

The Dynamic-Processing Model of Working Memory

Current Directions in Psychological Science
 2020, Vol. 29(4) 378–387
 © The Author(s) 2020
 Article reuse guidelines:
sagepub.com/journals-permissions
 DOI: 10.1177/0963721420922185
www.psychologicalscience.org/CDPS



Nathan S. Rose 

Cognitive Neuroscience of Memory & Aging Lab and Department of Psychology,
 University of Notre Dame

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 of dynamic, “activity-silent,” short-term retention processes diverges from conventional models positing that information is always retained in WM by sustained neural activity in buffers. Such evidence comes from machine-learning methods that can 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 can “ping” brain areas to both reactivate latent representations retained in WM and affect memory performance. On the basis of these findings, I argue for a supplement to sustained retention mechanisms. Brain-decoding methods also reveal that dynamic levels of representational codes are retained in WM, and these vary according to task context, from perceptual (sensory) codes in posterior areas to abstract, recoded representations distributed across frontoparietal 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, sensorimotor 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 (a) how the mind and brain accomplish WM tasks that require holding goal-relevant information in mind (such as names when meeting some people, as in the opening example), (b) what happens to such information when attention shifts away, and (c) 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 have been rapidly evolving in recent years as models of

behavior have become 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* WMs may occur either via “activity-silent” neural

Corresponding Author:

Nathan S. Rose, University of Notre Dame, Cognitive Neuroscience of Memory & Aging Lab, Department of Psychology, 390 Corbett Family Hall, Notre Dame, IN 46556
 E-mail: nrose1@nd.edu

mechanisms or, depending on the stimulus and task context, long-term-memory (LTM) processes.

The conventional view: sustained and active representations

Traditionally, both cognitive and neural models of WM have posited that information is retained in WM, either in *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 posit that information is transferred from sensory to central-executive control (frontoparietal) 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

Given early findings from human neuropsychology and lesion or recording studies in animals, neural instantiations of WM models have focused on regions of frontoparietal 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, recent advances are revolutionizing conventional WM theory, largely driven by advances in machine-learning analyses of neuroimaging data. Whereas traditional univariate analyses show elevated levels of activity in frontoparietal 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 systems and representations engaged to perceive information can also contribute to the short-term retention of that information” (D’Esposito & Postle, 2015, p. 118); *motor* is in the name “to accommodate the intimate, often inextricable, coupling between sensory attention

and motor intention” (D’Esposito & Postle, 2015, p. 119). Sensorimotor representation of items in WM is advantageous in many situations because it provides highly 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 lesions selective only 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 are eye-saccade plans to service WM—not the location of items in WM per se (Mackey, Devinsky, Doyle, Meager, & Curtis, 2016). Additionally, recordings of neurons in areas of prefrontal cortex (PFC) during the delayed-saccade task showed that although 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 (Cavanagh, Towers, Wallis, Hunt, & Kennerley, 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 (Spaak, Watanabe, Funahashi, & Stokes, 2017; Stokes, 2015).

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 frontoparietal cortex or with activity-silent mechanisms in regions of sensorimotor cortex. For example, regions of frontoparietal cortex and the hippocampus and surrounding structures of the medial temporal lobe (MTL) seem to be particularly involved in situations in which 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 that when attention shifts away from the memoranda, retrieval processes are required to return the information to focal attention for further processing and action. Thus, according to this view, in the vast majority of studies in the history of WM research, WM retention has been confounded with internal attention (LaRocque, Lewis-Peacock, & Postle, 2014; Sheldon et al., in press).

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

Such tasks (e.g., those that mimic the situation depicted in the beginning of this article 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, with a “two-step double-cue toodeloo” task (see Fig. 1), the primary finding was that in the postcue delay periods, evidence for a sustained, active neural representation existed only 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).

The synaptic theory of WM is a computational model based on biologically plausible neural mechanisms that can account for this finding (Mongillo, Barak, & Tsodyks, 2008; Trübtschek 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 because of the potentiated pattern of synapses. Indeed, using brain-decoding methods with simultaneous noninvasive brain stimulation (transcranial magnetic stimulation, or TMS), my colleagues and I transiently reactivated these passively retained (latent) WMs by recovering memory-specific patterns of neural activity and influencing memory performance (Rose et al., 2016; see also Wolff, Jochim, Akyürek, & Stokes, 2017).

Context-dependent dynamics: the role of stimulus representations. Much of the evidence supporting 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, Martin, Hamilton, & Rose, 2019). 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, Chun, & Johnson, 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, 2019).

