Is working memory domain-general or domain-specific? Implications for theory and practice

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Abstract

Given the widely accepted role of working memory (WM) in human cognition across tasks and domains, a central question has been, Is WM domain general? However, the term "domain-general" has been used in different, and sometimes misleading, ways. By reviewing recent evidence and biologically plausible models of WM, we show that the level of domain-generality varies substantially between three facets of WM: in terms of principles of processing, WM is largely domain-general. In terms of neural correlates, it contains both domain-general and domain-specific elements. Finally, in terms of application, it is mostly domain-specific. This variance encourages a focus shift towards uncovering domain-general principles and away from domain-general approaches to WM training, favoring newer perspectives, such as training-as-skill-learning, for the latter.

Keywords

Working memory, domain-generality, brain training, resource models, neural correlates

Highlights

We break down the domain-generality of working memory into three components. In terms of principles of processing, working memory is domain-general. In terms of neural correlates, it is both domain-general and domain-specific. In terms of application, it is mostly domain-specific.

Is working memory domain-general or domain-specific?

Working memory (WM) is the ability to maintain information over short periods of time, usually in the service of an ongoing task. Since different kinds of information may need to be temporarily maintained before they are acted upon, it is reasonable to ask whether WM is "domain-general", meaning whether the process has a shared component across domains. The assumption of domaingenerality is behind many practices in current psychological studies and interventions. When researchers correlate scores on a WM task with scores on a completely different task to analyze individual differences, they are tacitly assuming some level of domain-generality. Similarly, when brain training programs train WM using video games, the assumption is that improving a domaingeneral function will benefit all tasks that require WM. It is, thus, of both theoretical and clinical interest to verify the assumption of domain-generality of WM.

The goal of this paper is to show that domain-generality/specificity includes three distinct components: (a) domain-generality in principles of processing, (b) domain-generality in neural substrates, and (c) domain-generality in application. Critically, domain-generality in (a) does not logically imply domain-generality in (b), or (b) in (c), hence calling for separate investigation of each component (see Box 1).

Box 1. Logical inference about domain-generality

Even if assumed only tacitly, research on domain-generality has recognized the three different components (a. principles of processing, b. neural correlates, and c. application). An issue, however, has been the assumptions regarding the logical relations between these components in the form of $a \rightarrow b$ and $b \rightarrow c$. For example, $b \rightarrow c$ has been the logical assumption behind brain training studies: if the same neural region is involved in WM operations across domains, then training WM in one domain should lead to improved WM performance in another domain through inducing plastic changes in that region. Making such an assumption also implies that $\neg c \rightarrow \neg b$: if the evidence for transfer of training between domains is weak, then no shared neural correlates exist. A main point of the current paper is that this kind of logical relation does not hold between a, b, and c. Theoretically, it is perfectly possible to have the same principles of processing implemented in distinct neural tissue (domain-generality in principles of processing, domain-specificity in neural substrates). Similarly, it is perfectly possible to have the same brain region involved in implementing a function in different domains, without implying transfer of learning between domains (domain-generality of neural substrates, domain-specificity in application). Parts 2 and 3 of the current paper address these issues.

1. Domain-generality in principles of processing

One of the most fundamental and least disputed properties of human WM is its limited capacity [1-3]. As such, examining the principles that govern such capacity limitation across domains provides a good test of domain-generality of principles of processing. The theoretical debate regarding the source of capacity limitation in WM is still ongoing. Our goal in this paper is not to settle this debate. Rather, we review the evidence to arrive at the most biologically plausible account to date, and then test whether the same account applies to visual and verbal WM, given their largely different representations.

