Beyond Routine Maintenance: Current Trends in Working Memory Research

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Abstract

■ Working memory (WM) is an evolving concept. Our understanding of the neural functions that support WM develops iteratively alongside the approaches used to study it, and both can be profoundly shaped by available tools and prevailing theoretical paradigms. Here, the organizers of the 2024 Working Memory Symposium—inspired by this year's meeting—highlight current trends and looming questions in WM research. This review is organized into sections describing (1) ongoing efforts to characterize WM function across sensory modalities, (2) the growing appreciation that WM representations are malleable to context and future actions, (3) the enduring problem of how multiple WM items and features are structured and integrated, and (4) new insights about whether WM shares function with other cognitive processes that have conventionally been considered distinct. This review aims to chronicle where the field is headed and calls attention to issues that are paramount for future research. ■

INTRODUCTION

Working memory (WM) is an intuitive concept to grasp. Humans can relate to the idea of mentally rehearsing a to-do list or security code, and we appreciate the intrinsic importance of this ability to adaptive function. WM plays an important role in many everyday tasks, and we run up against our own WM limits with frustration. Yet, in part because of its ubiquity, WM has proven difficult to define.

WM is commonly understood as the act of keeping relevant information activated in mind, when it is not being perceived, so that it can be used to guide behavior. However, this definition remains open to interpretation. Although WM is widely described as a fundamental cognitive function, basic tenets about what should be considered WM, what it is for, and how it is supported by physiological processes are contested. WM has grown into an umbrella term that encompasses many potential subfunctions, and this breadth is evident in how WM is currently defined and studied. Conceptually, WM may refer to a cognitive workspace that contains transient content (i.e., "I'm holding the code *in* WM"), a short-term maintenance process (i.e., "I got distracted *during* WM"), or a distributed system for online goal coordination (i.e., "I plan my to-do list *with* WM"). Experimentally, tasks that are geared to test WM may also differentially engage other cognitive processes that generate unique neural signatures (e.g., encoding, binding, selection, manipulation, retrieval). Conceptual and experimental diversity are both a boon and a challenge to WM research. To characterize the core tenets of WM in a theoretically meaningful way, we must build an understanding that is generalizable across modalities and tasks and from the laboratory to the real world. Yet parsing out the generalizable versus task-constrained elements is a challenge, resulting in persistent debates about the neural code, functions, and architecture of WM as well as to what extent a unified theoretical account of WM is achievable (Ngiam, 2024; Nozari & Martin, 2024; Logie, Camos, & Cowan, 2020; Oberauer, 2020; Kiyonaga, 2019; Oberauer et al., 2018).

Starting in 2020, the WM research community has gathered online for 4 days each summer to hear and discuss talks from trainees across the globe and across WM subfields. This Working Memory Symposium (WMS2024) offers a snapshot of the emerging trends in the field, and the discussions crystallize the topics of greatest intrigue and theoretical value to the community. This year's meeting was permeated by themes of multimodality and interaction between WM and other cognitive systems, representational complexity and geometry, innovation in behavioral approaches, and searching questions about the nature, content, and purpose of WM. Research tackled these issues in a range of model systems and with various neuroimaging, neurostimulation, and computational modeling approaches—all unified by a thread of self-reflection and challenging long-held assumptions. Here, we highlight key issues for the state of understanding and inquiry in WM, in the hopes of illuminating a productive path forward for this evolving field.

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COMING TO OUR SENSE(S): WM ACROSS MODALITIES

Experimental methodologies indelibly shape scientific understanding. As the old adage goes: “When you have a hammer in hand, everything looks like a nail”—or, in this case, “When you have a Gabor patch in hand, everything looks like a visual memory.” Studies in verbal and visual modalities form most current knowledge about WM function, but WMS2024 highlighted the ways that examining beyond these modalities might challenge the explanatory power and generalizability of existing WM theories.

In daily life, we may need to temporarily retain information in any modality, and our experiences are not restricted to one modality at a time. For example, when you are cooking and call the next step of the recipe into mind (e.g., “chop the cilantro”), it evokes a mental representation that includes not only the cilantro’s green color and jagged leaves but also the texture, scent, and sounds that will result once you start chopping. In WM research, however, verbal and visual stimuli have played an outsized role. For example, the number of Google Scholar hits for verbal WM (109,800) or visual WM (80,800) eclipses other modalities by an order of magnitude or more (auditory = 12,100, motor = 981, tactile = 752, olfactory = 548, gustatory = 96, proprioceptive = 8). The focus on visual WM systems is largely explained by the disproportionate reliance of humans and other primates on the visual modality to guide behavior relative to other mammals (Bolt, 2022; Dominy, Ross, & Smith, 2004). Moreover, decades of well-developed models and observations of the primate visual system have outlined circuit principles for the representation and transformation of visual stimuli across a hierarchy of 35+ cortical areas (Pasternak, Bisley, & Calkins, 2003; Van Essen, Anderson, & Felleman, 1992). However, the WM field’s focus on verbal and visual WM is also partially one of convenience, with standard computer hardware and readily available software offering an out-of-the-box solution to precise stimulus timing and presentation. At WMS2024, we saw the extra technical complexity that goes into studying WM in other modalities, from “Kinneth” the kinematic robot (Hillman, Botthof, Forrence, & McDougle, 2024) and 3-D printed “greebles” (Ettensohn, Park, & Serences, 2024) to specialized apparati for delivering olfactory and gustatory stimuli (Lim et al., 2022). However, these efforts are crucial for developing a theoretical understanding of WM that captures the richness of our sensory world. Moreover, expanding into multiple modalities allows powerful tests of fundamental computational principles, the generalizability of WM theories, and common benchmarks for WM function (or lack thereof).