In a recent functional MRI study, univariate analyses showed similar results for phonological WM (Yue et al., 2019) as those observed for visual WM (Riggall & Postle, 2012); however, multivariate-pattern-classification analyses on delay-period activity during phonological WM diverged (see Fig. 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 versus non-speech captured different representations in the same region of sensory cortex when three stimuli were retained during the delay than when they were initially perceived and encoded. This result suggests that the sensory cortex was recruited only 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 sensory cortex or on “buffer” regions is context dependent.

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 because of neuropsychological and behavioral double dissociations between tasks purported to selectively measure WM and LTM (Ranganath & Blumenfeld, 2005), many researchers 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 because of the distributed and dynamic nature of information processing coded in activity across both local and large-scale brain networks. With regard to the role of the MTL in WM, there are many examples of profound WM deficits in MTL amnesiacs (Olson, Page,

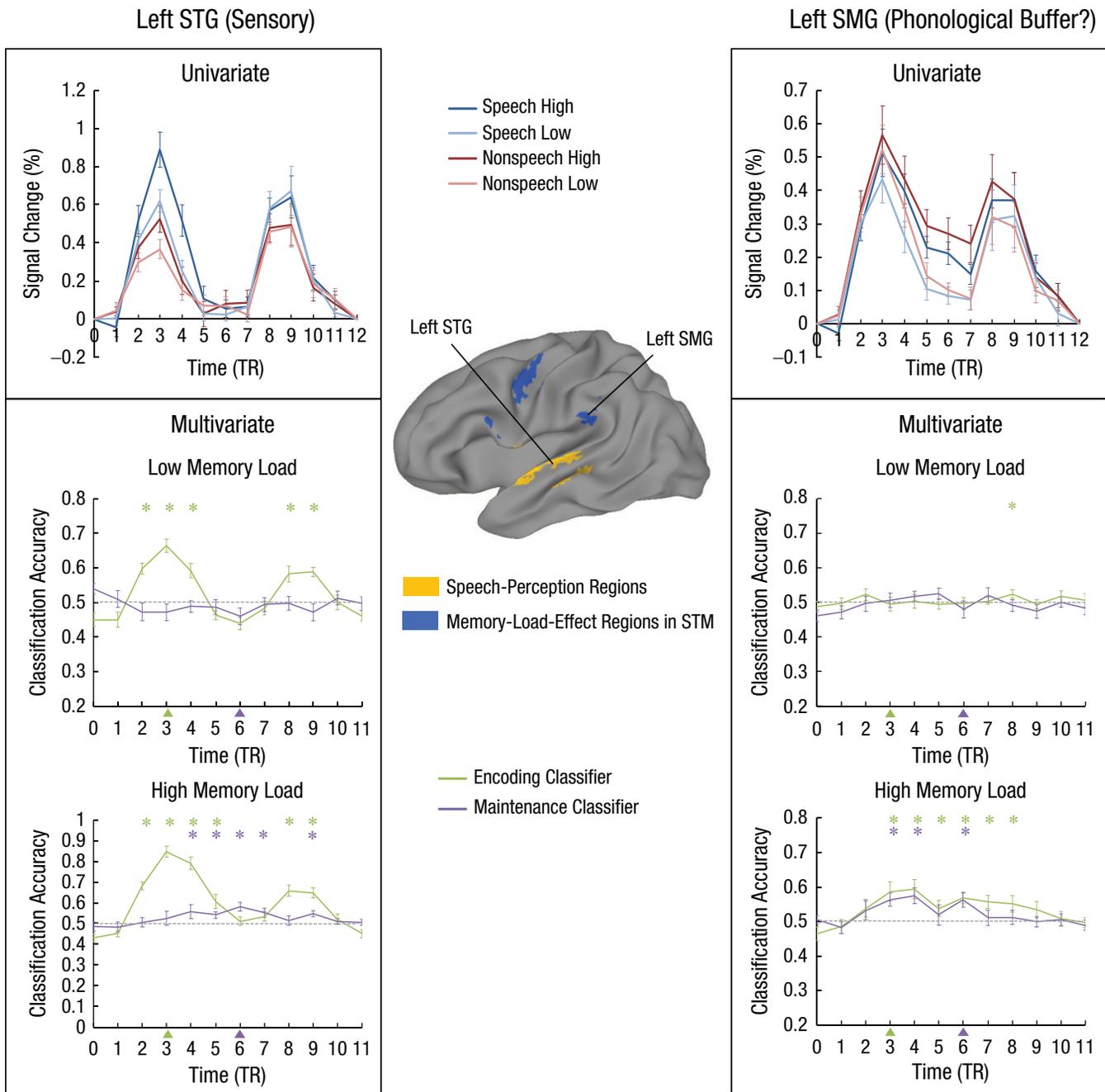


Fig. 2. Univariate and multivariate brain-decoding evidence during a phonological short-term-memory (STM) task with one (low memory load) versus three (high memory load) speech or nonspeech sounds from functional MRI activity in left superior temporal gyrus (STG; sensory cortex) and left supramarginal gyrus (SMG; the putative phonological buffer). For univariate results, the graphs show mean percentage of signal change as a function of repetition time (TR), load (low, high), and sound type (speech, nonspeech). 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). For multivariate results, the graphs show mean classification accuracy as a function of TR and classifier type (encoding, maintenance), separately for low-load and high-load conditions. 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 (indicated by the purple triangle at TR 6)—not during perception or encoding (indicated by the green triangle at TR 3)—which means that STM contents were recoded perceptual representations. The “buffer” region contained similar representations during encoding and maintenance during high load. Asterisks (color coded for each condition) indicate classification accuracy significantly greater than chance (.5). Error bars indicate standard errors of the mean. For further details and results, see Yue, Martin, Hamilton, and Rose (2019).

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 in situations requiring high-resolution representations in both WM and LTM and even perception (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 the 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 (see Fig. 3). I argue for a dynamic model because the nature of the representations and processes that are involved in supporting 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 in box-and-arrow 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.

The major tenets of the model are as follows. First, the mind and brain retain 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 or conceptual processing and associative activation of LTM. Second, whether retention is 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, Sreenivasan, Nee, Vandenbroucke, & D'Esposito, 2018; Rademaker, Chunharas, & Serences, 2019). Third, the nature of the neurocognitive representations and processes that support retention in WM is 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). Fourth, information may be simultaneously represented via multiple codes 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 previously (Christophel, Klink, Spitzer, Roelfsema, & Haynes, 2017; Myers, Stokes, & Nobre, 2017; Oberauer, 2019; Sreenivasan, Curtis, & D'Esposito, 2014); 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

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 "active" representations⁵ that are dynamic, recoded representations in frontoparietal 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 regard 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.

