***** In Press at *Current Directions in Psychological Science* *****

The Dynamic Processing Model of Working Memory

Nathan S. Rose

University of Notre Dame

Corresponding author:

Nathan S. Rose, PhD

William P. and Hazel B. White Assistant Professor of Psychology

Director, Cognitive Neuroscience of Memory & Aging Lab

Department of Psychology, University of Notre Dame

390 Corbett Hall, Notre Dame IN 46556

nrose1@nd.edu, www.RoseLab.org

Abstract

Recent shifts in the understanding of how the mind and brain retain information in working memory (WM) call for revision to traditional theories. Evidence for the existence of dynamic, “activity-silent” short-term retention processes in the brain diverge from conventional models that have argued that information is always retained in WM by sustained neural activity in buffers. Such evidence comes from the use of machine-learning analytic approaches to decode patterns of brain activity and the simultaneous administration of transcranial magnetic stimulation (TMS) to causally manipulate brain activity in specific areas and time-points. TMS has been used to 'ping' brain areas and reactivate latent representations retained in WM and affect memory performance. These findings argue for a supplement to the sustained retention mechanisms associated with attending to information in WM. Moreover, brain decoding methods reveal that dynamic levels of representational codes are retained in WM, which vary according to task context, from perceptual/sensory codes in posterior areas to more abstract, recoded representations distributed across frontal-parietal regions. A Dynamic Processing Model of WM is advanced to account for the overall pattern of results.

Keywords: activity-silent, short-term memory, working memory, sensory-motor recruitment

“Hey Nate, this is Alyssa, she’s new to our department. And this is her partner, Alex. He works in administration.”

“Hi, nice to meet you! Welcome! And where were you before moving over here... um... *Alexa?*”

The ability to retain and integrate information in working memory (WM) is fundamental for cognition. Yet students and researchers struggle to understand the construct because a comprehensive model does not exist to explain: 1) how the mind and brain accomplish WM tasks, such as holding goal-relevant information “in mind” (like names upon meeting some people, as in the opening example), 2) what happens to such information when attention shifts away, and 3) how it is recovered when needed for processing and action. The search for a comprehensive model of WM has been challenging, in part because of the dynamic, nuanced, and context-dependent nature of the neurocognitive processes that support WM across situations and individuals. However, ideas about how WM *works* are rapidly evolving in recent years as models of behavior are increasingly informed by the understanding of neural mechanisms that support WM.

Constraining cognitive models of WM with neuroscientific evidence

Identifying the neural substrates of WM is critical for testing theories of WM because revealing where information is stored in the brain and how the representations change over time or in response to task demands is fundamental to understanding the nature of WM-related behavior. Below, after briefly introducing key concepts of traditional WM theory, I review some evidence for emerging concepts that call for revision to, and integration with, traditional theory: namely, that the retention and reactivation of *latent* working memories may be held via either ‘activity-silent’ neural mechanisms or, depending on the stimulus and task-context, in long-term memory (LTM).

The conventional view: sustained/active representations

Traditionally, both cognitive and neural models of WM have posited that information is retained in WM, in either ‘*buffers*’—which are capacity-limited short-term stores that retain specific codes (visuospatial, phonological; Baddeley, 2000)—or in activated states of varying

levels of accessibility (Cowan, 1999; Oberauer, 2009), via sustained, elevated levels of neuronal activity.¹ Most models proposed that information is transferred from sensory to central-executive control (frontal-parietal) regions in the brain where the information is actively retained “in WM”, and that, when items are not actively maintained, they are stored with LTM processes (Jonides et al., 2008).

A supplemental view: activity-silent, sensorimotor representations

Based on early findings from human neuropsychology and lesion or recording studies in animals, neural instantiations of WM models have focused on regions of frontal-parietal cortex as the representational substrate of WM storage (Curtis & D’Esposito, 2004; Funahashi, 2017). For example, neurons in dorsolateral prefrontal cortex (DLPFC) have shown elevated levels of activity during WM delay periods that has been described as sustained, persistent, and stable. However, there are recent advances that are revolutionizing conventional WM theory. This is largely driven by advances in machine-learning analyses of neuroimaging data. Whereas traditional univariate analyses show elevated levels of activity in frontal-parietal regions during WM delay periods that scale with WM load, posterior sensory regions show stimulus presentation and retrieval-evoked responses, but generally little-to-no sustained activity throughout the delay; in contrast, newer multivariate analysis techniques reveal a different picture: machine learning algorithms can often learn to *decode* aspects of the retained stimuli from signals in sensory areas, but with little-to-no stimulus-specific information decoded from signals in frontal cortex (Riggall & Postle, 2012; Yu & Shim, 2017).