Research on individual sensory modalities has accentuated the unique coding schemes for features that a given modality is most sensitive to. For instance, visuospatial coding is typically considered a hallmark of visual processing (Steel, Silson, Garcia, & Robertson, 2024; Groen, Dekker, Knapen, & Silson, 2022), whereas auditory processing relies more strongly on temporal coding (Ahveninen, Uluç, Raij, Nummenmaa, & Mamashli, 2023; Kumar et al., 2016). In contrast, the chemical senses are less easily classified along traditional modality-general dimensions of time and space. As such, these senses provide an important test of generalizability. Recent studies of olfactory and gustatory WM show that many key behavioral hallmarks of WM are indeed recapitulated in these modalities, like decreased performance with increasing load, recency benefits, relative resilience to distractor interference, and cross-modal binding limits (Johnson & Allen, 2023; Lim et al., 2022). This olfactory and gustatory work highlights that some behavioral benchmarks may be shared across modalities but poses a challenge to our explanatory models. For instance, many explanations for visual WM capacity limits appeal to competition in sensory networks with strong spatial and/or feature organization (e.g., Schneegans, Taylor, & Bays, 2020). Analogous behavioral constraints in modalities that lack such organization inspire questions as to which structural features impose capacity limits and whether WM in chemical senses might show the same flexibility as other modalities—for instance, in sensitivity to factors like chunking, presentation format, or serial biases (Chung, Brady, & Störmer, 2024; Wang & Alais, 2024; Endress & Szabó, 2020; Lau & Maus, 2019). Comparisons between modalities also strike at broader questions about the extent to which processing limits arise via modality-specific competitive interactions or shared central bottlenecks (Pashler, 1984; Baddeley & Hitch, 1974; Broadbent, 1958) and how this issue impacts current theoretical explanations of WM capacity limits (e.g., Wennberg & Serences, 2024; Bouchacourt & Buschman, 2019). There are likely multiple mechanisms that constrain capacity, and delineating the shared versus distinct principles across modalities should illuminate those mechanisms.

In addition to querying the unique characteristics and constraints of WM in each individual modality, multimodal interactions may be especially instructive to how WM operates in daily life. The inherently different sensitivities of sensory modalities to timing, order, and spatial organization, as well as different timescales of sensory processing (Senkowski & Engel, 2024), present a unique challenge in understanding how multisensory inputs are integrated in WM to create a unified representation of a multisensory experience (i.e., thinking back to our cilantro example). However, such integrated and multimodal representations may confer WM benefits. Research assessing how WM capacity differs for cross-modal as opposed to modality-specific items reports superior capacity for audiovisual compared to modality-specific input under certain circumstances (Fougnie & Marois, 2011; Delogu, Raffone, & Belardinelli, 2009; cf. Saults & Cowan, 2007); however, reports conflict as to whether this reflects benefits of integration (Delogu et al., 2009) or modality-specific storage (Fougnie & Marois, 2011). Indeed, whether WM is domain general or specific has been a long-standing question (Nozari & Martin, 2024), and "dual-task costs" with stimuli from different modalities are a cornerstone in this debate. Considering multimodal benefits, in addition to dual-task costs, may help resolve this uncertainty. More recent work, together with its follow-up presented in WMS2024, suggests that audiovisual features are encoded as integrated cross-modal objects, even when participants attend to only one task-relevant modality (Arslan, Schneider, Getzmann, Wascher, & Klatt, 2024). In contrast to previous work, this study focused on behavioral and electrophysiological correlates of audiovisual conjunctions, rather than solely considering the two modalities as competitors. Moving forward, this sort of unified approach may clarify how integrated versus modality-specific WM representations are neurally coded and how it affects WM capacity limits.

Attempts to isolate unique domain-specific versus domain-general functions are also challenged by a growing appreciation that WM representations are not necessarily yoked to the sensory presentation format. Rather, the brain may flexibly recode sensory information depending on task demands. Such recoding may happen between features within a modality (Bae & Chen, 2024), for instance, when perceptually distinct visual WM stimuli (e.g., oriented gratings vs. moving dot arrays) are recoded into a shared abstract "line-like" format (Kwak & Curtis, 2022). Recoding may also occur from one modality to another, for instance, when visual information is reformatted into a motor code because a manual response can be prepared (Henderson, Rademaker, & Serences, 2022). Indeed, visual WM experiments have long incorporated "articulatory suppression" controls to limit recoding visual information into a verbal format, highlighting how common it may be to strategically transform whatever information you are given into a preferred or more task-oriented code. In addition to recoding, work at WMS2024 highlighted how multiple "types" of WM representation may be maintained simultaneously, such as coexisting abstract and effector-specific kinesthetic representations (Hillman et al., 2024) and "transfer" of somatosensory experience to visual WM (Ettensohn et al., 2024). WM representations may be more inherently multimodal than originally assumed, comprising information in modalities beyond the sensory stimulus or integrating available semantic and motoric information from long-term memory (LTM; Quak, London, & Talsma, 2015).