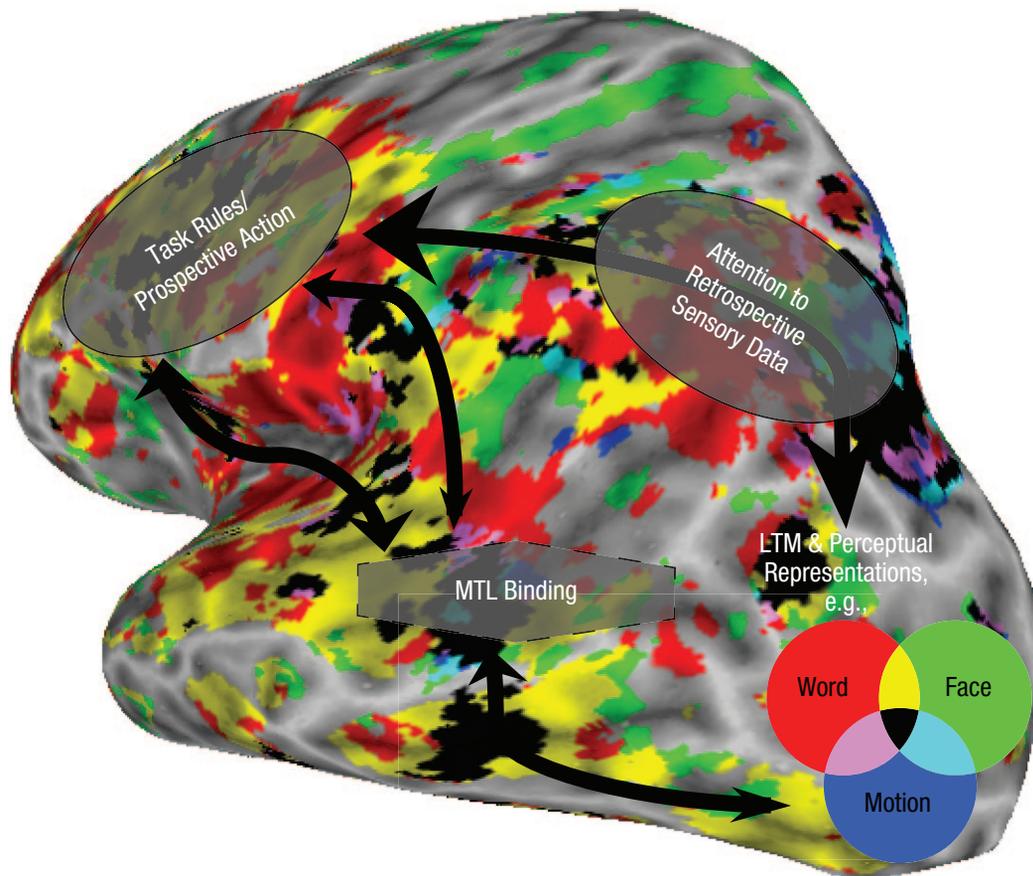


Fig. 3. Illustration of a dynamic-processing model of working memory (WM). According to this view, short-term memory and WM depend on both sustained and selective (transient and periodic) attention-control processes; representations emerge from sensorimotor processing during perception or activation of associations stored in long-term memory (LTM). Stimulus-specific and overlapping domain-general aspects of representations are distributed across the cortex. The hippocampal and medial temporal lobe (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 encoding, maintenance, or retrieval. The prefrontal cortex (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 examples of the distributed nature of WM representation from the selective or shared whole-brain decoding of a face, direction of motion, or word during a WM delay period (see Venn diagram). Figure adapted from Rose et al. (2016).

Recommended Reading

- Cowan, N. (2019). (See References). An excellent review with both similarities and differences to the current theoretical conceptualizations.
- D'Esposito, M., & Postle, B. R. (2015). (See References). An excellent historical survey of research that bridges the cognitive and neural sciences of working memory.
- Oberauer, K., Lewandowsky, S., Awh, E., Brown, G. D. A., Conway, A., Cowan, N., . . . Ward, G. (2018). (See References). An exciting “adversarial collaboration” of working memory researchers designed to have the field converge on key themes to be addressed by future

research and advance models of short-term and working memory.

- Serences, J. (2016). (See References). An excellent articulation of the sensory-recruitment hypothesis of working memory.

- Sreenivasan, K. K., & D'Esposito, M. (2019). (See References). An excellent recent review of neural data that calls for revision to thinking about the role of sustained neural activity for working memory retention.

Transparency

Action Editor: Randall W. Engle

Editor: Randall W. Engle

Declaration of Conflicting Interests

The author(s) declared that there were no conflicts of interest with respect to the authorship or the publication of this article.

Funding

The writing of this article was supported by a National Science Foundation CAREER Award.

ORCID iD

Nathan S. Rose  <https://orcid.org/0000-0002-7619-4441>

Notes

1. The scope of the current work cannot incorporate adequate discussion of the important, extensive debate about the source of WM capacity limits; for some excellent discussion, see Cowan (2017), Luck and Vogel (2013), and Oberauer et al. (2018).

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

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 that they may persistently fire or become synchronized with regions of PFC through oscillatory dynamics (theta–alpha coupling; Kamiński & Rutishauser, 2020; Kornblith, Quiroga, Koch, Fried, & Mormann, 2017); 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 article, but the reader is referred to related work regarding an intriguing concept of “labile long-term potentiation (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.

4. I use the term “prioritized” instead of “activity silent” because the latter refers to the phenomenon in which 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.

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, Herman, & Miller, 2018). Rather than indicating sustained neural firing, such sporadic bursts of delay-period activity may reflect the cognitive maintenance operation termed “refreshing” (Johnson, McCarthy, Muller, Brudner, & Johnson, 2015; Raye, Johnson, Mitchell, Greene, & Johnson, 2007). Note, however, that the neural data do not align with cognitive estimates of a refreshing rate of 10 ms to 40 ms per item (Barrouillet & Camos, 2015; see also Lemaire, Pageot, Plancher, & Portrat, 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 is positioned against interpretation of latent WM states (Schneegans & Bays, 2017), other computational models include both *attractor states* (which can sustain representations) and *transient states* (which support dynamic, recoded representations; Nachstedt & Tetzlaff, 2017). The future will undoubtedly see increasingly advanced neurocomputational and 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 (Bergström & 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 reconfigure what it means for something to be “in WM.”