Such findings are consistent with the *Sensorimotor Recruitment Hypothesis* (Postle, 2006), which states, “the same systems and representations that are engaged in the perception of information can also contribute to the short-term retention of that information” and *motor* is in the name “to accommodate the intimate, often inextricable, coupling between sensory attention and motor intention.” (D’Esposito & Postle, 2015, pp. 118-119). Sensorimotor representation of items in WM is advantageous in many situations because it provides highly-

¹ The scope of the current work cannot incorporate adequate discussion of the important, extensive debate about the source of WM capacity limits; see suggested readings for some excellent discussion (e.g., Cowan, 2017; Luck & Vogel, 2013; Mi et al., 2017; Oberauer et al., 2016).

selective tuning of stimulus-specific features with more efficient processes than sustained, elevated neuronal firing (Serences, 2016).

One example of how WM is tightly tied to action systems comes from observations that only lesions selective to the frontal eye fields of motor cortex—not DLPFC—impair performance on the delayed saccade (spatial WM) task, which suggests that what is retained is eye-saccade plans to service WM—not the location of items in WM per se (Mackey et al., 2016). Additionally, recordings of neurons in areas of PFC during the delayed-saccade task showed that, while many neurons appeared to demonstrate stable delay-period activity for the information in WM during a delay, the information represented in the population was dynamic (time-varying) and switched to reward-related information (Cavanaugh et al., 2018). Thus, delay-period activity across many regions of PFC seem to dynamically represent stimulus-specific information to the extent that the codes help produce the prospective actions that are most likely to result in optimal performance or, more specifically, the greatest reward (Stokes, 2015; Spaak et al., 2017).

Context-dependent dynamics: the role of attention. Various aspects of the WM task seem to determine whether items in WM are largely represented by sustained activity in frontal-parietal cortex and/or with ‘activity-silent’ mechanisms in regions of sensorimotor cortex. For example, regions of frontal-parietal cortex and the hippocampus and surrounding structures of the medial temporal lobes (MTL) seem to be particularly involved in situations when continuous attention to memoranda is disrupted by interference (e.g., from distraction, for reviews, see Sreenivasan & D’Esposito, 2019; Widhalm & Rose, 2019). It has been argued that active maintenance in WM is strongly dependent on continuous attention and, when attention shifts away from the memoranda, then retrieval processes are required to return the information to focal attention for further processing and action. Thus, according to this view, the vast majority of studies in the history of WM research has confounded WM retention with internal attention (LaRocque et al., 2014; Sheldon et al., in press).

Brain decoding evidence from tasks that shift a person’s focus of attention between items held in WM is consistent with the view that WM represents the intersection of attention and memory (LaRocque et al., 2014; Lewis-Peacock et al., 2012). Such tasks (like those that

mimic the situation depicted in the beginning of this paper of learning two names in conversation) require that two items (a face and a word) transition between being held either in a sustained, active state or transiently in an unattended, passive state. For example, in our “two-step double-cue toodeloo” task (see Figure 1), the primary finding was that in the post-cue delay periods, evidence for a sustained, active neural representation only existed for the attended/cued item; evidence for the unattended/uncued memory item returned to baseline levels of representation (Lewis-Peacock et al., 2012; Rose et al., 2016). When the initially uncued item was subsequently cued as the item that would be tested later in the trial, participants could quickly and accurately switch attention to it and there was a reinstatement of brain-decoding evidence for an active representation of it. Such findings challenge the assumption that holding information in WM always depends on sustained, elevated activity (Lewis-Peacock et al., 2012; Rose et al., 2016)

Figure 1. (A. Left Panel) Design of the “two-step double-cue toodeloo” task and brain decoding evidence from fMRI for the category of the initially cued, uncued, and irrelevant item (face, word, and motion, respectively, in this example); (B. Right Panel) the brain maps show distributed whole-brain decoding of category-selective areas used for targeting the TMS coil (see Venn diagram for color codes); the light blue ribbons show brain decoding of the unattended memory item (UMI) category on targeted and non-targeted trials relative to absent trials from presentation of the UMI (blue circle) and attended memory item (AMI, red circle; decoding not shown) 5-7 sec before cueing the AMI (red triangle), administering TMS, and testing the AMI (red rectangle) (see Rose et al., 2016, *Science*).