In the end, just because an experiment presents a Gabor patch, we cannot assume that is what participants are remembering in WM. Moreover, the principles that apply to remembering one stimulus class may not apply to other stimuli and domains, generating new challenges to defining neural substrates for WM (see Box 1). Examining WM within and between modalities represents a stress test of theory generalizability—and a requirement to obtain a true understanding of how WM operates in the multisensory world. Here, we have primarily focused on the WM representation of information from different modalities, but consideration of how WM control processes operate across sensory domains will also be an important area for further inquiry. For example, interdigitated areas in the lateral pFC preferentially encode visual versus auditory WM content, with differential connectivity to unimodal sensory areas (Noyce et al., 2022; Medalla & Barbas, 2014), but the selection and manipulation of domain-specific WM representations may rely on higher-level, modality-independent control mechanisms (Katus & Eimer, 2020; Mayer, Ryman, Hanlon, Dodd, & Ling, 2017). Identifying when modalities do or do not operate by shared motifs will be critical to reconciling competing takes on the fundamental questions of not only how WM content is stored but also what is stored.

Box 1. The Evolving Debate Over Sensory Cortical WM Storage

The multimodality of WM, and potential recoding between formats, can undermine efforts to clearly delineate the neural functions for representing WM content. For instance, prominent sensorimotor recruitment theories propose that WM shares representations and cortical territory with content-specific perceptual processing (D'Esposito & Postle, 2015; Harrison & Tong, 2009; Serences et al., 2009), but the theoretical predictions become murky if content can shift between domains. The sensory recruitment perspective is especially well supported by many human fMRI findings in visual WM, and work in other modalities suggests that other sensory cortices may similarly support WM (Dimakopoulos et al., 2022; Esmaeili & Diamond, 2019; Linke & Cusack, 2015; Zelano et al., 2009; Harris et al., 2002; Dade et al., 2001; Gottlieb et al., 1989), but it remains contested what mechanistic role sensory cortex might play. Work at WMS2024 underscored the methodological constraints on firmly proving or disproving such theories, given also that WM is increasingly understood to engage widely distributed and interacting brain regions (Courtney, 2022; Christophel et al., 2017; Sreenivasan et al., 2014; Courtney et al., 1997). Ongoing work strives to identify the unique mechanisms and functions of distributed representations (Chopurian et al., 2024), but researchers may come to different interpretations of the same data. For instance, if transcranially perturbing V1 degrades visual WM (e.g., Dake & Curtis, 2024), does that definitively implicate V1 as the storage site for high-fidelity, veridical WM content? Or might the stimulation propagate to other critical regions or impact other forms of multimodal representation that still manifest in behavioral impairments?

The topic of sensory recruitment has driven debate and discovery in WM research for decades (Curtis & Sprague, 2021; Iamshchinina et al., 2021; Lorenc & Sreenivasan, 2021; Scimeca et al., 2018; Xu, 2017). The question is fundamental to understanding neurocognitive architecture but has nonetheless evaded consensus. We suggest that this theoretical challenge be productively addressed through an "adversarial collaboration" approach (Melloni et al., 2023; Cowan et al., 2020), where scientists with competing perspectives collaborate together to agree a priori on which experimental protocols, analyses, and outcomes would lead to decisive support for key hypotheses. (Melloni et al., 2023; Cowan et al., 2020). Notably, disagreements about the role of sensory cortex in WM may be uniquely fueled by methodological differences across studies that can lead to discrepant outcomes and interpretations (Yiling, Klon-Lipok, Shapcott, Lazar, & Singer, 2024; Miller, Tambini, Kiyonaga, & D'Esposito, 2022; Leavitt, Mendoza-Halliday, & Martinez-Trujillo, 2017; Birman & Gardner, 2016). For example, although human fMRI studies typically find sustained multivariate decoding of visual WM content within V1 (e.g., Harrison & Tong, 2009; Serences et al., 2009), electrophysiological studies in nonhuman primates tend to find feature-specific WM activity in association cortices and little WM-related spiking in early sensory cortex (e.g., Leavitt et al., 2017). A targeted effort to bring together researchers from different research subfields—who study different modalities, use different methods and model organisms, and may otherwise rarely interact—could yield significant advances toward resolving this debate.

WHAT IS WM FOR?

> "*I will propose that memory evolved in service of perception and action in a three-dimensional environment, and that memory is embodied to facilitate interaction with the environment*" (Glenberg, 1997, p. 1).

The way that WM is studied and the conclusions we draw about its underlying mechanisms are shaped by assumptions about why the function evolved. Although WM is often construed as a rehearsal process (e.g., remembering a to-do list or security code), we also engage WM in the service of action, learning, multistep planning, and maintaining a stable understanding of an ever-changing world. For example, we might also use WM to follow a conversation and prepare a response, to reason through a series of chess maneuvers, or to hold a mental picture of the traffic while we prepare to cross the street. Just as we have seen that visual WM content can be reformatted based on task demands (e.g., Henderson et al., 2022), the different contexts in which we use WM will shape the neural circuitry and fundamental mechanisms that support WM. WMS2024 showcased the variety of ways that researchers frame the "purpose" of WM and how appreciating the ultimate task goal can enrich our understanding of flexible WM function.