References

- Baddeley, A. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences*, 4, 417–423.
- Barrouillet, P., & Camos, V. (2015). *Working memory: Loss and reconstruction*. Hove, England: Psychology Press.
- Bergström, F., & Eriksson, J. (2018). Neural evidence for non-conscious working memory. *Cerebral Cortex*, 28, 3217–3228.
- Boran, E., Fedele, T., Klaver, P., Hilfiker, P., Stieglitz, L., Grunwald, T., & Sarthein, J. (2019). Persistent hippocampal neural firing and hippocampal-cortical coupling predict verbal working memory load. *Science Advances*, 5(3), Article eaav3687. doi:10.1126/sciadv.aav3687
- Buchsbaum, B. R., & D'Esposito, M. (2019). A sensorimotor view of verbal working memory. *Cortex*, 112, 134–148. doi:10.1016/j.cortex.2018.11.010
- 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), Article 3498. doi:10.1038/s41467-018-05873-3
- 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, 111–124.
- Cowan, N. (1999). An embedded-processes model of working memory. In A. Miyake & P. Shah (Eds.), *Models of working memory: Mechanisms of active maintenance and executive control* (pp. 62–101). Cambridge, England: Cambridge University Press.
- Cowan, N. (2017). The many faces of working memory and short-term storage. *Psychonomic Bulletin & Review*, 24, 1158–1170.
- Cowan, N. (2019). Short-term memory based on activated long-term memory: A review in response to Norris (2017). *Psychological Bulletin*, 145, 822–847.