Two major classes of theories have been proposed to explain capacity limitations of WM, discrete and continuous models [1,3,4]. Discrete models were based on a clever observation in early studies, namely that the number, and not the complexity, of stimuli determined WM capacity [3]. Correspondingly, it was proposed that WM has a fixed capacity, defined as k slots, within which items are stored perfectly and beyond which performance is at chance. The introduction of continuous reproduction paradigms [5,6], which allowed for measuring *precision* of a memory, revealed a problem in the predictions of the older discrete models: the old models predicted that below the capacity limit k, precision should be near-perfect and independent of the number of items, whereas empirical data showed a decline in precision even from 1 to 3 items. To account for this finding, Zhang and Luck (2008)[6] proposed a new version of discrete models, the slotplus-averaging model, according to which, when the number of items is below k, multiple copies of the same item are stored independently in multiple slots and their average determines performance. The idea of slots-plus-averaging was later adopted by more models [7], but has also received criticism [8–13]. The success of models that averaged over slots brings up the question of whether slots are necessary if information is averaged across them. This is the idea behind continuous resource models [4,12]. These models assume WM to be a continuous resource with no upper bound k. As the number of items increases, the precision with which they are encoded decreases. Thus, these models can account for the data using a single process of continuous resource division, although such division may be unequal among items [11,12,14–16]. Opposing this view are mixed-state models, which assume a dual process, a primary memory process and a second process of pure guessing [17–20], whereas in continuous models, guessing is simply the extreme end of the continuous process when an item receives almost no resources (see [21] for a unifying view).

Importantly, while mixed-state models were originally built off of discrete models, the assumption of discreteness of slots has not been maintained as a critical one [9]. Importantly, continuous resource models are biologically more plausible. The notion of slots is hard to define at the neural level, and even if defined within certain frameworks, such as binding, it is difficult to justify why a certain value of k should be applicable [22]. In contrast, in continuous resource models, resource limitation is simply defined as neural gain, i.e., the amplitude of activation at the level of a neural population which has encoded a probability distribution over a given feature [21–25]. Higher gain means higher precision. Moreover, defining resource limitation as neural gain provides a natural link between WM and attention, which corroborates the close correspondence between the two at the level of brain [26], as well as behavior [27,28].

To summarize, despite some of the ongoing debates regarding the role of guessing as a qualitatively different process, there is much evidence that resource division between items that do get stored is continuous. Most of this evidence, however, comes from visual WM paradigms. But can the same principle be applied to verbal WM? Historically, visual and verbal WM have been assumed to be separate [29]. Empirically too, performance on visual and verbal domains are dissociable [30]. This dissociation is understandable given the very different nature of representations in these two domains. For one thing, visual stimuli are spread in *space*, whereas verbal stimuli are spread in *time*. Moreover, while the influence of category (color or phoneme labels) on perception has been reported in both domains [31–34], cf., [35,36], this influence is much stronger in the verbal domain, a finding known as categorical perception [33]. When presented with a series of artificially created stimuli between two phonemes, such as /b/ and /d/, participants do not experience them as

a smooth continuum, but as either /d/ or /b/. Categorical perception is a desirable property of speech processing, as differentiating between minimal pairs such as /beer/ and /deer/ critically depends on the identification of the right phoneme and not its acoustic details.

The continuous nature of visual representations makes a continuous resource model an intuitive model of visual WM, whereas the categorical nature of speech representations makes slot-based models a prime candidate for verbal WM. However, if the same principles operate across domains, continuous resource models should be able to account for the data in verbal WM. This proposition is not unreasonable, given that despite categorical perception, listeners are sensitive to subtle changes in the distribution of statistical information in acoustic dimensions even when the information does not flip the category [37,38], and such sensitivity is powerful enough to change production [39].

To test this, Hepner and Nozari (2019) [40] adapted the continuous reproduction paradigm to the auditory domain. Four continua (/ba/–/da/, /ka/–/ga/, /ıa/–/la/, and /sa/–/ʃa/) were created, each manipulating one acoustic property of the pair to generate seven syllables from one end of the spectrum to the other. In the baseline phase, participants heard a single syllable from one of the four continua, and were asked to move a continuous slider to mark the position of the syllable on the continuum (Fig. 1a). This allowed for the calculation of a "deviation score" between the actual and the indicated position of the syllable, to measure precision. The results (Fig. 1a, b) showed that while the effect of category was not eliminated, participants were able to hear intermediate syllables. The authors then played 1, 2, or 4 syllables, sequentially, from different continua on each trial and probed one continuum at the end of the trial. After accounting for positional differences, the pattern was similar to that uncovered in visual WM paradigms, with a gradual increase in the deviation score as a function of increased set size even from 1 to 2 (see also [41] but see [40], for the criticism of their methodology).