Although it is largely agreed that WM keeps relevant information activated in mind so that it can be used to guide behavior, WM research has often focused on the mechanisms for keeping information in mind while paying less heed to the behavior that it is geared to guide. Despite earlier formulations of WM for prospective cognition and action (Glenberg, 1997; Fuster, 1973), WM has often been construed as a retrospective storage system. However, in the field of movement science, it has long been recognized that a plan or motor program is basically "a memory for what is to come" (Rosenbaum, Cohen, Jax, Weiss, & van der Wel, 2007, p. 528). Accordingly, in recent years, WM research has increasingly recognized the prospective nature of WM (Nasrawi, Boettcher, & van Ede, 2023; van Ede & Nobre, 2023; Henderson et al., 2022; Boettcher, Gresch, Nobre, & van Ede, 2021; Heuer, Ohl, & Rolfs, 2020; Miller, Kiyonaga, Ivry, & D'Esposito, 2020; Olivers & Roelfsema, 2020; Nobre & Stokes, 2019; van Ede, Chekroud, Stokes, & Nobre, 2019). This work has formalized the output or "use" function of WM and examined how WM content can modulate motor effectors or how prospective task demands can influence WM representational format. The appreciation that WM may be held in various functional or "use-dependent" states has ushered in a WM subfield that examines the mechanisms and consequences of this modulation.

To understand the nature of use-dependent WM effects, one important step is to dissect how neural representations of WM sensory feature content may coexist or interact with WM action plans. Electrophysiological evidence supports the idea that prospective motor codes emerge concurrently with sensory WM storage signals (Rösner, Sabo, Klatt, Wascher, & Schneider, 2022; van Ede, Chekroud, Stokes, et al., 2019; Schneider, Barth, & Wascher, 2017). For instance, when remembering visual orientation stimuli, both visuospatial codes and effector-specific motor codes emerge in the EEG signal at encoding, highlighting that action preparation begins early in WM maintenance and may be a major contributor to delay activity (Boettcher et al., 2021). New research at WMS2024 addressed how action codes might not only exist alongside but also alter or interact with WM behavior and feature contents. For example, action codes associated with WM representations render the respective representation more salient (Trentin, Slagter, & Olivers, 2023), and perceptually similar representations are remembered as more distinct when they are coupled with different actions (Trentin, Olivers, & Slagter, 2024). Thus, action preparation processes may change or reweight other aspects of the WM representation itself. More generally, what actions to use—and when to prepare them—are further determined by superordinate goals and contexts. Tasks that manipulate hierarchical and associative relationships in WM show that neural responses in pFC (Rouzitalab, Boulay, Park, Martinez-Trujillo, & Sachs, 2023) and in computational models (Soni & Frank, 2024; Ehrlich & Murray, 2022) reflect combinations of task rules, stimulus properties, and response-outcomes. Such task contexts illuminate how the structure and selection of WM representations guides actions, how those actions in turn influence WM representation, and how pFC subserves sensory-to-motor transformations (Fuster, 1990). Thus, converging behavioral and neural evidence suggest that how the WM content will be used has consequences for how it is encoded and stored (Saito, Bae, & Fukuda, 2024; Saito, Duncan, & Fukuda, 2023; Saito, Kolisnyk, & Fukuda, 2023; Machizawa, Goh, & Driver, 2012).

Taking into account the relationship between WM and action preparation might also clarify uncertainties about the effect of perceptual interference during WM maintenance (Lorenc, Mallett, & Lewis-Peacock, 2021; Hakim, Feldmann-Wüstefeld, Awh, & Vogel, 2020; Xu, 2018, 2020; Mallett & Lewis-Peacock, 2019; Rademaker, Chunharas, & Serences, 2019; Allen & Ueno, 2018; Barth & Schneider, 2018; Hitch, Hu, Allen, & Baddeley, 2018; Bettencourt & Xu, 2016; Rademaker, Bloem, De Weerd, & Sack, 2015). Considering the involvement of the BG in both selection of motor plans and input/output gating of more abstract WM representations, movements might function as a trigger for WM updating (Chatham & Badre, 2015). Likewise, the stage of action processing might determine when WM is vulnerable to interference (Hautekiet, Langerock, & Vergauwe, 2024). Namely, recent work suggests that visual WM items may be more susceptible to interference when they are in use (Lout, Golomb, & Dube, 2023). Thus, considering the role of action preparation—and how that modulates the WM representational format—might help to solve why WM is inconsistently vulnerable to interference (Zhang & Lewis-Peacock, 2023a, 2023b).

Actions are of course not limited to manual responses, and visuospatial WM is tightly intertwined with oculomotor function. Since the discovery of pFC delay activity, WM theorizing has questioned the distinction between response preparation and WM content storage in neural signals, especially during oculomotor delayed response tasks (Jonikaitis, Noudoost, & Moore, 2023). Recent work has demonstrated how WM content can be read out from eye movements and pupil size (de Vries & van Ede, 2024; Dong & Kiyonaga, 2024; van Ede, Chekroud, & Nobre, 2019; Zokaei, Board, Manohar, & Nobre, 2019) and that great care must be taken to ensure that eye movements do not confound the interpretation of neural WM signals (Quax, Dijkstra, van Staveren, Bosch, & van Gerven, 2019; Mostert et al., 2018; Drisdelle, Aubin, & Jolicoeur, 2017; Foster, Sutterer, Serences, Vogel, & Awh, 2016; Kang & Woodman, 2014). WM research has exploited the tight-knit relationship between gaze and WM to detect more complex WM representational content from eye movement features (Linde-Domingo & Spitzer, 2024), and work at WMS2024 highlighted how gaze reflects WM task demands (Liu, Alexopoulou, Kong, Zonneveld, & van Ede, 2024). Oculomotor WM is a prime illustration of the reciprocal perception–action cycle (Fuster, 2004), as the eyes are positioned to both filter the sensory input and enact the motor output for WM. That is, WM-driven eye movements not only serve as a read-out or response modality but also may change what information gets processed in the environment. Jointly, this work underlines the role of WM as a temporal bridge over which traffic flows both ways (van Ede & Nobre, 2023).

