaker, R. L., Park, Y. E., Sack, A. T., & Tong, F. (2018). Evidence of gradual loss of precision for simple features and complex objects in visual working memory. *Journal of Experimental Psychology. Human Perception and Performance*, 44(6), 925–940. <https://doi.org/10.1037/xhp0000491>
- Rademaker, R. L., & Serences, J. T. (2019). Manipulating attentional priority creates a trade-off between memory and sensory representations in human visual cortex. *Journal of Vision*, 19(10), 205b – 205b. <https://doi.org/10.1167/19.10.205b>
- Rademaker, R. L., van de Ven, V. G., Tong, F., & Sack, A. T. (2017). The impact of early visual cortex transcranial magnetic stimulation on visual working memory precision and guess rate. *PloS One*, 12(4), e0175230. <https://doi.org/10.1371/journal.pone.0175230>
- Rämä, P., Poremba, A., Sala, J. B., Yee, L., Malloy, M., Mishkin, M., & Courtney, S. (2004). Dissociable Functional Cortical Topographies for Working Memory Maintenance of Voice Identity and Location. *Cerebral Cortex*, 14(7), 768–780. <https://doi.org/10.1093/cercor/bhh037>
- Regan, D. (1985a). Storage of spatial-frequency information and spatial-frequency discrimination. *JOSA A*, 2(4), 619–621. <https://doi.org/10.1364/JOSAA.2.000619>
- Regan, D. (1985b). Masking of spatial-frequency discrimination. *Journal of the Optical Society of America. A, Optics and Image Science*, 2(7), 1153–1159. <https://doi.org/10.1364/josaa.2.001153>
- Riggall, A. C., & Postle, B. R. (2012). The Relationship between Working Memory Storage and Elevated Activity as Measured with Functional Magnetic Resonance Imaging. *Journal of Neuroscience*, 32(38), 12990–12998. <https://doi.org/10.1523/JNEUROSCI.1892-12.2012>
- Rose, N. S., LaRocque, J. J., Riggall, A. C., Gosseries, O., Starrett, M. J., Meyering, E. E., & Postle, B. R. (2016). Reactivation of latent working memories with transcranial magnetic stimulation. *Science*, 354(6316), 1136–1139. <https://doi.org/10.1126/science.aah7011>
- Rosenthal, R. (1979). The file drawer problem and tolerance for null results. *Psychological Bulletin*, 86(3), 638–641. <https://doi.org/10.1037/0033-2909.86.3.638>
- Scolari, M., Byers, A., & Serences, J. T. (2012). Optimal Deployment of Attentional Gain during Fine Discriminations. *Journal of Neuroscience*, 32(22), 7723–7733. <https://doi.org/10.1523/JNEUROSCI.5558-11.2012>

- Seo, H., Schaworonkow, N., Jun, S. C., & Triesch, J. (2016). A multi-scale computational model of the effects of TMS on motor cortex. *F1000Research*, 5, 1945. <https://doi.org/10.12688/f1000research.9277.3>
- Serences, J. T. (2016). Neural mechanisms of information storage in visual short-term memory. *Vision Research*, 128, 53–67. <https://doi.org/10.1016/j.visres.2016.09.010>
- Serences, J. T., Ester, E. F., Vogel, E. K., & Awh, E. (2009). Stimulus-Specific Delay Activity in Human Primary Visual Cortex. *Psychological Science*, 20(2), 207–214. <https://doi.org/10.1111/j.1467-9280.2009.02276.x>
- Shin, H., Zou, Q., & Ma, W. J. (2017). The effects of delay duration on visual working memory for orientation. *Journal of Vision*, 17(14), 10. <https://doi.org/10.1167/17.14.10>
- Siebner, H. R., Hartwigsen, G., Kassuba, T., & Rothwell, J. C. (2009). How does transcranial magnetic stimulation modify neuronal activity in the brain? Implications for studies of cognition. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, 45(9), 1035–1042. <https://doi.org/10.1016/j.cortex.2009.02.007>
- Silvanto, J., & Cattaneo, Z. (2010). Transcranial magnetic stimulation reveals the content of visual short-term memory in the visual cortex. *NeuroImage*, 50(4), 1683–1689. <https://doi.org/10.1016/j.neuroimage.2010.01.021>
- Soto, D., Heinke, D., Humphreys, G. W., & Blanco, M. J. (2005). Early, Involuntary Top-Down Guidance of Attention From Working Memory. *Journal of Experimental Psychology. Human Perception and Performance*, 31(2), 248–261. <https://doi.org/10.1037/0096-1523.31.2.248>
- Soto, D., Llewellyn, D., & Silvanto, J. (2012). Distinct Causal Mechanisms of Attentional Guidance by Working Memory and Repetition Priming in Early Visual Cortex. *Journal of Neuroscience*, 32(10), 3447–3452. <https://doi.org/10.1523/JNEUROSCI.6243-11.2012>
- Spiridon, M., & Kanwisher, N. (2002). How distributed is visual category information in human occipito-temporal cortex? An fMRI study. *Neuron*, 35(6), 1157–1165. [https://doi.org/10.1016/s0896-6273\(02\)00877-2](https://doi.org/10.1016/s0896-6273(02)00877-2)