Two follow-up experiments investigated the interaction between attention and WM, by using probabilistic cues. In the *pre-cue* condition, a number was presented before the sequence was played, indicating the position in the sequence where the syllable had the highest chance of being probed. In the *retro-cue* condition, the same cue was presented but only after the syllables had been heard (Fig. 1d). The results showed that, for both pre- and retro-cues, deviation scores for the uncued items (i.e., those with a lower chance of being probed on a cued trial) were significantly

higher than a baseline with no cueing. On the other hand, only pre-cues were successful at significantly decreasing deviation scores of the cued items (Fig.1e, f). Collectively, these experiments showed that the cued-item advantage was due to more price encoding, whereas the uncued-item disadvantage was likely due to the release of the uncued items during maintenance. Importantly, this pattern was very similar to that reported for visual WM [42].

To summarize, when WM in speech perception is probed using a continuous reproduction paradigm, the results look strikingly similar to visual WM. This pattern is compatible with a continuous resource model, but, in theory, also with a mixed-state model that combines a discrete slot model with a pure guessing process. To minimize the chance of guessing, Black and Nozari (2023) [43] applied the framework to speech *production* (see Box 2).

Using a case-series approach, Black and Nozari (2023)[43] analyzed phonological errors from four individuals with aphasia. Extensive research has shown that the cognitive processes underlying aphasic error production are similar to those in neurotypical individuals, making such errors a powerful tool for studying cognition (See [44] for a review). Precision of an error was defined as the distance between the target and error phoneme in the articulatory-phonetic space, weighted more heavily for features more diagnostic of minimal pairs, using ALINE ([45]; Fig. 1g). WM load was simply word length, which varied between 3 and 9 letters (see Box 2). If phonological WM stores phonemes as discrete units, one would expect an increased probability of committing a phonological error with increasing word length, but there would be no reason to expect that such errors show a gradual increase in deviation from the target. Conversely, if phonemes in the phonological buffer have a graded representation, one would expect a continuous increase in deviation scores as a function of word length, as predicted by continuous resource models. This was indeed what Black and Nozari (2023) observed (Fig. 1h). The results held after ruling out the influence of position, differences in the number of correct segments, differences in the phonological composition of long and short words, and articulatory simplification. These findings match those reported for verbal WM in perception, as well as visual WM. Moreover, since phoneme selection within a word is unlikely to be driven by pure guessing (see Box 2), this pattern of results endorses the applicability of continuous resource models to verbal WM, despite the much

greater utility of discrete categorical representations in speech vs. vision, pointing to domaingenerality in a core principle of processing.



Figure 1. Paradigms and results for testing WM in speech perception and production. (a) Continuous ratings of the seven tokens for the four continua in the perceptual task. (b) Full distributions of responses averaged in (a). (c) Changes to mean deviation scores in the perceptual task as a function of number of items and position of presentation. (d) Examples of pre-cue and retro-cue trials in the cueing paradigm in the perceptual task. Baseline (not shown) had no cues. (e) Summary of mean deviations for cued, uncued and baseline items in pre- and retro-cue conditions in the perceptual task. (f) Same data as (e), broken down by position. (g) An example trial and ALINE coding in the production task. (h) Mean ALINE distance as a function of word length in the production task.

Box 2. Where do phonological errors come from and why are they a good tool for studying working memory?

Origin of phonological errors. The word production system is a hierarchical system comprising several layers of representations, from semantics to articulatory-phonetic features that guide motor production (Fig. 2; [46–48]. To say a word like "cat", speakers must first activate the concept of cat (shown here schematically as distributed semantic features). Activation then spreads to lexical items, phonemes and articulatory phonetic features. The system has three key properties that create potential for errors: (a) Spreaidng activation activates all the representations that are connected to the currently activated nodes, regardless of their target/non-target status. (b) The system is cascaded, meaning that even items that are not selected in one layer still send some activation down to subsequent layers. (c) The system is interactive [49,50], meaning that activation not only flows from upper to lower layers, but also backwards. This feature is important for producing phonological errors (e.g., "mat" instead of "cat"). When the lexical item "cat" is activated, it activate "mat", which in turn activates its onset /m/, the misselection of which leads to the phonological error "mat". As such, activation reverberates between phonemes and lexical items that support them, making the retrieval of other phonemes in the same words easier.