Ongoing WM research, as presented at WMS2024 and beyond, shows an acute appreciation for the prospective nature of WM. Rather than overcorrecting as a field by construing WM as primarily oriented toward overt physical actions, however, examining the full scope of potential WM purposes and their implications for individual WM processes presents a compelling open challenge for future work (e.g., planning and integration; Ying, Callaway, Kiyonaga, & Mattar, 2024; Fedorenko, Gibson, & Rohde, 2007).

WM CAUGHT IN A BIND: SHAPES AND STRUCTURES OF FUNCTIONAL WM

The recent focus on WM across a variety of sensory experiences and goal states presents an exciting scientific opportunity but calls attention to an algorithmic challenge for WM systems. How do we parse and maintain rich streams of multimodal sensory information, while being able to access individual objects and their features? For example, when hosting a dinner party, you may walk to the kitchen to get drinks for your guests and have to remember where each guest is sitting and what they requested. How we tie together different sources of information into coherent unit(s) and experience(s) is a fundamental question in cognitive psychology and neuroscience, sometimes called the "neural binding problem":

> To generate a perceptual experience and to be able to act on it, we need to specify the current details of how an object looks, where it is, how it is oriented, and many other often arbitrary details of its current instantiation. Thus we must construct a temporary token ("object file") that binds together these current features with the more permanent identifying characteristics of its type. (Treisman, 1999)

Ongoing WM research examines the cognitive and neural algorithms for solving this binding problem—by integrating object features via LTM and associative learning systems, using pointers ("object files") to tag and access stimulus attributes, and by organizing multiple WM items in temporal and spatial structures.

In LTM systems, binding of stimulus information across modalities and presentation formats is reflected by "concept" selective cells (Rutishauser, Reddy, Mormann, & Sarnthein, 2021; Quiroga, Reddy, Kreiman, Koch, & Fried, 2005). Recently, pioneering studies of single-unit activity in the human hippocampus and medial temporal lobe (MTL) show the involvement of "concept" cells—and other neuron types—in maintaining stimulus-specific information during WM tasks (Daume et al., 2024; Kyzar et al., 2024; Kamiński et al., 2017; Kornblith, Quian Quiroga, Koch, Fried, & Mormann, 2017). In line with these neuronal findings, lesions to hippocampus and MTL areas can cause specific deficits in WM binding performance: Patients are impaired in linking an object's location and color together, but not recalling either one individually (Borders, Ranganath, & Yonelinas, 2022; Dundon et al., 2018; Yonelinas, 2013). Flexible WM systems for immediate behavior, then, can recruit functionality of long-term associative learning for items and features. However, considering how features—such as the color and location of a square—can be bound together requires a deeper consideration of how to exactly define an "item" versus a "feature" in WM. In the laboratory, we often study the binding of features to objects or locations using abstract, clearly delineated stimuli (e.g., a red, oriented bar on a blank, gray background). Natural vision, however, both presents a definitional challenge and reinforces the task dependence of defining objects in the laboratory (e.g., in a photograph of a forest, is the "object" the tree line, the tree, the branch, or the leaf?). More exploration of natural image and stimulus spaces will be critical to identify how object files are constructed to serve WM—and how sensory information processing may constrain WM capacity (Bates, Alvarez, & Gershman, 2024; Xie, Duan, et al., 2023).

Beyond the binding of simple visual features to objects, ongoing work is highlighting how higher-order and semantic knowledge structures may influence binding in WM. For example, carefully crafted stimulus sets can leverage deeply ingrained bindings: A "pink flamingo" is a much stronger association than a "blue flamingo," and such learned associations enhance WM retrieval for bound object identity and color (Sobrinho & Souza, 2023). Recruiting knowledge structures can also be done through semantic tagging. For instance, conceptual similarities between WM objects can influence WM performance more than the visual similarity of items alone (Yu, Thakurdesai, & Xie, 2024). Linking basic sensory with abstract, higher-level object properties may be accomplished through proposed modality-independent pointers (Yu & Lau, 2024; Thyer et al., 2022; Adam, Vogel, & Awh, 2020). Along with more general top–down control signals, examining the mechanistic implementation of such pointers should clarify how neural circuits integrate and separate sensory information to best guide adaptive WM. Greater complexity and semantic depth of WM content, for example, places a high demand on retrieval and readout properties (Desbordes, King, & Dehaene, 2024). However, open questions remain about how multiple items and bindings are managed in WM systems. For instance, how would pointers associated with WM storages relate to or interface with proposed mechanisms of flexible selection in WM? One possibility is that these systems may share circuitry in primate pFC, whereby certain representations are selected to guide behavior via pFC–striatal loops (Soni & Frank, 2024; Manohar, Zokaei, Fallon, Vogels, & Husain, 2019).