The Synaptic Theory of WM is a computational model based on biologically plausible neural mechanisms that can account for this finding (Mongillo et al., 2008; Trubetschek et al., 2017). It posits that a stimulus-evoked pattern of neural activity could be retained during a delay by transiently strengthening the synaptic weights between the neurons. Thus, a memory could be temporarily retained without elevated, neural firing. The model further suggests that if a nonspecific burst of energy is applied to the network during this period, then the memory would be reactivated due to the potentiated pattern of synapses. Indeed, using brain-decoding methods with simultaneous noninvasive brain stimulation (TMS, transcranial magnetic stimulation), we transiently reactivated these passively retained ('latent') working memories by recovering memory-specific patterns of neural activity and influencing memory performance (Rose et al., 2016; Widhalm & Rose, 2018; see also, Wolff et al., 2017).

Context-dependent dynamics: the role of stimulus representations. Much of the evidence to support the notion of 'activity-silent' representations in WM comes from visual WM research, particularly in situations with minimal interference. In contrast, some evidence exists for a putative storage 'buffer' for *phonological* WM (Yue et al., 2018). Neuropsychological, neuroimaging and neurostimulation evidence has been used to argue for a specialized storage site for phonological WM in the supramarginal gyrus (Majerus, 2019). The distinct coding schemes are sensible because fleeting visual representations can be 'refreshed' by attending to goal-relevant visual information in the retinotopically coded visual field (Park et al., 2010). In contrast, because auditory information unfolds over time and must be sequenced with both preceding and succeeding acoustic information, distinct processes support the short-term retention and reactivation of auditory information (Buchsbaum & D'Esposito, 2018).

In a recent fMRI study, *univariate* analyses showed similar results for phonological WM (Yue et al., 2018) as those observed in visual WM (Riggall & Postle, 2012); however, *multivariate pattern classification* analyses on delay-period activity during phonological WM diverged (see Figure 2). WM content could be decoded from patterns of activity in sensory (auditory) cortex during a maintenance period, but only during conditions of high load with a classifier trained during the maintenance period--not by a classifier trained during a separate perception task or during the encoding period of the WM task. That is, the classifiers that

decoded the activity patterns for speech vs. nonspeech captured *different* representations in the *same* region of sensory cortex when three stimuli were retained during the delay than when they were initially perceived/encoded. This result suggests that the sensory cortex was only recruited during high load and that the neural representation during the delay was a *recoded* pattern that differed from the pattern established during perception. That is, whether WM retention relies on either sensory cortex or ‘buffer’ regions is context dependent.

Figure 2. Univariate and multivariate brain decoding evidence during a phonological STM task with 1 (low-load) vs. 3 (high-load) speech or non-speech sounds from fMRI activity in left superior temporal gyrus (STG, sensory cortex) and the left supramarginal gyrus (SMG, the putative phonological buffer).

Univariate results are analogous to visual STM results with ‘activity-silent’ sensory regions but sustained elevated activity in ‘buffer’ regions during STM delay periods (Riggall & Postle, 2012); multivariate results show delay-period decoding of STM contents only for high memory load conditions in the sensory region, but only for a classifier trained to discriminate speech patterns during maintenance (purple)--not during perception/encoding--which means STM contents were recoded perceptual representations. The ‘buffer’ region contained similar representations during encoding and maintenance during high load. Asterisks indicate decoding timepoints significantly greater than chance (.5). See Yue, Martin, Hamilton, & Rose, 2018, *Cerebral Cortex*.

These results are consistent with the hypothesis that recoding perceptual (e.g., phonological) representations, which are vulnerable to interference, by attending to deeper (conceptual) levels of processing during encoding changes their neural substrate and makes them robust to interference by recruiting LTM processes (Rose, Craik, & Buchsbaum, 2015).²