Relationship to WM. Several findings suggest that sequencing phonemes within a word taps into similar memory processes as memorizing items within a list, albeit less explicitly. The evidence includes the length effect, i.e., an increase in the probability of phonological errors as the word length increases, above and beyond chance [51], as well as strikingly similar positional effects in phonological errors in picture naming and reading and memory errors in serial recall tasks [52]. Furthermore, the inability to maintain information about phonology in WM (e.g., whether a probe word rhymed with another word in a list) is predictive of phonological errors [53]. However, while items in a typical serial recall task are usually independent of one another, hence giving rise to responses that are simply guesses, phonemes within a word are not. Even if a phoneme is hard to retrieve, it still receives support from the lexical item, as well as other correctly retrieved phonemes. This dynamic makes selection by pure guessing a much less likely scenario in word production compared to a typical memory experiment.



Figure 2. A schematic of the interactive word production system when the target is CAT. For simplification, only some articulatory-phonetic features are shown. Similarly, feedback (orange) is only shown between MAT and its phonemes, but exists everywhere in the system.

2. Domain-generality in neural substrates

A general framework has emerged in which WM is argued to be implemented in a network comprising sensory and fronto-parietal regions, with contribution from cerebellum, as well as subcortical regions including hippocampus, thalamus and basal ganglia [54–63]. Comprehensive reviews of the role of these regions exists elsewhere (e.g., [57,64], as do reviews of debates on the relative importance of sensory vs. non-sensory regions in WM [65,66]. Rather, our goal in the current paper is to examine the existing evidence as it relates to domain-generality or specificity of the neural correlates of WM. The target of such investigation will, obviously, not be the sensory cortex, as domain-specificity is undisputed in those areas. Rather, the focus will be on regions that are not clearly specialized to process a certain type of sensory information, such as the frontoparietal regions.

Although parietal regions have been implicated in both visual and verbal WM, different parts of the parietal lobe have been identified in these two domains. Specifically, the bulk of evidence in visual WM points to posterior parietal and intraparietal sulcus (IPS), whereas verbal WM studies often implicate the supramarginal gyrus (SMG) [67–76]. Even within the domain of language processing, researchers have identified separable neural correlates for semantic and phonological

WM [77]. For example, Yue and Martin (2021) [75] used representational similarity analysis (Fig. 3c) on data from participants judging either the phonological or semantic similarity of a memory item to a probe item (Fig. 3a, b). For the phonological task, they were able to decode phonological representations in superior temporal gyrus (STG, the speech perception region [48]) during encoding but not during maintenance across a delay period (Fig. 3d), whereas in the SMG, the opposite was the case (Fig. 3e; see also [74,76] for similar evidence using multi-voxel pattern analysis (MVPA) and transcranial magnetic stimulation (TMS)). On the other hand, semantic representations could not be decoded in either STG or SMG during either encoding or maintenance, showing the specificity of these regions for phonological WM. In contrast, both types of information could be decoded from angular gyrus (AG; Fig. 3f), although in a task-specific manner, e.g., phonological information could only be decoded in the phonological task but not in the semantic task.

Also informative about the neural correlates of WM are studies using voxel-based lesionsymptom mapping (VLSM), which examine the relationship between brain lesions and behavioral deficits in individuals with brain damage. Although several studies have examined the neural correlates of WM using this method (e.g., [78-80], very few studies have compared the neural regions involved in semantic and phonological processing within the same participants in tasks with comparable demands. One such study was conducted by Ding et al. (2020) [81], who used a multivariate approach to lesion symptom mapping to assess whether different brain regions support phonological vs. semantic WM. The 94 participants were tested at the acute stage (most within one week) of left hemisphere stroke, ruling out reorganization of function. Participants' single-word semantic and phonological processing abilities were controlled for by partialing out performance on a picture-word matching task, which included semantic and phonological distractors. To tap phonological WM, a digit matching task was used in which participants judged whether two lists were the same or different (e.g., 3 5 2 1 9, 3 5 1 2 9) and to tap semantic WM, a category probe task was used in which participants heard a word list and judged whether a probe word was in the same semantic category as any list word (e.g., list: table shirt apple rose; probe: chair). For both tasks, WM load was manipulated by presenting lists of increasing length. Control for the other WM measures was employed to identify regions specific to either semantic or phonological WM, as many regions might be expected to be drawn on in common for the two tasks (e.g., general attentional regions). Figure 4 (a) shows the number of individuals with damage to