Classic tests of WM capacity such as the Sternberg paradigm present a series of stimuli—typically verbal (words or letters) or visual stimuli—and require the binding of an item's order and identity (Sternberg, 1975). Such serial order tasks are critically dependent on pFC (Petrides, 1991), but it has been difficult to parse the neural circuit mechanisms for binding in these scenarios, given overlapping signals for similar items with related features. New theoretical frameworks for flexible selection and binding in WM now provide a mechanistic basis for how these serial order tasks may be solved and explain set size and order effects from decades of human behavioral studies (Murdock, 1968). First, when objects are bound to a spatial location, computational modeling shows that units develop selectivity for conjunctions of item features with their spatial location (Schneegans & Bays, 2017), and other such "mixed-selective" tuning has been observed across WM studies (Badre, Bhandari, Keglovits, & Kikumoto, 2021; Fusi, Miller, & Rigotti, 2016). Individual conjunctive units for item-location and/or item-position binding enable population representations that are robust for solving complex serial order tasks: In primate pFC, the activity of hundreds of neurons shows similar, but separable, subspaces for item location and order (Xie et al., 2022). Second, the order of items in WM can be resolved by temporal binding and frequency/spiking coherence. New evidence for foundational theories of temporal binding through cross-frequency coupling (Lisman & Jensen, 2013) shows stimulus-related activity in category-selective areas in phase-locked theta/alpha cycles, enabling binding of stimulus order and content (Bahramisharif, Jensen, Jacobs, & Lisman, 2018; Hakim & Vogel, 2018). Moreover, swap (or binding) errors in WM emerge when phase-locking of oscillatory activity is reduced during WM (Pagnotta et al., 2024). In a key connection to neural circuit properties, subpopulations of single neurons in the hippocampus were recently shown to be disproportionately involved in phase-amplitude coupling during WM, helping to preserve dynamics of spiking activity with ongoing frequency modulations (Daume et al., 2024). Finally, proposed mechanisms of dynamic WM involve the coordination of activity via synaptic weights, with spiking serving to maintain these patterns across longer periods (Barbosa et al., 2020; Stokes, 2015). Recent computational modeling of synaptic augmentation processes now considers various timescales of synaptic activity, whereby longer timescales enable temporal information—like primacy and order—to be encoded in synaptic changes (Mongillo & Tsodyks, 2024). These three mechanisms likely all help to ensure optimal WM performance for sequences of items, offering new insight into classic task paradigms that require binding items across time in WM.

How item and temporal binding effects in time and space either contribute to or determine constraints on WM capacity remains an important unresolved question. Does the process of binding, selection, and tagging itself impose a bottleneck on WM functioning (see Yu & Lau, 2024), or does such a constraint emerge when loading information into WM (Huang & Luo, 2024; via encoding; Stroud, Watanabe, Suzuki, Stokes, & Lengyel, 2023) or when retrieving and selecting information from WM to guide behavior (Mongillo & Tsodyks, 2024; Inoue & Mikami, 2006)? Conflicting results, ideas, and models may encourage the field to broaden our ideas of binding to a more diverse array of tasks and stimulus modalities and to better capture the complexity of stimuli in our sensory experiences.

n-BACK TO THE FUTURE

Forgetting curves are one of the best-known phenomena in the study of memory, and scientists are not immune to the foibles of forgetting. As a field, we go through cycles of forgetting earlier work and rediscovering its relevance when new experiments are conducted (Lamers, Van Hal, & Clercx, 2020; Parolo et al., 2015). Accordingly, several historical themes have resurfaced in WM research, but with innovation in approach and new tools to shed light on old questions.

One of the most long-standing debates in memory surrounds the relationship between WM and LTM systems. WM had historically been considered distinct from LTM (Squire & Zola, 1996; Squire & Zola-Morgan, 1991; Warrington & Shallice, 1969), and key evidence for this dissociation stems from profound impairments of LTM but relative sparing of WM in MTL lesion patients like H. M. (Drachman & Arbit, 1966; Scoville & Milner, 1957; Milner & Penfield, 1955). Yet, there has been robust debate about whether WM and LTM are truly independent memory systems. Other accounts have proposed a more unitary view, with information passing through WM on its way to LTM (Davachi & Wagner, 2002; Ranganath & D'Esposito, 2001; Atkinson & Shiffrin, 1968).

After a relative lull in attention to the topic, LTM is again at the forefront of WM research. First, recent work has revisited the question of whether and when the MTL supports WM, bringing high-resolution fMRI and human intracranial recordings to bear on the issue (Daume et al., 2024; Xie, Cappiello, et al., 2023; Xie, Chapeton, et al., 2023; Boran, Hilfiker, Stieglitz, Sarnthein, & Klaver, 2022; Boran et al., 2019; Kamiński et al., 2017). Complementary work shows that causally perturbing the MTL reduces WM precision, supporting a close-knit relationship between MTL activity and WM maintenance (Xie, Chapeton, et al., 2023; Boran et al., 2019). Second, there has been a renewed interest in how prior knowledge supports WM behaviors. Early work has long-posited that "chunking" and prior knowledge are important means to get more mileage out of capacity-limited WM (e.g., it is much easier to hold in mind "DOG-CAT-TURTLE" than "XKY-QJC-PLZWDU"; Bower, 1972; Ebbinghaus, 1885, 1913). New work is shedding light on how familiarity and meaningfulness of stimuli boost WM performance (Brady & Störmer, 2022; Asp, Störmer, & Brady, 2021; Xie & Zhang, 2017), how chunks are acquired and "built" via learning (Adam, Zhao, & Vogel, 2024; Soni & Frank, 2024; Zhong, Katkov, & Tsodyks, 2024; Musfeld, Souza, & Oberauer, 2023; Ngiam, Brissenden, & Awh, 2019; Brady, Konkle, & Alvarez, 2009), and how neural representations transform with long-term learning (Huang et al., 2024; Miller & Constantinidis, 2024; Miller et al., 2022; Starr, Srinivasan, & Bunge, 2020). However, although it is increasingly recognized that WM interfaces with LTM, the boundaries of that interaction and parallels in their functioning are in question (Hirschstein & Aly, 2023; Cotton & Ricker, 2022; Beukers, Buschman, Cohen, & Norman, 2021; Forsberg, Guitard, & Cowan, 2021). For example, when information enters WM via perception or LTM, there are broad similarities in neural load signals and representational formats (Vo et al., 2022; Sutterer, Foster, Serences, Vogel, & Awh, 2019; Fukuda & Woodman, 2017; Lewis-Peacock & Postle, 2008). Yet, recent work has highlighted how WM representations may transform with long-term learning and retrieval (Miller et al., 2022; Sabo & Schneider, 2022) and how the spatial tuning of mnemonic representations across retinotopic regions differs from the feedforward perceptual signals for the same feature (Woodry, Curtis, & Winawer, 2024; Favila, Kuhl, & Winawer, 2022). Parsing what neural machinery and algorithms are shared versus distinct between WM and LTM, and under which circumstances, will be critical to understand how the continuum of memory guides adaptive behavior.