Context-dependent dynamics: the role of LTM processes. Although WM has been considered to be distinct from LTM due to neuropsychological and behavioral double-dissociations between tasks purported to selectively measure WM and LTM (Ranganath & Blumenfeld, 2005), many have posited an integral contribution of LTM processes to short-term retention (Jonides et al., 2008), and acceptance of this view is growing (Cowan, 2019; Foster, Vogel & Awh, in press). Baddeley (2000) added an “episodic buffer” (as well as language and visual semantics) to his model to accommodate interactions between WM and LTM. However, attempts to localize components of “box-and-arrow” models has been challenging due to the distributed and dynamic nature of information processing coded in activity across both local and large-scale brain networks (Kriegeskorte & Douglas, 2018). With regards to the role of the MTL in WM, there are many examples of profound WM deficits in MTL amnesics (Olson, Page, Moore, Chatterjee & Verfaellie, 2006), but the deficits depend on whether the tasks involve binding associations among less familiar features, especially during distraction (Rose, Olsen, Craik, & Rosenbaum, 2012). Results from neuropsychological cases and neuroimaging studies (see Jonides et al., 2008; Ranganath & Blumenfeld, 2005) point to a prominent role of the MTL

² Note that the same applies for visual WM as well (e.g., Curby, Glazek & Gauthier, 2009; Endress & Potter, 2014; Lewis-Peacock & Postle, 2008; Wolfe, 2012).

in situations requiring high-resolution representations in both WM and LTM, and even perception as well (Yonelinas, 2013).³

An accommodating view

It is important to acknowledge that there will be considerable differences in the neurocognitive retention mechanisms that support WM according to the participants and strategies they use to remember different types of memoranda across different task contexts. For example, considerable variance exists in inter- and intra-individual differences in WM capacity. This is hypothesized to result from variance in the engagement of cognitive control processes associated with active maintenance, controlled retrieval, and output monitoring processes, among others. Thus, WM is not a monolithic, isomorphic construct; rather, WM should be considered as a collection of *processes* associated with perception, attention, semantic and episodic memory, and prospective action that support one's current goal-relevant behaviors.

Therefore, attempts to define an all-encompassing, one-size-fits all WM model may ultimately prove futile. Building on the ideas of many others, I propose a *Dynamic Processing Model* of WM in an attempt to account for the diverse set of findings regarding the neurocognitive substrates of WM. I argue for a *dynamic* model because the nature of the representations and processes that are involved to support WM in the service of thought and action change over time and across contexts. I argue for a *processing* model to emphasize the need to specify the neurocognitive processes and informational codes represented by neuronal activity rather than trying to identify a system of stores, as was the tradition of box-and-arrow

³ In both human and nonhuman studies of WM, the involvement of LTM processes also appears to be dynamic and context dependent. Data from direct electrophysiological recordings suggest that stimulus-specific activity of “concept” cells in the MTL can reflect the contents of WM and they may persistently fire or become synchronized with regions of PFC through oscillatory dynamics (theta-alpha coupling) (Kaminsky et al., 2017; Kornblith et al. 2017); and this activity can predict WM load and successful WM performance (Boran et al., 2019; Kornblith et al., 2017). Other data suggest that afferent pathways from hippocampus to PFC code for spatial WM through gamma-frequency synchrony during encoding, but *not* maintenance or retrieval (Spellman et al., 2015). In depth discussion is beyond the scope of the current manuscript, but the reader is referred to related work regarding an intriguing concept of “labile LTP” codes in the hippocampus (Pradier et al. 2018). The main point here is that LTM processes *are* recruited during WM, likely via connectivity with PFC, but in a dynamic, context-dependent manner.

models in cognitive psychology. This approach is consistent with the cognitive neuroscience revolution over the past few decades that is pushing researchers to develop more biologically plausible models based on computational codes processed in neural networks.

Figure 3. Graphical depiction of a “Dynamic Processing Model of WM”: According to this view, STM/WM depends on both sustained and selective (transient/periodic) attention control processes; representations emerge from sensorimotor processing during perception or activation of associations stored in LTM; stimulus specific and overlapping domain general aspects of representations are distributed across the cortex; the hippocampal/MTL complex establishes high-resolution binding of task-relevant features; feedforward and feedback connections exist throughout task-relevant pathways with parietal nodes biasing attention to critical sensory features during either encoding, maintenance, or retrieval; the PFC *can* code for stimulus specific features during WM delay periods (e.g., locations of future eye movements), but the signals may be better conceptualized as representing task rules or the prospective actions predicted to maximize rewards for goal-directed behaviors; to this end, distributed subregions of PFC code for various processes such as active maintenance or periodic retrieval of relevant

representations and associations, decision-making, performance monitoring, and updating. Color coded data depict an example of the distributed nature of WM representation from the selective or shared/overlapping whole-brain decoding of a face, direction of motion, or word during a WM delay period (see Venn diagram; adapted from Rose et al., 2016, *Science*).