individual voxels. The results for phonological WM are shown in Figure 4 (b). In keeping with the neuroimaging results, the largest number of relevant voxels were in SMG (see also [82]). Several frontal and subcortical regions were also identified, all of which could plausibly be involved in articulatory rehearsal. Figure 4(c) shows the regions associated with semantic WM performance. Again, in line with the neuroimaging findings, the largest regions was AG, as well as a region spanning the opercular portion of the inferior frontal gyrus and the insula [83,84]. The next largest region was in the posterior superior temporal sulcus – a region often thought to link phonological with semantic representations [85]. These results show a clear double dissociation in neural correlates of semantic and phonological WM.

To summarize, studies of WM across visual and verbal domains, and even subdomains of language processing have implicated largely separable neural correlates for different types of information, pointing to domain-specificity in neural correlates. That said, there is also evidence that certain regions may be involved in aspects of processing that have a more domain-general flavor. For example, Guidali et al. (2019) [86] showed that transcranial magnetic stimulation (TMS) of SMG affected the maintenance of a sequence regardless of the nature of items (verbal, spatial or motor), bringing up the possibility that the sequencing demand of certain WM tasks may also critically involve this region. Similarly, as discussed earlier, both phonological and semantic representations could be decoded from AG, although each in a task-specific manner [75]. This finding fits well with the role of AG in episodic (as opposed to non-episodic) memory [87]; see also [88], which would predict its involvement in processing various kinds of information but each related to a specific context. Finally, there is ample evidence for the involvement of prefrontal regions, thalamus and basal ganglia in balancing maintenance and updating functions of WM (Box 3). It is reasonable to assume that, in so far as balancing these demands are required in WM tasks, the neural correlates involved in this gating processes could be shared between tasks. However, as shown in Box 3, these loops are triggered by sensory-motor mapping and task goals, which are, by definition, domain and task-specific.



Figure 3. Design and results from Yue & Martin (2021). (a) An example trial with a highly similar probe in the phonological WM task. A somewhat similar probe would be "post" and a dissimilar probe would be "tease". (b) An example trial with a highly related probe in the semantic WM task. A somewhat related probe would be "asphalt" and an unrelated probe would be "laugh". (c) ROI-based RSA data analysis strategy. For a given ROI, the neural dissimilarity was calculated for each pair of words based on the neural activation pattern across all voxels in that ROI, to estimate the neural representational dissimilarity matrix (RDM) (green). Then, the neural RDM was compared to either the phonological RDM (blue) or the semantic RDM (red). This procedure was conducted for activation pattern obtained during the encoding period and the delay period of the phonological task and the semantic task, respectively. (d, e, f) The graphs show the average neural-model similarity index (i.e., Spearman correlation coefficient) at each time point spanning the encoding period to the delay period, with the one calculated based on the average activation pattern across the delay period on the rightmost side in (d) the left superior temporal gyrus (STG), (e) the left supramarginal gyrus (SMG), and (f) the left angular gyrus (AG). The colors indicate the task with the blue for the phonological WM task and red for the semantic WM task. The dark colors represent correlations with the target models whereas the light colors represent correlations with the contrasting control models. Error bars represent the standard error of the mean. Dashed lines indicate the typical boundaries between the encoding period and the delay period. pho: phonological; sem: semantic. Asterisks indicate the significance of one-sample t-test: *p < .05, **p < .01, ***p < .001.



Figure 4. Lesion overlap distribution and lesion-symptom mapping results of Ding et al. (2020). (A) Lesion overlap in 94 acute left hemisphere stroke subjects where only regions damaged in at least 5 subjects (>5%) were included in the lesion-symptom mapping analyses. Beta values of the regions significantly associated with decreased performance in the phonological WM (B) and semantic WM (C) measures after accounting for lesion volume, input processing (input processing composite score of semantically and phonologically related word-picture matching d' scores), and the respective opposing WM task (p values < 0.05). pWM = phonological WM, sWM = semantic WM.

Box 3. What might domain-general neural regions do in WM tasks?