Beyond debates about memory systems, other foundational ideas from episodic LTM are now being viewed in the context of contemporary WM research. For example, there is growing interest in the impact of factors like effort, elaboration, labeling, and strategy choice on WM maintenance (Bartsch, Souza, & Oberauer, 2024; Master, Li, & Curtis, 2024; Vergauwe, Souza, Langerock, & Oberauer, 2024; AuBuchon & Wagner, 2023; Overkott, Souza, & Morey, 2023; Loaiza & Lavilla, 2021; Overkott & Souza, 2021; Forsberg, Johnson, & Logie, 2020; Kardan et al., 2020; Bartsch, Loaiza, Jäncke, Oberauer, & Lewis-Peacock, 2019; Rose, Craik, & Buchsbaum, 2015). This work harkens back to the influential "levels of processing" framework (Craik & Lockhart, 1972), whereby memory strength varies as a function of elaboration or processing depth at encoding. For instance, information is often (somewhat counterintuitively) remembered more robustly when it is more difficult to encode, presumably because that difficulty spurs deeper processing (e.g., McDaniel, Einstein, & Lollis, 1988). As has been shown for LTM, recent work suggests that self-selected elaborative strategies yield greater WM performance than rote rehearsal strategies (Bartsch et al., 2024). In contrast, some labeling strategies seem to uniquely benefit WM performance without carryover into LTM (Overkott & Souza, 2021). Although there is broad agreement that effort improves WM performance, the concrete mechanisms underlying effort-related improvements have remained elusive. New work uses trial-by-trial decoding of WM with fMRI to suggest that more effortful WM may increase recruitment of frontal control signals (i.e., sustained prefrontal activity) in the service of maintaining higher fidelity WM representations in sensory cortex (i.e., decoding accuracy in V1; Master et al., 2024). These neural results illustrate how effort may impact behavior via modulation of feature-specific sensory WM codes and show a path forward for investigating how other strategic factors (e.g., labeling, elaboration) impact neural WM representations.

Work at the intersection of LTM and WM at WMS2024 highlighted how looking back can open productive new paths forward. Beyond looking back, we also need to look "sideways"—outside our laboratory window and into the real world. Laboratory studies have pushed our understanding of the boundaries of human memory, but emerging work has highlighted how our laboratory understanding of WM may diverge from WM "in the wild." For example, laboratory studies have shown that humans can hold three to four visual items in mind. Yet, when given a more naturalistic task that affords the opportunity to "offload" task demands from WM to perception, we overwhelming chose to hold only one visual item in mind (Draschkow, Kallmayer, & Nobre, 2021; Somai, Schut, & Van der Stigchel, 2020; Ballard, Hayhoe, & Pelz, 1995). This work suggests that humans often prefer to offload from WM by sampling from the environment—either to evade cognitive effort or because sensory information is more precise and reliable (Berry, Allen, Mon-Williams, & Waterman, 2019; Risko & Gilbert, 2016). The discrepancy between hypothetical capacity limits in standard laboratory tasks versus self-imposed capacity constraints in naturalistic contexts highlights the need to also ask not only how WM content is represented but also whether WM is used at all. Bringing elements of the "real world" into the laboratory, from richer stimulus sets to VR tools, will be one important approach to filling in the gaps (Kristjánsson & Draschkow, 2021; Brady et al., 2019). However, targeted work is also needed to build an understanding of when the differences between the laboratory and the real world are merely products of context versus indicative of underlying WM function.

WM IS ALL AROUND US

Above, we have examined trends in WM research centered around four specific topics: (1) WM across senses, (2) WM for action, (3) the binding problem in WM, and (4) the relationship between WM and LTM. Although each topic is defined by a specific set of problems and approaches, they also call attention to broader issues that permeate WM research across topics. In this final section, we discuss some of those broad issues.