- Curtis, C. E., & D'Esposito, M. (2004). The effects of prefrontal lesions on working memory performance and theory. *Cognitive, Affective, & Behavioral Neuroscience*, *4*, 528–539.
- D'Esposito, M., & Postle, B. R. (2015). The cognitive neuroscience of working memory. *Annual Review of Psychology*, *66*, 115–142.
- Endress, A. D., & Potter, M. C. (2014). Large capacity temporary visual memory. *Journal of Experimental Psychology: General*, *143*, 548–565.
- Foster, J. J., Vogel, E. K., & Awh, E. (in press). Working memory as persistent neural activity. In M. Kahana & A. Wagner (Eds.), *The Oxford handbook of human memory*. Oxford, England: Oxford University Press.
- Funahashi, S. (2017). Working memory in the prefrontal cortex. *Brain Sciences*, *7*(5), Article 49. doi:10.3390/brainsci7050049
- 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*, 1823–1839.
- 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. *Annual Review of Psychology*, *59*, 193–224.
- Kamiński, J., & Rutishauser, U. (2020). Between persistently active and activity-silent frameworks: Novel vistas on the cellular basis of working memory. *Annals of the New York Academy of Sciences*, *1464*, 64–75. doi:10.1111/nyas.14213
- King, J. R., Pescetelli, N., & Dehaene, S. (2016). Brain mechanisms underlying the brief maintenance of seen and unseen sensory information. *Neuron*, *92*, 1122–1134.
- 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*, 1026–1032.
- 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*, Article 5. doi:10.3389/fnhum.2014.00005
- Lemaire, B., Pageot, A., Plancher, G., & Portrat, S. (2018). What is the time course of working memory attentional refreshing? *Psychonomic Bulletin & Review*, *25*, 370–385.
- 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*, 61–79. doi:10.1162/jocn_a_00140
- Lewis-Peacock, J. A., & Postle, B. R. (2008). Temporary activation of long-term memory supports working memory. *The Journal of Neuroscience*, *28*, 8765–8771.
- 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. *The Journal of Neuroscience*, *38*, 5267–5276.
- Luck, S. J., & Vogel, E. K. (2013). Visual working memory capacity: From psychophysics and neurobiology to individual differences. *Trends in Cognitive Sciences*, *17*, 391–400. doi:10.1016/j.tics.2013.06.006
- Lundqvist, M., Herman, P., & Miller, E. K. (2018). Working memory: Delay activity, yes! Persistent activity? Maybe not. *The Journal of Neuroscience*, *38*, 7013–7019.
- 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. *The Journal of Neuroscience*, *36*, 2847–2856.
- Majerus, S. (2019). Verbal working memory and the phonological buffer: The question of serial order. *Cortex*, *112*, 122–133.
- Mongillo, G., Barak, O., & Tsodyks, M. (2008). Synaptic theory of working memory. *Science*, *319*, 1543–1546.
- Myers, N. E., Stokes, M. G., & Nobre, A. C. (2017). Prioritizing information during working memory: Beyond sustained internal attention. *Trends in Cognitive Sciences*, *21*, 449–461.
- 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), Article 2473. doi:10.1038/s41598-017-02471-z
- Oberauer, K. (2009). Design for a working memory. *Psychology of Learning and Motivation*, *51*, 45–100.
- Oberauer, K. (2019). Working memory and attention – A conceptual analysis and review. *Journal of Cognition*, *2*(1), Article 36. doi:10.5334/joc.58
- Oberauer, K., Lewandowsky, S., Awh, E., Brown, G. D. A., Conway, A., Cowan, N., . . . Ward, G. (2018). Benchmarks for models of short-term and working memory. *Psychological Bulletin*, *144*, 885–958.