The major tenets of the model are as follows: 1) The mind and brain retains information that is predicted to be relevant for current, goal-directed processing and action either by A) actively attending to the representations by sustained/recurrent activity, or B) passively “prioritizing” the representations by synaptic plasticity dynamics.⁴ The representations themselves are the products of perceptual/conceptual processing and associative activation of LTM. 2) Whether retention is either active or prioritized depends on the need to protect these representations from interference (e.g., from distraction as delay, load, or stimulus similarity increases, or as motivation or capacity decreases) (e.g., Lorenc et al., 2018; Rademaker et al., 2019). 3) The nature of the neurocognitive representations and processes that support retention in WM are highly dynamic because they change over time and they depend on the context (including the to-be-performed action that is assumed to result in the most desirable outcome). 4) Information may be simultaneously represented via multiple codes and/or recoded over time. Such coding is important for representing information at varying levels of abstraction, particularly in the service of higher-order cognitive functions.

Many of these ideas have been articulated previously³³⁻⁴⁰; a goal of this review is to help integrate ideas from cognitive- and neural-sciences to foster better appreciation for the context-dependent nature of WM retention and representation. This review represents an attempt to tie together some of the big ideas that are emerging at a rapid rate. A more detailed treatise will be necessary as more empirical data and quantifiably testable computational models develop.

Conclusions and Outlook

⁴ I use the term prioritized instead of “activity-silent” because the term activity-silent refers to the phenomenon where the neuroimaging techniques that can decode a delay-period representation of a stimulus that is attended and actively retained can no longer decode that representation when it is unattended (i.e., passively retained); thus, other physiological (e.g., synaptic, electrochemical and oscillatory) processes retain the memory.

The research reviewed above and related results have considerable significance for theoretical and mechanistic accounts of WM. The findings suggest that short-term retention of goal-relevant information can be accomplished via either ‘active’ representations⁵ that are dynamic, recoded representations in frontal-parietal cortex (especially when there are competing demands on controlled attention during a delay) *or* latent, ‘prioritized’ representations in sensorimotor cortex via efficient, synaptic plasticity mechanisms (especially in situations that either involve minimal interference or require high-resolution representation).⁶ With regards to the future, it is important to address questions regarding the sources and site of latent WM representation, as well as the role of LTM processes in retaining and reactivating latent WM. Providing answers to such questions will advance WM theory in a way that will have widespread influence on the understanding of cognition more generally. My hope is that a dynamic processing model of WM will help to integrate the many mutually compatible views across the field.

⁵ Note that recent research suggests that sustained neural activity over a delay period may actually be an artifact of averaging trials in which brief bursts of activity occur sporadically over a delay period (Lundqvist et al., 2018). Rather than sustained neural firing, such sporadic bursts of delay-period activity may reflect the cognitive maintenance operation termed refreshing (Johnson et al., 2015; Raye et al., 2007). Note, however, that the neural data do not align with cognitive estimates of a refreshing rate of 10-40 ms per item (Barrouillet & Camos, 2015; see Lemaire et al., 2018). Pairing sophisticated manipulations in cognitive tasks with multivariate, single-trial analyses of neural data with high temporal and spatial resolution will provide important insight to help resolve this debate.

⁶ Note that, although some computational modeling argues against interpretation of latent WM states (Schneegans & Bays, 2017), other computational models argue for both “attractor states” (which can sustain representations) and “transient states” (which support dynamic, recoded representations) (Nachstedt & Tetzloff, 2017). The future will undoubtedly see increasingly advanced neurocomputational/neural-network modeling of biologically plausible mechanisms that support cognitive phenomena associated with WM. One intriguing phenomenon to explain is evidence of above-chance behavioral performance (Soto, Mäntylä & Silvanto, 2011) and brain decoding accuracy (King, Pescetelli, Dehaene, 2016) for trial-relevant memory-specific representations that are retained over WM delay periods *in the absence of conscious awareness* (Bergstrom & Eriksson, 2018). The extent to which goal-relevant representations are retained outside of conscious awareness in the service of WM has the potential to dramatically re-envision what it means for something to be ‘in WM’.

Recommended Reading (see references)

For some rather comprehensive, accessible overviews of what is known about the mind and brain of STM/WM see:

Cowan, N. (2019) Short-term memory based on activated long-term memory: A review in response to Norris (2017). *Psychological Bulletin*, 145, 822-847.

D'Esposito, M., & Postle, B. R. (2015). The cognitive neuroscience of working memory. *Annual review of psychology*, 66, 115-142.