Aside from regions in the parietal cortex discussed in the text such as AG, several other regions, including prefrontal cortex (PFC), thalamus, and basal ganglia have been implicated in domaingeneral WM processes. One of the most detailed accounts of the role of these regions is O'Reilly and Frank's (2006) [89] gating model, a schematic of which is shown in Figure 5. The model explains the trade-off between maintaining and updating memories in PFC over short periods of time. Sensory input is mapped onto motor outputs via posterior cortical regions. PFC's role is to modulate this mapping based on prior information and task goals. PFC's flexibility in updating is adjusted through gating via baso-cortical loops. Thalamus always excites the PFC, however this excitation is inhibited by substantia nigra (SN). Two pathways via dorsal striatum modulate this interaction. The direct pathway is activated when the Go neurons with excitatory D1 receptors in dorsal striatum are activated. They directly inhibit SN, which leads to the disinhibition of thalamus and updating in PFC. The indirect pathway is activated when the NoGo neurons with inhibitory D2 receptors in dorsal striatum are activated. This pathway counteracts the direct pathway by inhibiting globus pallidus. Since globus pallidus itself has an inhibitory effect on SN, its inhibition leads to the activation of SN and further inhibition of thalamus, which prevents updating in PFC.



Figure 5. Schematic of O'Reilly & Frank's (2006) model of gating in WM. GPe = globus pallidus, I =input, O = output, PFC = prefrontal cortex, SNr =substantia nigra.

3. Domain-generality in application

One of the key outcomes of the assumption of domain-generality has been the emergence of WM training programs. The general idea behind these programs is that extensive (and usually adaptive) training of WM using a small number of (computer-based) tasks will improve WM capacity across a wide array of tasks in real life (i.e., far transfer; [90–92]. The efficacy of brain-training methods

in general, and WM training in specific, has been one of the most hotly debated topics in the past two decades. The reason is that WM is considered to underlie a very wide range of cognitive tasks, act as a building block of general intelligence [93,94], and be a critical locus of impairment in many neuropsychiatric conditions such as schizophrenia and attention-deficit hyperactivity disorder [95,96]. Therefore, it is natural that an easy tool for training WM would be highly appealing to both neurotypical and impaired populations. In fact, sales in the digital-brain-health market already well exceed \$1 billion, with more than one case of charges brought up by Federal Trade Commission against brain-training companies for deceptive advertising practices [97].

There are numerous empirical studies, meta-analyses, and review papers arguing for or against the efficacy of WM training [98–102]. As with neural correlates of WM, our goal is not to review this literature here, but rather to examine whether far transfer is predicted by current, biologically plausible, theories of WM. Proponents of far transfer often cite neuroplasticity as the foundation of their theoretical perspective. It is well-established that training WM induces plastic changes in certain brain regions (e.g., dorsolateral prefrontal cortex, DLFC) by changing the local field potentials and recruiting a greater proportion of neurons with increased firing rates [103,104], and that such plasticity improves performance on trained tasks [105,106]. It is also well-known, as reviewed in the earlier sections, that there is some overlap in cortical and subcortical regions involved in WM processes across various tasks and domains [107]. Combining these two uncontroversial findings, it has been reasoned that, if there is some domain-generality in neural correlates of WM and if such neural regions show plasticity, then inducing plastic changes through one task should lead to improved performance in other tasks [105,108] (logical inference $b \rightarrow c$; Box 1). Indeed, single-cell recordings from the DLPFC of rhesus monkeys shows that changes induced during training are sufficient to benefit near-transfer, i.e., changes to the task parameters such as delay period or stimulus location in visual WM paradigms [104], and similar effects have been observed in humans [109]. The critical question, however, is whether far-transfer can be expected, when there is little or no overlap between stimuli and/or task goals, except for the necessity of holding on to information over short periods of time. The answer, according to recent neurobiologically plausible computational models of WM is no. Box 4 discusses an example model, proposed by Bouchacourt and Buschman (2019) [110] (Fig. 6). Critically, the model implements the uncontested assumptions of neuroplasticity and the undifferentiated neural space that overlaps across tasks. Nevertheless, while training does improve performance on the same

task, as well as new stimuli within task [111], far transfer is not predicted by these models (see Box 4 for details).

Box 4. Do biologically plausible models of WM predict far transfer?