- Stokes, M. G. (2015). “Activity-silent” working memory in prefrontal cortex: a dynamic coding framework. *Trends in Cognitive Sciences*, 19(7), 394–405. <https://doi.org/10.1016/j.tics.2015.05.004>
- Supèr, H., Spekreijse, H., & Lamme, V. A. (2001). Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neuroscience*, 4(3), 304–310. <https://doi.org/10.1038/85170>
- Tamber-Rosenau, B. J., Fintzi, A. R., & Marois, R. (2015). Crowding in Visual Working Memory Reveals Its Spatial Resolution and the Nature of Its Representations. *Psychological Science*, 26(9), 1511–1521. <https://doi.org/10.1177/0956797615592394>
- Teng, C., & Postle, B. R. (2021). Spatial specificity of feature-based interaction between working memory and visual processing. *Journal of Experimental Psychology. Human Perception and Performance*, 47(4), 495–507. <https://doi.org/10.1037/xhp0000899>
- Ungerleider, L. G., Courtney, S. M., & Haxby, J. V. (1998). A neural system for human visual working memory. *Proceedings of the National Academy of Sciences of the United States of America*, 95(3), 883–890. <https://doi.org/10.1073/pnas.95.3.883>
- van de Ven, V., Jacobs, C., & Sack, A. T. (2012). Topographic Contribution of Early Visual Cortex to Short-Term Memory Consolidation: A Transcranial Magnetic Stimulation Study. *Journal of Neuroscience*, 32(1), 4–11. <https://doi.org/10.1523/JNEUROSCI.3261-11.2012>
- van Kerkoerle, T., Self, M. W., & Roelfsema, P. R. (2017). Layer-specificity in the effects of attention and working memory on activity in primary visual cortex. *Nature Communications*,

- 8(1), 13804. <https://doi.org/10.1038/ncomms13804>
- van Lamsweerde, A. E., & Johnson, J. S. (2017). Assessing the Effect of Early Visual Cortex Transcranial Magnetic Stimulation on Working Memory Consolidation. *Journal of Cognitive Neuroscience*, 29(7), 1226–1238. [https://doi.org/10.1162/jocn\\_a\\_01113](https://doi.org/10.1162/jocn_a_01113)
- Vogel, E. K., Woodman, G. F., & Luck, S. J. (2006). The time course of consolidation in visual working memory. *Journal of Experimental Psychology. Human Perception and Performance*, 32(6), 1436–1451. <https://doi.org/10.1037/0096-1523.32.6.1436>
- Wolff, M. J., Akyurek, E. G., & Stokes, M. G. (2021). *What is the functional role of delay-related alpha oscillations during working memory?* <https://doi.org/10.31234/osf.io/z6y5b>
- Wolff, M. J., Ding, J., Myers, N. E., & Stokes, M. G. (2015). Revealing hidden states in visual working memory using electroencephalography. *Frontiers in Systems Neuroscience*, 9, 123. <https://doi.org/10.3389/fnsys.2015.00123>
- Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017). Dynamic hidden states underlying working-memory-guided behavior. *Nature Neuroscience*, 20(6), 864–871. <https://doi.org/10.1038/nn.4546>
- Xu, Y. (2017). Reevaluating the Sensory Account of Visual Working Memory Storage. *Trends in Cognitive Sciences*, 21(10), 794–815. <https://doi.org/10.1016/j.tics.2017.06.013>
- Xu, Y. (2018). Sensory Cortex Is Nonessential in Working Memory Storage [Review of *Sensory Cortex Is Nonessential in Working Memory Storage*]. *Trends in Cognitive Sciences*, 22(3), 192–193. <https://doi.org/10.1016/j.tics.2017.12.008>
- Xu, Y. (2020). Revisit once more the sensory storage account of visual working memory. *Visual Cognition*, 28(5-8), 433–446. <https://doi.org/10.1080/13506285.2020.1818659>
- Yörüük, H., Santacroce, L. A., & Tamber-Rosenau, B. J. (2020). Reevaluating the sensory recruitment model by manipulating crowding in visual working memory representations. *Psychonomic Bulletin & Review*, 27(6), 1383–1396. <https://doi.org/10.3758/s13423-020-01757-0>
- Zelano, C., Montag, J., Khan, R., & Sobel, N. (2009). A Specialized Odor Memory Buffer in Primary Olfactory Cortex. *PloS One*, 4(3), e4965. <https://doi.org/10.1371/journal.pone.0004965>
- Zhao, D., Zhou, Y.-D., Bodner, M., & Ku, Y. (2018). The Causal Role of the Prefrontal Cortex and Somatosensory Cortex in Tactile Working Memory. *Cerebral Cortex*, 28(10), 3468–3477. <https://doi.org/10.1093/cercor/bhx213>
- Zokaei, N., Manohar, S., Husain, M., & Feredoes, E. (2014). Causal Evidence for a Privileged Working Memory State in Early Visual Cortex. *Journal of Neuroscience*, 34(1), 158–162. <https://doi.org/10.1523/JNEUROSCI.2899-13.2014>