Serences, J. (2016). Neural mechanisms of information storage in visual short-term memory. *Vision Research*

Sreenivasan, K. K., & D'Esposito, M. (2019). The what, where and how of delay activity. *Nature Reviews Neuroscience*, 1.

For an exciting “adversarial collaboration” of WM researchers designed to have the field converge on key themes to be addressed by future research and advance models of STM/WM, see:

Oberauer, K., Lewandowsky, S., Awh, E., Brown, G. D., Conway, A., Cowan, N., ... & Ma, W. J. (2018). Benchmarks for models of short-term and working memory. *Psychological Bulletin*, 144(9), 885.

Declaration of Conflicting Interests

The author declared that he has no conflicts of interest with respect to his authorship or the publication of this article.

Funding

National Science Foundation CAREER Award

References

- 1 Baddeley, A. (2000). The episodic buffer: a new component of working memory?. *Trends in cognitive sciences*, 4(11), 417-423.
- 2 Cowan, N. (1999). An embedded-processes model of working memory. *Models of working memory: Mechanisms of active maintenance and executive control*, 20, 506.
- 3 Oberauer, K. (2009). Design for a working memory. *Psychology of learning and motivation*, 51, 45-100.
- 4 Jonides, J., Lewis, R. L., Nee, D. E., Lustig, C. A., Berman, M. G., & Moore, K. S. (2008). The mind and brain of short-term memory. *Annu. Rev. Psychol.*, 59, 193-224.
- 5 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.
- 6 Funahashi, S. (2017). Working memory in the prefrontal cortex. *Brain Sciences*, 7(5), 49.
- 7 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.
- 8 Yu, Q., & Shim, W. M. (2017). Occipital, parietal, and frontal cortices selectively maintain task-relevant features of multi-feature objects in visual working memory. *Neuroimage*, 157, 97-107.
- 9 Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, 139(1), 23-38.
- 10 D'Esposito, M., & Postle, B. R. (2015). The cognitive neuroscience of working memory. *Annual review of psychology*, 66, 115-142.
- 11 Serences, J. T. (2016). Neural mechanisms of information storage in visual short-term memory. *Vision research*, 128, 53-67.
- 12 Mackey, W. E., Devinsky, O., Doyle, W. K., Meager, M. R., & Curtis, C. E. (2016). Human dorsolateral prefrontal cortex is not necessary for spatial working memory. *Journal of Neuroscience*, 36(10), 2847-2856.

- 13 Cavanagh, S. E., Towers, J. P., Wallis, J. D., Hunt, L. T., & Kennerley, S. W. (2018). Reconciling persistent and dynamic hypotheses of working memory coding in prefrontal cortex. *Nature Communications*, 9(1), 3498.
- 14 Stokes, M. G. (2015). 'Activity-silent' working memory in prefrontal cortex: a dynamic coding framework. *Trends in Cognitive Sciences*, 19(7), 394-405.
- 15 Spaak, E., Watanabe, K., Funahashi, S., & Stokes, M. G. (2017). Stable and dynamic coding for working memory in primate prefrontal cortex. *Journal of Neuroscience*, 37(27), 6503-6516.
- 16 Sreenivasan, K. K., & D'Esposito, M. (2019). The what, where and how of delay activity. *Nature Reviews Neuroscience*, 20(8), 466-481.
- 17 Widhalm, M. L., & Rose, N. S. (2019). How can transcranial magnetic stimulation be used to causally manipulate memory representations in the human brain? *Wiley Interdisciplinary Reviews: Cognitive Science*, 10(1), e1469.
- 18 LaRocque, J. J., Lewis-Peacock, J. A., & Postle, B. R. (2014). Multiple neural states of representation in short-term memory? It's a matter of attention. *Frontiers in human neuroscience*, 8, 5.
- 19 Sheldon, A.D., Saad, E., Sahan, M.I., Meyering, E., Starrett, M.J., LaRocque, J.J., Rose, N.S., and Postle, B.R. (in press). Attention biases competition for visual representation via enhancement of targets and inhibition of nontargets. *Journal of Cognitive Neuroscience*.
- 19 Lewis-Peacock, J. A., Drysdale, A. T., Oberauer, K., & Postle, B. R. (2012). Neural evidence for a distinction between short-term memory and the focus of attention. *Journal of Cognitive Neuroscience*, 24(1), 61–79. https://doi.org/10.1162/jocn_a_00140
- 20 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.
- 21 Widhalm, M. L., & Rose, N. S. (2018). Can TMS to Visual Cortex Reactivate Unattended Representations Held in Visual Working Memory? Paper presented in a Nanosymposium at the Annual Meeting of the Society for Neuroscience, San Diego, CA.