- Olson, I. R., Page, K., Moore, K. S., Chatterjee, A., & Verfaellie, M. (2006). Working memory for conjunctions relies on the medial temporal lobe. *The Journal of Neuroscience*, *26*, 4596–4601.
- Park, S., Chun, M. M., & Johnson, M. K. (2010). Refreshing and integrating visual scenes in scene-selective cortex. *Journal of Cognitive Neuroscience*, *22*, 2813–2822.
- Postle, B. R. (2006). Working memory as an emergent property of the mind and brain. *Neuroscience*, *139*, 23–38.
- 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. *The Journal of Neuroscience*, *38*, 5750–5758.
- Rademaker, R. L., Chunharas, C., & Serences, J. T. (2019). Coexisting representations of sensory and mnemonic information in human visual cortex. *Nature Neuroscience*, *22*, 1336–1344.
- Ranganath, C., & Blumenfeld, R. S. (2005). Doubts about double dissociations between short-and long-term memory. *Trends in Cognitive Sciences*, *9*, 374–380.
- Raye, C. L., Johnson, M. K., Mitchell, K. J., Greene, E. J., & Johnson, M. R. (2007). Refreshing: A minimal executive function. *Cortex*, *43*, 135–145.
- Riggall, A. C., & Postle, B. R. (2012). The relationship between working memory storage and elevated activity as measured with functional magnetic resonance imaging. *The Journal of Neuroscience*, *32*, 12990–12998.
- 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*, 522–532.
- 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*, 1136–1139.
- Rose, N. S., Olsen, R. K., Craik, F. I., & Rosenbaum, R. S. (2012). Working memory and amnesia: The role of stimulus novelty. *Neuropsychologia*, *50*, 11–18.
- Schneegans, S., & Bays, P. M. (2017). Restoration of fMRI decodability does not imply latent working memory states. *Journal of Cognitive Neuroscience*, *29*, 1977–1994.
- Serences, J. T. (2016). Neural mechanisms of information storage in visual short-term memory. *Vision Research*, *128*, 53–67.
- Sheldon, A. D., Saad, E., Sahan, M. I., Meyering, E., Starrett, M. J., LaRocque, J. J., . . . Postle, B. R. (in press). Attention biases competition for visual representation via enhancement of targets and inhibition of nontargets. *Journal of Cognitive Neuroscience*.
- Soto, D., Mäntylä, T., & Silvanto, J. (2011). Working memory without consciousness. *Current Biology*, *21*, R912–R913.
- Spaak, E., Watanabe, K., Funahashi, S., & Stokes, M. G. (2017). Stable and dynamic coding for working memory in primate prefrontal cortex. *The Journal of Neuroscience*, *37*, 6503–6516.
- 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*, 309–314.
- 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*, 82–89.
- Sreenivasan, K. K., & D’Esposito, M. (2019). The what, where and how of delay activity. *Nature Reviews Neuroscience*, *20*, 466–481.
- Stokes, M. G. (2015). ‘Activity-silent’ working memory in prefrontal cortex: A dynamic coding framework. *Trends in Cognitive Sciences*, *19*, 394–405.
- Trübutschek, 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*, Article e23871. doi:10.7554/eLife.23871
- 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), Article e1469. doi:10.1002/wcs.1469
- Wolff, M. J., Jochim, J., Akyürek, E. G., & Stokes, M. G. (2017). Dynamic hidden states underlying working-memory-guided behavior. *Nature Neuroscience*, *20*, 864–871.
- 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.
- 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.
- Yue, A., Martin, R. A., Hamilton, C., & Rose, N. S. (2019). Non-perceptual regions in the left inferior parietal lobe support phonological short-term memory: Evidence for a buffer account? *Cerebral Cortex*, *29*, 1398–1413. doi:10.1093/cercor/bhy037