First, all four trends highlight the central role of WM in cognition, broadly construed, and the challenge in defining where WM ends and other cognitive processes begin. WM acts as a "hub" for broader cognition, interfacing between our internal and external worlds (Gresch, Boettcher, Gohil, van Ede, & Nobre, 2024; e.g., Gresch, Boettcher, van Ede, & Nobre, 2024; Poskanzer & Aly, 2023) and operating upon information in diverse formats (e.g., motor plans, information from different senses, language, prospective planning). Thus, it is especially difficult to isolate which aspects of cognition are distinctive to WM, versus shared across domains (e.g., decision-making, LTM, executive control). Cutting across the topics discussed above, this definitional challenge is central to longstanding debates about the relationship between WM and attention (Narhi-Martinez, Dube, & Golomb, 2023; Verschooren & Egner, 2023; Oberauer, 2019; Gazzaley & Nobre, 2012; Chun & Johnson, 2011; Awh & Jonides, 2001). WM and attention are now widely considered to be closely related constructs, as they often appear to be governed by shared operating principles, capacity constraints, and neural functions (Panichello & Buschman, 2021; Kiyonaga & Egner, 2014; Johnson et al., 2013; Saad & Silvanto, 2013; Cavanagh & Alvarez, 2005; Lepsien, Griffin, Devlin, & Nobre, 2005). Because of this close relationship, WM is sometimes folded into the larger attention construct, considered as a form of attention that is directed internally (Kiyonaga & Egner, 2013; Chun, 2011; Theeuwes, Kramer, & Irwin, 2011). Yet, other evidence highlights the distinctions between these constructs and cautions against using them interchangeably. For example, although attention is widely viewed as the entry point to WM, attentionally processing information is not sufficient to ensure reliable WM encoding (Chen & Wyble, 2015, 2016; cf. Dube & Golomb, 2021), and WM can elicit distinct neural signals from sustained spatial attention (cf. Hakim, Adam, Gunseli, Awh, & Vogel, 2019; Feldmann-Wüstefeld, Vogel, & Awh, 2018; Berggren & Eimer, 2016). Thus, glomming attention and WM together may often undermine attempts to understand component functions. Because WM has such strong ties to other cognitive processes, developing a comprehensive theoretical account of WM can sometimes snowball into an unwieldy attempt to explain all of cognition and motivated behavior. A key challenge for ongoing WM research is to develop theories that account for the richness and malleability of WM, while remaining falsifiable and appropriately bounded (Ngiam, 2024; Oberauer et al., 2018).

Second, all four trends highlight the importance of considering context and task demands when evaluating WM. Work manipulating predictive value, attentional state, and response goals has highlighted how WM behaviors and neural codes for the same stimuli can change with the unique demands of the task (Rademaker & Serences, 2024; Henderson et al., 2022; Gresch, Boettcher, van Ede, et al., 2021). How individuals approach a task may also vary not only with the task demands (e.g., what sort of response is required) but also with individual differences in stable traits and strategy use (Bartsch et al., 2024; Lin & Leber, 2024; Keogh & Pearson, 2014; Vogel, McCollough, & Machizawa, 2005). Our discussions of WM for action and LTM highlighted how behavioral goals can influence whether people rely on an active WM representation versus "offload" information to LTM or action planning (both of which may differ with individual tendencies). Our discussion of binding also highlighted how the "binding problem" can be definitionally arbitrary and flexible as to which features should be bound together as objects—which would also likely change with task context. Furthermore, ongoing work questions whether bound objects are the appropriate unit when considering WM operations and capacity limits, instead favoring whole-field characteristics operationalized as Boolean maps (Ji et al., 2024; Shen, Yu, Xu, & Gao, 2013). The fundamental challenge of the "binding problem" within one sensory modality (e.g., vision) also highlights the parallel problem that arises when scaling up to the study of rich, multisensory WM representations. Thinking back to our earlier example—where a mental image of cilantro evokes visual features, scents, sounds, and textures—the issue of task demands raises questions as to whether the richness of this multisensory experience is also context dependent. Is a multimodal representation a natural and obligatory byproduct of our representational systems or an optional outcome that arises only when there is spare capacity to accommodate all dimensions? Our precise behavioral goals and other ongoing tasks (like listening to a podcast) may very well influence the extent to which ancillary multisensory information is readily available. Such fluid contextual effects and wide individual variability make WM an ever-moving target.

At its core, the study of WM contains a paradox: WM is known for its starkly limited capacity, yet it has seemingly boundless flexibility—allowing us to store information from different senses, seamlessly transition between our internal and external worlds, and arbitrarily bind information together in infinite combinations. For many decades, there has been a prominent research focus on, arguably, the simpler side of this paradox: WM's limited capacity and the neural constraints that dictate this behavioral limit. Looking forward, there is a renewed energy toward addressing the more slippery side of WM. The flexibility of WM creates muddy boundaries—both cognitively and neurally—and a central challenge for contemporary WM research is to delineate the fundamental properties of WM in a landscape of shifting task demands, distributed neural processing, and deeply intertwined cognitive systems.

Conclusion

WMS2024 provides a unique opportunity to discuss the state of the field through the lens of new and emerging work from early career researchers. This year at WMS2024, we saw how contemporary WM research is rethinking the prevailing assumptions from the past few decades—and, in some cases, repurposing traditional ideas in light of new methodological capabilities. The current paradigm has an undercurrent of questioning when and why WM is used—what real functions it supports, how the system determines when it is worth the metabolic cost, and what level of representation is good enough for the task at hand. Ongoing work is imbued with the sense that building an accurate scientific understanding of WM requires considering the many ways that "real-world" WM differs from the laboratory, while also addressing how, even in controlled laboratory settings, WM is a "moving target" whose underlying neural representations are temporally dynamic and context dependent (Adam, Rademaker, & Serences, 2022; Wolff, Jochim, Akyürek, Buschman, & Stokes, 2020). Moving forward, the field looks to better capture the dynamic interplay between WM and other cognitive functions as well as how that further interacts with meaningful individual variability in strategy, experience, and motivation.

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Author Contributions

All authors contributed to the outline and initial draft of the article as well as revisions. The assignment of first and last authors reflects the higher degree of involvement of the respective individuals, whereas all other authors contributed equally.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be M/M = .549, W/M = .257, M/W = .109, and W/W = .085.

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