- 21 Mongillo, G., Barak, O., & Tsodyks, M. (2008). Synaptic theory of working memory. *Science*, 319(5869), 1543-1546.
- 22 Trübetschek, D., Marti, S., Ojeda, A., King, J. R., Mi, Y., Tsodyks, M., & Dehaene, S. (2017). A theory of working memory without consciousness or sustained activity. *Elife*, 6, e23871.
- 20 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.
- 21 Widhalm, M. L., & Rose, N. S. (in preparation). TMS to Visual Cortex Reactivates and Enhances Unattended Representations Held in Visual Working Memory
- 22 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.
- 23 Yue, A.; Martin, R.A.; Hamilton, C.; Rose, N.S. (2018). Non-perceptual regions in the left inferior parietal lobe support phonological short-term memory: Evidence for a buffer account? *Cerebral Cortex*, <https://doi.org/10.1093/cercor/bhy037>
- 24 Majerus, S. (2019). Verbal working memory and the phonological buffer: The question of serial order. *Cortex*, 112, 122-133.
- 25 Park, S., Chun, M. M., & Johnson, M. K. (2010). Refreshing and integrating visual scenes in scene-selective cortex. *Journal of Cognitive Neuroscience*, 22(12), 2813-2822.
- 26 Buchsbaum, B. R., & D'Esposito, M. (2018). A sensorimotor view of verbal working memory. *Cortex*.
- 24 Rose, N. S., Craik, F. I., & Buchsbaum, B. R. (2015). Levels of processing in working memory: Differential involvement of frontotemporal networks. *Journal of cognitive neuroscience*, 27(3), 522-532.
- 25 Ranganath, C., & Blumenfeld, R. S. (2005). Doubts about double dissociations between short-and long-term memory. *Trends in Cognitive Sciences*, 9(8), 374-380.
- 26 Foster, J.J., Vogel, E.K., & Awh, E. (In Press). Working memory as persistent neural activity. To appear in the *Oxford Handbook of Human Memory*. Eds. M. Kahana & A. Wagner.
- 27 Kriegeskorte, N., & Douglas, P. K. (2018). Cognitive computational neuroscience. *Nature Neuroscience*, 21(9), 1148-1160.

- 28 Olson, I. R., Page, K., Moore, K. S., Chatterjee, A., & Verfaellie, M. (2006). Working memory for conjunctions relies on the medial temporal lobe. *Journal of Neuroscience*, 26(17), 4596-4601.
- 29 Rose, N. S., Olsen, R. K., Craik, F. I., & Rosenbaum, R. S. (2012). Working memory and amnesia: the role of stimulus novelty. *Neuropsychologia*, 50(1), 11-18.
- 30 Yonelinas, A. P. (2013). The hippocampus supports high-resolution binding in the service of perception, working memory and long-term memory. *Behavioural brain research*, 254, 34-44.
- 31 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.
- 32 Lorenc, E. S., Sreenivasan, K. K., Nee, D. E., Vandenbroucke, A. R., & D'Esposito, M. (2018). Flexible coding of visual working memory representations during distraction. *Journal of Neuroscience*, 38(23), 5267-5276.
- 33 Sreenivasan, K. K., Curtis, C. E., & D'Esposito, M. (2014). Revisiting the role of persistent neural activity during working memory. *Trends in cognitive sciences*, 18(2), 82-89.
- 34 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.
- 35 Myers, N. E., Stokes, M. G., & Nobre, A. C. (2017). Prioritizing information during working memory: beyond sustained internal attention. *Trends in Cognitive Sciences*, 21(6), 449-461.
- 36 Leavitt, M. L., Mendoza-Halliday, D., & Martinez-Trujillo, J. C. (2017). Sustained activity encoding working memories: not fully distributed. *Trends in neurosciences*, 40(6), 328-346.
- 37 Xu, Y. (2017). Reevaluating the sensory account of visual working memory storage. *Trends in Cognitive Sciences*, 21(10), 794-815. + associated commentaries
- 38 Constantinidis, C., Funahashi, S., Lee, D., Murray, J. D., Qi, X. L., Wang, M., & Arnsten, A. F. (2018). Persistent spiking activity underlies working memory. *Journal of Neuroscience*, 38(32), 7020-7028.
- 39 Lundqvist, M., Herman, P., & Miller, E. K. (2018). Working memory: delay activity, yes! Persistent activity? Maybe not. *Journal of Neuroscience*, 38(32), 7013-7019.