Models of WM must explain many properties, such as its flexible nature for temporarily storing various kinds of information, its capacity limitation, and sensitivity to interference [112], as well as neural findings, such as the increase in neural activity with WM load [113], involvement of a distributed network comprising sensory cortex and frontoparietal and hippocampal regions [57], and the dual static-dynamic nature of neural representations in WM [114,115]. One recent model that successfully captures all of this is Bouchacourt and Buschman's (2019) [110], which models WM as random and recurrent connectivity between a structured network (representing sensory regions) and an unstructured random network (representing regions such as PFC and hippocampus; see also newer versions that also implement fast Hebbian synaptic plasticity [116].

The idea of WM as a workspace is instantiated by the random connections to the random network, which generate a high-dimensional space within which various types of information can be temporarily stored, such as those reported in PFC or the hippocampus [117]. As such, the model very much embraces the idea of undifferentiated neural regions involved in WM operations across various tasks and domains, and could be considered a great candidate for demonstrating domain-generality in application. Yet, even within such a model, while learning does optimize performance on trained items, benefits do not generalize to untrained items. The reason is that training increases the correlation between the input in sensory regions and the random network, and is therefore specific to those connections. Most recent advances, such as spatial computing models, allow generalization to new items within the same task, but even in these models, different tasks generate unique patterns of neural activity [111].



Figure 6. Flexible WM model of Bouchacourt and Buschman (2019). (A) Model layout. The sensory network is composed of 8 ring-like sub-networks. The inset shows center-surround connectivity within a sensory sub-network. The connections to the random network are randomly assigned and balanced. (B) Raster plot of an example trial with 8 sensory sub-networks (512 neurons each) randomly connected to the same random network (1,024 neurons). Six sensory sub-networks (1–6) receive a Gaussian input for 0.1 s during the "stimulus presentation" period (shaded blue region). Representations are maintained (without external drive) for four of the inputs. Reproduced with permission from Bouchacourt and Buschman (2019).

Aside from the neuroplasticity view, two other theoretical perspectives have been expressed regarding transfer (Box 5). The representational overlap view e.g., [94] emphasizes that transfer is limited to tasks that share overlap in representations and processes. However, defining these processes upfront has been a challenge. In a large-scale and well-controlled study, Gathercole et al. (2019) [118] demonstrated that overlap in stimulus, response, or task, alone was not sufficient to reliably predict transfer, casting doubt on the utility of the representational account. They, in turn, proposed the skill learning account. In contrast with the representational overlap account, this account emphasizes learning new routines during training. If such routines cannot be learned or

readily transferred to a new task, there will be no transfer (see Box 5). For example, N-back tasks, often used for WM training, entail routines that are not applicable to many other WM tasks, which explains the absence of transfer between them [119]. Similarly, Gathercole et al. (2019) reported substantial transfer between complex span tasks within the same stimulus domain, but not across domains. This result indicates that cognitive routines may depend strongly on task and domain, making the skill learning view the most restricted of the three perspectives in predicting generalization in WM training, but also the most compatible with both theoretical models of WM and empirical evidence. Critically, the success of the account hinges on the fact that it does not posit an automatic mechanism for far transfer solely based on shared representations or neural substrates. Rather, it emphasizes the development of new cognitive pipelines through learning, some of which are outside of primary WM operations.

Box 5. Working memory training benefit: plasticity, overlap or skill learning?

Theories of transfer for WM training fall under three general groups:

1- Neuroplasticity. This account assumes that automatic and undifferentiated plasticity of domaingeneral neural correlates of WM leads to transfer to a wide range of tasks that tap into the same neural regions, predicting far-transfer [e.g., 105,107].

2- Representational overlap. This account claims that the extent of transfer of WM training between two tasks depends on the degree of overlap between their features/processes. Although less general than the neuroplasticity account, the representational overlap account still predicts automatic transfer, and attributes the absence of transfer to the lack of overlap in the appropriate representations [e.g., 94,120]. It is, however, unclear which features and processes constitute the critical representational mediating transfer.

3- Skill learning. This account claims that transfer is only expected when a new cognitive routine is learned during training, which can later be applied to a new task [118,121]. Importantly, and in opposition to the other two views, transfer is not viewed as automatic and may very well comprise strategies that lie outside of core WM processes. No significant transfer is expected if the tasks are either too well-learned to allow room for new strategies to develop during training, or if they are too different to benefit from the application of the same newly developed cognitive routine.