- 40 Oberauer K. (2019). Working Memory and Attention – A Conceptual Analysis and Review. *Journal of Cognition*, 2(1): 36, pp. 1–23. DOI: 10.5334/joc.58

Footnote References:

- 1 Cowan, N. (2017). The many faces of working memory and short-term storage. *Psychonomic bulletin & review*, 24(4), 1158-1170.
- 2 Luck, S. J., & Vogel, E. K. (2013). Visual working memory capacity: from psychophysics and neurobiology to individual differences. *Trends in Cognitive Sciences*, 17(8), 391–400.
<https://doi.org/10.1016/j.tics.2013.06.006>
- 3 Oberauer, K., Lewandowsky, S., Awh, E., Brown, G. D., Conway, A., Cowan, N., ... & Ma, W. J. (2018). Benchmarks for models of short-term and working memory. *Psychological Bulletin*, 144(9), 885.
- 4 Kamiński, J., & Rutishauser, U. (2019). Between persistently active and activity-silent frameworks: novel vistas on the cellular basis of working memory. *Annals of the New York Academy of Sciences*.
- 5 Kornblith, S., Quiroga, R. Q., Koch, C., Fried, I., & Mormann, F. (2017). Persistent single-neuron activity during working memory in the human medial temporal lobe. *Current Biology*, 27(7), 1026-1032.
- 6 Boran, E., Fedele, T., Klaver, P., Hilfiker, P., Stieglitz, L., Grunwald, T., & Sarnthein, J. (2019). Persistent hippocampal neural firing and hippocampal-cortical coupling predict verbal working memory load. *Science Advances*, 5(3), eaav3687.
- 7 Spellman, T., Rigotti, M., Ahmari, S. E., Fusi, S., Gogos, J. A., & Gordon, J. A. (2015). Hippocampal–prefrontal input supports spatial encoding in working memory. *Nature*, 522(7556), 309.
- 8 Pradier, B., Lanning, K., Taljan, K. T., Feuille, C. J., Nagy, M. A., & Kauer, J. A. (2018). Persistent but labile synaptic plasticity at excitatory synapses. *Journal of Neuroscience*, 38(25), 5750-5758.

- 9 Lundqvist, M., Herman, P., & Miller, E. K. (2018). Working memory: delay activity, yes! Persistent activity? Maybe not. *Journal of Neuroscience*, 38(32), 7013-7019.
- 10 Johnson, M. R., McCarthy, G., Muller, K. A., Brudner, S. N., & Johnson, M. K. (2015). Electrophysiological correlates of refreshing: Event-related potentials associated with directing reflective attention to face, scene, or word representations. *Journal of Cognitive Neuroscience*, 27(9), 1823-1839.
- 11 Raye, C. L., Johnson, M. K., Mitchell, K. J., Greene, E. J., & Johnson, M. R. (2007). Refreshing: A minimal executive function. *Cortex*, 43(1), 135-145.
- 12 Barrouillet P., Camos V. (2015). *Working Memory: Loss and Reconstruction*. Hove: Psychology Press.
- 13 Lemaire, B., Pageot, A., Plancher, G., & Portrat, S. (2018). What is the time course of working memory attentional refreshing?. *Psychonomic Bulletin & Review*, 25(1), 370-385.
- 14 Schneegans, S., & Bays, P. M. (2017). Restoration of fMRI decodability does not imply latent working memory states. *Journal of Cognitive Neuroscience*, 29(12), 1977-1994.
- 15 Nachstedt, T., & Tetzlaff, C. (2017). Working memory requires a combination of transient and attractor-dominated dynamics to process unreliably timed inputs. *Scientific reports*, 7(1), 2473.
- 16 Soto, D., Mäntylä, T., & Silvanto, J. (2011). Working memory without consciousness. *Current Biology*, 21(22), R912-R913.
- 17 King, J. R., Pescetelli, N., & Dehaene, S. (2016). Brain mechanisms underlying the brief maintenance of seen and unseen sensory information. *Neuron*, 92(5), 1122-1134.
- 18 Bergström, F., & Eriksson, J. (2018). Neural evidence for non-conscious working memory. *Cerebral Cortex*, 28(9), 3217-3228.