In summary, while the assumption of domain-generality in neural implementation is very much part of the cutting-edge computational models of WM, this assumption does not lead to the prediction of domain-generality in application. Quite the opposite, these models predict taskspecific patterns of neural activity, and at best, generalization to new items within the same task (see also Box 6 for complementary evidence from the analysis of individual differences). At the same time, a new and more restrictive perspective on transfer, namely transfer by learning new cognitive routines, shows much promise, although there are still open questions regarding what constitutes a new cognitive routine and what factors promote the learning of such routines in individuals.

Box 6. Does neuropsychological evidence support domain-generality in application?

Aside from training studies, another informative source of evidence for assessing domaingenerality of WM in application is the analysis of individual differences. If WM is one general ability, that ability should be predictive of performance in all tasks that tap WM, regardless of domain. Conversely, if WM is domain-specific, WM abilities in specific domains should be predictive of task performance only within that domain. Following Shah and Miyake's (1996) seminal study pointing to the latter, other neurotypical and neuropsychological evidence has also supported a dissociation between the contribution of visual and verbal WM to visual and verbal tasks [e.g., 123–126]; see [77] for a review. Even more striking are reports of double dissociations within one domain, language processing, in individuals with brain damage. For example, double dissociations have been reported between semantic and phonological WM abilities in individuals with aphasia [127,128]; see [77,129] for reviews. Importantly, these two types of impairments have different consequences for language processing: phonological WM deficits lead to impaired verbatim repetition, whereas semantic WM deficits lead to greater disruption of comprehension and elaboration of content during language production [130,131]. In summary, both neurotypical and neuropsychological data on individual differences in WM point to domain-specificity of WM in application, complementing the data from training studies.

4. Concluding remarks

The goal of this paper was to show that while the question of domain-generality of WM is an important one, it must be posed separately for principles of processing, neural substrates, and application, to be truly informative, as the answer differs for each. We showed that, in terms of principles of processing, WM is indeed domain-general. In terms of neural correlates, it contains both domain-general and domain-specific elements. Finally, in terms of application, it is mostly domain-specific. Thus, if progress is to be made, researchers need to be clear about which aspect of domain-generality is being addressed, and mind the limits of logical inference when extending claims of domain-generality across these three components. The current review encourages a greater focus on cross-domain investigation of theoretical principles involved in WM operations, such as sequencing, and their potentially domain-general neural correlates, while at the same time implying a need for understanding why some non-sensory regions behave in a domain-specific manner in WM operations. This overview also encourages a major shift in perspectives regarding WM training, from an expectation of transfer as a natural and automatic consequence of domain-generality in neural correlates to a view of transfer as skill learning.

4. Outstanding questions

- Computational models have been instrumental in shedding light on the role of domain-general circuits underlying WM, such as the thalamo- and baso-cortical loops for gating operations (Box 3). Do similar loops exist for operations such as sequencing items in WM, and if so, what computations are carried out by each component of such loops?

- Current computational models include both sensory and domain-general regions in WM circuits, however neural data also point to non-sensory, domain-specific regions such as SMG and AG. What properties make these regions distinctly suitable for specific domains? Are different computations carried out by these regions across different domains?

- Cutting-edge models using spatial computing have been critical to explaining transfer and generalization in visual WM (Box 4). Do similar principles apply to stimuli from other domains, such as the auditory domain?

- The new perspective of learning new cognitive routines as the basis of transfer (Box 5) offers promise for real world application, but what constitutes a cognitive routine and what factors determine its overlap with new tasks? What characteristics in learners determine the ability to learn new cognitive routines and their transfer to new tasks?

- The dissociations reported in the analysis of individual differences suggest that using a single WM task as an index of "WM ability" is theoretically unmotivated (Box 6). Given the new perspectives on transfer, what types of measures may be more appropriate for analyzing individual differences in WM?

5. Acknowledgments

The authors would like to thank Rob Nosofsky for the helpful discussions regarding mixed-state models, and Flora Bouchacourt and Timothy Buschman for their permission to reuse Figure 6.

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